

CONSERVATION IMPLICATIONS
OF THE INVASION
OF SOUTHERN AFRICA
BY ALIEN ORGANISMS

VOLUME 1

by

Ian A W Macdonald

University of Cape Town

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**CONSERVATION IMPLICATIONS OF THE INVASION OF
SOUTHERN AFRICA BY ALIEN ORGANISMS**

by

Ian Angus William Macdonald

Thesis submitted to the Faculty of Science,
University of Cape Town
for the degree of Doctor of Philosophy

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This thesis, unless specifically indicated to the contrary in the introductory statement on the role of co-authors or in the Acknowledgement section of one of the published papers, is my own original work. It has not been submitted for a degree to any other university.

I.A.W. Macdonald

Signed by candidate

DEDICATION

I dedicate this thesis to all those conservation area managers I have been fortunate enough to meet and work with who are actually getting down to the hard business of controlling alien invasions rather than just talking about them.

In particular, this thesis is for ;

- Derek Clark, who, more than any other single individual, 'turned the tide' of alien tree invasions in that amazingly important little reserve, the Cape of Good Hope Nature Reserve
- Martin Schofield, who was the first warden to really get stuck into the Chromolaena odorata problem in Hluhluwe Game Reserve, and who taught me that research and management can work together
- George Zaloumis, who carried cochineal-infested cladodes of Opuntia in his rucksack as he walked the Umfolozi Wilderness Area so as to spread the biocontrol agent to isolated infestations
- Frank Woodvine and Dr Ion Williams, who have shown in the Fernkloof and Vogelgat reserves at Hermanus, that it really is possible to control alien woody plants in fynbos
- Mr J A Fenn, the former Director of Forestry for the Western Cape, who set in motion the enormous operation in the Mountain Catchments to control Hakea and Pinus which, if continued as vigorously as he initiated it, will do much to 'save the fynbos'
- the South African biological control 'team' who through their often unseen and unsung labours, have done much to reduce the long-term threat of alien invasions throughout the subcontinent
- the late Mr "Tut" Trainor who was a driving force in the volunteer "hack movement" in the Western Cape for many years and who, for me, epitomized all that is noble in the concept of nature conservation.
- the numerous, nameless, members of the Betty's Bay Hack Group who have met each and every month for over twenty years to keep the fynbos around their village free of alien trees.

If this thesis can in any way contribute to the practical achievement of the goal for which they and their like have striven, then it will all have been worthwhile.

A B S T R A C T

ABSTRACT

Alien species known to be invading untransformed ecosystems in southern Africa, and, more particularly, those inside nature reserves, were identified. The extent and ecological impacts of these invasions were assessed. Their control within reserves was also evaluated. Research approaches used were; literature review (which included an international review), a detailed questionnaire survey of alien plant invasions in 307 reserves, rapid field surveys of 60 reserves, intensive case studies of four reserves (Cape of Good Hope Nature Reserve, Hluhluwe-Umfolozi Game Reserve, Kruger National Park, Pella Fynbos Research Site), international comparison with case-study reserves in other savanna and Mediterranean-type biomes, and field evaluation of control methods for alien plants in the two fynbos reserves. Ecological impacts of alien invasions throughout the subcontinent were determined from historical changes in vertebrate populations, including detailed studies of three native birds (Bostrychia hagedash, Lybius leucomelas, Ploceus velatus) expanding their ranges, partly in response to the spread of invasive alien trees. The results are presented in eight chapters, comprising 26 published (or submitted) papers, an introduction and a concluding summary. One chapter covers contributions to the theoretical understanding of invasion processes, including a prediction of their interaction with rapid global environmental change. The conclusion is reached that alien invasions pose a serious challenge to nature conservation in the region. Mostly this comes from alien woody plants but the importance of herbaceous plants has possibly been underestimated regionally. Introduced mammalian pathogens and predatory fishes have also had important effects. Alien invertebrates have been poorly studied (the ant Iridomyrmex humilis poses a significant threat). Alien terrestrial vertebrates have generally had only localized effects. Alien plant invasions affect all biomes, with riparian ecosystems being regionally threatened. Mesic biomes and habitats are usually more invaded by alien plants than xeric equivalents. 281 alien vascular plant species were recorded invading vegetation within nature reserves (an average of 12 species per reserve) with an additional 200 species being possibly present but unrecorded (an average of 18 species per reserve). By 1984, the 54 plant taxa recorded invading reserves most frequently were estimated, on average, to be present in 30% of the 1km x 1km grid cells of the reserves they were invading. The average potential future extent of these invasions was estimated to be 51%. Control had, on average, been initiated for two plant species in each reserve and 18% of these operations had already resulted in complete eradication. Reported control costs were particularly high for the woody plants which pose a serious threat to the highly endemic flora of the fynbos biome, on average R48 284/reserve (R1,8/ha = US\$1,2/ha) in 1983. These high costs were validated experimentally. A computerized optimization model, aimed at minimizing the costs of controlling the most intractable shrub invader of fynbos, Acacia saligna, was developed from the results of a field experiment at the Pella site. Practical field-scale control of these invasions was assessed to be feasible, using the results of repeated monitoring of permanent plots in the Cape of Good Hope Nature Reserve. Control strategies and regional priorities, based on the theoretical and practical insights gained from this study, are proposed. Even though the intensity of invasions is likely to increase in the foreseeable future, in part as a result of rapid man-induced changes in global climate, it is predicted that these invasions can be controlled if the correct approaches are adopted timeously. Failure to control them, will ensure that the extinction rate of native species will markedly increase and that ecosystem functioning will be altered significantly at a local scale and, conceivably also, at a regional scale.

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ACKNOWLEDGEMENTS

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Finally and most of all, I must thank my wife, Susan, who acted as my assistant for the first year of this study and who has given me more support than I can ever adequately acknowledge. Also of course, my three sons, Angus, Jeremy and David, who accompanied me on my field surveys and put up with agonizing hours in the back of the survey vehicle. They must have been some of the only kids in the world who could identify alien plants from a fast moving vehicle at the age of five! In addition I thank my sister Jean who assisted with the Kings Park case study and gave up precious hours of her holiday to photostat papers for this thesis. Also my parents who never gave up asking when I was intending to finish this thesis.....and never stopped encouraging me to do so. I thank all my family for putting up with me during all these hundreds of hours spent in the office when I should have been at home.

Thanks for holding in there, all of you..... Dad is finally coming home!

CONTENTS

CONTENTS

	Page
VOLUME 1	1 to 246
Abstract.....	1
Acknowledgements.....	2
Contents.....	3
Role of the paper coauthors.....	7
Chapter 1. INTRODUCTION	10
 Chapter 2. THE OVERALL INVASION STATUS OF SOUTHERN AFRICAN BIOMES AND NATURE RESERVES	19 to 95
Introduction to the chapter.....	19
Paper 1. The differential invasion of southern Africa's biomes and ecosystems by alien plants and animals	21
Published 1986 in "The Ecology and Management of Biological Invasions in Southern Africa". (co-authors F.J. Powrie and W.R. Siegfried)	
Paper 2. Alien species in terrestrial ecosystems of the fynbos biome	38
Published 1986 in "The Ecology and Management of Biological Invasions in Southern Africa". (co-author D.M. Richardson)	
Paper 3. Advances in our understanding of alien invasions of the fynbos biome: 1980-1985	53
Published 1987 as an Occasional Report of the Ecosystem Programmes of the CSIR.	
Paper 4. Invasive alien organisms in central South West Africa/Namibia: results of a reconnaissance survey conducted in November 1984	74
Published 1987 in <u>Madoqua</u> . (co-author T.B. Nott)	
Summary of main points arising from the chapter.....	88
 Chapter 3. THE INVASION OF SOUTHERN AFRICAN NATURE RESERVES - SOME CASE STUDIES	96 to 246
Introduction to the chapter.....	96
Paper 5. The alien flora of the Cape of Good Hope Nature Reserve	99
Published 1987 in <u>South African Journal of Botany</u> . (co-authors D.L. Clark and H.C. Taylor)	

Paper 6. The history and effects of alien plant control in the Cape of Good Hope Nature Reserve, 1941-1987.....	105
Published 1989 in <u>South African Journal of Botany</u> . (co-authors D.L. Clark and H.C. Taylor)	
Paper 7. Introduced species in nature reserves in Mediterranean-type climate regions of the world.....	125
Published 1988 in <u>Biological Conservation</u> . (co-authors D.M. Graber, S. DeBenedetti, R.H. Groves and E.R. Fuentes)	
Paper 8. A list of alien plants in the Kruger National Park.....	155
Published 1988 in <u>Koedoe</u> . (co-author W.P.D. Gertenbach)	
Paper 9. The history, impacts and control of introduced species in the Kruger National Park, South Africa.....	169
Published 1988 in <u>Transactions of the Royal Society of South Africa</u> .	
Paper 10. The invasion of introduced species into nature reserves in tropical savannas and dry woodlands.....	195
Published 1988 in <u>Biological Conservation</u> . (co-author G. Frame)	
Summary of main points arising from the chapter.....	223
VOLUME 2.....	247 to 483
Contents.....	247
Chapter 4. THE INVASION OF SOUTHERN AFRICAN NATURE RESERVES - A QUANTITATIVE ANALYSIS OF ALIEN VASCULAR PLANTS.....	251 to 483
Introduction to the chapter.....	251
A questionnaire survey of alien plant invasions of protected areas in southern Africa.	
Paper 11. 1. Background, design and response.....	254
Submitted to <u>South African Journal of Wildlife Research</u> (coauthors F.J. Powrie, R.S. Knight & S.A. Macdonald)	
Paper 12. 2. Number, identity and characteristics of the species invading.....	297
Submitted to <u>South African Journal of Wildlife Research</u>	
Paper 13. 3. The extent of the areas invaded.....	339
Submitted to <u>South African Journal of Wildlife Research</u>	
Paper 14. 4. Habitats being invaded.....	394
Submitted to <u>South African Journal of Wildlife Research</u>	

Paper 15. Invasive alien plants and their control in southern African nature reserves	452
Published 1988 in "Proceedings of the Conference on Science in the National Parks, Volume 5".	
Summary of main points arising from the chapter	470
VOLUME 3	484 to 808
Contents	484
Chapter 5. SOME EFFECTS OF ALIEN INVASIONS ON NATURAL ECOSYSTEMS	488 to 646
Introduction to the chapter	488
Paper 16. Range expansion in the Pied Barbet and the spread of alien tree species in southern Africa	490
Published 1986 in <u>Ostrich</u> .	
Paper 17. Range expansion of the hadedah ibis <u>Bostrychia hagedash</u> in southern Africa	510
Published 1986 in <u>South African Journal of Zoology</u> . (co-authors D.M. Richardson and F.J. Powrie)	
Paper 18. Range expansion of the Masked Weaver <u>Ploceus velatus</u> in the Karoo facilitated by the spread of alien mesquite trees	522
Published 1990 in <u>Ostrich</u> .	
Paper 19. Vertebrate populations as indicators of environmental change in southern Africa	524
In press for <u>Transactions of the Royal Society of South Africa</u> .	
Paper 20. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective	595
Published 1989 in "Biological Invasions: A Global Perspective". (co-authors L.L. Loope, M.B. Usher and O. Hamman)	
Summary of main points arising from the chapter	636
Chapter 6. MANAGING ALIEN INVASIONS IN NATURE RESERVES ..	647 to 705
Introduction to the chapter	648
Paper 21. Strategies for limiting the invasion of protected areas by introduced organisms	651
Published 1990 in <u>Monographs in Systematic Botany of the Missouri Botanical Gardens</u> .	

Paper 22. Costing the initial clearance of alien <u>Acacia</u> species invading fynbos vegetation.....	662
Published 1989 in <u>South African Journal of Plant and Soil</u> . (co-author C. Wissel)	
Paper 23. Determining optimal clearing treatments for the alien invasive shrub <u>Acacia saligna</u> in the south-western Cape, South Africa.....	669
Submitted to <u>Agriculture, Ecosystems & Environment</u> . (co-author C. Wissel)	
Summary of main points arising from the chapter.....	700
Chapter 7. TOWARDS A CONCEPTUAL FRAMEWORK FOR UNDERSTANDING THE INVASION OF NATURAL ECOSYSTEMS BY INTRODUCED ORGANISMS.....	706 to 808
Introduction to the chapter.....	707
Paper 24. Is the fynbos biome especially susceptible to invasion by alien plants - a reanalysis of available data.....	710
Published 1984 in <u>South African Journal of Science</u> .	
Paper 25. The Australian contribution to southern Africa's invasive alien flora: an ecological analysis.....	719
Published 1985 in <u>Proceedings of the Ecological Society of Australia</u>	
Paper 26. Global change and alien invasions: implications for biodiversity and protected area management.....	731
Submitted for publication in the <u>Proceedings of the IUBS Symposium on Global Change and Biodiversity</u> .	
Summary of main points arising from the chapter.....	746
Chapter 8. A CONCLUDING SYNTHESIS OF THE IMPLICATIONS OF ALIEN INVASIONS FOR NATURE CONSERVATION IN SOUTHERN AFRICA.....	753 to 791
REFERENCES.....	792 to 808

ROLE OF COAUTHORS

THE ROLE OF MY CO-AUTHORS IN THE THESIS PAPERS

In a study as extensive and wide-ranging as the present one it has often been necessary to work in cooperation with others. In most cases this cooperation has simply been of a minor or purely technical nature and as such is simply referred to in the "Acknowledgements" section of the relevant paper. However, in several instances the cooperation was so extensive as to have warranted the inclusion of the person(s) as a co-author.

In all cases, I have been the senior author, have written all or virtually all of the text, have been responsible for planning the papers and have made the interpretations of their findings. In all cases the co-authors have read successive drafts of the manuscript and made suggestions for its improvement in the light of their specialised knowledge on any component of the paper. The role of the co-authors was undoubtedly greatest in the papers reporting the international comparative studies of nature reserves (Chapter 3). In these studies, particular co-authors were responsible for individual reserves. In all cases I was responsible for the southern African case-studies, at least one of the other case studies and for their integration.

The detailed role of the co-authors in each of the papers is given below.

Chapter 2

Paper 1. F.J. Powrie was responsible for the computerization of the databases and the execution of the statistical analyses. W.R. Siegfried advised on the interpretation of the results.

Paper 2. D.M. Richardson collated much of the information on the history of forestry and alien plant control in the biome, made available most of the plot data used in Figure 2 from his own unpublished data and calculated the regressions used in this figure.

Paper 4. T.B. Nott collected the field data used in this study together with the author and made available his unpublished observations on sparrows from Etosha National Park.

Chapter 3

Paper 5. D.L. Clark contributed his unpublished field observations on the recent status of alien plant species in the reserve and H.C Taylor made available his card index and field notebooks which listed the historical records of these species from the reserve.

Paper 6 D.L. Clark supervised most of the final surveys of the fixed plots, mapped the distribution of the remaining alien plant thickets in 1987 and provided details on the recent history of control in the reserve. H.C. Taylor provided the raw data from the first two plot surveys and made available his files on the early history of the reserve.

Paper 7 D.M. Graber collated the data for the Sequoia-King's Canyon case study (assisted in small measure by myself during my field visit to the reserve in June 1986) and wrote the first draft of this case study, S. DeBenedetti did the same for the Pinnacles National Monument case study, R.H. Groves collated much of the data used in the two Australian case studies but in both these case I did some of the basic data gathering and drafted the case-study accounts, E.R Fuentes provided the basic account for the La Campana case study and the references relating to its biota which were used in compiling the final account.

Paper 8 W.P.D. Gertenbach supplied a computer printout of the flora of the Kruger National Park and additional information on alien plant species from a survey of gardens in the park. In addition he provided first dates of specimens from the park's herbarium and drew the figure.

Paper 10 G. Frame provided the first draft of the Serengeti case study, unpublished data on its large carnivore community and references relating to introduced fauna in the Kakadu case study.

Chapter 4

Paper 11 F.J. Powrie, R.S. Knight and S.A. Macdonald were all employed as my research assistants during the questionnaire survey and were jointly responsible for the computerization and checking of the questionnaire data.

Chapter 5

Paper 17 D.M. Richardson was responsible for much of the correspondence soliciting unpublished data on the distribution of the hadedah ibis, and the extraction of forestry data relating to the spread of plantations in the Cape. F.J. Powrie checked some of the early literature for distribution records and helped with the mapping of records.

Paper 20. All three coauthors in this chapter provided examples and literature references from their own particular sphere of experience. Thus, most of the Hawaiian and North American input to the chapter came from L.L. Loope, the British and Antarctic data and insights from M.B. Usher and the Galapagos examples from O. Hamman. The data on the number of alien plant species in North American reserves came from an unpublished report of L.L. Loope but their use in the visitor numbers/ alien plant numbers analysis was my own initiative.

Chapter 6

Papers 22 and 23. C. Wissel was entirely responsible for the complex computerization aspects of this study. I planned and carried out the experiment and provided the biological/practical input to the model. I carried out the model runs necessary for these papers and wrote both of them (except for the first draft of the "Computational methods" section of Paper 22 and Appendix 1 of Paper 23).

I have approached my co-authors and asked if they have any objections to me using our jointly authored papers as a contribution towards my thesis. In all cases they have agreed to this use.

Chapter 1

INTRODUCTION

CHAPTER 1

INTRODUCTION

The invasion of untransformed ecosystems by plants, animals and micro-organisms introduced by man to areas outside their natural distribution ranges has recently been recognized as constituting an environmental problem of global significance (Anonymous 1985). As a consequence of this realization, the International Council of Scientific Union's Special Committee on Problems of the Environment (SCOPE) in 1983 initiated a project 'The Ecology of Biological Invasions' (Mooney & Drake 1989). The present study was conceived as part of the South African contribution to this project (Ferrar & Kruger 1983).

Prior to the SCOPE project, most of the concern about these invasions in southern Africa focused on three groups of plant species; those threatening the region's extensive grazing lands, such as Opuntia aurantiaca, Opuntia ficus-indica and Stipa trichotoma, those invading fynbos vegetation, such as Acacia cyclops, Hakea sericea and Pinus pinaster, and those invading aquatic ecosystems, such as Eichhornia crassipes and Salvinia molesta (Stirton 1978). Although there was an awareness that alien plant invasions posed a threat to nature conservation, particularly in the fynbos biome (Taylor 1977a and b, Hall 1978), only a few isolated attempts had been made to document the problem they posed in specific protected areas (e.g. Macdonald 1983a).

Faunal invasions had received even less attention: Although there was an increasing awareness that introduced sport fish endangered certain native fish species (e.g. Skelton 1983), other vertebrate invasions had only been documented in the most basic sense (e.g. Siegfried 1962). Only a handful of alien invertebrate species had been indicated as having potentially deleterious effects on native communities, for example Iridomyrmex humilis (Skaife 1955). There were no published accounts specifically detailing the faunal invasions of protected areas in the region, except for Bigalke's (1947) pioneering but incomplete account of the situation in the South African national parks. Although there was a wealth of published information on microbial pathogens affecting wildlife populations (e.g. Davis 1964, Neitz 1965), little distinction had been made between alien and native species and few accounts existed of their effects in protected areas (e.g. Pienaar 1960). Only one plant pathogen thought to have been introduced to the region, Phytophthora cinnamomi, was considered to pose a major threat to native plant species (Knox-Davies 1975). However, even the alien status of

this fungus was uncertain (Von Broembsen 1979).

Thus, although there were scattered indications that invasions by a diverse range of organisms were potentially of high significance for nature conservation in the region, there was a general lack of information of a synthetic nature that would allow for an objective assessment of their relative and absolute importance.

Several recent studies in man-modified areas within South Africa (Shaugnessy 1980, Wells *et al.* 1980) had illustrated the difficulty of differentiating between the relative contributions of invasion and of man-assisted spread to the current distribution of an alien organism. Accordingly, it was decided that this study should be focussed on protected areas where the latter component was generally minimal.

Objectives and scope of the study

The study was therefore initiated with the following objectives:

- i) To summarize all the available information relating to the invasion of protected areas in southern Africa by alien organisms.
- ii) Where necessary, to obtain information on this subject where it was not available.
- iii) To produce synthetic accounts of the problem which would enable research and management to be organized according to an objective system of priorities.
- iv) Wherever possible to use the information assembled to elucidate the processes giving rise to successful alien invasions.
- v) Similarly, to evaluate the ecological consequences of such invasions with particular reference to their implications for the conservation of the region's native biota.
- vi) Finally, to integrate the scientific understanding of these invasions gained during the study, into practically applicable guidelines for conservation management.

After the study was initiated, an international working group was established within the SCOPE Project, to study the invasion of nature reserves by introduced species on a global basis (Anonymous 1985, Usher *et al.* 1988). The local investigations

being carried out as part of the current study became an important component of this comparative international investigation. The exercise proved useful in placing the southern African situation in an international perspective.

Within the South African contribution to the SCOPE Project it soon became apparent that two facets of the subject were already well covered by the local scientific community. These were the biological control of alien plants (e.g. Naser and Annecke 1973, Annecke and Moran 1978, Zimmerman and Moran 1982) and the distribution and effects of alien vertebrates in freshwater systems (e.g. Gaigher et al. 1980, Skelton 1983). Both components were subjected to independent studies as part of the South African contribution and both have subsequently yielded several published syntheses (e.g. Moran et al. 1986, Hoffmann and Moran 1988, Bruton and Merron 1985, Bruton and van As 1986, de Moor and Bruton 1988). As a result of the existence of highly competent local research communities well-versed in both the above fields, no attempt was made to review these facets of the invasion phenomenon in the present study.

Approaches adopted in the study

The published literature on alien organisms in southern Africa was reviewed. As there were few publications dealing specifically with introduced species in reserves, this review mainly took the form of the analysis of published and unpublished inventories of all the species occurring in reserves. All data on introduced species present were summarised. In some cases there was virtually no information on alien species in certain taxonomic groups specifically from within reserves and more general syntheses were attempted for invasions into untransformed areas outside reserves, e.g. into the whole fynbos biome.

In order to supplement the published information, a questionnaire survey of alien plant invasions of protected areas was initiated in late 1983. The methodology of this survey is outlined in Chapter 4, Paper 11. Returns were received for 307 reserves. In addition, rapid field surveys were carried out in a sample of 60 of the subcontinent's reserves by the author and his assistants. These surveys allow for an assessment of bias in the results of the questionnaire survey. Estimates were made of the completeness of the species listed in the questionnaire returns and the accuracy of the estimates of the extent of invasions made by the respondents. Further checks were made on the completeness of the questionnaire returns by comparing the lists of species included in the questionnaires with lists compiled from the reserves' floras. The results of this survey of alien plant invasions of nature reserves constitutes the core of the present

study.

In order to increase the insights arising from this study, more detailed analyses were carried out for four protected areas; the Kruger National Park, Hluhluwe-Umfolozi Game Reserve, Cape of Good Hope Nature Reserve and Pella Fynbos Research Site. In the latter two reserves, quantitative field data were collected to assess the efficacy of control measures.

What is an alien invasion?

An alien invasion occurs when a species is introduced, deliberately or accidentally, by man to an area outside its natural range where it then spreads unaided into untransformed ecosystems, i.e. those still having natural or semi-natural vegetation. Such a species is often termed an invasive alien species or an invasive exotic.

In the present study no arbitrary limits were placed on the extent of a particular geographic region, species introduced from within which limits - "translocated native species" - being differentiated from those introduced from outside the region - "alien species" (c.f. Brooke et al. 1986). There are no a priori reasons for assuming that such introductions would be qualitatively different in any ecological sense.

It is important, for the purposes of this study, to discriminate between true alien invaders, as defined above, and the multitude of alien and native species that invade transformed ecosystems such as agricultural fields, plantations and urban areas. Although most alien invaders readily invade these areas, only a few of the many species invading such transformed ecosystems are capable of successfully invading areas where the native communities of plants and animals are relatively intact. It is, generally, only such invasive alien species that have a significant impact on nature conservation.

It is also important, from the conservation standpoint, to discriminate between indigenous (or 'native') species that increase in density in response to some man-induced or natural habitat change and alien species that can spread regardless of such a change. The appropriate management responses are generally very different (see discussion below under conceptual issues to be addressed in the thesis, and Chapters 7 and 8).

Why should conservationists be concerned?

Nature conservation can be simply defined as keeping the biosphere in a condition that will maximize naturally occurring genetic diversity while at the same time ensuring the maintenance of essential ecological processes. So defined, there are only two fundamental threats to nature conservation. These are, firstly, the stresses natural ecosystems are being subjected to as a result of the exponentially increasing human population and, secondly, those arising from biological invasions. Of these two categories of threats, those arising from the human population explosion are currently the most serious on a global basis (e.g. the destruction of natural ecosystems to make way for fields, plantations and cities, the effects of the waste products generated by humans on the atmosphere, oceans and terrestrial ecosystems, the degradation of the soil and the impoundment of rivers). Unless these direct threats are effectively combatted there is no hope for the successful conservation of nature (Ehrlich 1989a).

However, even if these rather obvious threats are contained or eliminated completely, the often more insidious threats posed by biological invasions are still serious enough to prevent nature being effectively conserved. As an extreme example to illustrate this point, one can think of an isolated, uninhabited oceanic island which is not seriously threatened by man-made pollutants and which therefore shows every potential for maintaining its native biota intact way into the future. If into this idyllic picture one introduces only one pregnant cat Felis catus, the entire conservation future can be radically altered: introduced domestic cats having successfully invaded numerous oceanic islands, invariably to the detriment of breeding seabird populations and other native fauna (Diamond 1984, Atkinson 1989). If the introduction had been of goats Capra hircus or rabbits Oryctolagus cuniculus, the end result could have been the total destruction of the island's vegetation cover with the concomitant loss of native plant and animal species and, in several known cases, of much of the invaded island's soil mantle (Coblentz 1978, Atkinson 1989).

In addition, the stewardship of natural areas for posterity, which is normally construed as falling within the realm of 'nature conservation', carries with it the implicit assumption that these areas will be maintained in some semblance of their natural or pristine state. This can generally only be achieved where the landscapes within such an area continue to be dominated by the plant and animal species native to the region. Thus alien invasions, or at least certain extreme examples of these invasions, need to be contained simply to preserve the "naturalness" (Usher 1986a) of the environment.

The conceptual issues addressed in this thesis

Although this study was not carried out with the primary intention of testing the hypotheses that have been proposed to explain the invasion of native communities by alien organisms, the data that were assembled have provided me with several opportunities for doing so.

In terms of my brief to investigate the nature conservation implications of these invasions, it was appropriate that I should direct my attention to those conceptual issues which might have significant implications for the formulation of preventative and ameliorative management strategies. Accordingly, the following were the major hypotheses that I attempted to address in the course of this study:

i) Alien invasions can only occur in man-disturbed ecosystems (Tansley 1939, Elton 1958, Kornas and Medwecka-Kornas 1967, Joenje 1987a).

ii) High levels of disturbance, either natural or anthropogenic, predispose an ecosystem to alien invasions (Hobbs 1989).

iii) For biogeographic reasons, certain biomes are intrinsically more susceptible to invasion by introduced organisms than are others (Elton 1958).

In a southern African context, the special case of this hypothesis, that had been formulated prior to the current study, was that the fynbos biome exhibits a heightened susceptibility to invasion (Taylor 1977a). So well established had this notion become in the minds of those people with practical experience of plant invasions within the subcontinent, that the initial South African proposal for the SCOPE Project included the definite statement; "Without doubt it is South Africa's mediterranean region - the fynbos biome - that is most threatened by invasions." (Ferrar and Kruger 1983). The corresponding null hypothesis, that the fynbos is indeed no more susceptible than are the other biomes of southern Africa, was extensively tested in several of the papers that make up this thesis. This was not purely an academic exercise, as, if it could not be refuted, it could well provide a theoretical underpinning for a differential approach to invasions in the various biomes of the subcontinent.

iv) Certain ecosystems are more susceptible to alien invasions than others (Fox and Fox 1986, Rejmanek 1989).

Recently several attempts have been made to synthesize the body of theory relating to the invasion of natural ecosystems by alien organisms. In some cases these syntheses have been carried out independently (e.g. Crawley 1987) but most have been stimulated

by the recently completed SCOPE programme on the "Ecology of Biological Invasions" (e.g. Fox and Fox 1986, Holdgate 1986, Kruger et al. 1986, Williamson and Brown 1986). These reviews have tended to draw upon data bases assembled for purposes other than the testing of hypotheses relating to invasions. As such they have frequently been considered to be inadequate for this purpose (c.f. the discussion of Crawley 1987).

In this thesis I present some results of research carried out specifically to test some of the hypotheses relating to the susceptibility of ecosystems to invasion. Insofar as the data I have collected in this thesis are invariably the results of "natural experiments", the caveat of Crawley (1987) still applies. The use of statistical tests should thus be viewed with caution.

I will not be dealing with the large body of theory relating to the characteristics of the invading organisms which make them successful invaders (e.g. Crawley 1986, Gray 1986, Newsome and Noble 1986, Ehrlich 1989b, Noble 1989, Simberloff 1989). However, the distinction between these two sets of hypotheses is not always absolute. For example, Williamson and Brown (1986) consider the "vacant niche hypothesis" to relate to the species invading rather than being a characteristic of the ecosystem invaded.

One of the aspects of ecosystem susceptibility that was singled out for detailed investigation in this study, was the community property sometimes termed "biotic resistance" (Simberloff 1989). According to this hypothesis, interspecific interactions between the alien species and the native biota (and in some cases, the previously established alien biota, e.g. Moulton and Pimm 1983) can determine the success or failure of the alien species' invasion (Diamond and Case 1986). As the composition of the community is one of the few characteristics of an ecosystem that is often amenable to manipulation within a wildlife management context, this was considered to be a particularly useful line of investigation.

v) Another important concept that had to be addressed was one that has never really been explicitly formulated in the theoretical literature dealing with invasions, although it had been alluded to by Elton (1958, p. 18) in his classic treatise on the subject: this is whether invasions by alien organisms are fundamentally different from the often rapid and extensive increases in range and numbers exhibited by native species when they "explode".

This is an important, although generally overlooked, conceptual issue as, if they are fundamentally different in their ecological origins, then any attempt to derive general principles to explain the differential success of invasions which draws examples from

both native and alien 'invasions' is almost certainly going to be doomed to failure.

The significance of obtaining some clarity on this issue was brought home to me during the early deliberations of the CSIR's Working Group on Invasive Biota (then called the Task Group). There were two viewpoints expressed in these meetings. The first was that all 'invasions' (including the historical increases in density of native woody plants - the so-called 'bush encroachment' that is so widespread in the subcontinent's savannas - and those of unpalatable native grass species in many grassland types) should fall within the group's terms of reference. The second was that only invasions by alien species should be considered.

The decision was made to adopt the second option, but, to at least some extent, this decision was driven by the practical consideration that native "encroachment-type phenomena" (Ferrar and Kruger 1983) were the subject of intensive research under existing programmes. The decision was not made on the basis that these were in fact two totally discrete phenomena.

That there is in fact no clear distinction between these two types of invasion in the minds of at least some of the authorities concerned with the management of the region's rangelands is demonstrated by their consistent treatment within single papers or books by the staff of what was formerly the South African Department of Agriculture's Botanical Research Institute (Henderson and Anderson 1966, Wells *et al.* 1983a, b and c, 1986b) and the inclusion of both native and alien species as "declared invaders" in terms of the most recent landuse legislation in this country (Anonymous 1984).

Internationally, this distinction has also not been clearly drawn. This can be seen, for example, in the inclusion of several papers on unassisted range expansions of organisms, e.g. trees (Bennett 1986) and birds (O'Connor 1986), in the British contribution to the SCOPE programme which otherwise mainly concentrated on invasions of introduced species (e.g. Usher 1986b). That there was no clear distinction made between these two categories of invasion in the British contribution is not surprising in the light of comments made in the introduction to the British synthesis volume (Williamson *et al.* 1986). Here, surprise is expressed that SCOPE, which normally deals with man-made problems in the environment, should be addressing biological invasions as "although most of the problems are caused by invasions induced by man, some can arise as a result of natural extensions of range." Similarly, in his summary of the introductory paper to the Dutch contribution to the SCOPE programme, Joenje (1987b) in fact states; "Apparently there are no fundamental differences between alien and native species involved in larger population increases." This matter obviously

warrants explicit treatment.

vi) Can invasive alien species have significant effects on the functioning of otherwise undisturbed, natural ecosystems (Vitousek 1986).

vii) Can invasive alien species have significant effects on the native biota of undisturbed, natural ecosystems (Diamond and Case 1986).

The latter two postulates had not been explicitly formulated in the theoretical literature relating to invasions when this study was initiated. Possibly this is a result of most previous studies of invasions having been conducted in disturbed systems where these issues were not relevant. That the issues had not been subject to detailed theoretical analyses from the viewpoint of conservation biology, probably can be ascribed to the general failure, until very recently, of scientists working in this field to acknowledge the significance of invasions (see Chapter 8).

It was the primary goal of this study to assess just how significant alien invasions actually are within the field of conservation biology in southern Africa.

Chapter 2

OVERALL INVASION STATUS

OF

BIOMES AND RESERVES

Introduction to the chapter

Paper 1

**The differential invasion of southern Africa's biomes
and ecosystems by alien plants and animals.**

Paper 2

**Alien species in terrestrial ecosystems
of the fynbos biome.**

Paper 3

**Advances in our understanding of alien invasions
of the fynbos biome: 1980-1985.**

Paper 4

**Invasive alien organisms in central
South West Africa/Namibia:
results of a reconnaissance survey
conducted in November 1984.**

Summary of main points arising from the chapter

CHAPTER 2

THE OVERALL INVASION STATUS OF SOUTHERN AFRICAN BIOMES AND NATURE RESERVES

Introduction to the chapter

In the papers that make up this chapter the basic questions addressed are: First, which taxonomic groups have alien species which are invading? Second, do the biomes of southern Africa show differential levels of invasion by alien species from any of these groups? Third, do the ecosystems within the biomes show differential levels of invasions? Fourth, can we discern any patterns in this differential invasion which could suggest its causation? Fifth, how extensive are these invasions? Sixth, what ecological effects are these invasions known or suspected to be having? Finally, are there any indications as to which invasions might be the most important from a nature conservation perspective?

In Paper 1, I first reviewed the fragmentary literature that related to differential invasions at a biome and ecosystem level. Then I assembled two novel data sets with which to investigate the matter: The first was the occurrence of the two widely established alien rodents, Mus musculus and Rattus rattus, in 193 samples of the prey of the barn owl Tyto alba collected from 164 different sites throughout the region. The second was the number of alien species in each of the major taxonomic groupings within vascular plants and terrestrial vertebrates in 57 nature reserves for which species lists were available. For each owl-prey sample site and nature reserve, I also assembled basic geographic, environmental and certain biotic data sets. The approach adopted in the analysis of the first data set was to see whether there were detectable differences in the frequency of occurrence of alien rodents in subsets of these samples which were defined in terms of variation in these site variables. In the case of the nature reserve lists, the number of alien species in similarly defined subsets of the total data set, expressed either as an absolute number or relative to the number of native species in the group, were compared using non-parametric tests of significance.

It must be emphasized that these tests did not prove what gave rise to different alien incidences, they simply suggested which of the site variables might be associated with variations in such incidence.

In the second paper in this chapter, I subjected the southern African biome which had previously been implicated as being the

one most severely affected by alien invasions, the fynbos biome, to a more detailed analysis. This was done mainly by reviewing and synthesizing data on the biome's biogeographic, historical and ecological characteristics and relating this to the available information on alien invasions. The syntheses of information relating to the ecological, floristic and faunistic effects of one of the biome's characteristic invasions, that of alien trees and shrubs, provided the first comprehensive review of this topic.

The third paper in this chapter complements the analysis of fynbos biome invasions presented in Paper 2. This paper is a fuller review of recent developments in the field of alien invasions in this biome. The taxonomic coverage is more complete than was possible in the broader overview paper and recent research findings relating to the causes and consequences of alien invasions are summarized.

The final paper in this chapter presents the results of a rapid survey of alien invasions occurring in central Namibia. This includes much of the Namib Desert, which is the only true desert in southern Africa, and the paper provides useful data for inter-biome comparisons, both within Namibia and within the subcontinent, and for comparisons between habitats in this arid and semi-arid area. The only groups included in this rapid survey were vascular plants and birds.

1986, *The ecology & management of biological invasions in Southern Africa.* (ed) I A W Macdonald; F J Kruger; A A Ferrar. Chapter 17 pp. 209-225

The differential invasion of southern Africa's biomes and ecosystems by alien plants and animals

I A W Macdonald, F J Powrie and W R Siegfried
University of Cape Town.

Introduction

It is commonly observed that natural ecosystems differ in the extent to which they have been invaded by alien organisms (Elton 1958). For example, islands and mediterranean climate regions often show a high incidence of alien invasions (Ferrar and Kruger 1983).

Within southern Africa, variations in the extent of alien plant invasions between biomes and between ecosystem types within biomes have been noted by several authors.

Differential invasion of southern African biomes by plants

Using as their measure of the extent of invasions the number of species of invasive alien plants recorded from different types of ecosystem within South Africa, Wells et al (1983) concluded that aquatic ecosystems were the most severely affected with streambank ecosystems second and the terrestrial habitats of the winter rainfall region third. Without data several other authorities have contended that the fynbos biome is especially susceptible to invasion by alien trees and shrubs (Hall and Boucher 1977; Taylor 1977; Campbell et al 1979). In attempting to test this hypothesis, Macdonald (1984) concluded that there were strong indications that the fynbos biome had more extensive infestations of alien trees and shrubs than the other South African biomes. However, the quality of the available data did not allow statistical tests of the hypothesis. In addition, any such differences in the extent of invasions could not be taken as being proof of differences in the inherent susceptibility to invasion of the biomes, because the patterns are confounded by differences in the extent of human disturbance and the history and extent of alien plant introductions to the various biomes (Macdonald 1984).

Address for correspondence: I A W Macdonald, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700.

Differential invasion of southern African ecosystems by plants

There have been several southern African studies which allow comparisons to be made of the relative extent of alien plant invasions of different types of ecosystem within a biome. However, most of these studies have been carried out for individual species and it is difficult to extract an overall index of the extent of alien plant invasions of the different ecosystems involved (eg Henderson and Musil 1984; Richardson 1984; Taylor et al 1985). In a study in the Hluhluwe-Umfolozzi Game Reserve a crude measure of the relative frequency of occurrence of 16 species of tree, shrub and woody creeper indicated that disturbed areas around human habitations were the most invaded, with riverine ecosystems being second (Macdonald 1983). In an intensive survey of the central Transvaal highveld, Wells et al (1979) found the average number of alien woody plant species and mean abundance rating to be highest in bushveld ecosystems, intermediate in bankveld (a transitional grassland type with scattered trees) and lowest in true grassland ecosystems. However, working as they did in an extensively transformed and otherwise man-modified area, they found alien plant infestations to be generally highly correlated with intentional plantings. Thus their data on the relative extent of infestations might not reflect inherent differences in susceptibility to invasion. Although the techniques used by Wells et al (1979) do not allow for a direct comparison between riverine and upland ecosystems it is apparent from their account that they, too, found the riverine ecosystems to be the most severely invaded. They classified the riverine ecosystems sampled into those along rivers, along perennial streams, and along temporary streams. Alien woody species were present in the riverine fringing vegetation in 100%, 69% and 16% of the samples in these three types of riverine ecosystems, respectively, with more than four species being present in 34,8%, 34,9% and 2,9% of the samples (Wells et al 1979). Alien plant

species in the arid regions of southern Africa are restricted almost entirely to riverine ecosystems, as has been recorded in the Kalahari Gemsbok National Park (Macdonald in preparation) and in the Namib Desert (Tarr and Loutit 1985; Vinjevold et al 1985; Macdonald and Nott in press).

The only quantitative study in southern Africa which has not shown riverine ecosystems to be more densely invaded than adjacent upland ecosystems is the aerial photographic assessment of Boucher (1981), working in the south-western Cape lowlands. Here he found 30% of the remaining areas of Coastal Renosterveld to be invaded by alien woody plants, 27% having dense stands. Seventeen per cent of the length of watercourses were invaded, with only seven per cent densely invaded. Strandveld had 16% of its remaining area invaded and Coastal Fynbos, eight per cent. The relatively low level of invasion of riverine ecosystems in this study is at variance with the consensus opinion of a panel of fynbos researchers and managers (Macdonald and Jarman 1984). It is possible that alien trees were undercounted in the aerial photographic analysis of riverine ecosystems, since this habitat has indigenous tree species present which would be difficult to distinguish from alien species.

Faunal invasions

The extent of faunal invasions of different biomes or ecosystems within southern Africa has not been analysed. However, Van Bruggen (1964) provides data on the number of alien terrestrial Mollusca recorded from different localities. It is possibly significant that the three port cities in the fynbos biome, Cape Town, Port Elizabeth and East London all showed high numbers of species (17, 9 and 5 respectively) compared to the two subtropical ports, Durban (4) and Maputo (1). The cities of Johannesburg and Bloemfontein, in the grassland biome, both had only a single species (Van Bruggen 1964).

Background to the present study

Alien rodent invasions in southern Africa

In this study, we have attempted to analyse the results of two naturally occurring experiments as a preliminary test of the hypothesis that South African biomes and ecosystems vary in their susceptibility to invasion. The first of these is the differential invasion of biomes and ecosystems by two introduced rodents the house rat *Rattus rattus* and the house mouse *Mus musculus*, as reflected in the incidence of their remains in owl pellets.

These rodents are commensal with man and have been unintentionally carried to localities scattered throughout the globe. Individuals have evidently been introduced into all but the most remote areas as they are accidentally translocated by road and rail transport and have been present in the sub-continent for centuries (cf Smithers 1975, 1983; Plug et al 1979). Both species are capable of surviving under a much wider range of climatic conditions than is present in the subcontinent (Hanney 1975). In a variety of insular ecosystems and in certain continental ecosystems both species have been recorded invading natural and seminatural ecosystems (Fox 1983; Smithers 1983; Atkinson 1985; Cooper and Brooke this volume). Although *Mus musculus* is stated to be "closely confined to dwelling houses, outbuildings, especially where foodstuffs are stored" within southern Africa (Smithers 1983), it has been recorded up to 1.5 km from human habitation and is known to live in burrows in these outlying areas (Shorridge 1934). *Mus musculus* has established a feral population in a small fynbos nature reserve completely surrounded by a suburban area (Middlemiss 1975). This is possibly analogous to the hillside habitat within Francistown, Botswana, where the species was also collected (Smithers 1971). The species is considered to have established a "feral population" at Sandvis Harbour in the Namib Desert (Stuart 1975a,b; Griffin and Panagis 1985), centered on a deserted building (C T Stuart personal communication). *Rattus rattus* has been found in several localities within natural and seminatural vegetation within the subcontinent: Davis (1974) states "wild-living populations not uncommon, but main habitat attachment is to houses, outbuildings and huts". *Rattus rattus* has been recorded in areas of natural and seminatural vegetation in the forests of the Transkei (Shorridge 1934), around Durban (Shorridge 1934) and at Oribi Gorge Nature Reserve in Natal, "two kilometres from nearest habitation" (Bourquin and Mathias 1984), on the Springbok Flats in Transvaal savanna "one kilometre from the nearest deserted farmhouse" (J Mendelsohn 1982 and personal communication), in the fynbos biome at the Cape of Good Hope (D L Clark personal communication) and Assegaaibos Nature Reserves (Stuart 1976), and at Sandvis Harbour on the Namib Desert coast (Griffin and Panagis 1985). Since the degree of invasion by *Mus musculus* and *Rattus rattus* is variable, an improved understanding might be achieved of factors limiting alien invasions by analysing the characteristics of localities where either or both of these rodents have invaded the small mammal com-

munity and contrasting these with those of localities where they are not known to be present.

The use of barn owl *Tyto alba* pellets for surveying for the occurrence of alien rodents

Rodents make up >75% of vertebrate prey items in the pellets of the barn owl *Tyto alba* in all regions of southern Africa (Vernon 1972a). The species composition of the diet varies between regions, within a region between sites, and at a site between years and seasons (Kolbe 1946; Vernon 1972a; Dean 1973, 1978; Macdonald and Dean 1984). *Tyto alba* is a generalist predator feeding on whatever prey items it can secure but with a preference for small mammals where these are available (Vernon 1972a; Macdonald and Dean 1984).

This low selectivity in prey choice is understandable given the owl's ability to locate its prey using sound cues alone (Payne 1971). However, the occurrence of prey species in the diet does not always reflect their abundance in the environment as determined by trapping (Hanney 1962; Coetzee 1963). This might be due to behavioural differences between prey species (Glue 1970; Perrin 1982) and habitat selection by the owls when hunting (Morton and Martin 1979). But the biases in the trapped sample are often marked (see references in Macdonald and Dean 1984) and there are no published data to show greater bias in the diet of the barn owl.

In southern Africa both *Mus musculus* and *Rattus rattus* are rarely recorded in *T. alba* pellet analyses (Vernon 1972a; Dean 1978; Macdonald and Dean 1984). Experience elsewhere has shown that these species are not behaviourally immune to predation by barn owls (Glue 1974; Herrera and Jaksic 1980). In some localities where these rodents have been introduced they have become the dominant prey items (Abs et al 1965; Morton and Martin 1979; Valente 1981).

The use of the number of alien species recorded from nature reserves as an index of their susceptibility to invasion

The second naturally occurring experiment considered here is the invasion of nature reserves by alien species. In these areas the general management objective is the maintenance of indigenous communities of species. Even in the most intensively managed reserves in the subcontinent an invasive alien plant species, once present, is very seldom completely eradicated from the reserve (Macdonald unpublished). Comparisons of the numbers of alien species recorded in reserves might provide some indication of the susceptibility of a reserve to invasion. This is

more particularly the case when one considers only those species invading the reserve which are not known to have been intentionally introduced to the reserve at some time in its history. Although there are uncontrolled variables present, such as the number of species that have been introduced into the reserve since its inception, there is little chance of controlling for these variables. Given the wide range of successfully invasive species present in the subcontinent (Wells et al 1986), and the extremely efficient dispersal mechanisms shown by many of these species, one may assume that the number of species established within a particular reserve is a measure of its susceptibility to invasion rather than simply reflecting its exposure to invasion. In order to test this assumption various measures such as the distance of the reserve from towns of different sizes, the presence of influent rivers and the annual number of visitors, were incorporated in the analysis.

Methods

The alien rodent/owl pellet data set

Data on the prey in pellets of the barn owl *Tyto alba* were collected for sites scattered throughout southern Africa (Figure 1). These data were assembled from the published literature (excluding those cited in previous sections these were Davis 1958, 1959; Bateman 1960; De Graaf 1960; Malherbe 1963; Pocock 1963; Nel and Nolte 1965; Winterbottom 1966; Niethammer 1968, 1975; Wilson 1970; Vernon 1971, 1972b, 1980a,b,c, 1981, 1983; Grindley et al 1973; Dean 1975; Avery 1977; Van der Merwe 1980; Brain 1981; Tilson and Le Roux 1983; Steyn 1984), from one of the authors' own records (Macdonald), and from unpublished records of ornithologists. These prey analyses were paired with data on the biome, climate, ecosystem type, extent of human disturbance and the number of species of predators of rodents likely to be present at the collection locality. The data were analysed to test for association between the presence or absence of alien rodents (*Rattus rattus* and *Mus musculus*) at each collection locality and such categorical information as biome type and ecosystem type. In addition, different derived variables describing the prey collection itself were analysed for differences between collections with and without alien rodents.

The collections made in different years at a site were analysed separately as, in some cases, these collections had been made by different workers and the exact collection locality might have differed. Also, invasions by alien rodents could have occurred in the

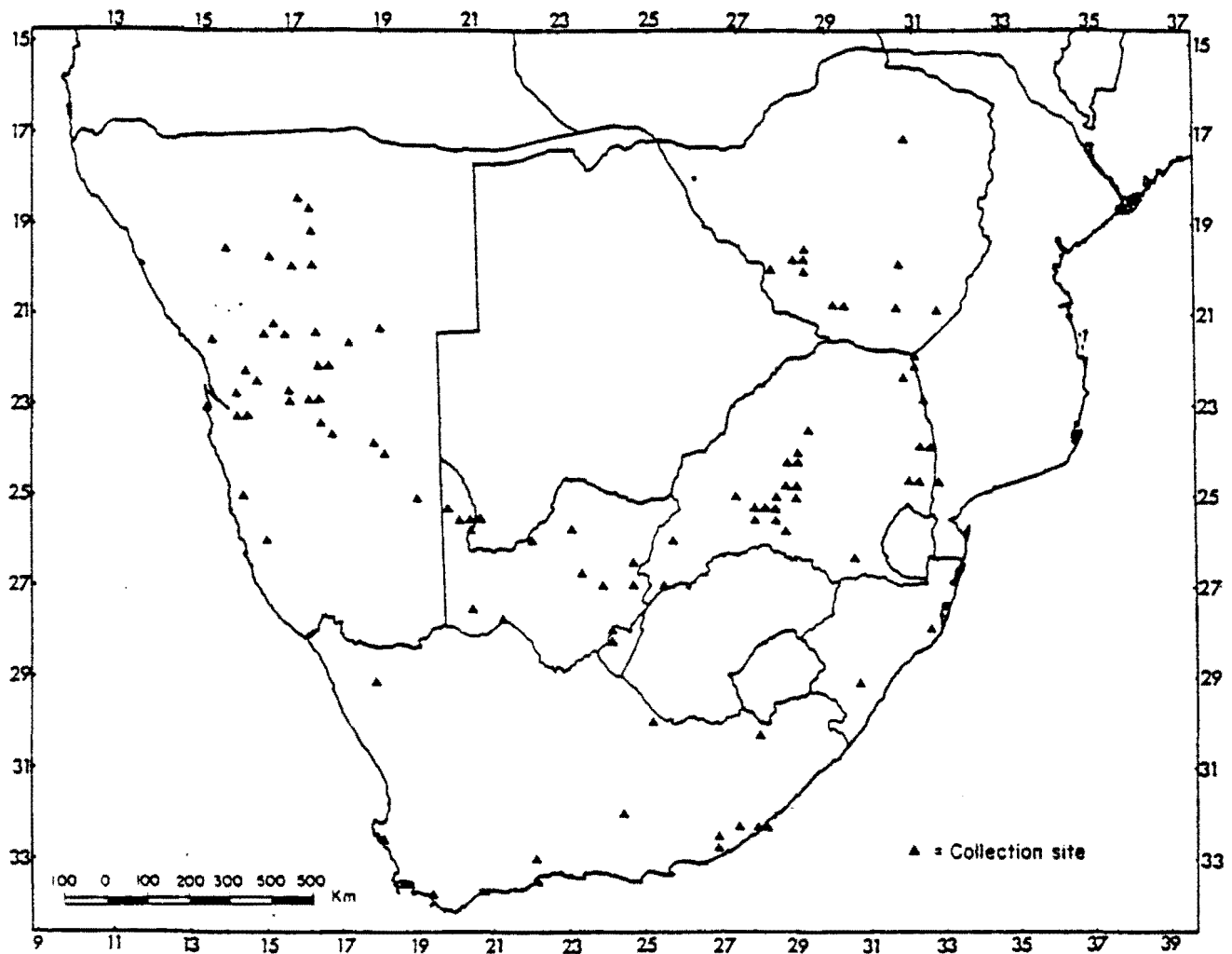


Figure 1. Map of the distribution of *Tyto alba* pellet collection sites by quarter degree grids.

interval between collections which sometimes exceeded a decade. Finally, the prey composition of the sample often differed markedly between years (cf Macdonald and Dean 1984).

Statistical tests employed in the alien rodent analysis

Statistical tests were applied to the data with the purpose of generating useful hypotheses. The analysis should not be viewed as definitive as there are problems with the randomness of the data sets, the cross-correlations between some of the classifications and the accuracy with which individual samples can be allocated to certain classes (eg those relating to ex-

tent of habitat modification). In the latter connection the sizes of *Tyto alba* hunting ranges in southern Africa have not yet been measured but a European estimate is that these have a mean radius of 2.5 km (Taberlet 1983). We classified collections on the basis of the location of the roost or nest where the collections were made; in some cases this might be different to the classification of the hunting range.

In all cases the frequencies of owl pellet collections with or without alien rodents were compared for two or more classes of these collections using the likelihood ratio chi-square G^2 test. Computations were carried out using the BMDP analysis P4F (Dixon 1985). Where the sample sizes for some of the

classes were small, and where the classes could not be meaningfully combined, eg in the inter-biome comparisons, the requirement for a valid contingency test, that the minimum expected value should not be less than one (Everitt 1977), could not be met. In these cases the results of the test are not presented, the data simply being tabulated for discussion.

The nature reserves data set

The second data set comprised the total number of indigenous and invasive alien vascular plants and vertebrate species recorded for a sample of nature reserves within southern Africa. The sample was selected to represent reserves in each biome, preference being given to those reserves which were known to have been reasonably well studied and those reserves which had been proclaimed for some time (ie those which can be considered reasonably "natural" rather than profoundly modified). In several cases it was found that data were not available for one of the selected reserves, and in most cases data were not available for every taxonomic group within a reserve. Some members of the initial sample were therefore rejected and, in a few cases, reserves with good species lists which were not previously in the sample were added. All were selected independent of their known invasion status. Most of the species lists were assembled from the unpublished records of the conservation agency responsible for the reserve, with a minority being obtained from published reports. Data on alien plant invasions were supplemented with the results of a questionnaire survey (Macdonald unpublished). Each reserve's species richness data were paired with data on the biome and climate, as well as various data relating

to the reserve itself. In many cases these data were obtained from Greyling and Huntley (1984).

Statistical tests employed in the nature reserves analysis

The 57 reserves in the sample were classified into two or more groupings according to their environmental or reserve characteristics (see Tables 3 and 7 for these characteristics).

The numbers of invasive alien species in a taxonomic group recorded for reserves were compared (either as absolute numbers or as percentages of the number of indigenous species in the reserves) using the Kruskal-Wallis nonparametric analysis of variance. Computations were carried out using the P3S programme of BMDP (Dixon 1985). In the case of the comparison of the fynbos biome reserves with all other reserves this test is identical to the Mann-Whitney U-test. Even here a two-tailed test of significance was appropriate as the mean number of invasive alien species in fynbos reserves was not always greater than that for the other reserves, even though the a priori hypothesis being tested was that fynbos reserves are more heavily invaded than other reserves.

The results of these analyses are presented simply as the significance of the overall analysis of variance. No detailed analyses using least significant differences between different classes of reserves have been attempted. The use of the number of species rather than a more quantitative measure of the extent of the invasions makes such analyses almost spurious. The intention of the analysis of this data set is the same as that of the alien rodent data set, ie the identification of potentially useful hypotheses

Table 1. A summary of the *Tyto alba* prey analyses used in the present study. All collections made from a site within a single calendar year were summed and called one collection. Collections made in different years were kept separate. Published sources of data are presented in the reference list.

Biome	No of sites	No of collections	No of vertebrate prey items	Decades of collections
Forest	0	0		
Fynbos	4	4	604	1950 - 70
Moist savanna	15	19	3 557	1960 - 70
Arid savanna	99	113	24 635	1950 - 70
Grassland	23	29	7 332	1930 - 30
Karoo/semidesert	14	16	2 722	1960 - 70
Desert	9	12	2 460	1960 - 70
Total	164	193	41 310	1930 - 30

Table 2. A summary of the nature reserves used in the analysis of indigenous and alien species richness.

Biome	No of reserves in sample	No of reserves for which species lists available (and mean number of invasive alien species per reserve)					
		Vascular plants			Vertebrate Classes		
		Angio- sperms	Spermato- phyta	All vascular + angiosperms	Reptilia	Aves	Mammalia
Forest	5	1(1.5)	1(3.2)	2(23.5)	3(0)	5(1.2)	2(0)
Fynbos	17	3(16.7)	6(40)	14(29.3)	7(0.1)	12(2.8)	11(2.7)
Savanna (arid or moist)	17	4(26.2)	4(68.7)	11(40.9)	15(0.1)	16(1.5)	12(1.2)
Grassland	8	0	5(32.2)	7(30.2)	5(0)	8(0.9)	6(0.5)
Karoo/semidesert	8	3(22.3)	1(1.5)	5(17.8)	4(0.2)	8(1)	5(1.2)
Desert	2	0	2(12.5)	2(12.5)	1(0)	2(1)	1(1)
Total	57	11	19	41	35	51	37

Table 3. Collection site or nature reserve data used in the analyses.

Parameter	Used in		Main Sources
	<i>Tyto alba</i> Study	Nature Reserve Study	
Biome	+	+	Huntley (1984); Brown et al (1985); Wild and Barbosa (1967)
Mean annual rainfall (mm)	+	+	Greyling and Huntley (1984); Weather Bureau (undated); Department of Met Services (1977)
Rainfall in 6 wettest months as % of annual rainfall	+	+	Department of Met Services (1977); Weather Bureau (undated)
Koppen climate classification	+		Schulze and McGee (1978, Figure 10)
Mean annual incidence of days having frost		+	Schulze (1965, Figure 85)
Reserve size (ha) and number of visitors per year		+	Greyling and Huntley (1984); NAKOR (1985)
Presence of influent rivers and distance from urban area		+	Trig Survey Maps, RSA and SWA
Number of species of rodent predators likely to be present in community:			
Birds	+		Tarboton (1968); Steyn (1982); Boshoff et al (1983); Tarboton and Allan (1984); Kemp et al (1985)
Mammals	+		Stuart (1975a, 1981); Smithers and Wilson (1979); Smithers (1983)
Reptiles	-		Rose (1962); FitzSimons (1970)

relating to the extent of invasions.

Summaries of the two data sets used

The full data sets are available in the archives of the Percy FitzPatrick Institute of African Ornithology. Summaries of the barn owl prey analysis data and reserve species richness data are presented in Tables 1 and 2. The parameters used in the paired data sets, together with their main source references, are listed in Table 3.

Patterns of incidence of alien rodents in owl pellets

Alien rodents were present at 19 (11,6%) of the

164 sites for which *Tyto alba* prey analyses were available (Figures 2 and 3). At three sites alien rodents occurred in the collections for more than one year, giving a total of 22 (11,3%) of the 195 collections with alien rodents.

The probabilities of the likelihood ratio chi-square tests of the frequency of occurrence of alien rodents in samples of these sites having different habitat or biotic characteristics are presented in Tables 4 and 5. Since alien rodents generally only occurred in very low numbers in any collection (15 of the 19 sites had fewer than five individuals present) it appeared likely that collections with few prey would be inaccurate predictors of the presence or absence of an alien ro-

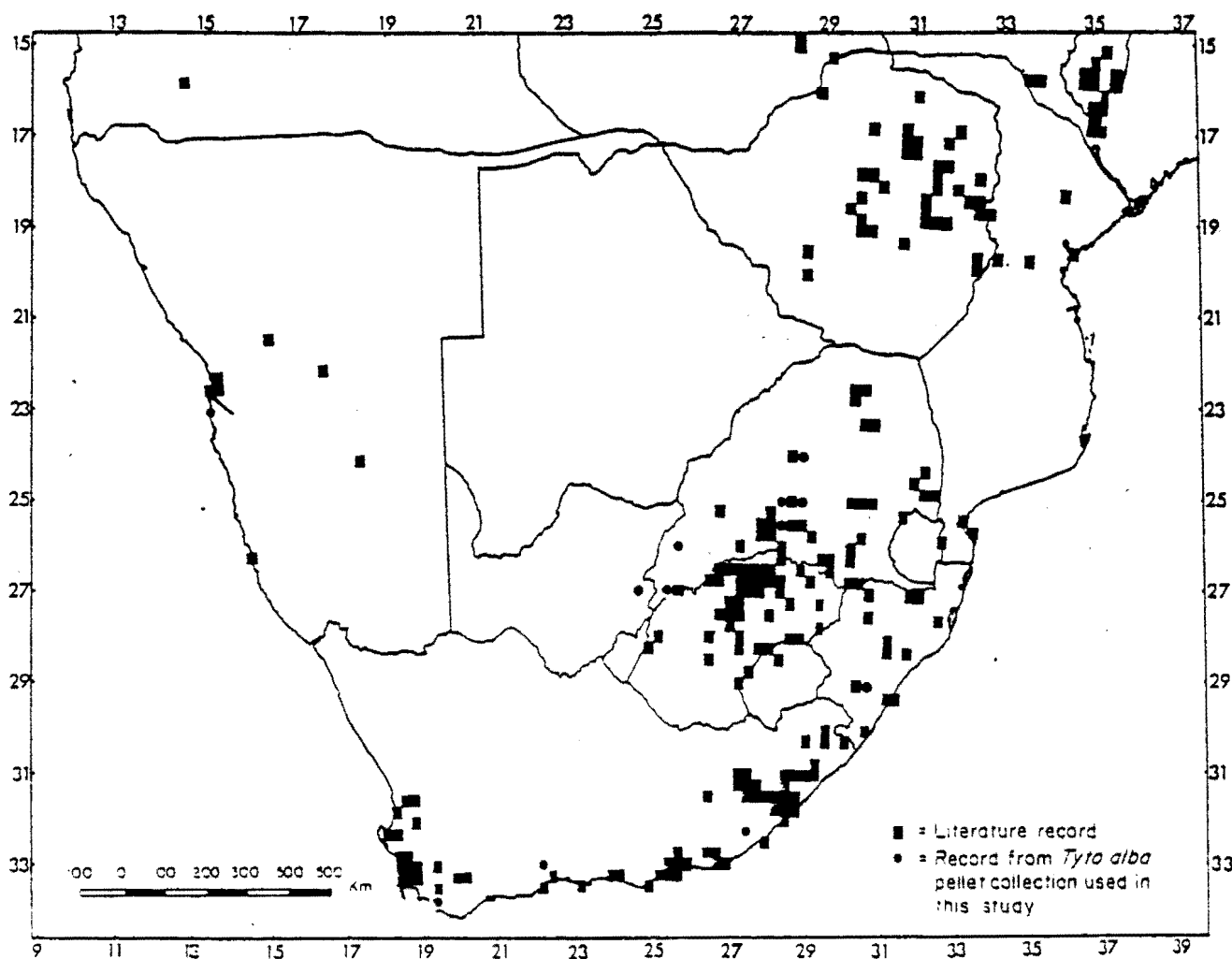


Figure 2. Map of the known distribution of *Rattus rattus* according to the quarter degree grid system (literature records from Davis 1974; Smithers and Tello 1976; Smithers and Wilson 1979; Bourquin and Mathias 1984; Brown et al 1985).

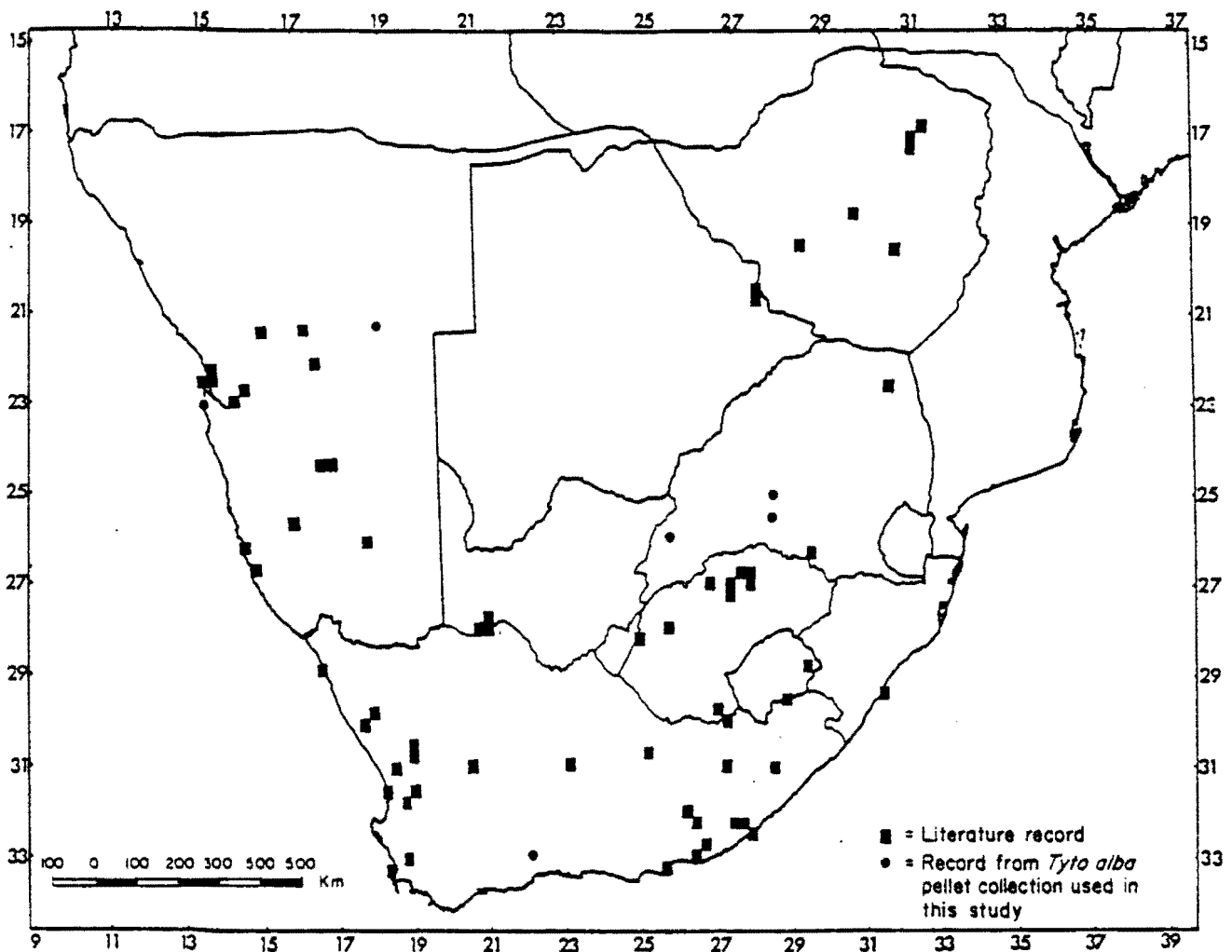


Figure 3. Map of the known distribution of *Mus musculus* according to the quarter degree grid system (literature records from Smithers 1971; Davis 1974; Smithers and Wilson 1979; Brown et al 1985).

dent. Alien rodents were significantly less frequent in collections with less than 75 prey items ($P < 0,01$), being present in only two per cent of such collections ($n = 59$). Several of the significant associations between habitat and biotic factors and alien rodent occurrence for the entire sample were found to be significantly different in terms of frequency of occurrence of sites having different prey sample sizes. The smallest category of prey sample size (< 75 prey items) was therefore eliminated from the final analyses, although the results of the tests using all samples are also included (Tables 4 and 5).

Differences between biomes

The ranking of those biomes showing relatively high occurrences of aliens does not appear to be significant. This ranking changed markedly between the analysis when sites with small prey sample sizes were excluded (Table 4) and that where all sites were included. In the latter, savanna was still the lowest, five per cent ($n = 114$), but desert was the second lowest, 22% ($n = 9$), fynbos third, 25% ($n = 4$), grassland fourth, 26% ($n = 23$) and karoo the highest, 29% ($n = 14$). In neither of these analyses could the results be tested statistically as minimum expected

values were much less than one for some cells in the contingency table (Table 4).

If the savanna sites are compared with those from all other biomes the statistical analysis is valid and the frequency of occurrence of aliens is significantly

lower in the savanna ($P < 0.01$). The only reason that the desert biome shows such a high frequency of occurrence is the presence of aliens in both collections from Sandvis Harbour. The susceptibility to invasion of mesic coastal sites surrounded by desert is sug-

Table 4. Probability values obtained in the likelihood ratio chi-square tests of the frequency of samples with or without alien rodents where samples were classified by habitat factors. Asterisks indicate cases where valid tests could not be made.

Factor	P		Frequency of occurrence (per cent) of alien rodents including only collections with more than 75 prey items (number of collections)
	All samples	Samples > 75 items	
Biome	*	*	Savanna - 7 (70), Fynbos - 25 (4), Grassland - 33 (18), Desert - 40 (5), Karoo - 50 (8)
Ecosystem types	*	*	Hillsides - 0 (15), Fynbos - 0 (1), Agricultural fields - 9(11), Open woodland - 12 (33), Riverine fringe - 19 (31), Grassland - 56 (9), Coastal dunes/estuaries - 67 (3)
Extent of modification	0,289	0,685	Natural - 12 (24), Seminarural - 17 (47), Transformed - 21 (33)
Pellet collection site	0,017	0,012	Cliff/cave roost - 5 (39), building roost - 20 (30), Tree roost - 30 (33)
Koppen climatic classification	*	*	BWh, Cfb, Dwa and Csa - 0 (7,6,1,1) Bsh - 15 (61), BWk - 18 (11), CWb - 20 (10), Csb - 50 (2), BSk - 67 (6)
Mean annual rainfall (mm)	0,951	0,632	400 to 600 - 14 (49), >600 - 16 (25), <400 - 23 (31)
% Rainfall in 6 main months	0,197	0,293	>85 - 10 (39), <80 - 20 (38), 80 to 85 - 23 (26)

Table 5. Probability values obtained in the likelihood ratio chi-square tests of the frequency of samples with or without alien rodents where samples were classified by biotic factors.

Factor	P		Frequency of occurrence (per cent) of alien rodents including only collections with more than 75 prey items (number of collections)
	All samples	Samples > 75 items	
Number of spp avian predators	0,001	0,006	>23 - 5(21), 15 to 23 - 9(47), <15 - 35(37)
Number of spp mammalian predators	0,174	0,386	>13 - 13(29), 11 to 13 - 15(26), <11 - 22(50)
Number of spp reptilian predators	0,009	0,060	<6 - 10(50), 6 to 8 - 24(55)
Total number of spp of predators	0,004	0,067	>40 - 7(29), 35 to 40 - 12(25), <35 - 25(51)
Total number of prey items from site	0,0016	0,200	75 to 300 - 13(61), 300 to 2150 - 23(44)
Total number of indigenous mammalian prey species from site	0,009	0,023	3 to 15 - 10(62), <3 - 21(28), 16 to 21 - 40(15)

gested by other results from the Namib Desert. In a limited sample of jackal *Canis mesomelas* scats from the small lagoon at Luderitz Bay only *Rattus rattus* and *Mus musculus* were present (Niethammer 1968). Similarly, pellets of an unidentified predator from Walvis Bay sewage settling ponds were composed entirely of *R rattus* (Niethammer 1975). Completely xeric sites and riverine ecosystems in the desert show no alien penetration (Niethammer 1968, 1975; Vernon 1972a; Tilson and Le Roux 1983). Mesic coastal isolates in the Namib Desert are possibly analogous to oceanic island ecosystems which have proven to be highly susceptible to alien rodent invasions (Atkinson 1985).

Differences between ecosystems

The individual ecosystem categories all had too few sites to allow for accurate statistical analysis (Table 4). The absence of aliens in hillside samples is possibly because most of these sites were from natural areas, eg the Kruger and Matopos National Parks. That hillside ecosystems are susceptible to invasion is exemplified by the occurrence of *Mus musculus* on a hill in Francistown, Botswana (Smithers 1971). The high frequency of occurrence in grassland and estuarine ecosystems (two of the latter were from different collections at Sandvis Harbour, one containing *R rattus* and the other *M musculus*) is in accordance with Smithers's (1983) observation that *R rattus* is dependent on dense low ground cover in natural and seminatural areas.

Extent of ecosystem modification

That this analysis failed to show significant differences in the frequency of occurrence of alien rodents in response to gross differences in the extent of ecosystem modification is puzzling (Table 4), given that the species are known to be human commensals. Where all sites are included in the analysis the frequencies of occurrence of alien rodents are: natural - six per cent ($n=48$), seminatural - 12% ($n=64$) and transformed - 16% ($n=50$). These results suggest higher levels of incidence in modified ecosystems (cf Hanney 1962; Macdonald and Dean 1984), but are not statistically significant.

Pellet collection site

The highly significant difference between the three categories of pellet collection sites (Table 4) is difficult to explain. The very low frequency of occurrence at sites on cliffs or in caves appears to be linked both to the high occurrence of such sites in natural areas and to the low occurrence of alien rodents in samples from hillside habitats.

Climatic factors

The Koppen climate zones each had too few sites to allow for valid statistical testing. However, there was a high occurrence of alien rodents in the Bsk climate zone, because of the presence of alien rodents at several sites in the Little Karoo around Oudtshoorn. Davis (1964) notes that this is one of the few areas in southern Africa that has not been penetrated by the bubonic plague bacillus *Yersinia pestis*. This disease, which was introduced to several South African ports in the early 1900's by infected *Rattus* species, has now become "endemic" throughout the region and causes periodic mass mortalities in indigenous rodents. It may also limit the penetration of indigenous rodent communities by the aliens.

Both mean annual rainfall and the seasonality of this rainfall (as measured by the percentage falling in the six consecutive heaviest rainfall months) had no significant effect on the incidence of alien rodents (Table 4).

Characteristics of the predator community

The highest level of statistical significance ($P=0,006$) was obtained for the association between the incidence of alien rodents and the number of species of avian predators of rodents likely to be present at a site (Table 5). It appears that sites having alien rodents were distinguished by a depauperate avian predator community. This trend was weaker and not significant for mammalian predators, possibly because the distribution data for mammalian predators was less exact than for avian predators. The relationship of reptilian predator species to alien rodent occurrence, which was significant ($P=0,009$) when all the sites were included in the analysis, was found to be highly confounded by differences in the total prey numbers of sites in the two categories of reptile species richness. The distribution data used for reptile species and the definition of which species preyed upon rodents were much less precise than was the case for both birds and mammals. The total number of species that prey on rodents that were likely to be present at a site was also linked to alien rodent occurrence when all samples were included in the analysis ($P=0,004$).

These results can be considered either to allow one to refute the hypothesis that ecosystems characterized by having different numbers of species which prey on rodents are equally susceptible to invasions by alien rodents, or to suggest the hypothesis that predation pressure exerted by a diverse predator community is an important factor limiting alien rodent penetration of an ecosystem. These results definite-

ly do not "prove" this latter hypothesis as there is no indication of causality in the observed correlation. That there is in fact causality in the relationship has been suggested as an explanation for the general lack of success of alien terrestrial vertebrates in southern Africa (Ferrar and Kruger 1983; Brooke et al this volume). Although it is widely recognized that predators do not eliminate established populations of these alien rodents it has been suggested that predation pressure exerted by domestic cats *Felis catus* can prevent the colonization of new areas by these species (De Graaf 1981).

Characteristics of the small mammal community

The number of species of indigenous small mammals present in the prey community (as reflected in the *Tyto alba* pellet analysis) was another biotic factor significantly associated with the frequency of occurrence of alien rodents (Table 5). In the analysis of all sites, regardless of the number of prey items, highest frequencies of alien rodents were found in the most species-rich prey communities. However, richness was strongly linked to the number of prey items in a sample. Moreover the results of this analysis were strongly influenced by the choice of cut-points between the different categories of species richness. If these were changed to six and eight there was no statistical significance to the differences in frequencies of occurrence of alien rodents in the analyses of all samples and samples having more than 75 prey items. The frequencies of occurrence for the latter analysis were: 8-21 species - 16% (n = 68), 6-8 species - 18% (n = 17), and <6 species - 20% (n = 20).

In order to test for a relationship between the occurrence of alien rodents and the diversity of the indigenous small-mammal community which would not be so heavily influenced by the variations in total prey numbers, the Shannon-Wiener index of diversity was calculated for each collection. This index was calculated twice for each collection, using both the total small-mammal prey community excluding bats, Chiroptera, and the total rodent prey community. The values of this index for sites with and without alien rodents and for sites having either one or two species of alien rodents present were compared using the Kruskal-Wallis non-parametric test. The comparisons of sites without alien rodents, with one species and with two species of alien rodents were not statistically significant for either the entire small-mammal community ($P = 0,69$) or for the rodent community ($P = 0,90$). The same comparisons between sites free of aliens and all sites with alien species were also not significant ($P = 0,91$ and $P = 0,94$).

The hypothesis that the species richness or diversity of the indigenous small-mammal community is irrelevant to the invasion of the community by alien species can thus not be convincingly refuted on the basis of this sample. This result is in accordance with the observation that *Rattus* is capable of invading southern African areas having highly diverse indigenous small mammal faunas (Shortridge 1934; Mendelsohn 1982; Bourquin and Mathias 1984). The species has, however, never been found to be common in such areas. Smithers (1983) suggests that the invasion of continental ecosystems in southern Africa by *Mus musculus* is prevented by the "high level of competition from indigenous species".

Results of the nature reserve analyses

The statistical significance of the Kruskal-Wallis analyses of variance of the number and proportion of invasive introduced species in the reserves are presented in Tables 6 and 7. All significance values with $P = 0,1$ or less are shown.

Differences between biomes

Two tests were carried out for each taxonomic group; the first comparing each biome independently and the second comparing the fynbos biome reserves with all other reserves regardless of biome. This latter test was carried out to test the a priori hypothesis that the fynbos biome is more susceptible to alien invasions than the other southern African biomes.

The number of accidentally introduced invasive species of Spermatophyta was significantly higher in arid savanna reserves with forest second, grassland third, fynbos fourth, karoo fifth and desert last. This effect was not manifest in any other grouping of plant species. When reserves were analysed for the number of invasive alien species of vascular plants (or of angiosperms where total vascular plant lists were unavailable) which had originally been intentionally introduced to the reserve, a total of 41 reserves could be compared. The biomes were shown to be significantly different ($P = 0,05$) in their mean rankings of this parameter: grassland reserves had the highest number, with arid savanna second and fynbos third.

When the fynbos biome reserves were compared against all the other reserves the only variable which was significantly different was the number of accidentally introduced invasive species expressed as a percentage of the total indigenous flora. This was significantly lower for fynbos where reserves with total lists of vascular plant species were compared

Table 6. Significance of the Kruskal-Wallis tests for differences in the number or proportion of alien plant and vertebrate species in the sample of nature reserves when classified by biomes and climatic parameters.

Taxonomic Group	Category of alien species	Biome	Probability of significance (P)				No of reserves in sample
			Fynbos vs all others	Mean annual r/fall	% Rainfall in 6 main months	No days frost per year	
Plants							
Angiosperms	all invasive spp	NS	NS	0,08	NS		11
	accidental spp	NS	NS	0,07	NS		
Spermatophyta	all invasive spp	NS	NS	NS	NS		19
	accidental spp	0,1	NS	NS	NS		19
All vascular	all invasive spp	NS	NS	0,08	NS		30
	accidental spp	NS	NS	0,1	NS		
	accidental spp as % of indigen spp	NS	0,03	NS	NS		
All vascular or angiosperm species	all invasive spp	NS	NS	0,04	NS	NS	41
	intentional spp	0,05	NS	NS	NS	NS	
	accidental spp	NS	NS	0,05	NS	NS	
	accidental spp as % of indigen spp	NS	0,05	0,03	NS	NS	
Reptiles	all invasive spp	NS	NS	NS	NS		35
	intentional spp	NS	NS	NS	NS		
	accidental spp	NS	NS	NS	NS		
Birds	all invasive spp	0,03	0,001	NS	0,05		51
	intentional spp	NS	NS	NS	NS		
	accidental spp	0,01	0,0002	NS	0,03		
Mammals	all invasive spp	NS	0,07	NS	NS		37
	intentional spp	NS	NS	NS	NS		
	accidental spp	0,07	0,07	NS	NS		

($P=0,03$) and where reserves with either vascular plant lists or angiosperm plant lists were compared ($P=0,05$). This reflects the rich floras of fynbos reserves relative to reserves in other southern African biomes and is not related to variations in the number of alien species.

The results of these analyses do not allow us to reject the hypothesis that southern African biomes are equally susceptible to alien plant invasions.

Amongst the vertebrate fauna the fynbos biome reserves had significantly higher numbers of accidentally introduced invasive alien species (see also mean numbers of all invasive species in Table 2). This resulted from the inclusion of the southern African helmeted guinea fowl *Numida meleagris* as an accidentally introduced alien species in most fynbos reserve lists (see Brooke et al this volume) as well as

the presence of the European starling *Sturnus vulgaris* and the house sparrow *Passer domesticus* in most of these reserves. In most other biomes only *P domesticus* was present. Similarly, in the analyses for mammals, fynbos reserves ranked higher than all other reserves. This was due to the frequent occurrence of *Rattus* species (both *R rattus* and the brown rat *R norvegicus*) and *M musculus* in fynbos reserves, as well as localized occurrences of the Himalayan tahr *Hemitragus jemlahicus*, the fallow deer *Dama dama*, the feral pig *Sus scrofa* and the grey squirrel *Sciurus carolinensis* in these reserves. In some fynbos reserves there were also southern African ungulates which did not formerly occur in the area which had been intentionally introduced. In other biomes virtually the only accidentally introduced mammals were the alien rodents *R rattus* and *M musculus* and even these were

not invariably recorded as being present. The fynbos biome appears to be more heavily invaded by birds and mammals than are the other terrestrial biomes. Whether this is a reflection of a heightened inherent susceptibility to invasion rather than of introduction pressure and the depression of indigenous predator populations in this biome is uncertain. It is possibly of note that the only feral population of *H jemblicus* in the biome is located in the only mountain chain from which all the larger carnivores have been exterminated. In the case of *S scrofa*, predation of piglets by indigenous carnivores has been identified as one of the factors limiting the successful establishment of some of the populations within the biome (Botha 1985).

Differences associated with rainfall regimes

The different groupings of plant species all showed the same trend, with the total number of invasive alien plant species and number of accidentally introduced species positively associated with annual rainfall. This is in accord with the observation within biomes that mesic habitats tend to have more alien species than do xeric habitats (Wells et al 1979; Macdonald 1983; Taylor et al 1985).

None of the vertebrate groups showed trends associated with variations in mean annual rainfall.

Surprisingly, the seasonality of the rainfall, as reflected in the extent of concentration of annual rainfall in the six main rainfall months, appeared to have no effect on the number of alien plant species

invading a reserve. Alien bird species were recorded as being present in greater numbers in reserves with aseasonal rainfall patterns (less than 70% of annual rainfall in six main rainfall months) than in those experiencing moderately (70-85%) and highly seasonal (more than 85%) rainfall regimes. This is possibly related to the autecological requirements of one of the major alien bird species in the region, *Sturnus vulgaris*. This species feeds by probing into soft ground with its beak (Feare 1984) and, as a result, it tends to be excluded from natural ecosystems in areas where surface soils harden during the prolonged dry seasons.

Differences due to variations in frost incidence

This parameter was only tested for lists of all vascular or angiosperm species, where available (Table 6). Contrary to expectations, there were no significant differences in the number of introduced plant species in reserves having less than five days of frost per year and reserves having more than sixty days of frosts.

The effect of reserve features

Although reserves varied in size from approximately 20 ha to 2 000 000 ha the number of alien plant species was not significantly associated with reserve size. Similarly, the presence or absence of influent rivers, often considered to be a factor of major importance in the introduction of alien species into

Table 7. Significance of the Kruskal-Wallis tests for differences in the number or proportion of invasive species of vascular or angiosperm plants in a reserve classified by reserve characteristics.

Category of alien species	Probability of significance (P)					
	Reserve Size	Presence of influent River	Distance from			Number of visitors per year
			Village	Town	City	
Total number of invasive alien spp	NS	NS	NS	NS	NS	0,1
Accidentally introduced alien spp	NS	NS	NS	NS	NS	0,08
Intentionally introduced alien spp	NS	NS	NS	NS	NS	NS
Accidental as % of total indigenous spp	NS	NS	NS	0,06*	NS	NS

*This is considered a spurious effect, showing no logical trend with increasing distance.

reserves (eg Macdonald 1983; Tarr and Loutit 1985; Vinjevoled et al 1985), had no significant effect. The distances of the reserves from the nearest small town (= village), medium town (= town), and metropolitan area (= city), as determined from maps were shown also to have no statistically significant effect. What was significant was the relationship between the annual number of visitors to a reserve and both the total number of invasive alien plant species and the number of accidentally introduced species. This relationship might be direct (visitors or their vehicles acting as the major vector for the introduction of alien plant species) or might be indirect, the number of visitors in the reserve possibly being correlated with factors such as the extent of disturbance of natural ecosystems within the reserve (eg through rest camp or roadbuilding activities).

Conclusions

The two studies carried out here indicate that faunal and plant invasions are possibly controlled by different suites of factors. The savanna biome appears to be highly resistant to faunal invasions, while possibly being susceptible to alien plant invasions. Similarly, whereas a high mean annual rainfall appears to indicate a high susceptibility to alien plant invasions, no such relationship apparently holds for faunal invasions. There are indications from both these studies that faunal invasions might be limited by indigenous predation pressure.

The alleged heightened susceptibility of the fynbos biome to alien plant invasions was not borne out by this analysis, based as it was on the number of species invading. Quantitative analyses, based on the extent of alien plant infestations, have still to be carried out (cf Macdonald 1984). The analysis of the number of species of invasive alien animals present in nature reserves indicated that the fynbos biome has been more severely invaded.

Neither of the analyses served to indicate the relative susceptibility to invasion of 'pristine' ecosystems. The extent of human modification of southern African ecosystems appears to be positively correlated to their susceptibility to alien plant invasions (Macdonald 1984). Even ecosystems in the subcontinent's nature reserves cannot now be considered to be pristine and some have been extensively modified.

In attempting to analyse natural experiments such as these, considerable caution must always be exercised in interpretation of the observed relationships. Significant relationships should not be taken to be a proof of causation. The validity of such relation-

ships can only be determined through carefully planned experimentation.

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Chapter 6

Alien species in terrestrial ecosystems of the fynbos biome

I A W Macdonald* and D M Richardson†

*University of Cape Town and †South African Forestry Research Institute.

Introduction

In this chapter we review alien invasions of the fynbos biome and address the following questions: (a) which species have invaded? (b) what are the characteristics of the invasions? and (c) do any of these characteristics appear to be unique to the biome? An outline of the salient features of the environment of the fynbos, the biotic communities which constitute it, and the history of human activities in the biome serve as background to the review.

Geographic extent

The fynbos biome is defined by Moll and Bossi (1984) and is here taken to also include all the Mountain Renosterveld (Acocks 1975). As such it occupies 77 172 km². The biome lies at the southern tip of Africa and includes the Cape Fold Belt Mountains and the coastal lowlands lying to the west and south of these mountains. The biome has a latitudinal range from 31° S on the west coast to 34° 50' S at Cape Agulhas to 33° 15' S near Grahamstown in the east. The longitudinal range is from 17° 51' E to nearly 27° E near Grahamstown. Various outlier patches occur in the mountains of the Karoo and further north in Transkei and Natal but their extent is small and their identity as true fynbos communities disputed (Kruger 1979).

Geology and soils

The predominant geological features are the quartz arenites of the Table Mountain and Witteberg Groups of the Cape Supergroup which form the main mountain and ridge crests. Shales of the Malmesbury Series of the Nama System and Bokkeveld Series of the Cape System form outcrops on the valley floors and coastal lowlands. Extensive areas of Quaternary and Tertiary sands are found along the southern and western coasts. Soils derived from sandstone rock

types are predominantly acid and poor in nutrients. Those derived from shales are relatively fertile and often saline. Granites occur locally, especially along the west coast at lower altitudes (Lambrechts 1979) and limestones and calcareous rock are largely restricted to the south coast.

Climate

The biome has climatic gradients from west to east, south to north, coast to interior and also a pronounced altitudinal gradient (Campbell 1983). These gradients, superimposed on the mountainous topography, give rise to a mosaic of spatially diverse climates (Fuggle and Ashton 1979). In the west, the lower mountain slopes experience a true Mediterranean-type climate with cold, wet winters and dry, hot summers (Köppen's climatic type Cs); summer drought is less severe on the upper peaks (Campbell 1983). Further east, rain falls throughout the year, with maxima in spring and autumn (Köppen's climatic type Cf; Fuggle and Ashton 1979). The biome is comparatively well watered and 19% of the major catchments of southern Africa fall within the biome (van der Zee 1981), an area comprising only about four per cent of the area of the subregion (Goldblatt 1978). Persistent high speed winds are an important factor in most fynbos ecosystems (Taylor 1984; Van Wilgen and Kruger 1985).

Fire regime

Possibly the most important aspect of the climate is that, in combination with the low-nutrient soils, it gives rise to patterns of plant production and combustibility that favour a fire regime of high intensity fires at intervals varying from 10-40 years depending on site conditions and sources of ignition (Kruger and Bigalke 1984). This fire regime is the single factor that most clearly differentiates the fynbos biome from the adjacent biomes. Fynbos plant species have characteristic adaptations that enable them to survive these periodic high-intensity fires (eg serotiny, myrmecochory and the ability to resprout).

Address for correspondence: I A W Macdonald, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700.

Biogeography

The combination of topography, geology and climate has given rise to environments that are ecologically unique in southern Africa, so much so that the area has been classified as a separate floral kingdom, distinct from the rest of Africa (Goldblatt 1978). The flora of the biome is renowned for its high alpha, gamma and delta species diversities (Kruger and Taylor 1979; Bond 1983). There is a high degree of endemism in several taxonomic groups: the flora (Goldblatt 1978); archaic invertebrates (Stuckenberg 1962); terrestrial molluscs (Van Bruggen 1978); Coleoptera (Endrödy-Younga 1978); Lepidoptera (Cottrell 1978); amphibia (Poynton 1960) and fishes (Bowmaker et al 1978). This reflects the antiquity and quasi-insular nature of the fynbos biome. Although a distinct biotic zone is recognized for the mammalian fauna (Rautenbach 1978), the species richness and endemism in this and other higher vertebrate classes does not parallel that of the flora (Bigalke 1978; Siegfried and Crowe 1983).

Vegetation and fauna

The vegetation of the biome is usually characterized by the presence of proteoid shrubs which form an upper storey of highly variable density. Ericoid shrubs and restioid hemipterophytes together usually form the understorey. In mid-high sparse to tall mid-dense shrublands (Campbell et al 1981), woody shrubs make up the greatest part of the above-ground living phytomass but the contribution of this component is very variable (van Wilgen 1984). Trees are generally restricted to ravines and riparian habitats and seldom dominate the landscape. Towards the east, grasses become more important in the understorey. Populations of the dominant plant species are generally even-aged with recruitment occurring directly post-fire (Kruger 1979). Plants are often protected by secondary chemicals and the level of herbivory is generally low except for the period directly after fire.

In general, the lowland environment comprises a few different plant communities, usually covering relatively large areas (Siegfried and Crowe 1983) whereas in the montane environment, a much greater variety of communities, often widely dispersed, occur as relatively small entities over the landscape. The great diversity of plant communities in this zone reflects the influence of geographic factors and of a complex landscape.

Populations of small mammalian granivores are of the same order as in other biomes (Cody et al 1983), but avian granivores are scarce except in some

instances after fire when they take advantage of serotinous seed releases. Avian communities are generally sparse. Nectarivores, feeding mainly on nectar of Proteaceae and Ericaceae and the associated insect fauna, and small insectivores are the most important guilds represented (Siegfried and Crowe 1983). Low bird density in the biome is ascribed to the low insect density (Siegfried 1979).

Patterns of land use and disturbance

Overall impacts of man

Man has been present in the fynbos biome for at least 600 000 years and the implications of the activities of prehistoric man for alien invasions have been extensively reviewed (Deacon this volume). The impacts on the biome of the burning, hunting and stock grazing of these peoples, although profound, have probably been smaller than those arising from man's activities since European colonization. Within 330 years, settled agriculture and the cultivation of a wide variety of alien plants has led to the complete transformation of at least 68% of the 28 508 km² of lowland ecosystems (Moll and Bossi 1984).

Transformation of the montane ecosystem has been less extensive, only 10% of the 42 064 km² occurring in the main block having been transformed by 1981 (Moll and Bossi 1984), and 10 823 km² (or 26%) currently being protected in State Forests or as proclaimed Mountain Catchment Areas (NAKOR 1984).

Simplification of faunal communities

Indigenous large mammals have been virtually eliminated throughout the biome (Skead 1980) and domestic livestock now graze much of the remaining areas of natural vegetation on the lowlands. Large mammalian predators (Stuart et al 1985) and a few of the large avian predators (Boshoff et al 1983) have been eliminated or reduced in numbers within the biome.

Alteration of fire regimes

One of man's main impacts throughout the biome, as it relates to alien invasions, has been the alteration of the natural fire regime (Macdonald 1984). We suggest the main changes have been: (a) increased fire frequency; (b) altered seasonal incidence (Van Wilgen and Richardson 1985a) and (c) reduced fire size. Lower mean fire intensities would have resulted from

(a) and (b). As in the precolonial era, the altered fire regime is virtually the only direct human impact on large tracts of the montane environment. Intensive grazing of recently burnt veld by domestic stock has, in places, led to severe degradation of natural communities (Wicht 1945). The degree to which fire regimes have been altered is greatest around urban areas (Kruger and Bigalke 1984) where alien organisms are also most prolific.

Afforestation with alien trees

One of the first actions of the European colonists was the planting of alien tree species (eg Krüger 1966) and afforestation was strongly advocated by authorities in the Cape of Good Hope in the late nineteenth and early twentieth century (Shaughnessy 1980 and this volume). Trees were planted for fuel and timber, to stabilize driftsands and for aesthetic reasons. Afforestation in the biome was on a limited scale up to the time of the First World War. It reached a peak in the period between the First and Second World Wars and again after the Second World War. Mainly *Pinus radiata*, *P. pinaster*, *P. canariensis* and *Eucalyptus* species were planted for commercial use. *Acacia cyclops* and *A. saligna* were planted widely for driftsand reclamation and by 1938, 102 km² of lowland fynbos had been thus treated (King 1943).

History of introduced species

The role of prehistoric man

The early Khoi and San inhabitants of the area apparently introduced few species, if any, and not even commensals such as the house rat *Rattus rattus* and domestic cat *Felis catus* (Skead 1980; Deacon this volume). The introduction of alien species began with European settlement in 1652, although there is a putative record of *Rattus rattus* from Robben Island in 1614 (Skead 1980).

Plant introductions

Shaughnessy (1980 and this volume) has documented the history of the more important invasive alien trees and shrubs in the Cape Town area. Most were intentionally introduced for shade, timber and sand-binding over the period 1830 to 1900, although *Pinus pinaster* was introduced as early as 1680. Many of the species that have spread were extensively propagated and cultivated throughout the biome (Shaughnessy 1980; Stirton 1978). Notable exceptions are *Hakea sericea* and *Sesbania punicea* where the extent of the invasions are dispropor-

tionately greater than the extent of their cultivation (Kruger et al this volume).

Faunal introductions

Most vertebrate introductions have been intentional. Examples are the grey squirrel *Sciurus carolinensis* (Millar 1980), European starling *Sturnus vulgaris* and chaffinch *Fringilla coelebs* (Siegfried 1962). However, in cases such as the Himalayan tahr *Hemitragus jemlahicus* and *Felis catus*, the species have established from individuals which escaped from captivity (Siegfried 1962). Still other introductions have been inadvertent. The slow worm *Ramphotyphlops braminus*, for example, was possibly introduced to the Kirstenbosch Botanical Gardens with potted plants (McLachlan 1978). By contrast almost all invertebrate introductions have been unintentional. These include the numerous alien molluscs, the termite *Cryptotermes brevis*, the ant *Iridomyrmex humilis* and the wasp *Vespula germanica* which are thought to have been introduced in cargo or in ships' ballast (Skaife 1955; van Bruggen 1964; Whitehead and Prins 1975; Coaton 1981).

Introductions from elsewhere in southern Africa

Several southern African species have been introduced into the biome and have established free-living populations here, eg the guineafowl *Numida meleagris* (Skead 1962), the gecko *Pachydactylus bibrani* (Siegfried 1962), several species of trees and shrubs (Moll and Scott 1981; de Villiers and McDowell 1982) and grasses (Adamson and Salter 1950). Within southern Africa, the fynbos biome seems to be uniquely susceptible to invasion by species from elsewhere in the subcontinent. Possibly this is a reflection of the quasi-insular nature of the biome, a situation mirrored by the mesic south-west of Australia which is also being invaded by intracontinental aliens (Macdonald 1985a,b).

Patterns of invasions by some successful alien species

Figure 1 shows patterns of invasion by four alien organisms in the fynbos biome and serves to illustrate differences in patterns and rates of spread of plants, molluscs, birds and mammals.

Hakea sericea has spread to occupy most mountain veld around Cape Town, Franschhoek and George. Spread was rapid in all directions and was not significantly aided by human dissemination, in marked contrast to most of the other important woody plant species (Shaughnessy this volume). Invasion by the snail *Theba pisana*, after its introduc-

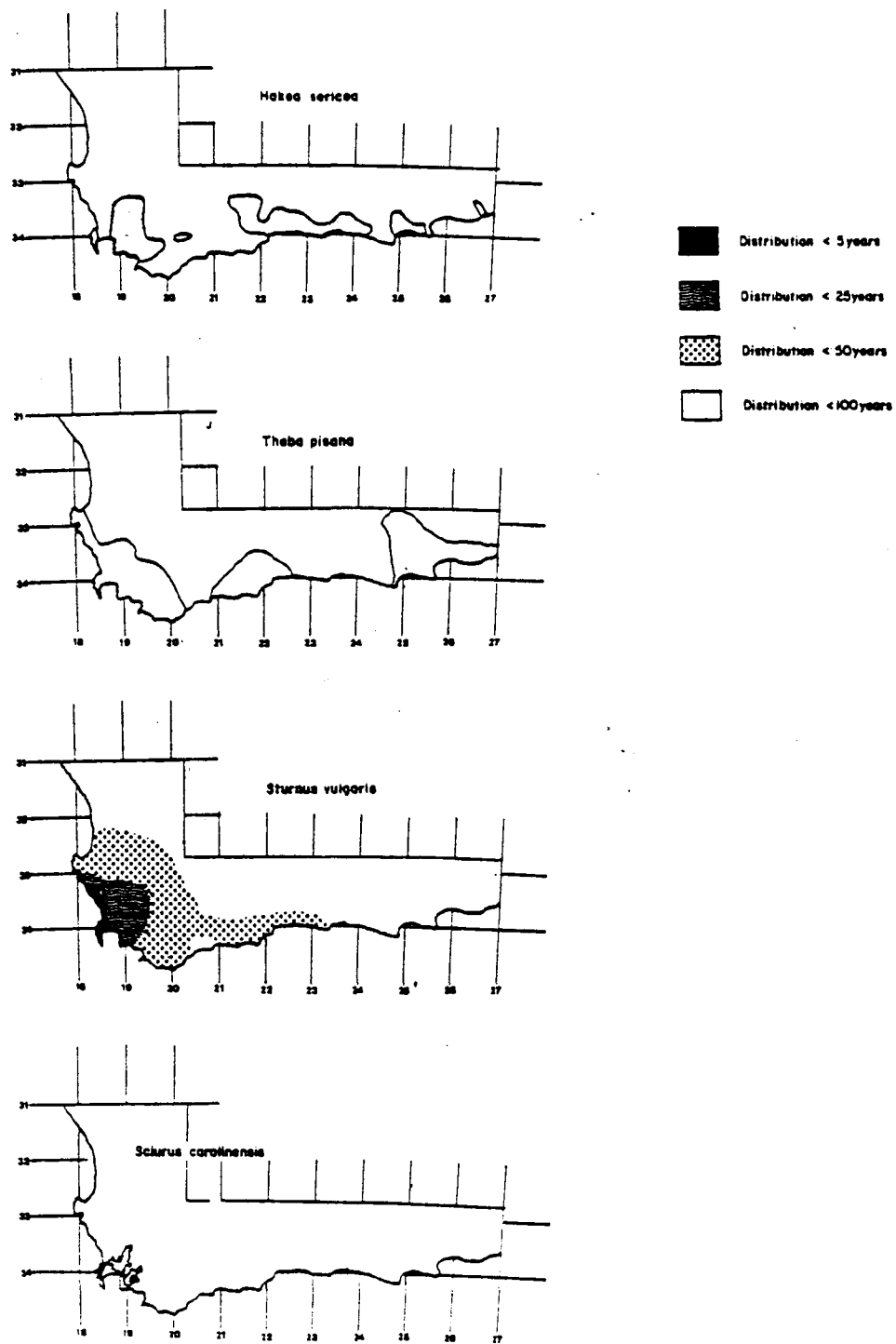


Figure 1. Distributions of some successful alien invaders of the fynbos biome.

tion to ports was facilitated by artificial dispersal by rail, road or ship though natural dispersal over short distances is apparently also implicated (Van Bruggen 1964). The starling *Sturnus vulgaris*, introduced in 1899, spread along a front in all directions from Cape Town to occupy the entire biome within 70 years of introduction. Spread was most rapid eastwards, where the availability of alien trees and man-made structures for roosting and nesting facilitated rapid colonization (Winterbottom and Liversidge 1954). The squirrel *Sciurus carolinensis* spread rapidly to occupy all potential habitat around Cape Town but further spread in the biome was prevented by the absence of suitable habitat. The slow increase in this species range has apparently been facilitated by the increase and maturation of stands of its favoured alien tree species (Millar 1980).

The nature of the invasions

Invasions of Mountain Fynbos by trees and shrubs

The most important alien invaders of the biome are numerous tree and shrub species, most of which have spread from cultivation and now cover small portions of the biome entirely. Coastal mountain ranges throughout the biome are invaded by *Hakea sericea*, *Pinus pinaster* and *Acacia longifolia* which form dense impenetrable thickets. *Hakea sericea*, introduced to the biome in around 1830 and planted on a very limited scale around Cape Town, Franschhoek and George, spread rapidly eastwards from Cape Town and Franschhoek and in all directions from George to cover almost 4 800 km² or 14% of the area of Mountain Fynbos about 130 years after its introduction (Kluge and Richardson 1983; Macdonald 1984). The present distribution of this species is positively associated with the occurrence of soils derived from quartzite and sandstone and its spread eastwards from Cape Town and northwards from George has been restricted to some extent by barriers of unsuitable nutrient-rich substrates (Fugler 1979; Richardson 1984). Typical stands of this species consist of three to four metres tall shrubs at a density of around 9 000 stems per ha ten years after a fire (Van Wilgen and Richardson 1985b). The other major invader of Mountain Fynbos, *P. pinaster*, has been found to be the most widely dispersed species in the Cape Peninsula mountains where it was present in 82% of 98 circular quadrats (10,5 ha) systematically located throughout the northern Peninsula mountains (Hall 1961). The spread of *P. pinaster* on Steilenboschberg has been analysed from successive aerial

surveys (Smit and De Kock 1984). The area covered by "dense infestations" (more than 50 plants km⁻²) increased from four per cent in 1938 to 36% in 1977. The most recent estimate of the area invaded by *Hakea* and *Pinus* species throughout the biome is 7 592 km² (Macdonald et al 1985a).

Hakea sericea and *P. pinaster* have the following factors in common which may have contributed to their success: both are dispersed by wind; both have winged seeds which are held in heat-resistant serotinous cones and which are often released after fire has killed the parent plants. However, the degree of serotiny is much higher in *H. sericea* than in *P. pinaster* (F J Kruger personal communication).

Acacia longifolia is a comparatively recent arrival in most Mountain Fynbos areas. However, it has recently shown rapid increases in both its distribution and density (McLachlan et al 1980; Taylor et al 1985) and is currently ranked the second most important alien plant invader in the biome (Macdonald and Jarman 1984). Its seeds are spread both by birds and water and it often forms dense thickets following fire, alien clearing operations or soil disturbance (McLachlan et al 1980; Pieterse 1984; Macdonald and Richardson unpublished).

Invasions of lowland areas and riparian communities by trees and shrubs

In contrast to the situation in Mountain Fynbos, *Acacia cyclops* and *A. saligna* are the most important species in the Strandveld and Coastal Fynbos. A survey of the western lowlands between the Berg River and False Bay revealed that by 1971, 17% of the remaining area of natural vegetation was invaded by alien woody plants (Boucher 1981). The seeds of the most important woody plant invaders of the lowlands are dispersed by birds and mammals (Middlemiss 1963; Knight and Macdonald 1985), man and water (Macdonald and Jarman 1984; Macdonald et al 1985a). Studies of sequential air photos have shown that certain *Acacia* species invade most rapidly along watercourses. The direction and rate of spread suggest that seed dispersal in water is the major cause of these patterns (Brownlie 1982). Possibly as a consequence of the efficacy of waterborn seed dispersal, riparian habitats throughout the biome are heavily invaded by numerous species, eg *A. longifolia*, *A. saligna*, *A. mearnsii*, *Albizia lophantha* and *Sesbania punicea* (Macdonald and Jarman 1984). A helicopter survey of the lowlands in the western Cape showed that *Sesbania punicea* was present in 64% of the 532 km of rivercourse surveyed (Bruwer 1983). *Acacia* and other thicket-forming alien woody plant species

in the biome were estimated to have invaded some 8 962 km² in 1984 (Macdonald et al 1985a). The extent of invasion by herbaceous alien plants has not been studied.

Vertebrate invasions

Of the vertebrate invaders, only the starling *Sturnus vulgaris* and the house sparrow *Passer domesticus* have spread throughout the biome. *Fringilla coelebs* is confined to the Cape Peninsula and is declining in numbers (Cape Bird Club 1979). Of the introduced mammals only the Himalayan tahr *Hemitragus jemlahicus* has been able to invade unmodified fynbos ecosystems and even it has not spread from Table Mountain because of intensive shooting since the early 1970's and because there are no corridors to other suitable habitats. The house mouse *Mus musculus* and *Rattus rattus* both have extensive ranges in the biome but are thought to occur mainly in areas of human habitation especially in drier areas (Smithers 1983). However, instances are known where both species have invaded areas of indigenous fynbos vegetation (Macdonald et al this volume). The brown rat *R. norvegicus* is mainly restricted to ports and coastal towns (Smithers 1983) but has been recorded invading seminatural areas within the biome (Middlemiss 1975; Stuart 1976). The squirrel, *Sciurus carolinensis*, introduced to Cape Town in 1900, rapidly became naturalized but is entirely dependent on introduced tree species (*Pinus* species and *Quercus robur*) and has not invaded natural ecosystems (Millar 1980).

Invertebrate invasions

A possibly important alien invertebrate that has invaded natural communities in the biome is the Argentine ant *Iridomyrmex humilis* (Skaife 1955; Donnelly 1983). The extent of invasion by this species is, however, related to the extent of disturbance in the form of roads and human habitation (De Kock 1984). *Iridomyrmex humilis* was found at 42% of 83 sites sampled within the fynbos between the Cederberg and the De Hoop Nature Reserve during 1983/84 (De Kock 1984). *Theba pisana* and *Helix aspersa* are the two most widely distributed alien molluscs in the biome, although at least 17 terrestrial species are known from the Cape Peninsula alone (Van Bruggen 1964). *Theba pisana*, first noted in the biome in 1881, is now found along most of the coastal strip south of St Helena Bay and has extended its range on the lowlands inland around Cape Town and Port Elizabeth (Van Bruggen 1964).

The case of *Phytophthora cinnamomi*

The pathogenic root fungus *Phytophthora cinnamomi* was thought to have been introduced to the biome and was considered to pose a considerable threat to its flora (Knox-Davies 1975). More recently, analyses of the current distribution of *P. cinnamomi* in the river systems of the biome (Von Broembsen 1984a), its host range (Von Broembsen 1984b) and the patterns of mortality in indigenous vegetation (Von Broembsen and Kruger 1985) have led to the conclusion that the species is indigenous. However, the possibility that one of the two genetic strains of the species present in the biome is alien requires further investigation.

Ecological impacts

Effects of woody plants on soil erosion rates

The only known impacts of invasive alien organisms on ecosystem processes in the fynbos biome are those of woody plant species. Soil erosion and deposition are considered to be severely affected in several ways. River bank erosion has been accelerated following the invasion of riparian vegetation by species such as *Acacia mearnsii*, *A. longifolia*, *A. saligna*, *Sesbania punicea* and *Pinus pinaster*. These species establish in and grow up through the indigenous vegetation which is well adapted to the flash floods that occur in most fynbos catchments. The alien trees, however, are not able to withstand these floods and are ripped out, often dislodging mats of indigenous vegetation such as those of *Prionium serratum* (Beyers 1959; Heydorn and Tinley 1980; Macdonald unpublished). The exposed mineral soil is then subjected to accelerated erosion.

Soil erosion is also considered to be accelerated under dense stands of certain woody alien species such as *Pinus* species which characteristically have a very sparse ground cover (Cowling et al 1976; Jacot Guillarmod 1980). However, other writers consider the establishment of alien woody plants to have decreased erosion rates, both of water erosion, as on Table Mountain (Lückhoff 1951), and of wind erosion, as on the Cape Flats (Wicht 1945). Following the clearing of long-established infestations of these species, particularly where the plants are felled, allowed to dry out and then burned, soil erosion is often accelerated on steep slopes (Cowling et al 1976; Richardson and Van Wilgen in press).

Effects of woody plants on coastal sand movements

Alien trees and shrubs have had a marked effect

on the movement of coastal dune sands, thus altering sediment dynamics. The species mainly responsible for this are the Australian watties *Acacia cyclops* and *A. saligna*. These have been extensively planted by the state forestry authorities to stabilize areas of windblown sand (Walsh 1968; Shaughnessy 1980; Shaughnessy this volume). Although some of this area was caused by man-induced changes in the vegetal cover (King 1943), recent research has shown that there are naturally occurring unvegetated dunes within the biome (McLachlan et al 1982; Lord et al 1985; Lubke and Avis 1985). Where the dunes that have been stabilized form part of a headland bypass dunefield, the reduction in sand movement can have profound effects on the distribution and extent of sandy beaches in the vicinity (Heydorn and Tinley 1980; Lord et al 1985; Lubke 1985). The ability of alien plants to establish and grow more successfully than indigenous plants on coastal sand dunes has been observed in southern and eastern Australia and has been recorded as having had profound effects on coastal sediment dynamics in these areas as well (Heyligers 1985; Sauer 1985).

Effects of woody plants on hydrology and fire regime

Although it is widely contended that dense stands of alien woody plants reduce the flow of water from fynbos catchments (eg Jacot Guillarmod 1980) there are no data available on this point. Extrapolation from plantations of alien tree species indicates that this reduction does occur (Van Wyk 1977; Bosch and Hewlett 1982).

Fuel loads are greater in dense stands of aliens than in fynbos but fires are generally more easily ignited in fynbos where there is an abundance of fine material in the herbaceous layer. Only under extreme weather conditions is fire intensity much higher in invaded areas. Fires under these conditions are more difficult to contain and are potentially more damaging to ecosystems than fires in indigenous vegetation (Van Wilgen and Richardson 1985b).

Effects of woody plants on geochemical cycling

Dense infestations of alien *Acacia* species affect geochemical cycling. *Acacia cyclops* has been shown to fix nitrogen (Roux and Warren 1963) and soil nitrogen levels have been shown to be increased by an order of magnitude following dune stabilization with this species (McLachlan et al 1982). Carbon cycling is also radically changed with above-ground biomass and mean litterfall rates being approximately three times higher in thickets of *A. cyclops* and *A.*

saligna than in indigenous fynbos vegetation (Milton 1981; Milton and Siegfried 1981). Soil organic matter content under a thicket of *A. cyclops* has been found to be twice that under indigenous dune thicket on the Alexandria dunefield east of Port Elizabeth (McLachlan et al 1982).

Milton (1981) has calculated from litterfall data and information on the chemical composition of alien and indigenous plants, that annual inputs of nitrogen and phosphorus to the soil under a dense thicket of *Acacia* would be about nine times greater than those under indigenous fynbos vegetation. Subsequent investigations of soil phosphorus levels in Strandveld have shown that both total and available phosphorus are approximately 50% greater under *Acacia* thickets than under fynbos (E. Witkowski and D.T. Mitchell unpublished). No work has yet been conducted on the relative rates of mineral cycling in alien and indigenous communities. Because fynbos plants are generally adapted to conditions of low soil nutrients the eutrophication of fynbos soils possibly has important implications for the survival or re-establishment of indigenous species on invaded sites. In the comparable heathlands of South Australia Hedde and Specht (1975) showed that three years' application of phosphate fertilizer resulted in the elimination or reduction in density of several indigenous species and their replacement by a range of herbaceous alien plants as measured twenty years after the fertilization.

Effects of woody plants on species richness of indigenous plant communities

Impacts on community properties have been more extensively documented than have those on ecosystem properties. Once again it is the impacts of alien woody plants that are best known. Plant species richness has been shown to be reduced in communities dominated by alien plants relative to uninvaded indigenous communities (Figure 2). This reduction in species richness has been best documented in a 'before and after' study of the fynbos in an area planted to *Pinus radiata* (Richardson and Van Wilgen 1986). The alien trees were planted in small pits in the fynbos with minimal disturbance to the indigenous vegetation. After 35 years the mean number of species per 0,1 m² quadrat was 2,1 (1,3 if alien species were excluded) compared with 3,5 prior to planting. The cover of the indigenous vegetation had decreased from 74 to 19% and plant density from 260 to 78 plants m⁻². Different life forms showed varying degrees of resistance to suppression by alien plants. Proteaceous shrubs with canopy-stored seeds

and limited dispersal capabilities were particularly susceptible (Richardson and van Wilgen 1986).

All the studies where paired estimates had been made of indigenous plant diversity, density or cover show these parameters to be reduced by dense or moderately dense infestations of alien plants (Cowl- ing et al 1976; Behrens 1985). The poor development of understorey vegetation in dense stands of alien trees is similar to that shown in indigenous forest vegetation in the south-western Cape (Bester 1976). Allelopathy, documented for *Pittosporum un- dulatum* in Australia (Gleadow 1982), has become evident where this species has invaded scrub and forest patches in parts of the biome (Richardson and Brink 1985).

Measures applied to control invasive trees and shrubs sometimes reduce the rate of recovery of in- digenous elements relative to recovery following nor- mal disturbance. Burning of slashed *H sericea* shrubs under severe weather conditions has resulted in very intense fires which kill subterranean rootstocks and seeds on or in the soil (Richardson and Van Wilgen, in press). Following the felling of an infestation, with or without subsequent burning, species richness is still depressed. Species richness has not been monitored

in the long term so that it is not known if it ever returns to preinfestation levels and, if it does, how long it takes to do so. In eastern Cape grassy fynbos it has been shown that, six years after the eradica- tion of a 15 to 20-year old multispecies alien infesta- tion (primarily *Pinus* species), the fynbos had regenerated sufficiently for a fire to be followed by normal post-fire regeneration of the vegetation (Jacot Guillardmod 1980, 1983; Richardson et al 1984). This agrees with the unsubstantiated assertion of Lückhoff (1951) that if *Pinus pinaster* infestations up to 20 years old are removed, recovery of the fynbos is still possible.

If infestations are not removed there is little doubt that local populations of at least certain indigenous species will become extinct. An analysis of a sample of 70 plant species in the south-western Cape which were evidently threatened with extinction showed that 33 were affected thus by invasive alien woody plants (Hall et al 1980). Similarly, of the 58 threatened plant species occurring on the Cape Peninsula, 31 are jeopardized by alien woody plants (Hall and Ashton 1983). As the extent of the remaining areas of natural vegetation decreases and alien plant invasions in- crease, more indigenous species will become en-

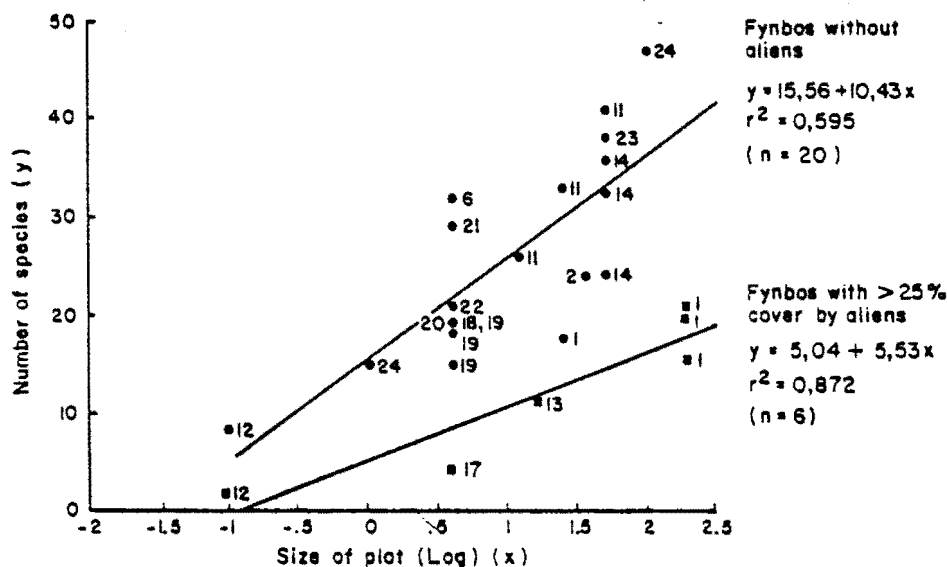


Figure 2. The relationships between the number of indigenous vascular plant species and plot size in fynbos areas densely infested (■) by alien woody plants and in uninfested areas (●). Each number indicates a different site. Numbering system relates to an unpublished study of the authors which is being prepared for publication. Sources of data are: (1) Cowling et al 1976; (2) Behrens 1985; (6) Richardson and Van Wilgen in press; (11) Van Wilgen and Kruger 1985; (12) Richardson and Van Wilgen 1986; (13) Milton 1976; (14) Van Wilgen 1981; (17) Richardson and Forsyth unpublished; (18) Richardson and Van Wilgen unpublished; (19) (20) and (21) le Maitre unpublished; (22) Richardson and Forsyth un- published; (23) Taylor 1984; and (24) Bond 1983.

dangered. Several authors have predicted the almost total disappearance of the fynbos flora if the spread of alien plants is not checked (Wicht 1945; Taylor 1977).

Effects of woody plants on the indigenous fauna

The impacts of alien woody plants on the fauna of the biome have also been considerable. Thickets of *Acacia cyclops* and *A saligna* have been shown to have a depauperate avifauna (total species number 86 with 37 occurring on five per cent or more of the bird lists made in this habitat) compared to the coastal fynbos they had replaced (total = 146 with 56 occurring on five per cent or more of lists) (Winterbottom 1970). The avifauna shows a reduced percentage of insectivores and an increase in granivores. The species that decrease most in frequency of occurrence in these thickets are those dependent on the smaller ericoid and graminoid plants within the indigenous vegetation eg Karoo robin *Erythropygia coryphaeus*, grassbird *Sphenoeacus afer*, greybacked cisticola *Cisticola subruficapilla* and lesser doublecollared sunbird *Nectarinia chalybea*. Of the 14 species most frequently recorded in these thickets 10 are generalist species that are also amongst the 14 species most frequently recorded in gardens eg Cape turtle dove *Streptopelia capicola*, laughing dove *S senegalensis*, fiscal shrike *Lanius collaris* and Cape sparrow *Passer melanurus* (Winterbottom 1970). The alien woody plants are not merely having local effects on the avifauna; studies have shown that at least two species, the hadeda ibis *Bostrychia hagedash* and pied barbet *Lybius leucomelas*, which are dependent on trees for roosting and nesting, have invaded the biome at least partly in response to the spread of alien trees (Macdonald 1986; Macdonald et al 1986). Historical analysis of the avifauna of terrestrial habitats in the south-western portion of the biome indicates that 36 species have invaded the area as a result of alien vegetation. A further 27 species have markedly expanded their ranges within the biome. Thus 63 of the current total avifauna of 224 species (28%) have been favoured by these alien plants (Macdonald et al 1985b).

Small mammal communities are reduced in species richness in some instances. In the Alexandria dune field, pure stands of *Acacia cyclops* were found to have only a single species of rodent, the four-striped fieldmouse *Rhabdomys pumilio*, while five species were recorded on adjacent littoral dunes having an indigenous plant cover (McLachlan et al 1982). Biomass of *R pumilio* in mixed thickets of *A cyclops* and *A saligna* on the Cape Flats has been estimated

at 2.5-9.4 kg^{-ha} (David 1980). This is approximately five to 10 times higher than the total rodent biomass in fynbos (David 1981). Its diet in the alien thicket was primarily *Acacia* seed (Shelton 1975). On the other hand, in *Hakea sericea* stands of varying density (1%, 35% and 95% of canopy cover) communities of indigenous small mammals, birds and arthropods were found to be similarly rich, both in species and in numbers (Breytenbach this volume). The effects of these faunal communities on their indigenous food plants were, however, much greater in the densely infested stand to the extent that recruitment of these plants following a fire could be jeopardized.

Impacts of other alien groups

Ecological impacts have not been investigated for herbaceous alien plants which, within this biome, are generally restricted to modified ecosystems, such as along railway lines (Raitt 1983), or are present only briefly following fire in areas of natural vegetation.

The browsing and trampling of *Hemitragus jemlahicus* is considered to have given rise to a reduction in plant cover and a concomitant increase in soil erosion (Lloyd 1975).

Iridomyrmex humilis displaces indigenous ant species (Skaife 1955; Donnelly 1983; De Kock 1984). The implications of this for the regeneration of the many myrmecochorous indigenous plant species has been stressed by Bond and Slingsby (1984). Such displacement has changed the pattern and reduced the abundance of seedling recruitment in *Mimetes cucullatus*, for example (Bond and Slingsby 1984).

History of control

The evolution of control programmes

Invasive trees and shrubs have long been a cause of concern in the biome. Phillips (1938) reported that farmers in the Bathurst district first met to discuss the spread of *Hakea sericea* in about 1863. Shaughnessy (1980) defines three phases of opinion by authorities concerning alien trees around Cape Town between 1884 and 1936: i) a determination to achieve total cover of trees (1884-1905); ii) defined plantations plus areas of abandoned plantations beyond which a policy of laissez faire applied (1906-1935); iii) areas beyond demarcated plantations were to be actively cleared of pines (1936 onwards). This is an accurate reflection of developments in the fynbos biome as a whole.

The control of *Hakea* and *Pinus* species in Mountain Fynbos areas

In the case of *Hakea* species and *Pinus pinaster*, the Weeds Act of 1937 did little to stop their spread. The lack of a definite mountain catchment management policy, together with the general opposition to the use of controlled burning as a management tool, made the attainment of control objectives impossible. A biological control programme for *H. sericea* was initiated in 1962, resulting in the release of two species of host-specific seed-attacking insects (Neser and Annecke 1973; Moran and Neser this volume; Neser et al this volume). The other important development in the control of *H. sericea* and other alien plants in mountain land has been the initiation of an active control policy by the Forestry Branch (Fenn 1980). With the initiation of regular prescribed burning in the late 1970's, proclaimed catchments were divided into management units. Each unit was to be burned at approximately 15-year intervals. All woody alien plants are felled prior to a burn and the area is burned about 18 months later to kill seedlings (Kruger 1977; Fugler 1983). This programme has been very successful and of the 7 592 km² once infested by *Hakea* and *Pinus* species, 1 579 km² (21%) had been successfully cleared by the end of 1984 (Macdonald et al 1985a). Assuming that the current rate of progress is maintained, most areas for which the Forestry Branch is responsible will have been cleared by around 1995 (Kluge and Richardson 1983).

The relatively recent emergence of the hard-seeded *Acacia* species and *Albizia lophantha* as important invaders of Mountain Fynbos is complicating control programmes. Prolific regeneration of these species after fire is now having to be treated with herbicides which is both expensive, often ineffective, and potentially damaging to indigenous plant regeneration (Macdonald et al 1985a).

The control of woody aliens in the lowlands

Acacia saligna and *A. cyclops*, the most important aliens in lowland vegetation of the biome, were, until very recently, widely planted for driftsand reclamation and a variety of other purposes. The use of these species has been strongly discouraged by the Forestry Branch since 1980 and official management instructions currently stipulate that indigenous species should be used for reclamation. In contrast to the montane environments of the biome, where some control is exercised over land use in proclaimed catchments, most land invaded by *A. saligna* and *A. cyclops* falls outside the area of jurisdiction of the

Forestry Branch. Control of these species is carried out by a number of smaller organizations, municipalities and volunteer groups. In total it is estimated that of the 8 962 km² infested by alien plants other than *Hakea* and *Pinus* species, ie mainly *Acacia* species, only 870 km² (10%) had been successfully cleared by 1984 (Macdonald et al 1985a). The ability of several of these species to coppice after felling and the density and longevity of the soil-stored seed bank makes control of these species difficult and expensive (Milton and Hall 1981; Macdonald et al 1985a). The control of these species, particularly on privately owned farm land, poses one of the most significant challenges to fynbos conservation.

The control of herbaceous alien plants

The large-scale control of herbaceous alien plant invaders in areas of natural vegetation has not yet been undertaken within the biome. The only exceptions have been the subshrub *Hypericum perforatum* and the grass *Stipa trichotoma*, both of which are confined mainly to areas of modified vegetation within the biome. The former has been the subject of a successful biocontrol programme (Kluge and Gordon 1983) while the latter is being controlled manually in at least one of the small areas currently known to be infested (Hall and Bulley 1980). Both these species are being controlled primarily on account of their potential threat to agriculture.

The control of alien fauna

The control of alien animals has not yet been accorded a high priority. Early attempts to limit the spread of *Sciurus carolinensis* through the application of a bounty system were abandoned as being futile (Millar 1980). The control of *Hemiragus jemlahicus* on Table Mountain is possibly the only example of the control of an alien animal for nature conservation reasons in the biome. The population density has been reduced to and kept at low levels through a programme of shooting initiated in the early 1970's and no increase in distribution range has been observed since then (Lloyd 1975). Research is being conducted on the ant *Iridomyrmex humilis*, to define the extent of its distribution, to analyse its effects and explore methods of control; recommendations have been made for limiting its further spread into fynbos areas (Macdonald and Jarman 1984; De Kock 1984). Until the ecological impacts of faunal aliens such as *Theba pisana* and *Vespula germanica* have been investigated, no rational basis exists for evaluating the importance of controlling these species.

Control priorities within the biome

The obvious impacts of alien woody plants has led to their control being accorded overriding significance in the management of natural and seminatural vegetation throughout the fynbos biome. This situation will not change unless major progress is made in the control techniques available for these species. In this respect, the biological control of the Australian *Acacia* species should be given the highest priority.

Conclusions

No attempt is made to draw conclusions regarding the assertion that the fynbos biome is especially susceptible to alien plant invasions, as this matter is dealt with in detail elsewhere (Macdonald 1984; Macdonald et al this volume). Instead conclusions will be made on the three questions posed at the start of this review.

Which species have invaded?

The most important alien invaders, both in terms of the extent of their infestations and their impacts, are undoubtedly the numerous species of woody trees and shrubs. However, the biome has been invaded by species from most taxonomic groups, with normally only a few species proving to be important in each of the faunal groups.

What are the characteristics of the invasions?

The invasions by woody plant species have been widespread and have often resulted in dense stands which radically alter biotic and abiotic features of the invaded landscape. These species have been able to invade relatively undisturbed ecosystems and the regular occurrence of fire in these ecosystems has tended to favour their spread and proliferation.

The impact of these woody plant invasions on the indigenous flora has been marked. Most indigenous plants in the biome appear to be intolerant of shade and decline in vigour or die once overtopped by invading tree species.

The invasions of herbaceous species and alien animals have generally been much less successful, with many of the alien species being restricted to sites of human disturbance.

What appears to be unique about alien invasions of the fynbos?

The dominance of the biome's invasive alien flora by trees and shrubs, at least in terms of the more important species, is possibly one of the features unique to the biome. Another is the large reduction in plant species diversity that follows the invasion of fynbos vegetation by alien woody plants.

The apparent high susceptibility of the biome to invasion by species from elsewhere in the subcontinent is also possibly unique. That more alien animal species have been able to establish populations in this biome than elsewhere in the subcontinent might also be unique (see Macdonald et al this volume). However, this could simply be the result of the extensive modification to ecosystems and impoverishment of the fauna that has characterized the biome in recent times.

The apparent occurrence of a "vacant" tree niche in the biome (Campbell et al 1979), the alleged occurrence of a "vacant" fish niche in the biome's rivers (Bruton this volume) and its susceptibility to invasion from elsewhere in the subcontinent all agree with the hypothesis that this small biome is in several ways akin to an island. The high levels of endemism in its indigenous biota strengthen this hypothesis. As in many "insular" environments throughout the world, alien organisms have wreaked havoc in the fynbos biome and will continue to do so until effectively controlled.

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A REPORT OF THE TERRESTRIAL ECOSYSTEMS SECTION
ECOSYSTEM PROGRAMMES

ADVANCES IN OUR UNDERSTANDING
OF ALIEN INVASIONS OF THE FYNBOS BIOME:
1980 - 1985

Occasional Report No 19

I A W Macdonald

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Author's address:

I A W Macdonald
Percy Fitzpatrick Institute
of African Ornithology
University of Cape Town
Private Bag
RONDEBOSCH
7700

PREFACE

The National Programme for Ecosystem Research (NPER) is one of several South African national scientific programmes administered by the CSIR. NPER is a cooperative undertaking concerned with research related to environmental problems. Within NPER, Ecosystem Programmes comprises a co-ordinated group of research projects and related scientific activities aimed at improving understanding of the structure and functioning of natural ecosystems and the solution of environmental conservation problems. The Fynbos Biome Project is one of these. The uniqueness of the biome was the focus of considerable research in the past. The project was initiated in 1977 in order to synthesize available scientific information, co-ordinate current activities and stimulate new research in the region.

Occasional Reports 12 and 18 in this series, which dealt, with 'community structure and species interactions' and 'nitrogen and phosphorus cycling' in the fynbos biome respectively, represented the first two of a set of preliminary reviews of recent literature (post 1978) concerning the fynbos biome. These reviews attempt to highlight the management implications of recent research activities carried out within the biome, and to identify future research priorities.

This report continues the review process in presenting a summary of the advances in our understanding of invasive alien organisms in the fynbos biome, documented in the literature during the period 1979 - 1985. A few 1986 references are included where the paper had been submitted at the time of review in July 1985.

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The author was particularly well placed to write this review, because of his involvement in the SCOPE (Scientific Committee on Problems of the Environment) project on the ecology of biological invasions, which fell under the auspices of the Nature Conservation Research (NCR) Committee of the NPER. The degree of collaboration which existed between the Working Group for Invasive Biota of the NCR and the Fynbos Biome Project is very much appreciated.

ABSTRACT

This report presents a summary of the advances in the understanding of invasive alien organisms in the fynbos biome, documented in the literature during the period 1979 - 1985.

During this period research has aided management in the following five main fields:

- in identifying where alien problems exist;
- in documenting the extent of the invasions;
- in quantifying alien impacts;
- in elucidating the mechanisms of invasion; and
- through the development of control strategies and techniques.

Research on control measures is not covered in this review.

TABLE OF CONTENTS

	<u>Page</u>
Preface	(iii)
Acknowledgements	(iii)
Abstract	(iv)
INTRODUCTION	1
IDENTIFYING THE PROBLEM.....	1
QUANTIFYING THE EXTENT OF THE PROBLEM	2
UNDERSTANDING THE INVASION PROCESS	4
QUANTIFYING ALIEN IMPACTS	6
RECOMMENDATIONS FOR FUTURE RESEARCH	8
REFERENCES.....	10

INTRODUCTION

The invasion of untransformed ecosystems by alien organisms has been identified as a serious environmental problem within the fynbos biome (Hall and Boucher 1977; Hall 1979; Kruger 1982; Bond and Slingsby 1984; Macdonald 1984). Combating these invasions has become one of the major tasks confronting fynbos managers (Fenn 1980; Macdonald et al 1985). This paper reviews the contribution research has made to the identification and resolution of problems posed by alien organisms.

Only research completed or initiated since 1979 is included in this review. Earlier research on alien organisms in most taxonomic groups is covered by the accounts in Werger (1978) while that on the alien plant problem was reviewed by Hall (1979) and early work on the biological control of these plants was reviewed by Annecke and Neser (1977).

IDENTIFYING THE PROBLEM

The problems posed by alien woody plants, known now for decades, have been quantified by some recent studies on rare and endangered plants. In a sample of 70 threatened plant taxa from the south western Cape, 33 had invasive alien woody plants threatening them (Hall et al 1980). Similarly, of 58 threatened taxa on the Cape Peninsula 31 were affected by alien woody plant infestations (Hall and Ashton 1983). In both these studies alien woody plants were the most frequent causal factor.

By contrast, recent studies of what was thought to be an alien organism of great significance for the biome, the fungus Phytophthora cinnamomi (Knox-Davies 1975), have failed to confirm the problem (Von Broembsen 1979). From an analysis of its current distribution in the river systems of the biome (Von Broembsen 1984b), its host range (Von Broembsen 1984a) and the patterns of mortality in indigenous vegetation (Von Broembsen and Kruger 1985) it has been concluded that the species is indigenous to the area. However, the possibility that one of the two genetic strains of the species currently present in the biome is alien to the region requires further investigation.

Amongst the biome's faunal invaders recent studies have indicated two species as impacting indigenous communities. The Argentine Ant Iridomyrmex humilis has been shown to have penetrated an area of untransformed Mesic Mountain Fynbos near Stellenbosch (Donnelly 1983). The European Starling Sturnus vulgaris has been reported competing for nesting holes with indigenous birds (Currie 1981; Van der Merwe 1984) and nesting in sandbanks (Brooke 1984a). Two other species of introduced animals have been shown to pose only limited hazards to indigenous communities. The American Grey Squirrel Sciurus carolinensis was found to be almost totally dependent on alien nut and seed-bearing tree species (Pinus species and Quercus robur) and, as such, to pose little risk to indigenous communities (Millar 1980). In depth analysis of the effects of introducing African Honeybees Apis mellifera adansonii into the fynbos biome have shown that the Cape Bee A. m. capensis is capable of withstanding this man-aided invasion with only minimal genetic pollution occurring (Tribe 1983).

Two introduced termite species, Coptotermes formosanus and Cryptotermes brevis have both been shown to be restricted to urban areas within the biome (Coaton 1981a and b) while another insect presumably introduced by ships to the biome, the Oriental Latrine Fly Chrysomya megacephala, is not thought to be having any significant impact (Prins 1979). Other alien insects recently discovered in the biome have been found to be restricted to their alien plant hosts eg the Pine Woolly Aphid Pineus pini (Bruzas 1981), the Eucalyptus Tortoise Beetle Trachymela tincticollis (Cillie 1984) and the Nectar Fly Drosophila flavohirta (Buys 1984).

The Red-eyed Turtle Dove Streptopelia semitorquata, which was thought to have a population in the south western portion of the biome only as a result of an intentional introduction (Winterbottom 1956), has been shown to have occurred here naturally, although the population present here shows genetic contamination from the south eastern subspecies introduced (Brooke 1984b).

QUANTIFYING THE EXTENT OF THE PROBLEM

The results of the most extensive survey undertaken to date of alien plant infestations in the biome, those of the Hakea species, were published during the review period (Fugler 1979, 1982, 1983; Fenn 1980; Richardson 1984). It was concluded that Hakea sericea was by far the most widespread of the three invasive species present in the biome with dense infestations (stems less than four metres apart) covering 314 km², medium infestations 2158 km² and sparse infestations 2428 km² (Fugler 1983). On those mountain ranges in the western Cape where Hakea species were present, the infestations were estimated to cover 25 per cent of the total area (Richardson 1984).

The other major invader of mountain regions, Pinus pinaster was studied on the slopes of the Stellenboschberg (Smit 1983; Smit and de Kock 1984). Using aerial photographs it was found that the area covered by dense infestations (>50 plants/km²) increased from four per cent in 1938 to 36 per cent in 1977.

A further study utilizing aerial photography was reported on during the period (Boucher 1981). A survey of the western lowlands between the Berg River and False Bay revealed that by 1971, 17 per cent of the remaining area of natural vegetation was infested by alien woody plants. A helicopter survey of rivers in the western Cape carried out in 1983 revealed that 64 per cent of the 532 kilometres of rivercourse surveyed were infested with Sesbania punicea (Bruwer 1983).

The results of two studies that compared the occurrence and densities of aliens in permanent plots at two points in time were published during the period of review. The first reported on 87 - 10,5 ha circular plots on the northern Cape Peninsula mountains (McLachlan et al 1980). Pinus pinaster and Hakea gibbosa were the most frequently recorded alien species in both surveys with the former decreasing from 82 per cent in 1959/60 to 75 per cent in 1976 and the latter increasing from 21 per cent to 27 per cent. Acacia saligna was the species showing the biggest absolute

increase in frequency between the two surveys (16 per cent to 25 per cent). The second reported on 99 of these circular plots located in the Cape of Good Hope Nature Reserve which were surveyed in 1966 and again over the period 1976 to 1980 (Taylor et al 1985). In these plots Acacia cyclops and Acacia saligna were the most frequent species at both surveys, the former increasing from 79 per cent to 86 per cent and the latter from 40 per cent to 59 per cent. Once again it was A. saligna which showed the biggest absolute increase in frequency. Pinus pinaster was only the third most frequent species at the first survey (23 per cent) and, as in the northern Peninsula study, it had shown the biggest absolute decrease by the time of the second survey (a seven per cent decrease to 16 per cent).

These and other earlier published estimates of the extent of alien plant infestations in the fynbos biome were collated in a review exercise (Macdonald 1984). It was concluded that the proportion of the fynbos biome's natural vegetation areas infested by woody plants is generally higher than that of other South African biomes.

The final contribution to our knowledge of the extent of these infestations arose from a collation of unpublished local knowledge carried out as part of the workshop meeting on the 'management of alien plants in the fynbos biome' held in October 1984 (Macdonald et al 1985). At this workshop, infestation and control operation maps were drawn up for the whole biome.

A conspicuous gap in our information on the extent of alien plant infestations is that relating to herbaceous alien species, in particular grasses. The only grass species that has been surveyed at all is Stipa trichotoma (Hall and Bulley 1980). As these authors emphasize, no efficient means exists for the surveying of the extent of herbaceous alien infestations. As they predicted, previously unknown infestations of S. trichotoma have been discovered during the five years since their review (A V Hall personal communication, 1985).

Very little research has been directed towards quantifying the extent of faunal invasions of the biome. Gaigher et al (1980) have published distribution maps for the southern African fish species that have been introduced to the fynbos biome but, although the records exist, the extent of the distributions of the fish species introduced from outside Africa have not as yet been published.

No published reports on the extent of alien bird invasions of the biome have appeared during the period. Ongoing research as part of the Cape Bird Club's Atlas project has shown that the Helmeted Guineafowl Numida meleagris, European Starling and House Sparrow Passer domesticus are now present in every quarter degree grid square in the western portion of the biome. The Chaffinch Fringilla coelebs is still restricted to the Cape Peninsula (Cape Bird Club unpublished records).

The quantification of the invasions of the biome by invertebrates, such as the White Dune Snail Theba pisana, is a conspicuous research gap. The only alien insect species that has had the extent of its infestation surveyed is the Argentine Ant (De Kock 1985). Of the 83 disturbed sites within or adjacent to natural fynbos areas that were surveyed in 1983/84 a total of 35 (42 per cent) were infested.

UNDERSTANDING THE INVASION PROCESS

Considerable advances have been made in our understanding of the processes involved in woody plant invasions of fynbos. One of the most fundamental additions to our knowledge has come from a unique study in historical ecology. Shaughnessy (1980) has shown how important human propagation has been in the spread of several tree species in the Cape Town area. Without a knowledge of the extent and timing of intentional plantings it is impossible to draw any sound conclusions on the relative speed of invasions of different species from a simple survey of current distributions.

The reproductive biology of Australian Acacia species in the biome has been the subject of intensive study (Milton and Hall 1981). It was shown that the mean densities of Acacia seedbanks fell between 2×10^3 and 4×10^4 seeds m^{-2} which is similar to those of ruderal weeds and most unusual for woody plant species. The seeds were shown to have high percentage viabilities and to show high levels of dormancy. Although their reproductive performance alone does not account for their successful invasion of the fynbos it does to a large extent explain the difficulties encountered in their control.

Ongoing studies on the seed dispersal of bird-dispersed alien trees have indicated that those species which have been successful invaders have fruit displays which equal those of the most successful indigenous fruiting species (Knight 1986). Even Acacia saligna, which is not generally considered to be specifically adapted for bird-dispersal, has been shown to be effectively spread by a ground feeding korhaan (Knight and Macdonald in preparation). Similarly, A. longifolia which is another species seemingly not well adapted for bird-dispersal, has been shown to be dispersed by Redwinged Starlings Onychognathus morio (Pieterse 1983). A. cyclops, which has a seed pre-eminently suited to bird-dispersal and which is known to be eaten by a wide variety of bird species, was shown to have a seedling distribution pattern concomitant with this mode of dispersal (Glyphis et al 1981). Initial studies of the Australian species Pittosporum undulatum near Stellenbosch have also documented the dispersal of this alien tree by birds (Richardson and Brink 1985).

Less progress has been made in understanding how alien Acacia species outcompete indigenous plants once they have germinated. Allelopathy was not demonstrated for A. saligna or for Albizia lophantha and seedlings of both these species were shown to be less competitive than those of the indigenous Virgilia oroboides (McDowell and Moll 1981). There is a suggestion that the success of Pittosporum undulatum is at least in part due to allelopathy (Richardson and Brink 1985).

Studies on the phenology of Acacia species (Milton and Moll 1982) and other alien woody plants (Sommerville 1981) in the western parts of the biome have indicated that the aliens possibly derive a competitive advantage over indigenous woody plants from their ability to grow earlier in spring. These studies also showed the extremely high rates of shoot growth these aliens are capable of in this area. The end result of these

growth rates, the biomass of alien Acacia thickets was estimated for 15 sites by Milton and Siegfried (1981). Mean above-ground biomass was 104 t/ha (dry mass) which is about three times the biomass of indigenous fynbos vegetation.

Recent studies on Hakea sericea have also increased our understanding of the invasion processes. Mitchell and Allsopp (1984) have shown that the seeds of H. sericea contain greater phosphorus reserves than those belonging to indigenous Proteaceae. H. sericea seedlings can grow longer in P-deficient substrates than can those of indigenous species. This, they suggest, could confer a competitive advantage to H. sericea in the generally P-deficient soils that cover so much of the fynbos biome.

In an analytical experiment, Richardson and Van Wilgen (1984) showed that, at least on a small plot basis, the germination and establishment of H. sericea was not significantly affected by either the season of seed release or the burning of the fynbos into which the seed was released. However, over all treatments the mean percentage of seeds that produced surviving seedlings was only 1,7 per cent. This low survival rate they ascribed to seed predation by rodents and birds. In further investigations Richardson (1985) showed that more than 99 per cent of H. sericea seeds were consumed by granivores 12 months after a dense (± 5000 stems/ha) stand had been felled and left unburned.

Two other investigations have shown the importance of indigenous seed predators for alien woody plants. In a two-year study carried out in alien Acacia thickets on the Cape Flats David (1980) showed an annual loss of Acacia seed from the litter layer of approximately 80 per cent. An estimated 20-30 per cent reduction could be attributed to predation by the Four-striped Fieldmouse Rhodomys pumilio. However, the remaining decrease was not accounted for. In some small-scale analytical trials in the western Cape, Pieterse (1984) showed that within a week rodents and birds removed an average of 66 per cent of Acacia longifolia seeds exposed on the soil surface.

Some data on the factors influencing the invasion process have emerged from a historical analysis of the Pella Fynbos Research Site (Brownlie 1982; Macdonald 1984). This, in combination with the results of a detailed enumeration of alien woody plants on this site carried out during 1984, has enabled a quantitative analysis to be made of the factors associated with the invasions of Acacia cyclops, A. saligna and Pinus pinaster (Macdonald et al in preparation). The investigation of Acacia seed bank densities and distributions carried out here has helped to elucidate the origins of some of the observed patterns (Beeston 1984).

The only research that has been carried out that throws light on the process of invasion by herbaceous alien plants is that of Harding (1983) on Stipa trichotoma. Once again the enormous annual seed production of a successful alien invader plant was documented; in this case an estimated 70 000 seeds/m². Plants were shown to have positive growth rates throughout the year with peaks in leaf extension occurring in October. The observed ability of this grass to grow and reproduce even under conditions of total shade emphasizes its invasive potential.

Among the faunal invaders the only research that has been carried out on the invasion process is that of De Kock (1985) on the Argentine Ant. In an analysis of the factors influencing whether or not a site was infested, a long history of vehicle access and occupancy by man were shown to be the most important factors. However many of the records of absence could not be explained on this basis and the researcher concludes that several of the sites surveyed could well be invaded in the near future given recent increases in development.

A general point that has emerged from numerous studies of a diverse range of alien invaders of the fynbos biome is the importance of man-induced disturbances in promoting these invasions. Another generalization is that the phenomenon of "ecological release" from natural predators and pathogens is of major importance in increasing the competitive ability of the aliens. Where indigenous pathogens, for example the gummosis and die back fungus Colletotrichum gloeosporioides of Hakea sericea (Morris 1982; 1983; Richardson and Manders 1985), or predators such as the Alydid seed predators of Acacia cyclops (Dennill 1983) emerge, the invasive potential of an alien is much reduced. Similarly, where a natural predator is introduced from the alien's country of origin, as in the case of the fruit weevil Erytenna consputa and Hakea sericea (Kluge 1983; Kluge and Siebert 1985) and the gall wasp Trichilogaster acaciaelongifoliae and Acacia longifolia (Dennill 1985), the reproductive output has been shown to decrease. This is in agreement with several recent studies which have contrasted seed production rates and seed bank sizes in the native and introduced portions of a single species' distribution (Weiss 1981; Weiss and Milton 1984; Gill 1984). What is currently unknown is whether the growth rates of aliens in their native habitat differs from that in the countries into which they have been introduced.

QUANTIFYING ALIEN IMPACTS

Although it is the deleterious impacts of alien organisms on ecosystem functioning and indigenous community structure and composition that provide the rationale for controlling aliens, very little research has been carried out on these impacts. To my knowledge there has not been a single published analysis of the economic impact of any alien organism in the biome.

One of the most important recent research findings on alien impacts relates to the Argentine Ant. Although it has been known for several decades that this alien displaces indigenous ants (see references in De Kock 1985), it was only recently that this displacement was shown to be occurring in areas of natural fynbos vegetation and to be primarily affecting those ant species responsible for dispersing the seeds of up to 20 per cent of the plant species occurring in the biome (Bond and Slingsby 1983). Where these indigenous ant species were excluded, myrmecochorous Proteaceae showed total recruitment failures (Bond and Slingsby 1984; Slingsby and Bond 1985).

Several studies have served to increase our knowledge on the impacts of alien woody plants. Two studies have detailed the effects of Pinus stands on indigenous plant community composition (Jacot Guillarmod 1980; Richardson and van Wilgen 1986). Both showed a loss of species richness. However, the eastern Cape study indicates that if the infestation was removed within 15 years of establishment most of the species regenerated. When the same study area was then burnt only six years after alien clearing operations had been initiated, the initial stages of the post fire regeneration were normal (Jacot Guillarmod 1983).

No research has been conducted specifically on the influences of aliens on ecosystem functioning. Increasing observational evidence has, however, been accumulated on the impacts of aliens, primarily Acacia cyclops, on sand movement on the coastal dune systems (Heydorn and Tinley 1980; Ascaray 1982; McLachlan et al 1982; Lubke 1983 and 1985). Aliens are apparently capable of naturally colonizing mobile dune systems and, having stabilized these, preventing sediment movement patterns which are often fundamental to existing coastal configurations. The resultant redistribution of beach sand can have serious economic impacts. The ecological impacts have not yet been detailed but may be considerable.

The effect of alien plants in destabilizing riverbanks continues to be stated as being one of their deleterious ecosystem impacts (Heydorn and Tinley 1980). No critical research has yet been carried out on this aspect.

The massive effects that dense infestations of alien plants have on geochemical cycling have been investigated for the first time in this biome. Milton (1981) found that the mean litterfall rate for the four species of Acacia she studied was approximately $700 \text{ g m}^{-2} \text{ pa}$. This is roughly three times higher than the rate measured for indigenous fynbos vegetation. Using published data on the composition of alien and indigenous plants she estimated that this would result in annual inputs of nitrogen and phosphate from Acacia thickets that would be some nine times higher than those of indigenous fynbos plant covers. Subsequent investigations of soil phosphorus levels have shown these to be elevated under Acacia stands (Witkowski and Mitchell in preparation).

Numerous workers have predicted that invasions by woody alien plants would lead to increases in fire intensity (Kruger 1982; Cole 1984; Macdonald and Jarman 1984). However, by using data on the fuel load characteristics of Acacia and Hakea thickets and indigenous fynbos communities, and inserting these in a fire behaviour model, Van Wilgen and Richardson (1985) have predicted that fire intensity will be decreased by these aliens. One of the possible confounding factors in this prediction is that, whereas almost all the above-ground fuel is removed in a fynbos fire, much remains standing following the first burning of an alien thicket. Repeated burning of an alien infestation might thus show elevated fire intensities as a result of this large contribution of standing dead material. It is desirable that empirical data be collected on this aspect.

The first critical studies of the effects of alien woody plant invasions on the composition of faunal communities were undertaken during this

period. In Hakea stands of varying density (one per cent, 35 per cent and 95 per cent of canopy cover) the composition of indigenous small mammal, bird and arthropod communities remained unchanged (Breytenbach et al 1984). However, the effects of these faunal communities on their indigenous food plants was much higher in the densely infested stand, to the extent that post-fire recruitment of these plants could be jeopardized.

In studies on the effects on bird communities of Acacia cyclops invasions, similar findings were made as regards species composition of the avifauna (Fraser et al 1985). However, bird density decreased to approximately 50 per cent of the level in a 10 per cent infested plot in two plots where A. cyclops had covers of 40 per cent and 75 per cent. Most of the reduction in avian density was due to reductions in nectarivore populations following the suppression of indigenous nectar producing Proteaceae.

The biome-wide influence of alien plant invasions was demonstrated in studies of two indigenous bird species, the Pied Barbet Lybius leucomelas (Macdonald 1986) and Hadedah Ibis Bostrychia hagedash (Macdonald et al 1986), which have recently expanded their distributions within the biome. Both expansions have been shown to have depended, at least in part, on the nesting and roosting substrates provided by alien tree species.

The only research that has been carried out on the impacts of herbaceous aliens in the biome is an investigation of the effects of the grass Briza maxima on indigenous plant regeneration following fire (Knight in preparation). The grass was shown to influence the survival of indigenous woody plant seedlings.

Research into the impacts of faunal aliens is a major gap in our current understanding of aliens in the fynbos biome. For example the current range expansion of the European Wasp Vespula germanica in the fynbos biome (Cooke 1984) is difficult to evaluate in terms of its significance for the biome's natural ecosystems as no research has been carried out on its impacts. Even long-established aliens such as the White Dune Snail Theba pisana, which are known to occur at high densities throughout certain fynbos ecosystems, have been completely neglected as regards their impacts. Unless this dearth of objective data on alien impacts is rectified no rational basis for the allocation of research and management funds will be possible.

RECOMMENDATIONS FOR FUTURE RESEARCH

Hall (1979) gave four broad priorities for research on invasive alien plants in the fynbos biome as:

1. determining their distributions;
2. studying their autecology and phenology;
3. developing integrated control programmes for each species; and
4. taxonomic studies, both of native plants, to enable the impacts of invasions to be better evaluated, and of invader species to enable the identification of appropriate biocontrol agents.

In the intervening years, some headway has been made on priorities one and two, and at least one integrated strategy has been developed and is being applied ie that for Hakea sericea (Kluge and Richardson 1983). Undoubtedly more work is required under topic two, particularly on some of the biome's lesser species which might prove to be major problems in the future eg Leptospermum laevigatum, Myoporum serratum and Nerium oleander.

Particular priorities that have emerged in recent years as being of major importance are the dynamics of soil stored seed banks of the hard seeded Acacia species. Another priority is an in depth assessment of the ecological impacts of herbaceous alien plants in the biome. These have largely been overlooked while the more obvious tree and shrub invasions were commanding attention. However, even the impacts of woody plant invasions have still not been adequately evaluated. This is particularly the case where the invasions have occurred in streambank situations. Erosion, water use and nutrient cycling impacts all require detailed research. The impacts of control measures on these aspects of ecosystem functioning, as well as on the subsequent regeneration of native plants need also to be researched.

In the field of faunal invasions research is needed to quantify the impacts of introduced fish species. We now know that alien fish are widespread throughout the biome's aquatic ecosystems and yet decisions as to whether or not they should be eliminated from certain of these water bodies have to be based on guesswork.

Finally there is an obvious need for research into the invasion of fynbos by alien invertebrates. Not only do we not know the impact of these aliens, but in many cases we do not even know what alien species are involved, let alone the extent of the invasions. This will be the major challenge facing zoologists concerned with alien invasions of the fynbos in the years ahead.

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Invasive alien organisms in central South West Africa/Namibia: Results of a reconnaissance survey conducted in November 1984.

I.A.W. Macdonald

Percy FitzPatrick Institute of African Ornithology,
University of Cape Town,
Rondebosch
7700
Tel. 6503300
021

T.B. Nott

Etosha Ecological Research Institute,
P.O. Okaukuejo,
via Outjo.
South West Africa/Namibia
9000

CONTENTS

1 Introduction	21
2 Methods	21
2.1 Alien plants	21
2.2 Alien birds	23
3 Results	23
3.1 Alien plants	23
3.2 Alien birds	24
4 Discussion	26
4.1 Alien plants, general	26
4.2 Alien plants, species accounts	27
4.3 Alien birds	33
5 Conclusions	34
6 Acknowledgements	34
7 References	34

ABSTRACT

Alien plants were surveyed from a moving vehicle along 2270 km of roads and 115 km in the courses of four rivers of central South West Africa/Namibia. Frequency of occurrence and abundance rating by 10 km road-lengths and 1 km river-lengths are presented for the 20 alien plant species observed. Although most species were infrequently recorded away from rivers, certain of the riverbeds held dense infestations of *Datura innoxia*, *Nicotiana glauca* and *Prosopis* sp.

The only alien bird species found to be widespread, the House Sparrow *Passer domesticus*, was recorded at 13 of the 21 areas of human habitation inspected.

1 INTRODUCTION

In South West Africa/Namibia, alien organisms invading natural and semi-natural ecosystems have received little attention from biologists. In order to collate the available information on the subject, a workshop meeting was held in November 1984 (Brown *et al.*, in press). In preparation for this meeting, the authors carried out a rapid survey of the central portion of South West Africa/Namibia during 20 — 26 November 1984. This paper presents the results of the survey.

2 METHODS

2.1 Alien plants

Infestations of alien plants were surveyed using the road transect method developed by the South African Botanical Research Institute, during their survey of alien plants in the Transvaal province of the Republic of South Africa (Henderson and Musil, 1984). The method used was to rate all infestations seen from a moving vehicle over each 10 km-section of road transect and over each 1 km-section of river bed traversed. The abundance ratings used were the modified ratings developed by Macdonald and Macdonald (in prep.) in South Africa (Table 1).

In total, 2 270 km of open road was traversed and rated in 10 km sections (Fig. 1) and 115 km of riverbed over four rivers was rated in 1 km sections (Fig. 1). In addition, 20 km of roads and firebreaks was traversed along the southeastern edge of the Waterberg Plateau Park.

For vegetation types, the frequency of occurrence (F) of species X in vegetation type i was computed as

$$F_{xi} = \frac{\text{No. of 10 km-sections in vegetation type i having species X}}{\text{Total No. of 10 km-sections in vegetation type i}} \times 100$$

The same approach was adopted using the 1 km-sections of each river transect. All frequencies were expressed as percentages, even though sample sizes were less than 100 (this is purely for facilitating comparison with other similar statistics, and the large error terms associated with these estimates should be borne in

mind). Mean abundance (A) for species X in vegetation type i was computed as

$$A_{xi} = \frac{\text{Sum of abundance ratings for sp. X in vegetation type i}}{\text{No. of 10 km-sections in vegetation type i having sp. X}}$$

The same approach was adopted in calculating the mean abundance ratings using the 1 km-sections of the river surveys. Mean abundance (A_{qd}) for species X in a quarter degree grid area was computed as

$$A_{qd} = \frac{\text{Sum of abundance ratings for sp. X in a quarter degree grid area}}{\text{No. of 100 km-section in quarter degree grid area}}$$

The mean abundance ratings for vegetation types and rivers are thus not comparable with those for quarter-degree grid areas, the latter being a mean over all 10 km-sections regardless of whether or not the species was present.

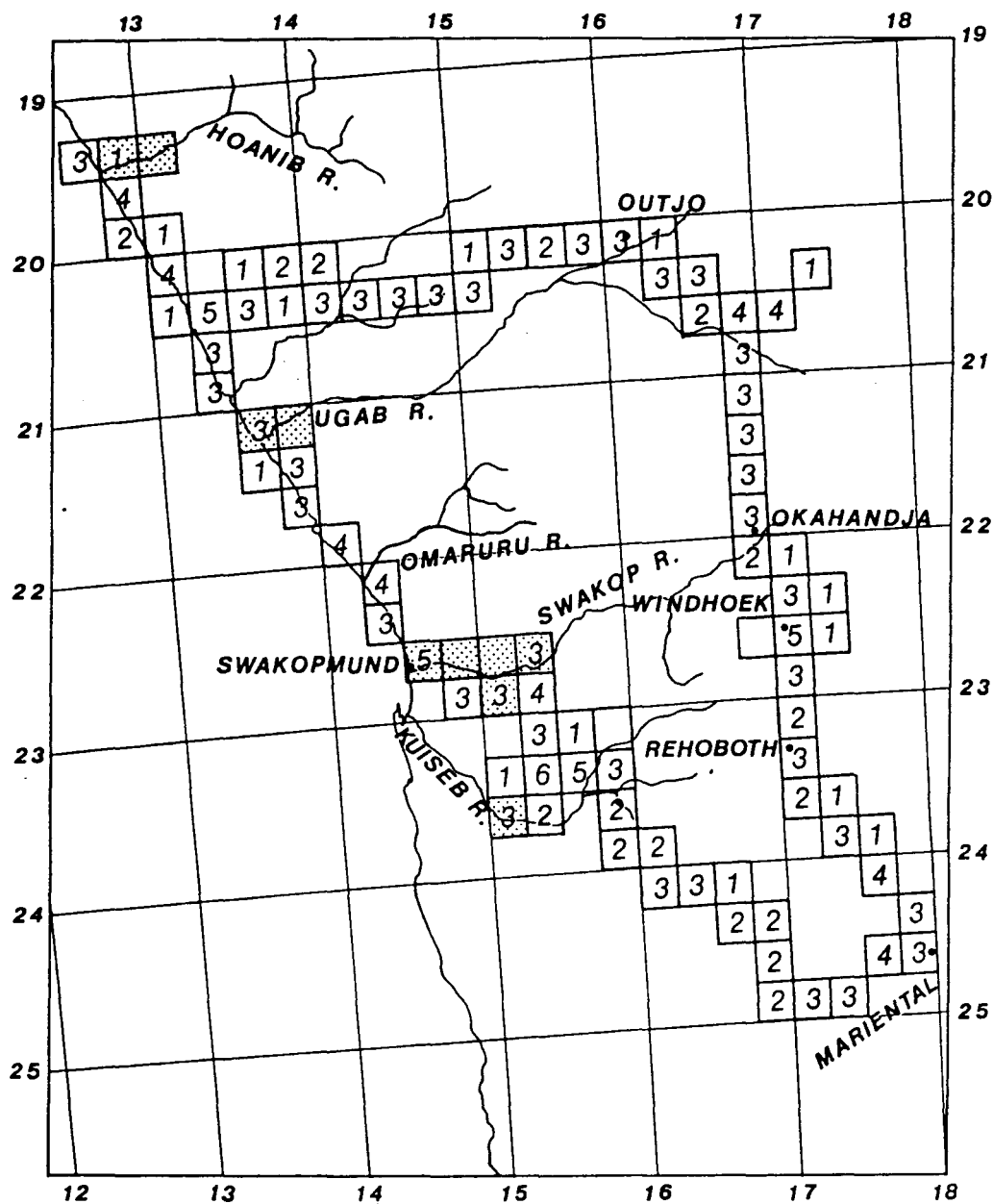


FIGURE 1: Route travelled showing number of 10 km transect sections surveyed per $\frac{1}{4} \times \frac{1}{4}^\circ$ area () and $\frac{1}{4} \times \frac{1}{4}^\circ$ areas where 1 km-sections were censused along riverbeds ().

TABLE 1: Abundance ratings used for alien plant species in the survey.

RATING	DEFINITION	
9	Species forming a virtually continuous, almost monospecific stand at least 1 ha in extent.	
8	Species co-dominant in a virtually continuous stand at least 1 ha in extent.	
	LESS ABUNDANT THAN "8" WITH THE NUMBER OF PLANTS SEEN PER:	
	10 km-section	1 km-section
7	200 or more	20 or more
6	100 - 199	10 - 19
5	50 - 99	5 - 9
4	20 - 49	2 - 4
3	5 - 19	1
2	2 - 4	N/A
1	1	N/A

2.2 Alien birds

All birds recorded in 29 quarter-degree grid areas visited were listed (Fig. 2). In particular, the environs of 12 restcamps and isolated stations, eight small towns and one city encountered on the journey were searched for alien birds (Fig. 2).

3 RESULTS

3.1 Alien plants

The results of the roadside survey are presented according to the seven vegetation types of South West Africa/Namibia (Geiss, 1971) traversed during the survey (Table 2; Fig. 3). The distribution and mean abundance ratings in each quarter-degree grid area

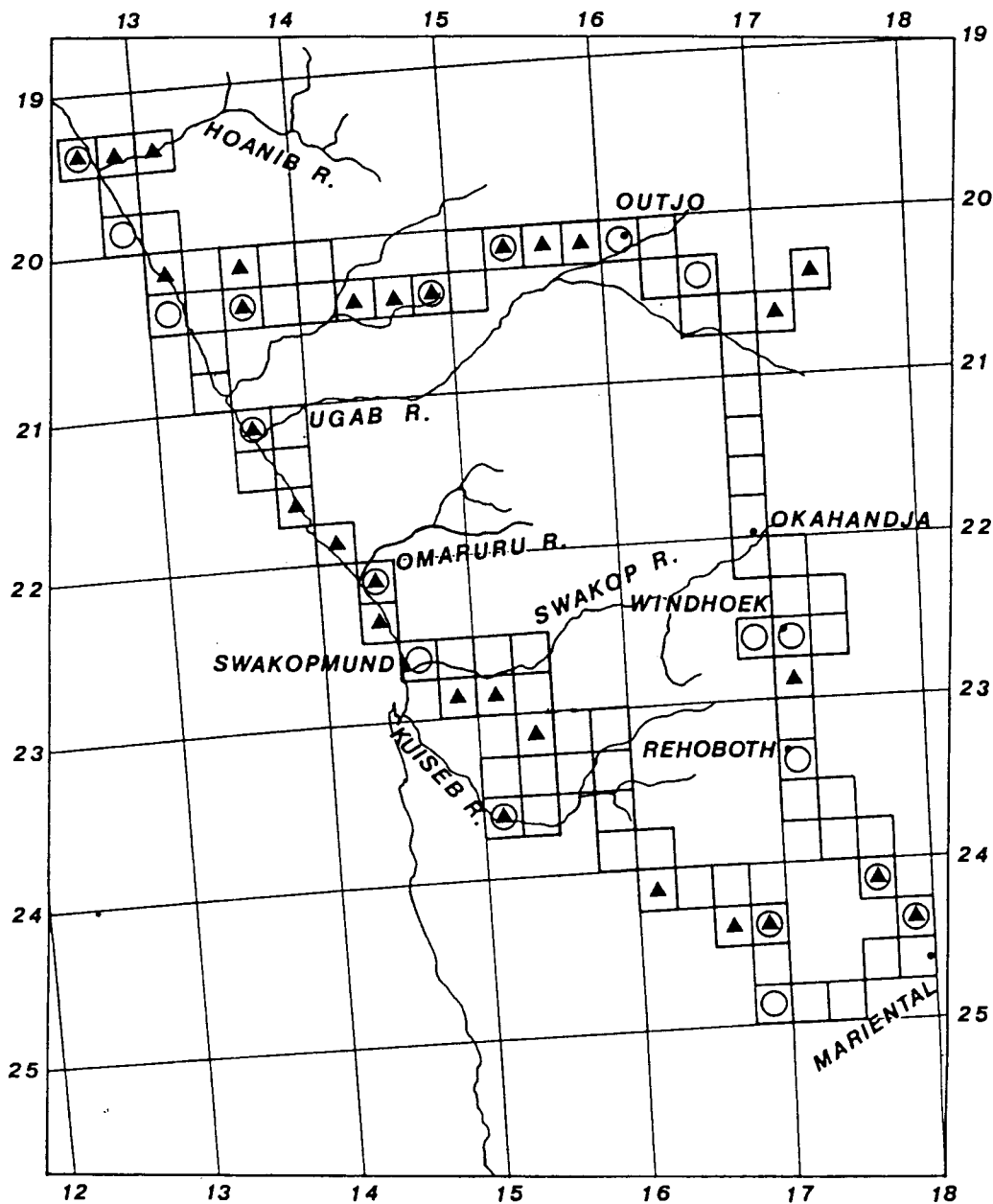


FIGURE 2: Grid squares for which all bird species were recorded (▲) and grid squares in which habitations were checked for occurrence of sparrows (○).

traversed for the most important species are presented in Figures 4 to 9. The results of the four riverbed surveys are presented in Table 3.

3.2 Alien birds

The only alien bird species recorded in the wild during the survey were Feral Pigeons *Columba livia* and

House Sparrows *Passer domesticus*. Feral Pigeons were only recorded in one quarter-degree grid area (Windhoek, 2217CA), whereas House Sparrows were recorded in 13 quarter-degree grid areas and around 13 of the 21 sites of human habitation surveyed. The observations made on sparrows around habitations are summarized in Table 4. No alien birds were encountered away from areas of human habitation.

TABLE 2: The percentage frequency of occurrence (F) in 10 km-sections and mean abundance ratings (A) for alien plant species in seven vegetation types sampled on the road transects (see Fig. 3 for names and distribution of vegetation types).

Veld type no.	1		2		4		5		7		8		9	
No. 10 km sections	30		55		25		31		40		12		36	
SPECIES	F	A	F	A	F	A	F	A	F	A	F	A	F	A
<i>Argemone subfusiformis</i>			4	5,0	12	3,0	10	2,6	40	5,3	75	3,8	33	4,8
<i>Asclepias fruticosa</i>					20	3,4	13	4,0	55	4,2	50	3,0	25	1,9
<i>Caesalpinia gilliesii</i>									3	3,0	8	1,0		
<i>Cereus peruvianus</i>							3	3,0						
<i>Datura ferox</i>							3	3,0	8	1,3	8	2,0		
<i>Datura innoxia</i>			4	3,0	4	3,0	26	4,0	23	2,2	25	2,3	8	2,3
<i>Datura stramonium</i>					4	3,0	3	3,0	3	3,0	8	5,0		
<i>Dodonaea viscosa</i>							3	4,0	3	1,0				
<i>Melia azedarach</i>							3	1,0	3	1,0	8	3,0		
<i>Nicotiana glauca</i>			4	7,0	8	2,5	6	3,0	5	1,0	8	6,0	3	1,0
<i>Opuntia ficus-indica</i>							3	2,0			17	2,5		
<i>Opuntia imbricata</i>											8	1,0		
<i>Opuntia inermis</i>							3	7,0						
<i>Opuntia microdasys</i> var <i>lutea</i>											8	4,0		
<i>Opuntia</i> sp. <i>unident.</i>											8	1,0		
<i>Prosopis</i> sp.					12	3,3	6	2,0	13	5,4	25	3,7	53	2,6
<i>Ricinus communis</i>	3	1,0	2	3,0	12	3,0	3	2,0						
<i>Schinus molle</i>							3	2,0	3	1,0				
<i>Tagetes minuta</i>							3	4,0	8	4,3	42	4,6		
<i>Tecoma stans</i>									3	1,0				

TABLE 3: The percentage frequency of occurrence (F) in 1 km-sections and mean abundance ratings (A) for alien plant species within the riverbeds of four west-flowing rivers in the Namib desert.

River (veld type no. of area)	Section of river surveyed	No. km	SPECIES											
			<i>Argemone subfusiformis</i>		<i>Datura innoxia</i>		<i>Datura stramonium</i>		<i>Nicotiana glauca</i>		<i>Prosopis sp.</i>		<i>Ricinus communis</i>	
			F	A	F	A	F	A	F	A	F	A	F	A
Hoanib (1)	Mouth of river to 35 km up river	35	9	3,7	94	7,2	9	4,0					6	4,0
Ugab (2)	Main road to 11 km upriver	11	73	5,9	100	6,4	45	5,2	100	8,3	27	3,0	18	3,0
Swakop (2 & 4)	Western boundary of Namib-Naukluft Park to 11 km east of Salem	47	6	3,0					21	3,5	94	5,1		
Kuiseb (border of 2 & 3)	Gobabeb to Homeb	22	32	4,1	73	6,0	55	5,7	82	6,0			27	4,2

TABLE 4: Presence (P) or absence (A) of sparrow species around human habitation in central South West Africa/Namibia. Where breeding activities were seen these are indicated by B. Where numbers were counted in the survey these are shown e.g. -6.

Locality	Quarter degree area	Presence of sparrows:				No. of spp. co- existing
		House	Cape	Great	Grey -headed	
REST CAMPS, ISOLATED STATIONS AND FARM HOMESTEADS						
Daan Viljoen Rest Camp	2216DB	P	A	P	A	2
Gobabeb Research Station	2315CA	PB	PB*	A	A	2
Hardap Dam Rest Camp	2417BD	PB	A	PB	A	2
Jackalsput Fishing Camp	2214AB	A	P-6	A	A	1
Mowe Bay Ranger Station	1912BC	P-2**	A	A	A	1
Nomtsas Farm	2416BD	A***	P	P	A	2
Power Station	2214DA	A	A	A	A	0
Springbokwater Ranger St	2013BC	PB-8****	A	A	A	1
Spykersbron Farm	2015AB	A	A	A	P	1
Terrace Bay Rest Camp	2013AC	A	A	A	A	0
Torra Bay Fishing Camp	1912DD	A	A	A	A	0
Ugabmund Ranger Station	2113BA	A*****	A	A	A	0
SMALL TOWNS						
Hentjies Bay	2214AB	PB-13	P-3	A	A	2
Kalkrand	2417BA	PB-6	A	A	A	1
Khorixas	2014BC	P	A	P	A	2
Maltahöhe	2417DC	P	?	?	?	?
Otjiwarongo	2016BC	P	A	A	A	1
Outjo	2016AA	P	?	?	?	?
Rehoboth	2317AC	A	?	?	?	?
Swakopmund	2214DA	P	?	?	?	?
CITIES						
Windhoek	2217CA	P	?	?	?	?

* Nesting in a hole in the wall of a building

** Only 1 pair, male arrived ca 2 months prior to our survey, female ca 1 month prior. Feeding far from habitation and also being fed kitchen scraps.

*** The occupant informed us that the species had been present here but that the birds has disappeared during "the drought". Numerous sparrow nests of uncertain origin were present in thorn branches intentionally placed in the rafters of a metal-roofed farm building for this purpose.

**** Has apparently been here since at least 1980 (Titos pers. comm.)

***** Vagrants turn up here irregularly but they are discouraged (B. Loutit pers. comm.)

? Areas searched too rapidly for the observers to be confident that a sparrow species had not been missed.

4 DISCUSSION

4.1 Alien plants, general

This survey showed that a variety of alien plant species is present in most of the vegetation types traversed in central S.W.A./Namibia. Alien plants were recorded at very low frequencies in vegetation types 1 and 2 of Giess (1971) the "Northern Namib" and "Central Namib" (Table 2). However, even in these extremely arid areas, the beds of irregularly flowing rivers were found to sustain alien plant assemblages which were sometimes diverse and normally had at least one spe-

cies occurring at both a high frequency and density (Table 3). Although most of the species were present in each river surveyed, different species were dominant in each of them. *Datura innoxia* was the most important alien species in the lower Hoanib, *Nicotiana glauca* in the lower Ugab, *Argemone subfusiformis* at the mouth of the Omaruru river (vegetation type 2 — quarter-degree area 2214AB, surveyed as part of the main road transect), and *Prosopis* sp. in the lower Swakop. *Datura innoxia* and *N. glauca* were co-dominant in the middle Kuiseb. The infestations of *D. innoxia* in the Hoanib, *N. glauca* in the Ugab and *Prosopis* sp. in the Swakop had already assumed mas-

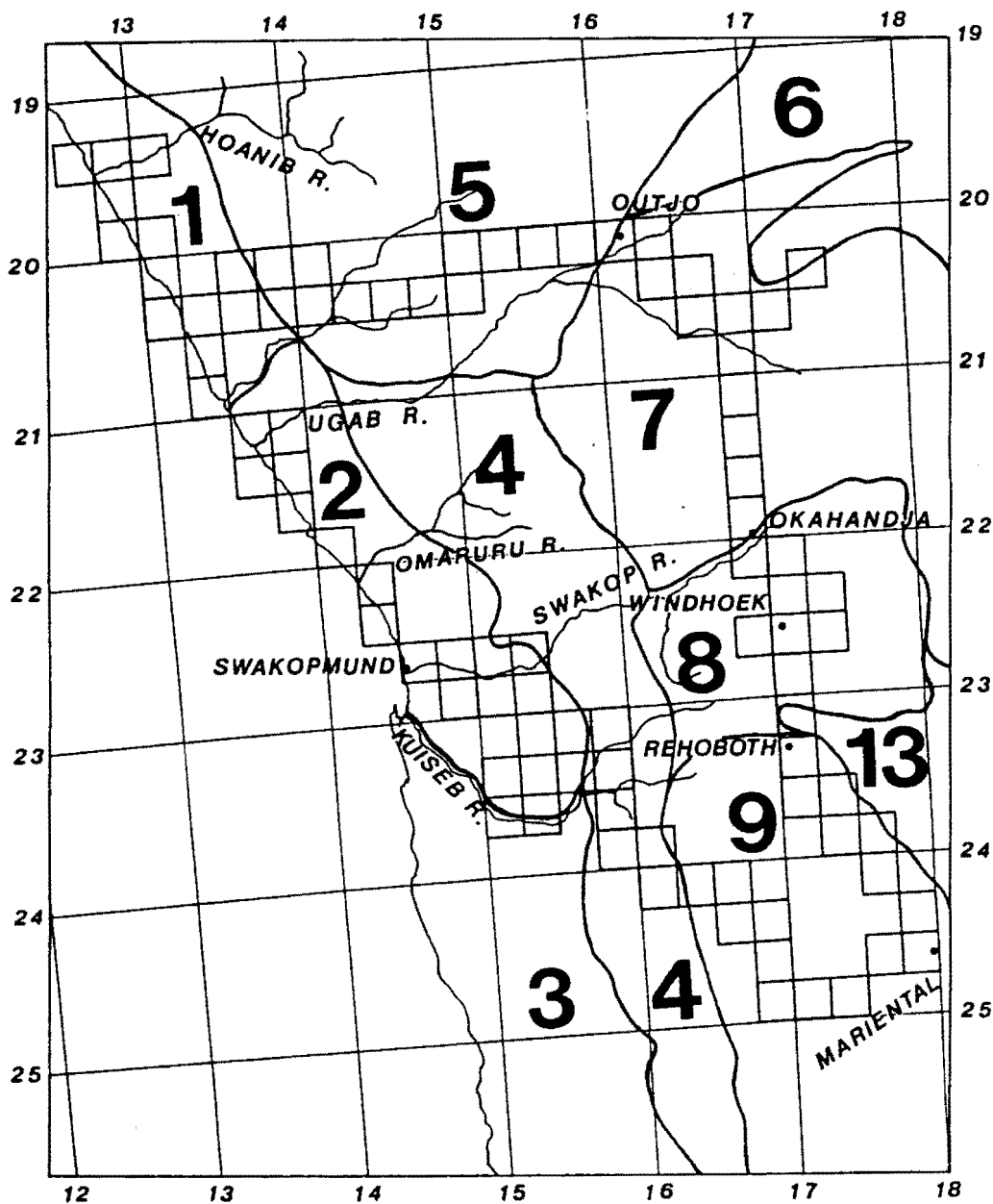


FIGURE 3: Grid squares surveyed within different vegetation types (after Giess, 1971). 1 — Northern Namib; 2 — Central Namib; 3 — Southern Namib; 4 — Semi-desert and savanna transition (escarpment zone); 5 — Mopane savanna; 6 — Mountainous savanna and Karstveld; 7 — Thornbush; 8 — Highland savanna; 9 — Dwarf shrub savanna; 13 — Mixed tree and shrub savanna (Southern Kalahari).

sive proportions. Each infestation occurred as a virtually monospecific stand covering considerable portions of the surveyed sections of the river courses. We consider it likely that these species are already responsible for undesirable impacts on the natural ecological functioning of these river systems which fall within proclaimed nature conservation areas. In this respect, it was gratifying to see that attempts had been made to control the *Prosopis* infestation on the Swakop and to learn that preliminary trials on the feasibility of controlling the other two major infestations had been initiated (P. Tarr, in litt. and R. Loutit, pers. comm.).

4.2 Alien plants, species accounts

Argemone subfusiformis was generally found in low density in sites of disturbance, such as roadsides, in

the higher rainfall vegetation types (Fig. 4). Denser stands were found in river courses and the beds of dry impoundments. The species (called *A. mexicana*) was recorded in 1911 at Orab south of Mariental (Grid 2417DD) on the Fish River, and Dinter (1918) commented that it was already found "quiet often" in S.W.A./Namibia soon after the turn of the century. Presumably the species has now reached virtually all suitable areas in central S.W.A./Namibia. The few scattered plants found in the Hoanib appeared to be pioneers, and it would possibly be worth attempting to eradicate the species there.

Asclepias fruticosa was mainly found in roadside ditches and other sites of water run-in in the higher rainfall vegetation types (Table 2, Fig. 5). It was most

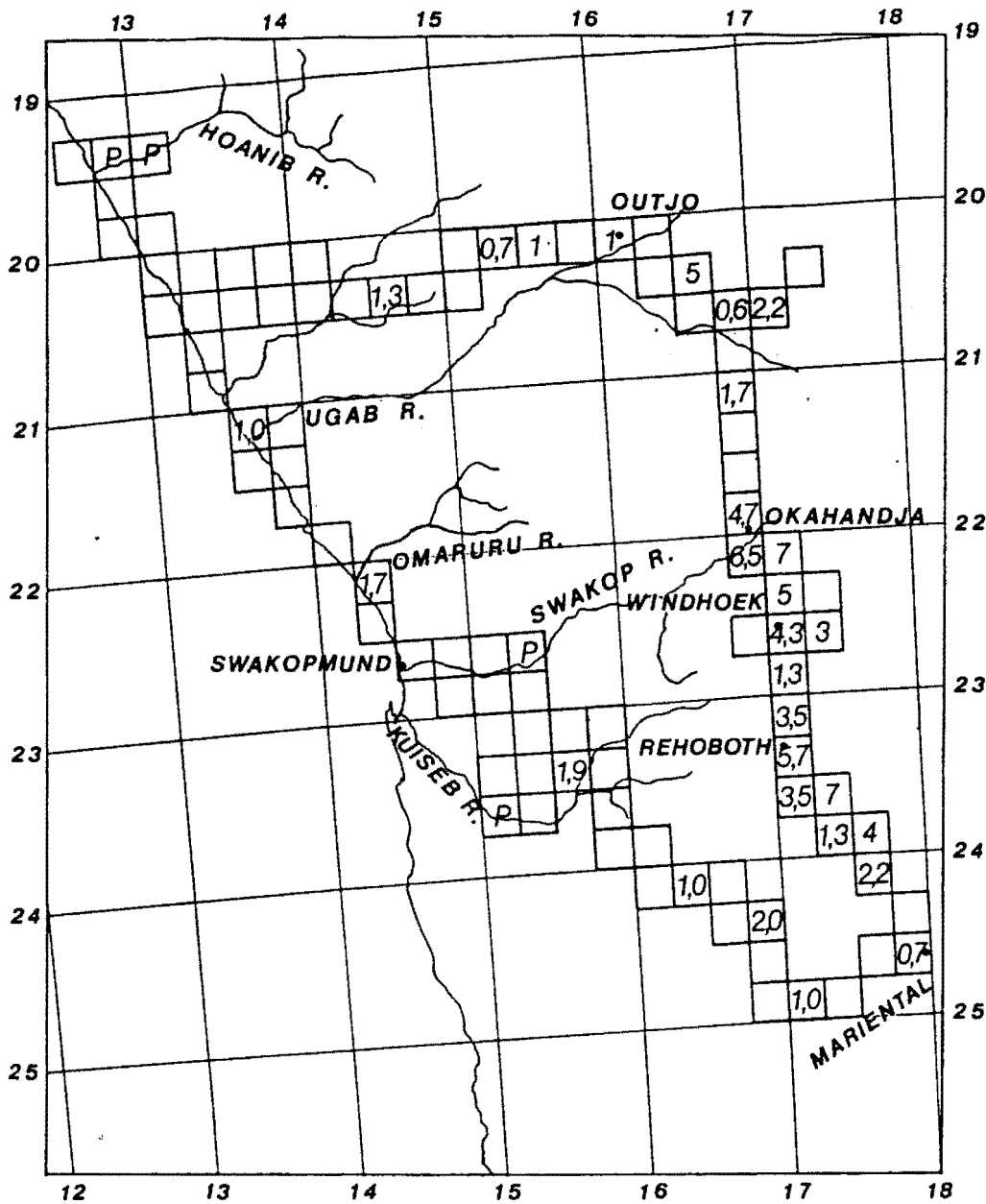


FIGURE 4: Mean abundance ratings for 10 km-sections (A_{qd}) for *Argemone subfusiformis*. P = where recorded outside the main road survey.

abundant in the road reserve between Outjo and Okahandja where the woody vegetation had been removed i.e. where competition for moisture would have been considerably reduced. Whether this species is alien to S.W.A./Namibia has not been conclusively established. However, Dinter (1909) reported that the species had been introduced from South Africa, that it indicated where there was water close to the surface and that by this date it was already one of "the commonest plants" in S.W.A./Namibia. As a ruderal in disturbed sites the species appears to pose little ecological threat in S.W.A./Namibia.

Caesalpinia gilliesii showed limited short distance spread into indigenous vegetation in the vicinity of Okahandja, Windhoek and Aris. This species could be eliminated with ease, at its present levels of infesta-

tion. However, its continued use in gardens would require that these operations be repeated at regular intervals in the future.

Cardiospermum grandiflorum was not recorded during the road transect but was found spreading into the indigenous vegetation at Rodenstein in the Waterberg Plateau Park. This species has become a major problem in localized areas in Natal (Macdonald and Jarman, in press) and should be eradicated wherever present in S.W.A./Namibia.

Cereus peruvianus was only recorded showing limited (? vegetative) spread from a cultivated plant on Spykersbron (Omasima) farm (2015AB). This species has become a major problem in certain of the savanna regions in the Republic of South Africa (Taylor &

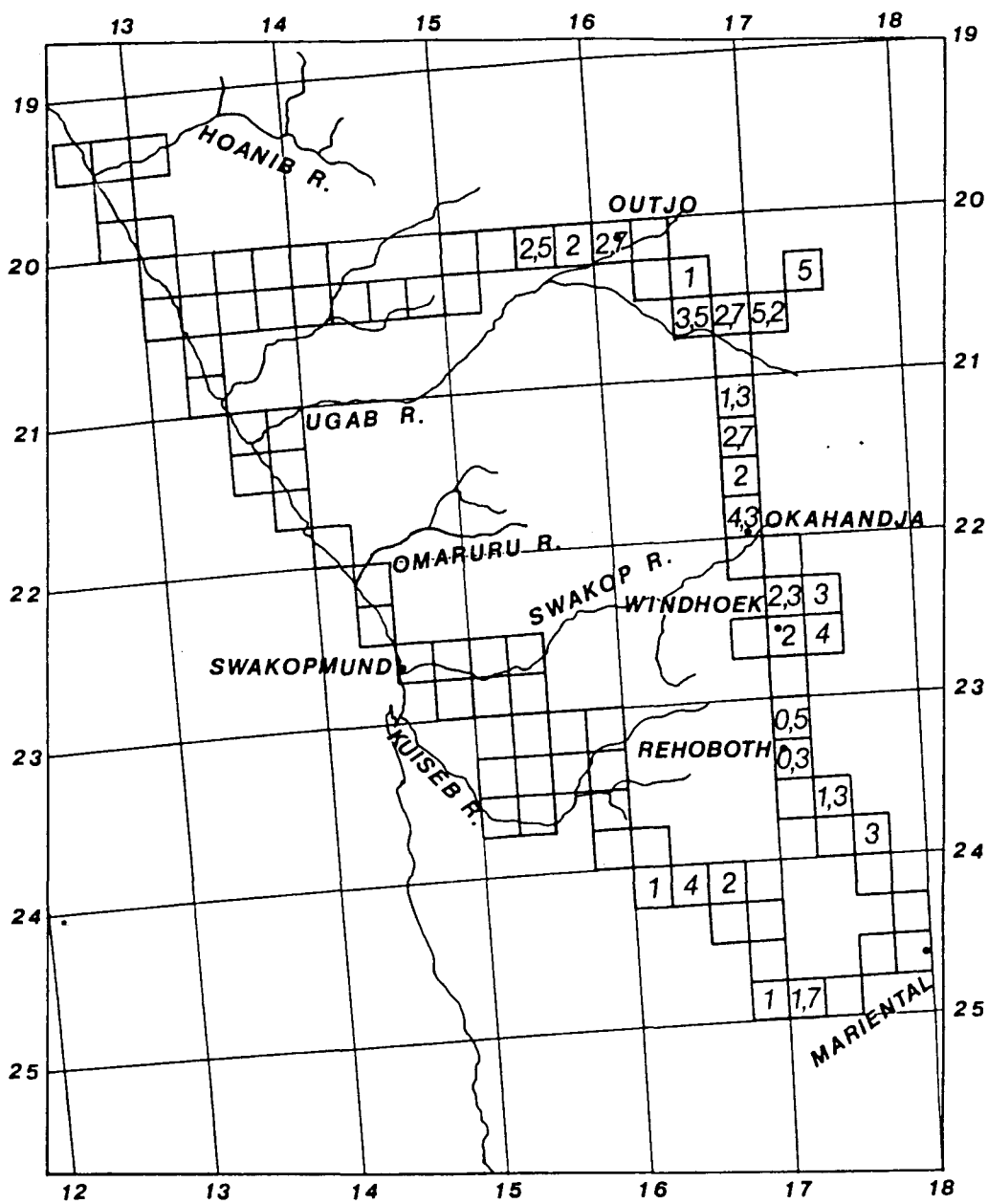


FIGURE 5: Mean abundance ratings (A_{qd}) for *Asclepias fruticosa*.

Walker 1984 and Macdonald pers. obs) and should be eliminated from S.W.A./Namibia wherever possible.

Datura ferox was found at low densities in scattered roadside infestations in the higher rainfall vegetation types (Table 2).

Datura innoxia was found in every vegetation type surveyed (Tables 2 & 3, Fig 6), although in all of them the species was restricted to river courses. This localized occurrence resulted in the species showing low quarter-degree abundance ratings (Fig. 6) compared to widespread aliens such as *A. subfusiformis* (Fig. 4). It was only in the riverbeds of the Namib that the species was abundant (Table 3). The species is apparently absent from the Swakop river system and efforts should be made to maintain this situation.

Datura stramonium was not found in the dry Dwarf Shrub Savanna (Table 2), and in the Namib vegetation types was only found in river courses (Tables 2 & 3). It was always less common than *D. innoxia* and nowhere was seen to form a dense infestation. This species does not appear to pose a major threat to any of the ecosystems it has invaded in S.W.A./Namibia. If *D. innoxia* were to be controlled, *D. stramonium* could possibly increase in systems such as the Ugab and Kuiseb where it is already widespread. In this respect, it would possibly be advisable to attempt to eradicate this species from the Hoanib before a major control programme is initiated there for *D. innoxia*.

Dodonaea viscosa was seen to be showing limited spread in the vicinity of Outjo and Otjiwarongo. This

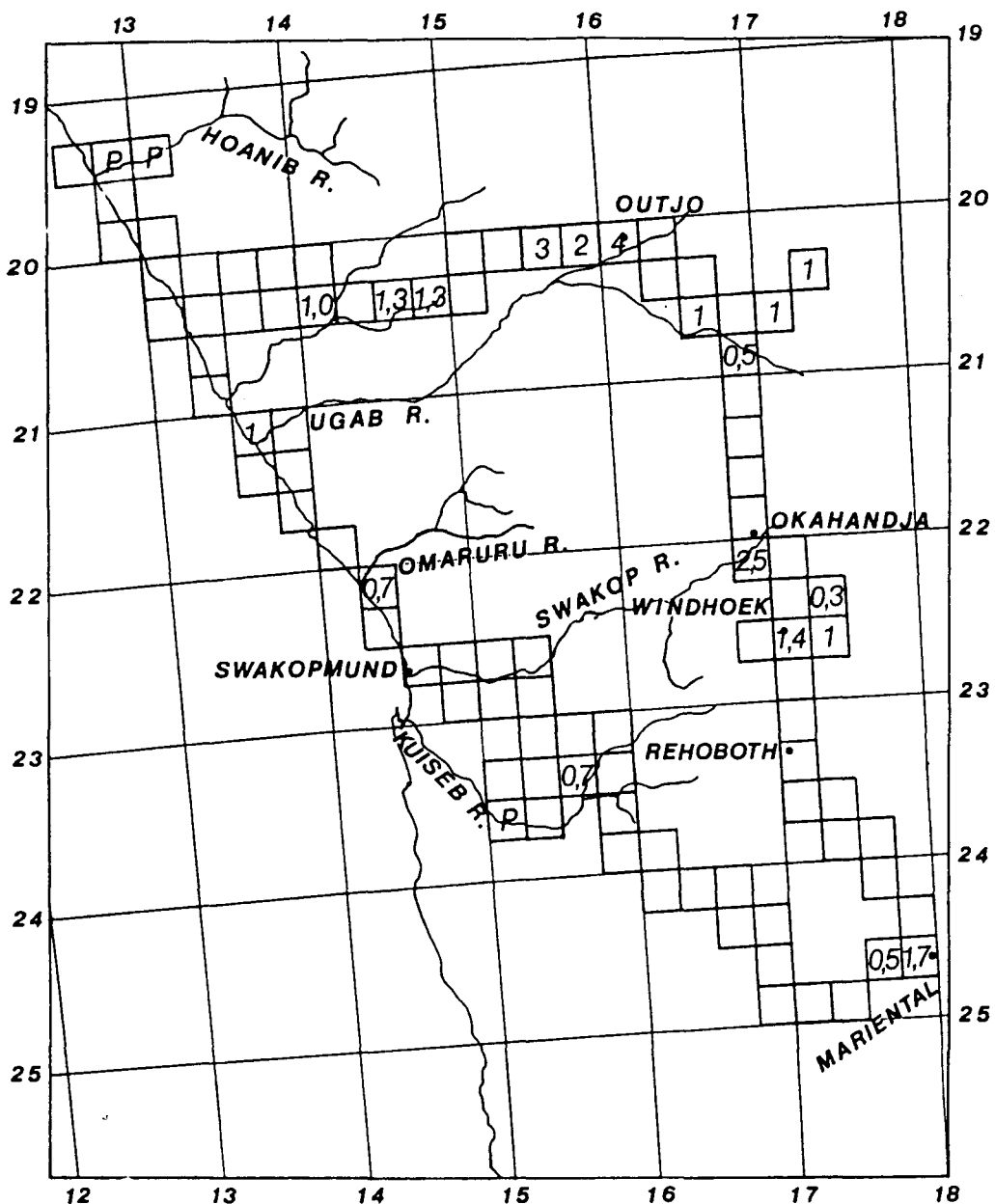


FIGURE 6: Mean abundance ratings (A_{qd}) for *Datura innoxia*. P = where recorded outside the main road survey.

species has spread into natural vegetation in areas outside its original range elsewhere in southern Africa and should be controlled while infestations are still light. The species should not be cultivated within nature conservation areas in the higher rainfall areas of the territory.

Lantana camara, although not recorded on the road transect, was seen to be invading indigenous vegetation in a kloof of the Waterberg Plateau Park around an old farm homestead. The plants observed had all been heavily browsed and the infestation was not dense. Browsing by indigenous ungulate communities can limit the spread of this species in southern Africa (Macdonald 1983).

Melia azedarach was seen as single individuals on the roadside near Outjo, Otjiwarongo and Windhoek. Whether these individuals had been planted or were self sown could not be determined. If the species is invasive in this area it is apparently not very successful and was certainly not posing a problem in any of the areas visited during this survey. The species is highly invasive in the moister eastern part of the subcontinent (Macdonald 1983) and should, ideally, not be planted in the vicinity of perennial or seasonal rivers in the northeastern areas of S.W.A./Namibia.

Nicotiana glauca was one of the most widespread alien plants found in this survey (Tables 2 & 3, Fig. 7). Although not recorded in the southernmost portion of

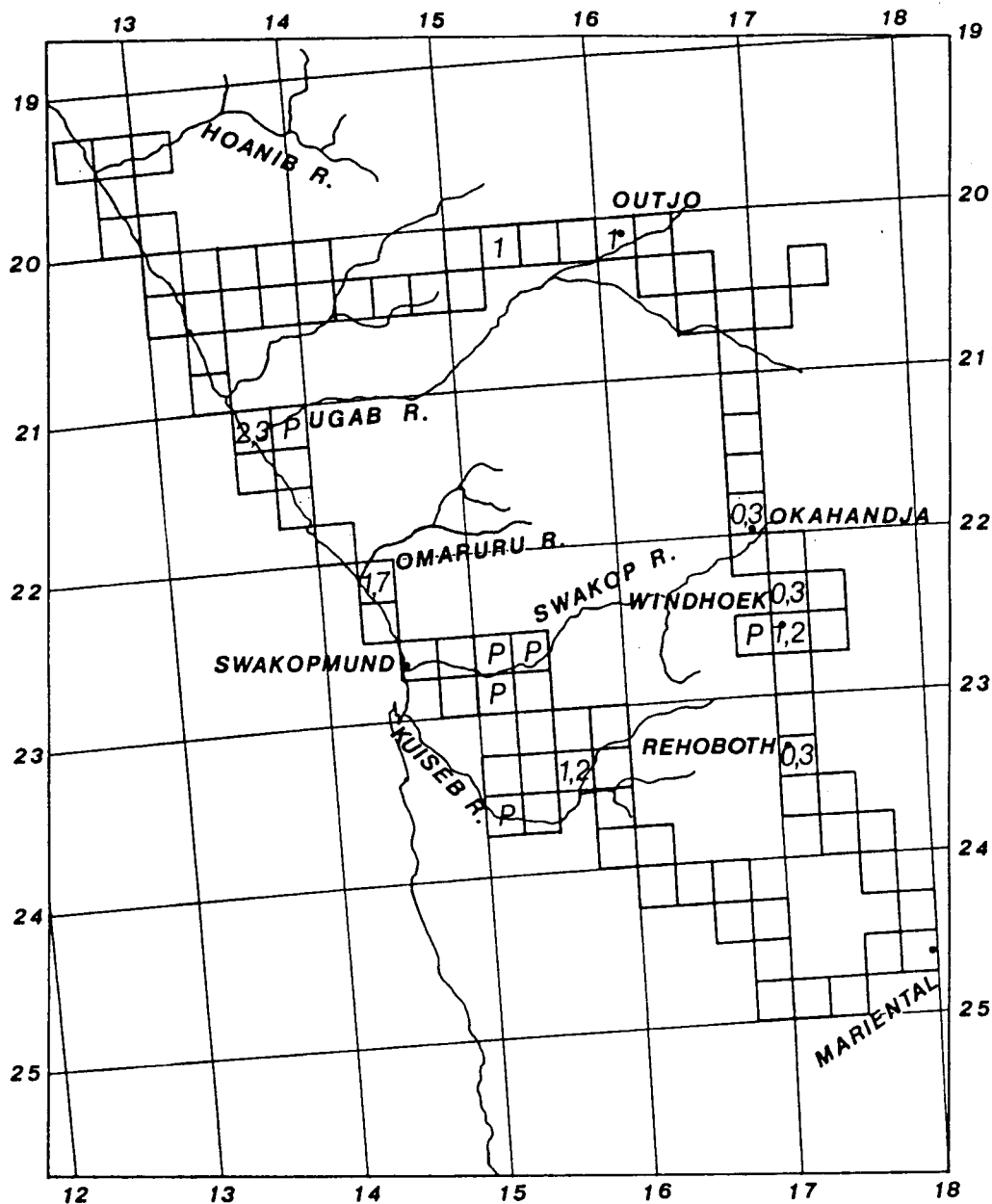


FIGURE 7: Mean abundance ratings (A_{qd}) for *Nicotiana glauca*. P = where recorded outside the main road survey.

the survey, this species was recorded in 1911 by Dinter (1918) on the Fish River at Orab south of Mariental (2417DD). That *N. glauca* was already well established in the territory by 1918 is borne out by it having been one of the four most common species at the mouth of the Swakop River in 1913 (Dinter 1918). The species is apparently absent from the Hoanib River system and considerable effort should be expended to maintain this desirable situation.

Opuntia ficus-indica was observed in the Mopane Savanna only as a light infestation around Spykersbron (Omasima) farm (2015AB). In the Highland Savanna it was observed as a few scattered individuals near Windhoek and Aris. The most extensive infesta-

tion observed was on the edge of the plateau in the Waterberg Plateau Park. In this locality it was being well controlled by an introduced Cochineal insect *Dactylopius* sp. The species has apparently become less common than was the case early this century (Dinter 1909).

Opuntia imbricata, *Opuntia microdasys* var *lutea* and *Opuntia* sp. unident. were all observed showing very limited spread from garden plantings around Windhoek.

Opuntia inermis was observed as an extensive infestation in Mopane veld around the homestead of Spykersbron (Omasima) farm (2015AB). None of

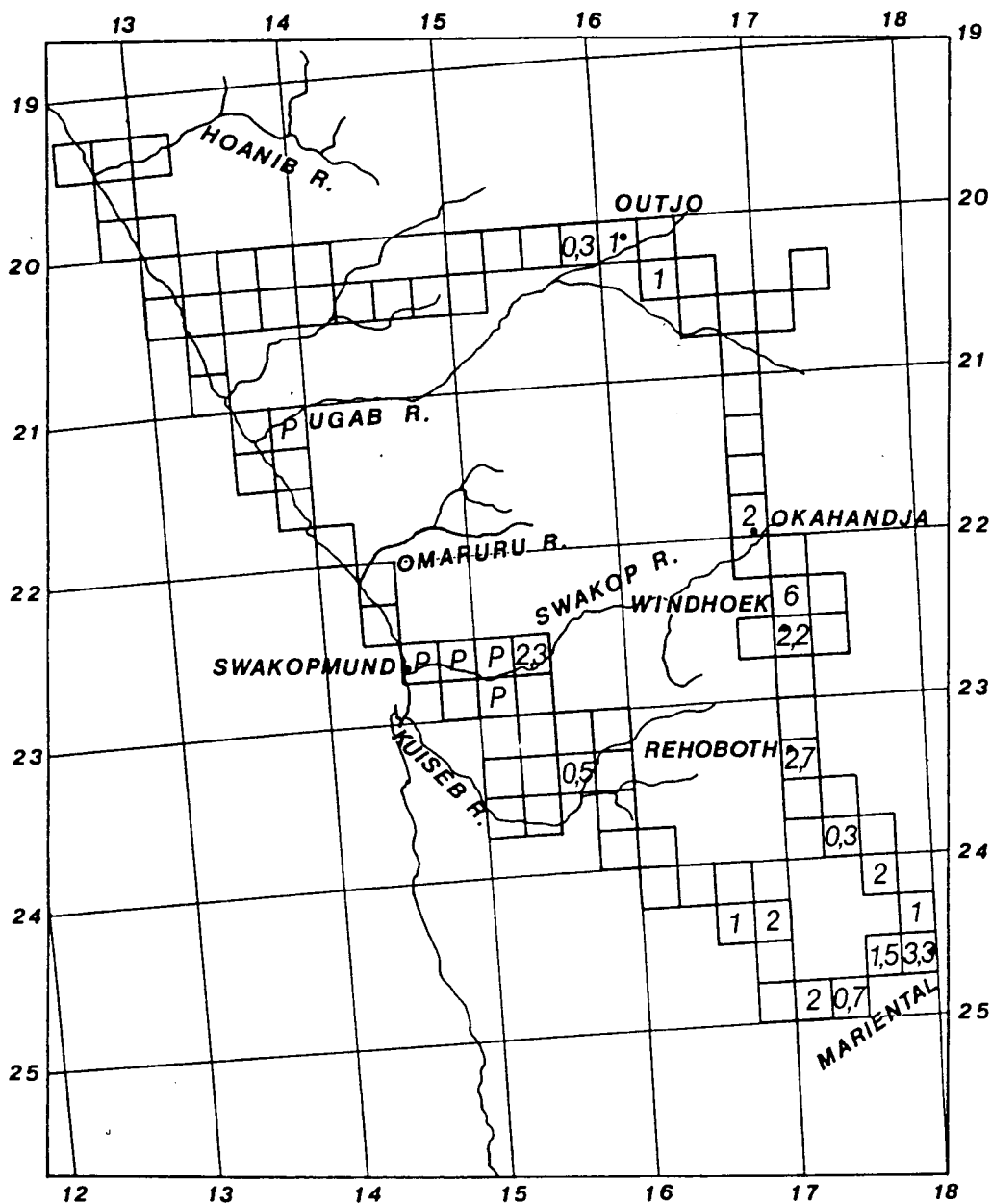


FIGURE 8: Mean abundance ratings (A_{qd}) for *Prosopis* sp. P = where recorded outside the main road survey.

these plants showed signs of being attacked by introduced biocontrol insects.

Prosopis sp. was found to be cultivated around most of the towns and farm homesteads visited during this survey. The species was first introduced to S.W.A./Namibia in 1912 (Müller, in press). The most extensive infestations seen were on the Swakop River and around Windhoek. Infestations were most widespread in the Dwarf Shrub Savanna (Table 2, Fig. 8), possibly as a consequence of the long history of cultivation at the numerous farm homesteads found in this vegetation type. Although present at low density in the upper catchment of the Kuiseb River (on the Gaub River) no individuals were seen in this river between Gobabeb and Homeb. The upper reaches of this river warrant clearing in order to prevent dense infesta-

tions, such as those found in the Swakop River, from developing. Similarly, the elimination of the few *Prosopis* trees established in the lower Ugab River should be accorded a high priority. In all cases where riverine infestations of this species are to be controlled, operations should be initiated at their source. In this respect the control operations observed near Riet Gaop on the Swakop River are clearly not ideal. Although it is uncertain how far *Prosopis* seed is transported by flood waters in such a river, it is certain that seed will continue to be brought into the cleared portion from the farming areas east of the Namib Naukluft Park. An infestation of *Prosopis* was observed on the banks of the upper Swakop River near Okahandja. That this species is still being planted as a roadside shade tree in S.W.A./Namibia (as was observed at a lay-bye on the road between Otjiwarongo and Oka-

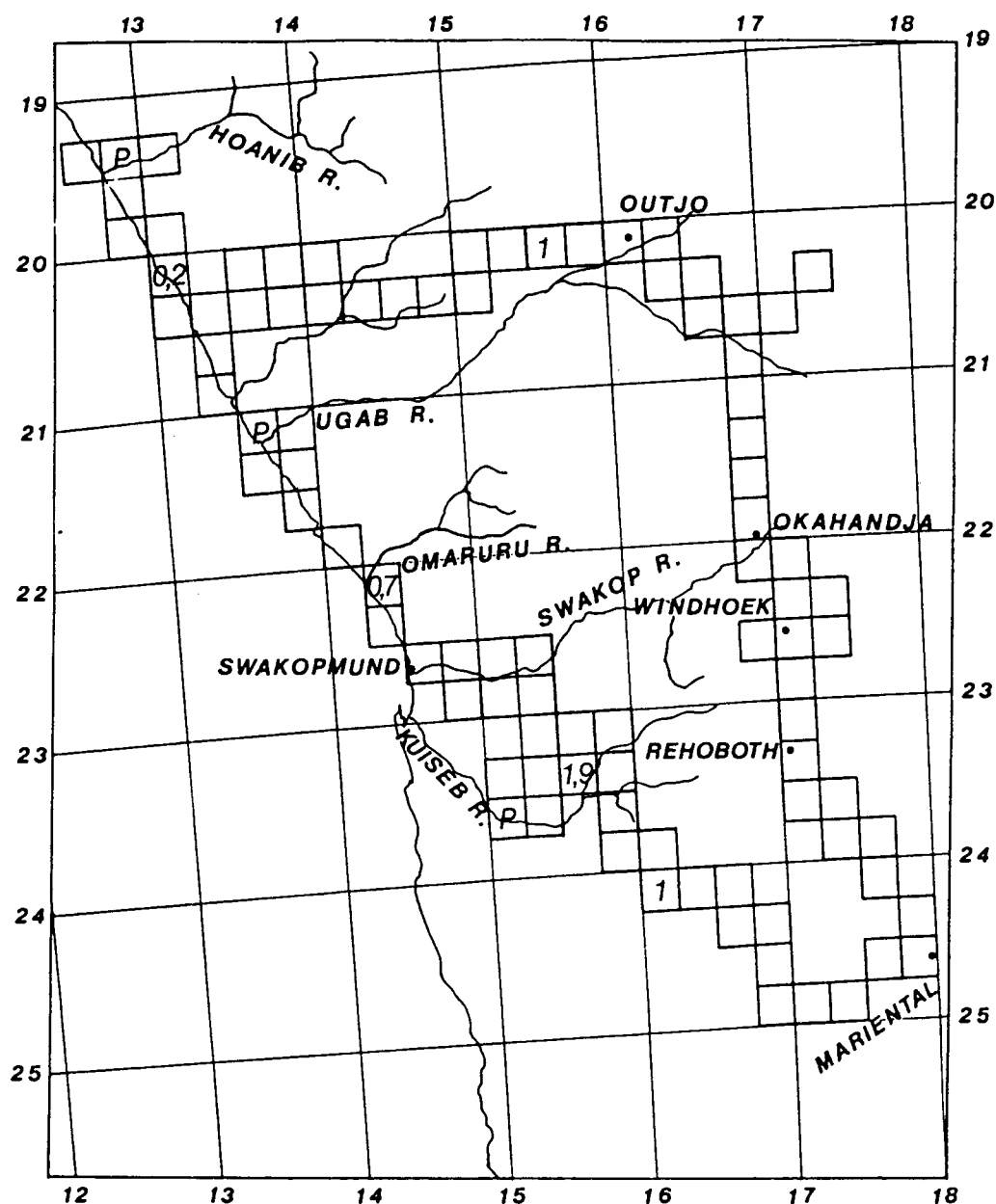


FIGURE 9: Mean abundance ratings (A_{qd}) for *Ricinus communis*. P = where recorded outside the main road survey.

handja) is remarkable, given its obvious invasive potential in the territory. Although *Prosopis* has not been shown to have deleterious ecological effects in S.W.A./Namibia, extrapolation from elsewhere indicates that this will be the case (Macdonald, 1985). Already the species has been shown to have deleterious effects on human health in S.W.A./Namibia (Ordman 1959).

Ricinus communis was only found as scattered plants, mainly along rivers such as a tributary of the Tsondeb, the Gaub, Kuiseb, Omaruru, Ugab and Hoanib. One plant was observed growing next to an isolated pump-house on the road between Torra Bay and Terrace Bay, indicating that the species is inadvertently spread by man in this area. On the middle Kuiseb River the species was being extensively browsed and the only relatively intact individuals seen were those growing in the protection of fallen branches. The browsing was probably being carried out by goats *Capra hircus* which were herded by the Topnaar inhabitants of the Namib-Naukluft Park and which had consumed most of the palatable herbage within their reach by the time of our survey of the river. The species was already common in S.W.A./Namibia early this century and Dinter (1909) was not certain as to whether or not the species was indigenous to the territory. If it is an alien it is certainly having a negligible impact on the rivers it was found in at the time of this survey.

Schinus molle was found as a few self-seeded individuals in the vicinity of Outjo and Otjiwarongo. This species has been found invading, albeit very slowly, karoo riverine fringe vegetation in the Republic of South Africa (Macdonald pers. obs).

Tagetes minuta occurred mainly in the relatively well-watered Highland Savanna region (Table 2). It was present almost exclusively as a roadside ditch invader. It was also recorded below the plateau in the Waterberg Plateau Park.

Tecoma stans was seen once growing on the road-verge south of Outjo. Whether this plant was self sown or not could not be determined.

In addition to the above species, the alien forb *Flaveria bidentis* was seen growing as a roadside weed between Nomtsas and Gamis where rain had fallen recently. This species could not be adequately surveyed from a moving vehicle, because there are several indigenous species which are similar in appearance and it was flowering in only one area. Similarly, *Bidens biternata* was observed in the Waterberg Plateau Park. The alien grass *Polypogon monspeliensis* occurs in the bed of the Swakop River (H. Kolberg, pers. comm.) but was not recorded by us during this survey. The preceding list is neither comprehensive nor complete for the alien plant species present in S.W.A./Namibia. It is a list of the conspicuous species that could be observed in a rapid survey such as the present. The value of our survey lies not in its completeness but in its repeatability for those conspicuous species surveyed.

4.3 Alien birds

The House Sparrow was the only widespread alien bird species seen in S.W.A./Namibia. Since Uys (1962) first recorded this species at Grünau (2718CB) in 1961, the species has apparently colonized the whole of the territory, at least as far north as was surveyed on this trip. At this most northerly point, Möwe Bay (1912BC), the species had only arrived during 1984 (Ryan *et al.*, 1984, P. Tarr pers. comm.).

Although three and, in some areas, four species of *Passer* occur sympatrically in those portions of S.W.A./Namibia traversed during this survey (Maclean 1985), in no locality were more than two species found around an area of human habitation (Table 4). At the small, intermittently occupied, sites in the Namib often no sparrow species were recorded. These sites appear marginal for House Sparrows as, apparently, was the Nomtsas farm homestead where the species had disappeared after an initially successful colonization.

At Gobabeb both House Sparrows and Cape Sparrows *Passer melanurus* were breeding at the time of our visit. As the House Sparrow was already present here by 1966 (Willoughby & Cade 1967) it is apparent that the two species have been able to coexist here for at least 19 years. This is made more interesting by the observation that the Cape Sparrow was nesting in a hole in the wall of a building at Gobabeb which is the preferred nest site of the House Sparrow. The Grey-headed Sparrow *Passer griseus* was observed entering the roof of a farm outbuilding on Spynersbron farm.

The Great Sparrow *Passer motitensis* which is generally considered "has not adapted to human settlement" in southern Africa (Maclean 1985) was found around two restcamps, one homestead and one small town. At Hardap Dam Rest Camp the species was nesting in a small indigenous shrub growing approximately 30 m from the buildings. At this locality the recently constructed buildings do not apparently offer many suitable nest sites for House Sparrows and the population of these was small. One pair of House Sparrows was observed nesting in a Greater Striped Swallow's *Hirundo cucullata* nest at the reception building and several individuals were seen at the entrance gate building. At Khorixas the Great Sparrow was observed to be far more abundant than the House Sparrow. These observations agree with those of Winterbottom (1964), who observed farther north in the territory that the statement "that the Greater Sparrow is a shy and retiring species of the bush and does not frequent human habitations is certainly not true of S.W.A.". It will be interesting to see whether the relatively recent arrival of the House Sparrow in these areas gives rise to any long term changes in the abundance of indigenous sparrows around habitations. At Kalkrand, where House Sparrows were already present in July 1968

(Macdonald pers. obs), no other species of sparrow was observed in November 1984. However, farther north in S.W.A./Namibia at Okakuejo, where the House Sparrow arrived in December 1976, both the Grey Headed and Great Sparrows were still present in the restcamp in 1985 (Nott pers. obs). The observation that no more than two species of sparrow were present at any of the habitations visited in the central portion of the territory indicates that sparrow "niche space" is limited in S.W.A./Namibia and potential interspecific competition should be watched for.

5 CONCLUSION

Alien plants were found to be invading most of the vegetation types observed. Infestations of *Datura innoxia*, *Nicotiana glauca* and *Prosopis* sp. in some of the west-flowing rivers were considered to constitute a conservation problem.

The only alien bird found to be widespread was the House Sparrow which was only found in close association with human habitation.

6 ACKNOWLEDGEMENTS

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THE OVERALL INVASION STATUS OF
SOUTHERN AFRICAN BIOMES AND NATURE RESERVES

Summary of main points arising from the chapter

One of the most important points that emerged from the papers in this section is that all the subcontinent's biomes have been invaded by alien species. In terms of the basic questions which these papers set out to address the answers are as follows.

Which taxonomic groups have alien species which are invading?

The nature reserve species-list analyses reported in Paper 1 showed that vascular plants, birds and mammals all had alien species present in reserves in every South African biome (the 0 recorded for mammals in forest biome reserves in Table 2 of this paper can be discounted as Bourquin and Mathias (1984) have trapped Rattus rattus in the forests of the Oribi Gorge Nature Reserve).

Only reptile faunas within these reserves tend to be totally lacking in alien species from outside the subcontinent. The few alien reptile records included were mainly of extra-limital introductions of native tortoises (most of which fail to breed cf. Paper 7). The aquatic red-eared terrapin Chrysemys scripta elegans from the New World is possibly the only real exception to this generalization (c.f. Paper 10 and Newbery 1984). Subsequent to the completion of this facet of the study, there were in fact several additional records published of introduced reptiles from reserves along the eastern seaboard, in particular of the commensal house gekko Hemidactylus mabouia (Paper 19). In the fynbos biome there is also the fossorial slow worm Ramphotyphlops braminus (Paper 2) but there is no indication that this has successfully invaded nature reserves there. Possibly the ectothermic lifestyle, in combination with the other factors militating against successful establishment of an alien vertebrate in a southern African native community, have proved generally insurmountable for introduced terrestrial reptiles. That an aquatic form should be the only real exception, agrees with this explanation, as aquatic habitats appear to me to be much more similar, environmentally, between continents than is generally the case for terrestrial habitats. This assumption is supported by the much higher success rate of inter-continental introductions of fish species, both into southern Africa and elsewhere (e.g. Bruton and van As 1986, Werner 1986).

However, it is not only endothermic animals that have shown

themselves capable of invading southern African ecosystems; numerous species from the relatively poorly studied invertebrate groups, which are all ectotherms, have shown themselves to be quite capable of doing so (Papers 1,2 and 3).

The number of alien plant species that are known to have invaded the different biomes far exceeds that of all the animals, including the invertebrates. However, the need for more detailed surveys of alien invertebrates is one of the main conclusions in this section (Paper 3).

Have the biomes of southern Africa been differentially invaded?

At a gross scale, as reflected for instance by the mean number of invasive alien species in a taxonomic group invading nature reserves (Paper 1), there were some indications that the biomes were showing different levels of invasions: contrary to predictions (Taylor 1977a, Ferrar and Kruger 1983, see Chapter 1) this measure did not indicate the fynbos biome as being the most severely invaded by alien plants. The savanna biome instead had the reserves with the highest mean number of alien plant species. The reserves in this biome were shown to have statistically significantly higher numbers of accidentally introduced vascular plant species than those in any other biome (Paper 1).

Terrestrial vertebrates were indicated as having their highest number of invasive alien species in fynbos reserves. To a certain extent this was the result of certain southern African birds and mammals having been intentionally introduced to the biome, or to nature reserves within it, and having then become successfully established there (Paper 1). However, the trend was also still apparent when only inter-continental introductions of vertebrates were considered (Paper 1 and 2). The same trend was also present for alien molluscs (Paper 1).

The ability of species of vascular plants, birds and insects from elsewhere in the subcontinent to become successfully established following introduction into the fynbos biome, was indicated as being a phenomenon which was almost restricted to this biome within southern Africa (Paper 2).

The hyper-arid Namib Desert biome was shown to have the lowest mean number of alien vascular plant species in its nature reserves relative to the other biomes (Paper 1) and the lowest frequencies and abundances of these species relative to the adjacent semi-desert (karroid) and savanna biomes as ascertained by road censuses (Paper 4).

Have certain ecosystems been differentially invaded?

Riparian ecosystems were shown to be much more severely invaded by alien vascular plants than were the adjacent upland ecosystems in the Namib Desert (Paper 4). This agreed with the general conclusion derived from a review of published studies in southern Africa (Paper 1). Surprisingly, nature reserves having influent rivers were not shown to have higher-than-average numbers of alien plant species in this same study (Paper 1). Presumably this was because there were just too many confounding variables in the sample of nature reserves used in this analysis, to enable the statistically significant determination of such a difference. Virtually everything we know about the distribution of invasive alien plants in southern Africa indicates that reserves with influent rivers ought to be more severely invaded by alien plants than equivalent reserves without such rivers (Wells et al. 1980, Macdonald 1983a, Henderson and Musil 1984, Macdonald and Jarman 1985, Brown et al. 1985, Henderson 1989 and in press, Brown and Gubb 1986).

Another possible case of the differential susceptibility of ecosystems to invasion, also came from the desert biome: in this case, it was an apparently heightened susceptibility to invasion by alien rodents of mesic coastal isolates in the Namib Desert (Paper 1).

Are there indications as to the factors causing any such differences?

There were several indications, both from the owl-pellet study and that of the nature reserve species-lists (Paper 1) and from considerations in the fynbos biome (Paper 2), that predation by generalist predators was a significant factor in limiting the success of invasions by alien vertebrates. This finding was explained by the notion that alien vertebrates would be particularly susceptible to local extinction as a result of predation when the population was still very small during the early stages of invasion (Paper 1).

The identical conclusion was reached, totally independently, by Diamond and Case (1986) in their overview of invasions - based mainly on studies of invasions of oceanic islands. They term such extinctions "bridgehead extinctions". This concept goes a long way towards explaining the remarkably low success rate of vertebrate invaders in 'intact' terrestrial ecosystems in southern Africa (c.f. Brooke et al. 1986, Brown and Gubb 1986) - and the relative ease with which such species can be introduced in areas where native predation pressure has been eliminated or severely reduced (see Chapter 3, Papers 7 and 10, and Chapter 8,

Papers 24 and 25, where the concept is applied also to plants, i.e. herbivory by generalist herbivores is equated to predation).

Competition, at least as reflected in the species richness or diversity of the native small mammal fauna of a site, was not reflected as being a significant factor in controlling the incidence of alien rodents in the owl-pellet study (Paper 1). However, the observation that the proportion these species made up of the prey population was always very small in untransformed habitats possibly indicates that competition is intense in all southern African communities. This is the conclusion that has been reached by mammalogists working intensively in the region (Smithers 1983). That these same rodent species make up a much larger proportion of the prey of barn owls elsewhere in the world, where the native rodent fauna is less diverse, supports this contention (Paper 1). Even in such low-diversity small mammal communities as are found in the temperate regions of Australia, this competition has been demonstrated experimentally (Fox and Pople 1984).

The observation that most other vertebrate invaders, in both the fynbos biome (Papers 2 and 3) and central Namibia (Paper 4), are also virtually confined to transformed habitats, can be interpreted as indicating that competition from the native fauna in untransformed habitats is intense (c.f. Diamond and Chase 1986). Even the invertebrate aliens recorded from the fynbos biome tend to be confined to transformed habitats (Papers 2 and 3). However, the tendency seems to be less well-defined in the case of carnivorous invertebrates than herbivorous species, which are generally limited to plantings of alien species in this biome (Papers 2 and 3).

As far as alien plant invasions were concerned, these studies indicated that the total number of species, and the number of accidentally introduced species, present in nature reserves were both significantly higher in areas with higher mean annual rainfall (Paper 1). This trend of a more diverse alien flora in association with a higher mean annual rainfall was also detected by the roadside survey in central Namibia (Paper 4). This agrees with the trend found within individual reserves within the subcontinent: In the Hluhluwe-Umfolozi complex in Natal it was the high-rainfall northern portion of Hluhluwe Game Reserve which had the most diverse alien flora (Macdonald 1983a), and, in the Cape of Good Hope Nature Reserve in the fynbos biome, more species were found within plots in the high-rainfall zones than in the low-rainfall zones (Taylor *et al.* 1985). The same situation is recorded in the Kruger National Park (see Chapter 3, Paper 9). Road surveys conducted in the Transvaal (Henderson and Musil 1984) and throughout the southeastern part of the subcontinent (Chapter 8, Paper 25) have also demonstrated this same tendency; the drier western areas having, in both cases, the

least diverse and least abundant alien plant invasions.

The indication is, then, that the more xeric the environment is in southern Africa, the less likely it is to have a diverse alien flora. It appears that either aridity acts as a "selective non-botanical barrier" (sensu Johnstone 1986) to plant invasions in the subcontinent, or that fewer alien plant species that are potential invaders of arid ecosystems have been introduced (c.f. discussion in Chapter 8, Paper 25). The lower human population densities (Zietsman and Van der Merwe 1986) and lower levels of ecosystem transformation (Macdonald 1989), that characterize the more arid areas of the subcontinent, provide further alternative explanations for this pattern when it is observed at a regional scale, i.e. outside individual nature reserves. The difficulty of distinguishing between such alternative explanations for observed patterns is one of the continual draw-backs of utilising 'natural experiments' such as these (c.f. Diamond and Case 1986). However, that the same pattern has been observed within individual nature reserves located in different biomes, indicates that there is indeed a greater likelihood of an alien plant successfully invading a mesic ecosystem than a xeric ecosystem in this subcontinent. This same tendency has subsequently been born out by the results of the questionnaire survey (Chapter 4, Papers 12, 14 and 15) and indicated as being globally applicable (Rejmanek 1989 and Chapter 6, Paper 20, where the principle is expanded to include all "harsh environments" as being less likely to be invaded).

There is no obviously equivalent relationship shown by faunal invasions to mean annual rainfall, in fact the owl-pellet study tended to show the converse, i.e. it was the arid sites which had the highest incidence of alien rodents, but the tendency was not statistically significant (Paper 1).

The whole concept of "environmental harshness", which is virtually synonymous with that of Johnstone's (1986) "selective non-botanical barriers", impeding alien invasions, was not born out by the analysis of the number of alien plant species in reserves having different annual incidences of frost (Paper 1). Possibly this is a result of many of the alien plants present in southern Africa having come from areas having a higher frost incidence than occurs locally, e.g. 54% of the invasive flora comes from Europe, Asia and North America, all predominantly cooler continents (Wells et al. 1986a). In her analysis of indigenous and alien barrier plants in southern Africa, Henderson (1987) showed that of 105 indigenous species suitable for use as security hedge plants only 17 had "appreciable frost hardiness" and 26, "moderate frost resistance". By contrast, of the 284 alien species used, or recommended for use, as barrier plants in the region, 227 were rated as suitable for use in the frost-prone cold climate zones in the region. She concludes that "the cold

interior of southern Africa is poorly endowed with indigenous woody plants, which is partly the reason for the almost exclusive use of alien woody species in these regions." Such selective biases in the introduction and dissemination of frost-hardy aliens could have led to this surprising lack of a significant response to frost incidence, as reflected in the number of alien species present in the subcontinent's nature reserves.

The final result of consequence for the understanding of factors controlling invasions was that relating numbers of alien plant species in nature reserves to numbers of people visiting these reserves (Paper 1). The interpretation of the observed positive correlation is that either people are significant vectors of introduction for alien plants or that visitation rate is correlated with some measure of disturbance. However, no distinction between these two alternatives could be made on the basis of the data collected in these studies.

How extensive are the invasions?

The indications from these studies were that invasions were more extensive in the fynbos biome than in the central section of Namibia. Within both these areas, alien plant invasions were much more extensive than alien vertebrate invasions (Papers 2, 3 and 4). Alien invertebrate invasions of the fynbos biome were generally intermediate in extent to those of the above two groups, with a few, such as the snail Theba pisana being extremely widespread (Paper 2 and 3).

Alien plant invasions were only extensive in the rivers of central Namibia and in the immediate vicinity of transformed areas (Paper 4). By contrast, the fynbos biome had extensive woody plant invasions in what were formerly untransformed upland areas (Papers 2 and 3). Two statistics included in the fynbos synthesis indicate just how extensive these woody plant invasions were: Hakea sericea was estimated to cover 14% of the Mountain Fynbos and all woody aliens had invaded 17% of the remaining areas of natural vegetation in the west coast lowlands of the biome (Paper 2).

What are the ecological effects of these invasions?

As could be predicted, the only ecosystems which were judged to be experiencing major ecological effects of invasions were those where aliens were reaching high densities, i.e. fynbos areas (Papers 2 and 3) and Namibian rivers (Paper 4) severely infested by alien plants. As the woody plant invasions of the fynbos had been much more intensively studied than had the riverine

invasions in Namibia, it was only possible to elaborate on the former.

The major categories of such effects were;

- i) geomorphological, e.g. accelerating soil erosion, as along infested riverbanks, and fixing mobile sand dunes on the coast,
- ii) geochemical, e.g. changing the sizes of carbon, nitrogen and phosphorus pools in the phytomass and the soil,
- iii) hydrological, e.g. postulated reductions in stream flow,
- iv) fire regimes, e.g. altered fire intensities (see Paper 3), and
- v) community effects, both floristic, e.g. reductions in native species richness in severely infested sites, and faunistic, e.g. alterations in the avifauna and small mammal community following such invasions.

In the case of the latter category, the effects were shown to be occurring at both small-plot and whole-biome scales, e.g. for plants, species richness was shown to be reduced in 4m² plots as well as, potentially, at the scale of the whole biome as indicated by the threatened extinction of species if these invasions were not controlled (Papers 2 and 3).

Historically, herbaceous plant invasions have generally not been considered to pose any serious threats to ecological functioning in the fynbos biome (Paper 2) but recent research indicated that there were potentially serious effects on the regeneration of native plants following disturbance (Paper 3). Certainly, sites subjected to unnaturally frequent disturbances, e.g. by fire alongside railways, had been observed to become totally dominated by herbaceous alien plants (Paper 3).

The potential effects of invertebrate invasions were considered to be generally too poorly researched to enable any proper evaluation to be made. However, those predicted for the Argentine ant on both native insects and on myrmecochoorous plants were considered potentially serious (Papers 2 and 3).

Which invasions are most important for nature conservation?

The simple conclusion which can be made in this respect, on the basis of these studies, is that those invasions with the greatest potential to alter the invaded ecosystem are those which are most important for nature conservation (Papers 2, 3 and 4).

In terms of the history of control in the two areas, it was

apparent that invasions of woody plants had been perceived to be the highest priority for control: Prosopis species was already being controlled in the Swakop River within the Namib Naukluft National Park (Paper 4) and extensive control measures were being implemented for alien trees and shrubs in the fynbos biome (Papers 2 and 3). Control on herbaceous alien plant invaders had been attempted in the Namib rivers but this had not yet been initiated on a large scale (Paper 4). In the fynbos biome, what little had been done to control herbaceous plant invaders had been done for agricultural reasons, i.e. because of the perceived threat of certain species to livestock grazing (Paper 2).

The only alien animal that was currently being controlled for nature conservation reasons within the biome was the Himalayan thar on Table Mountain (Paper 2). The control of the Argentine ant was considered to be a possible future priority for nature conservation (Papers 2 and 3). The control of other invertebrate invaders might also prove to be necessary for conservation reasons, but data with which this need could be objectively evaluated, were lacking (Papers 2 and 3).

Chapter 3

SOME CASE STUDIES

Introduction to the chapter

Paper 5

**The alien flora of the
Cape of Good Hope Nature Reserve.**

Paper 6

**The history and effects of alien plant control
in the Cape of Good Hope Nature Reserve,
1941-1987.**

Paper 7

**Introduced species in nature reserves
in Mediterranean-type climate regions
of the world.**

Paper 8

**A list of alien plants
in the Kruger National Park.**

Paper 9

**The history, impacts and control of introduced species
in the Kruger National Park, South Africa.**

Paper 10

**The invasion of introduced species into nature reserves
in tropical savannas and dry woodlands.**

Summary of main points arising from the chapter

CHAPTER 3**THE INVASION OF SOUTHERN AFRICAN NATURE RESERVES
- SOME CASE STUDIES****Introduction to the chapter**

In the papers that make up this chapter, the basic questions addressed are mainly the same as those in the previous chapter. However, there is one major difference: As these studies focus on particular reserves, there is now a greater chance of relating attributes of the invading species to the characteristics of the ecosystems they are invading. The questions addressed in these papers are, therefore, as follows: First, which taxonomic groups have alien species invading the case study reserves? Second, do these reserves show differential levels of invasion by alien species from any of these groups? Third, within the reserves do the ecosystems show different levels of invasion? Fourth, can we relate the characteristics of the invading species to those of the ecosystems they are invading? Fifth, can we infer the causal mechanisms underlying any such relationships? Sixth, how extensive are these invasions? Seventh, what ecological effects are these invasions known or suspected to be having? Are there any indications as to which invasions might be the most important from a nature conservation perspective? Finally, the recognition of the importance of these invasions within reserves is often expressed in the existence of control programmes. These are reviewed in order to ascertain what determines the relative ease with which different invasions can be controlled.

In Paper 5, I review and analyse all the available information on the alien flora of the Cape of Good Hope Nature Reserve, which is located in South Africa's fynbos biome. In Paper 6, I first present the detailed history of the alien plant control campaign that had been waged in this reserve for more than forty years. The success of this campaign is then evaluated, using the extent of infestations as mapped at irregular intervals and the results of three surveys of fixed plots located within the reserve. These surveys were conducted at roughly ten-year intervals, the final survey having been carried out specifically for this paper.

In Paper 7, the above reserve is one of six included in an intercontinental comparative study of the invasions of reserves having Mediterranean-type climates. This analysis covered both plant and animal invasions.

In Paper 8, I tabulate and briefly analyse the alien flora of the largest nature reserve in South Africa, the Kruger National Park. In the next paper of the chapter, I review the available

information on alien invasions of this reserve. This review covers all taxa for which information could be obtained and is the most comprehensive investigation of its sort yet made for any area in southern Africa. The invasions and their control are described within the context of the reserve's history.

The final paper in this chapter, Paper 10, is another intercontinental comparative analysis of alien invasions of nature reserves, this time of five reserves in the savanna and dry woodland biomes of the world. Kruger National Park and the Hluhluwe-Umfolozi Game Reserve are the two southern African case studies included in this chapter.

By studying invasions within proclaimed nature reserves, it was hoped to see more clearly the role ecological factors play in determining the success or failure of these invasions. Even when it was Man's control of these invasions that was being analysed, the emphasis was always on ascertaining the ecological principles that determined the relative ease with which different species (or even different invasions of the same species) could be controlled.

The alien flora of the Cape of Good Hope Nature Reserve

I.A.W. Macdonald*, D.L. Clark and H.C. Taylor

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700 Republic of South Africa,
Cape of Good Hope Nature Reserve, P.O. Box 62, Simonstown, 7995 Republic of South Africa and
Botanical Research Institute, P.O. Box 13, Clanwilliam, 8135 Republic of South Africa

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An annotated species list of the alien vascular plant flora of the Cape of Good Hope Nature Reserve is presented. The flora comprises five gymnosperm and 68 angiosperm species that are definitely alien to the reserve and four angiosperm species that are possibly alien. The life-form distribution of the alien flora is shown to be significantly different from that of the indigenous flora; trees, shrubs and annual herbs are more important in the alien flora, and dwarf shrubs and perennial herbs are much less important. Biotic factors are suggested as being important in determining the success of alien invasions, in particular grazing by ungulates. The invasion rate is currently about one new species per year. By ceasing to introduce tree species and by restricting human disturbance, the rate of invasion of new species could be reduced.

'n Benaamde lys van die uitheemse vaatplantsoorte van die Kaap die Goeie Hoop Natuurreserveaat word aangebied. Die flora bestaan uit vyf gimnosperm- en 68 angiospermsoorte wat sonder twyfel uitheems is en vier angiospermsoorte wat moontlik uitheems is. Daar word aangedui dat die lewensvormverspreiding van die uitheemse flora opvallend van dié van inheemse plantegroei verskil; bome, struik en eenjarige kruide is van meer belang by die uitheemse flora terwyl dwergstruik en meerjarige kruide baie minder belangrik is. Dit wil voorkom van biotiese faktore, veral beweiding deur hoëdiere, 'n belangrike rol kan speel by die indringing van uitheemse plante. Tans word die tempo van indringing op ongeveer een nuwe spesie per jaar geskat. Deur die invoer van boomsoorte te staak en versteuring deur mense te beperk, kan die indringingstempo van nuwe plantsoorte verminder word.

Keywords: Alien plants, Cape, fynbos, invasive species

*To whom correspondence should be addressed

Introduction

The invasion of natural vegetation by alien plants constitutes one of the Cape of Good Hope Nature Reserve's major management problems (Taylor 1977; Taylor & Macdonald 1985; Taylor *et al.* 1985; Clark 1985). In this paper we list for the first time all the species involved, providing details of their history, distribution and status in the reserve, and present some analyses of the problem, based on this information.

The reserve is located at the southern tip of the Cape Peninsula (34°12'S 18°22'E), is 7750 ha in extent, ranges in altitude from 0 to 366 m.a.s.l. and experiences mean annual rainfall ranging from 300 to 700 mm. The geology, ecology and history of the reserve have been described by Opie (1967) and Taylor (1969). The vegetation and flora of the reserve have been documented by Taylor (1984a, b; 1985). The vegetation is primarily mountain fynbos on the central plateau which is underlain by Table Mountain sandstone, with strandveld vegetation on the littoral shelf which is widest on the western side of the Peninsula.

Methods

In order to compile this list the alien species (Wells *et al.* 1986) were extracted from the published flora of the reserve (Taylor 1985). Additional species were obtained from the published accounts of alien plant invasions of the reserve (Taylor *et al.* 1985) and from the unpublished observations of the authors. These species were annotated using the conventions of Wells *et al.* (1986), the data provided by this text being supplemented where necessary from a range of botanical reference books. Details of each species' distribution and status within the reserve were based on field observations of the authors, supplemented by data recorded by H.C. Taylor in his card index of the area's flora and in the raw data and field notes from the fixed-plot surveys (Taylor *et al.* 1985). Only alien plant species that are known to have self-seeded on the reserve

are included. Species that are known to invade areas of natural vegetation within the reserve are asterisked (*). Species that are or have been a major problem in the reserve are given a double asterisk (**). Species were defined as constituting a 'major problem' when they have been observed to form dense stands in areas of natural vegetation. These stands tend to exclude the native flora and have generally required active control measures to prevent their spread. Those species which are not undoubtedly alien to the reserve are bracketed.

The term 'disturbed' is used throughout this paper to refer to anthropogenic disturbance. Within the reserve this mainly takes the form of soil disturbance arising from road building activities and that around picnic sites and human habitation. The clearance of dense stands of alien trees is also considered to give rise to 'disturbed' areas. Prior to the reserve's proclamation, certain areas were cultivated. These are also termed 'disturbed'.

A map giving the location of most of the places named in the present account and the location of the permanently marked alien plant-monitoring plots (numbered 1 to 100) is presented as Figure 1 of Taylor & Macdonald (1985) and Taylor *et al.* (1985).

In the list that follows, collections are given by the name of the collector followed by the collector's number. In the case of collections by H.C. Taylor these are given in the form (T2355). All the Taylor collections are lodged with STE and the other collections cited are either in NBT or BOL.

The alien flora

Gymnospermae

Pinaceae

**Pinus halepensis* Mill.

Aleppo pine. Tree, perennial from Europe and Asia.

A single small plant recorded in plot 23 (near Wolfkop) in the 1976 survey.

**** *P. pinaster* Ait.**

Cluster pine. Tree, perennial from Europe and Asia. Established as plantations and windbreaks in several locations in the north-west of the reserve. Low density self-sown stands had established throughout the central portions of the reserve by 1966 but were relatively easily controlled. Currently only a problem in the previous high density areas.

*** *P. pinea* L.**

Stone pine. Tree, perennial from Europe and Asia. Planted around homesteads in north-west of reserve with limited spread into immediate surrounds. This species does not pose a problem in the reserve although adult specimens still grow around Klaasjagersberg.

*** *P. radiata* D. Don**

Monterey pine. Tree, perennial from North America. Only recorded on a single plot (No. 75) in the Hoek van Bobbejaan area of the reserve in 1976. Possibly this species had been planted at a cottage in this vicinity.

Cupressaceae

*** *Cupressus macrocarpa* Hartweg.**

Monterey cypress. Tree, perennial from North America. A few adult trees planted and still growing around the Homestead Restaurant. A few saplings have established in the natural vegetation in the near vicinity, the furthest of these was growing near the main road some 700 m from the planted specimens.

Angiospermae

Monocotyledones

Poaceae

*** *Aira cupaniana* Guss.**

Herb, annual from ?Europe. This small grass has been recorded from the hills between Ribboksdam and Platboom in the south of the reserve by Taylor (T5282).

*** *Ammophila arenaria* (L.) Link.**

Marram grass. Herb, perennial from Europe. Growing on dunes north of Die Mond where it had probably been planted in a dune 'reclamation' campaign. Not considered to be spreading in the reserve.

*** *Avena barbata* Brot.**

Wild oats. Herb, annual from Europe & Asia. Widespread in reserve but is mainly confined to disturbed areas such as road verges, old lands and around present and old homesteads and picnic sites. Does not generally invade natural veld. Very palatable and is probably being kept in check by grazers. In areas of 100% alien tree cover that were cleared in 1986, dense stands of *A. barbata* have germinated. These areas were apparently cultivated at some time in the past.

*** *Briza maxima* L.**

Quaking grass. Herb, annual from Europe. Same comments as for *A. barbata*.

*** *B. minor* L.**

Small quaking grass. Herb, annual from Europe. Not as common as *Briza maxima*. The species shows a

preference for damp areas, eg. vleis and stream banks. Frequently found in natural veld in these areas, but usually in vicinity of old homesteads.

*** *Bromus diandrus* Roth**

Ripgut brome. Herb, annual from Europe & Asia. Associated with disturbed areas, and in and around picnic sites and old and present homesteads. Often in moist areas.

***Bromus molliformis* Lloyd**

Soft brome. Herb, annual from Europe & Asia. Recorded from the reserve in July 1982.

*** *Cortaderia selloana* (Schult.) Aschers. & Graebn.**

Pampas grass. Herb, perennial, South America. One specimen known from road verge on Circular Drive. New growth (especially after fire) heavily grazed by Hartman's Mountain Zebra *Equus zebra hartmannii*. Two plants growing in stream at Smitswinkel Bay. No seedlings noticed.

[*Digitaria sanguinalis* (L.) Scop.

Crab finger grass. Herb, annual, pantropical. Occasional in disturbed areas such as road verges, homestead sites, picnic sites and gravel borrow pits.]

***Hordeum murinum* L.**

Wild barley. Herb, annual, Europe & Asia. As for *D. sanguinalis*.

***Lagurus ovatus* L.**

Hare's tail grass. Herb, annual, Europe & Asia. As for *D. sanguinalis*.

***Lolium loliaceum* (Bory & Chaub) Hard**

Darnel. Herb, annual, Europe & Asia. Recorded at Platboom in November 1941 (Compton 12306).

***Lolium perenne* L.**

Perennial rye grass. Herb, perennial, Europe & Asia. Often found on road verges and in lawns at picnic sites and homesteads.

*** *Paspalum dilatatum* Poir.**

Common paspalum. Herb, perennial, South America. Common on stream banks in disturbed areas. Found in picnic sites, road verges and homesteads. Collected in 1979 at the Kaasjagers River Bridge (T9938).

***P. urvillei* Steud.**

Tall paspalum. Herb, perennial, South America. Recorded by Taylor (1969) in Appendix 4.

*** *Pennisetum clandestinum* Chiov.**

Kikuyu. Herb, perennial, East Africa. Found mainly at Klaasjagersberg, Perdekloof, the Homestead Restaurant and at picnic sites. Spreads in wet areas and outcompetes indigenous species. Isolated patches are scattered around the reserve, often where lawn cuttings have been dumped or used in erosion-control operations. This species is currently heavily grazed in the reserve.

*** *Polypogon monspeliensis* (L.) Desf.**

Beardgrass. Herb, annual, Europe & Asia. Recorded at Buffels Bay near spring (Adamson 728).

* *Vulpia myuros* (L.) C.C. Gmel.

Rat's tail fescue. Herb, annual, Europe & Asia.
Recorded from the reserve by Taylor (1985).

Cyperaceae

[* *Cyperus textilis* Thunb.

Matsedge. Herb, perennial, elsewhere in South Africa.

A few small clumps occur in the Klaasjagersberg river near the offices and a large stand in the lower reaches of this river near Die Mond. Also occurs in the marsh at Olifantsbos. This species has been cultivated in ornamental ponds at Klaasjagersberg and was not included in the reserve's flora by Taylor (1985). If this species is indeed alien to the reserve it could pose a significant conservation problem in the future.]

Arecaceae

* *Phoenix dactylifera* L.

Date palm. Tree/shrub, perennial, North Africa and Asia. One plant recorded on Plot 7 in the 1976–80 resurvey. Possibly a remnant of past cultivation as there is an old homestead in the vicinity of this plot. *Phoenix* sp. is recorded as spreading in natural vegetation on the slopes of Table Mountain (Moll & Scott 1981).

Agavaceae

Agave sisalana Perrine.

Sisal. Shrub, perennial, North America. Planted at Klaasjagersberg and at the Main Gate. In the latter locality has shown regeneration in an adjacent firebreak. Not known to spread into undisturbed fynbos on the reserve.

Dicotyledones

Salicaceae

* *Populus* × *canescens* (Ait.) J.E. Sm.

Grey poplar. Tree, perennial, Europe & Asia. Found along streams at Olifantsbos and Perdekloof near old homesteads. Does not appear to be spreading rapidly. In these areas it is competing with *Acacia longifolia* and *A. saligna* and spread might be more rapid in pure fynbos communities.

Urticaceae

* *Urtica urens* L.

Small stinging nettle. Herb, annual, Europe & Asia. Recorded on the Gifkommetjie Road dune slack in October 1971.

Proteaceae

** *Hakea gibbosa* (Sm.) Cav.

Rock hakea. Tree/shrub, perennial, Australia. Currently there are no seed-producing plants of this species in the reserve. Used to occur at scattered localities on the reserve's northern boundary especially near Modderdam, Wolfkop, Spookhuis and The Camp, but never in large numbers. These plants have been removed on discovery, e.g. seven plants from Modderdam in October 1973.

** *Hakea suaveolens* R.Br.

Sweet hakea. Tree/shrub perennial, Australia. Found in relatively moist sites between Modderdam and Tuinkop, in the north-west of the reserve. No seed-producing trees left by 1987. Previous infestations were not really dense but this area held dense stands of both *Acacia saligna* and *Eucalyptus lehmannii* and competition from these species had probably limited the spread of *H. suaveolens*.

Chenopodiaceae

* *Chenopodium botryodes* Sm.

Herb, ?annual, Europe & Asia. Found in disturbed areas, e.g. old lands, homesteads and kraals.

Caryophyllaceae

* *Spergularia media* (L.) C. Presl.

Middle-sized sand spurry. Herb, perennial, Europe & Asia. Recorded in the rocky coastal strip throughout the reserve, also in dried-up vleis (Olifantsbos) and on the margins of blackwater lakelets (Sirkelsvlei). Collected several times from the reserve, (Adamson 716) and (T6692, 7257, 7413).

* *S. rubra* (L.) J&C. Presl.

Purple sand spurry. Herb, annual, Europe & Asia. Included in Taylor (1985). Apparently only recorded by Adamson (2619) at a locality called Oudekraal. No such locality name currently in use in the reserve.

[* *Silene clandestina* Jacq.

Herb, annual, Europe & Asia. Recorded on the coastal flats at Buffels Bay in October 1966 (T6945) and in the Gifkommetjie turnoff plot in October 1971 (T7952). Not listed as alien by Wells *et al.* 1986.]

Fumariaceae

* *Fumaria muralis* Sond. ex Koch

Fumitory. Herb, annual, Europe & Asia. Common on lawns of picnic sites. Also found in disturbed areas such as old lands, homesteads and kraals.

Pittosporaceae

* *Pittosporum undulatum* Vent.

Sweet pittosporum. Tree/shrub, perennial, Australia. A few specimens along Klaasjagersberg river near office complex. Does not seem to be spreading.

Rosaceae

* *Rubus* sp. indet

Bramble. Shrub/climber, perennial, ?origin. A few plants occur at Perdekloof as an understory in alien *Acacia* thicket.

Pyracantha angustifolia Schneid.

Orange firethorn. Tree/shrub perennial, Europe & Asia. A single plant growing on the road verge on Circular Drive. The plant is kept low by persistent heavy browsing.

Fabaceae (Leguminosae)

** *Acacia cyclops* A. Cunn. ex G. Don

Rooikrans. Tree/shrub, perennial, Australia. Adult, seed-bearing trees now (1987) occur only south of a line drawn between Paulsberg, the Homestead Restaurant and Platboom. The species occurs throughout the reserve in dry, disturbed areas and is an aggressive invader.

** *A. longifolia* (Andr.) Willd.

Long-leaved wattle. Tree/shrub, perennial, Australia. Predominantly a riverine habitat invader which is often outcompeted by *A. saligna*. With the exception of isolated patches at Klaasjagersberg, Olifantsbos and Schuster river valley, all adult plants have now been removed.

* *A. mearnsii* De Wild.

Black wattle. Tree/shrub, perennial, Australia.

Scattered plants occur around the Klaasjagersberg complex and a few individuals have germinated along the Klaasjagersriver — generally in disturbed areas.

* *A. melanoxylon* R. Br. Blackwood.

Blackwood. Tree/shrub, perennial, Australia.

Has been found invading moist fynbos at Klaasjagersberg and near Plot 78 adjacent to the main road near the Homestead Restaurant. Several mature specimens still grow in the Klaasjagersberg complex.

** *A. saligna* (Labill.) H.L. Wendl.

Port Jackson willow. Tree/shrub, perennial, Australia.

Distribution generally confined to moist habitats. Isolated patches of seeding trees now only occur at Klaasjagersberg and in the southern portion of the reserve. Small plants are scattered throughout the reserve, often on road-verges.

* *Albizia lophantha* (Willd.) Benth.

Stinkbean. Tree/shrub, perennial, Australia.

Occurs in riverine and marshy habitats at Klaasjagersberg, Perdekloof, Olifantsbos, Smitswinkel Bay, Modderdam and near the Homestead Restaurant.

* *Medicago laciniata* (L.) Mill

Little burweed. Herb, annual, Europe & Asia.

Collected in the hills between Ribboksdam and Platboom in October 1963 (T5263).

* *M. polymorpha* L.

Burclover. Herb, annual, Europe & Asia.

Occurs on lawns of picnic sites throughout the reserve. Has been recorded from the hills in the south of the reserve and on disturbed ground near Sirkelsvlei (T5275 & 8224).

* *Melilotus indica* (L.) All.

Annual yellow sweet clover. Herb, annual, Europe & Asia.

Recorded at Ribboksdam near the sea and on the adjacent hills in October 1963 (Taylor).

Ornithopus sativus Brot.

Seradella. Herb, annual, Europe & Asia.

This species was introduced to the reserve as a fodder legume in the Circular Drive area. These plantings were initiated in 1959 in order to improve the reserve's grazing for large ungulates (Opie 1967). The introductions of forage legumes all failed as a result of over-utilization by these ungulates (Opie 1967; Millar 1970). Apparently this species is now no longer present on the reserve.

* *Sesbania punicea* (Cav.) Benth.

Red sesbania. Shrub, perennial, South America.

One stand of this species was discovered in the reserve in the early 1980s. The plants are growing on a borrow pit adjacent to the main road near Plot 58. The patch is approximately 500 m² in area. Clearing every second year has not proven successful so annual clearing is now being undertaken.

Trifolium fragiferum L.

Strawberry clover. Herb, annual, Mediterranean & southern Europe.

Listed by Taylor (1969) in Appendix 4.

* *T. subterraneum* L.

Subterranean clover. Herb, annual, Mediterranean & Western Europe.

Recorded in a plot at the Gifkometjie turnoff in October 1971 (T7957).

Vicia benghalensis L.

Narrow-leafed purple vetch. Climber, annual or biennial, Europe & Asia.

Scattered plants are found in disturbed areas around homesteads in the north of the reserve.

Geraniaceae

* *Erodium moschatum* (L.) L'Herit.

Musk heron's bill. Herb, annual or biennial, Europe & Asia.

Recorded in a disturbed area at Buffels Bay in September 1972.

Tropaeolaceae

* *Tropaeolum majus* L.

Garden nasturtium. Herb, annual, Central America.

Common in the Perdekloof area following the burning of a dense alien *Acacia* stand in 1986.

Euphorbiaceae

* *Ricinus communis* L.

Castor-oil bush. Tree/shrub, variable, elsewhere in Africa.

Scattered plants are found in disturbed areas in the reserve. Young plants were found in Plot 56 on the Smitswinkel Flats in 1986 where material had been imported for erosion control.

Lythraceae

* *Lythrum hyssopifolium* L.

Hyssope loosestrife. Herb, variable, North America.

Recorded at Klaasjagersberg as a weed near the river in December 1974 (T8875).

Myrtaceae

* *Callistemon rigidus* R.Br.

Australian bottle brush. Tree/shrub, perennial, Australia.

One plant known. Occurs in fynbos on road verge on the Circular Drive.

* *Eucalyptus cladocalyx* F. Muell.

Sugar gum. Tree, perennial, Australia.

This species, like the other *Eucalyptus* spp., was planted around homesteads, mainly in the north of the reserve. It shows localized spread, mainly into disturbed areas such as firebreaks. Thinning of the fynbos community around established individuals or patches allows the establishment of further seedlings.

* *E. ficifolia*

Red flowering gum. Tree, perennial, Australia.

Found around Klaasjagersberg. Although seedlings are found, the species does not appear to be an aggressive invader.

* *E. globulus* Labill.

Blue gum. Tree, perennial, Australia.

Only recorded in north of the reserve near Perdekloof.

* *E. gomphocephala* A.DC.

Tuart. Tree, perennial, Australia.

As for *E. cladocalyx*.

** *E. lehmannii* (Schau.) Benth.

Spider gum. Tree, perennial, Australia.

Found near old human habitations. Invasive capabilities are greatly enhanced by fire. This species has shown itself capable of forming extensive monospecific stands. Recovery of the fynbos after felling stands of this and other *Eucalyptus* species tends to be slower than where other alien tree species are involved.

* *E. sideroxylon* A. Cunn. ex Woolls.

Black iron bark. Tree, perennial, Australia.

Found around Klaasjagersberg. Although seedlings are found, the species does not appear to be an aggressive invader.

* *Leptospermum laevigatum* (Soland. ex Gaertn.) F.J. Muell.

Australian myrtle. Tree/shrub, perennial, Australia.

Seems to show a preference for drier, sandy areas — occurs at Skilpadsvei, Old Spookhuis and in the northern area where all adult plants have now been felled. This species spreads rapidly after fires (from seed) although adult plants are killed by fire.

Primulaceae

* *Anagallis arvensis* L.

Scarlet pimpernel. Herb, annual, Europe and Asia.

Grows mainly in disturbed areas, e.g. on road verges and where clearing activities have been carried out around old dwellings. Occasionally found in areas of natural vegetation such as in the coastal communities at Booiseskerm and the Old Lime Kiln. These areas have been severely disturbed in the past.

Apiaceae (Umbelliferae)

* *Centella asiatica* (L.) Urb.

Pennywort. Herb, perennial, Europe & Asia.

Recorded at Smiths Farm (now the Homestead Restaurant) near the vlei margin (Adamson 912) and in west coast swamps of the reserve (Adamson 3329). Apparently no recent records.

* *Torilis arvensis* (Huds.) Link.

Herb, annual, Europe & Asia.

Recorded on sand at Buffels Bay (Adamson 723), on the hills between Ribboksdam and Platboom in October 1963 (T5260), in the Gifkommetjie turn-off plot in October 1971 and under bushes at Sirkelsvlei in September 1972.

Verbenaceae

* *Lantana camara* L.

Lantana. Shrub/climber, perennial, South America.

A single plant was recorded in Plot 24 at the Spookhuis in the 1966 survey. Not known from anywhere on the reserve since this time.

Solanaceae

* *Datura* sp.

Thorn apple. Herb, annual, ?North America.

Occurs at the Homestead Restaurant and below the Homestead Dam in dunes next to river. Also at old rubbish dump.

* *Nicotiana glauca* R.A. Grah.

Wild tobacco. Tree/shrub, perennial, South America.

A few specimens in the disturbed area around the Theefontein homestead in 1986.

Solanum nigrum L. Scop.

Nightshade. Herb, variable, origin uncertain, thought to be alien to South Africa.

This species is found in disturbed areas around old human habitations and in old cultivated fields.

Orobanchaceae

* *Orobanche ramosa* L.

Blue broomrape. Herb, root parasite, annual, Europe & Asia. One patch found at gate at Scarborough in 1986 growing near the coast in sandy soil. Also present near beaches and at Cape Point next to footpath near the lookout spots.

Myoporaceae

* *Myoporum serratum* R.Br.

Manitoka. Tree/shrub, perennial, Australia.

This is a coastal species which occurs in the dunes at the Homestead Restaurant, Olifantsbos and Die Mond. Also found at Black Rocks. Numerous seedlings come up after clearing *Acacia cyclops* in these areas.

Plantaginaceae

Plantago lanceolata L.

Narrow-leaved ribwort. Herb, variable, Europe & Asia.

Occurs mainly on roadverges and other disturbed sites in the reserve.

Asteraceae (Compositae)

Conyza canadensis (L.) Cronq.

Horseweed fleabane. Herb, annual, North America.

Grows on roadverges and along gravel tracks. Common around buildings.

* *Hypochoeris radicata* L.

Hairy wild lettuce. Herb, perennial, Europe & Asia.

As for *Plantago lanceolata* but also recorded in the Gifkommetjie turn-off plot in October 1971.

* *Sonchus oleraceus* L.

Sowthistle. Herb, annual, Europe & Asia.

As for *P. lanceolata* but also recorded on the western shore of Sirkelsvlei in September 1972.

Discussion

The naturalized alien vascular plant flora of the Cape of Good Hope Nature Reserve comprises 5 species belonging to the Gymnospermae and 68 definitely alien species belonging to the Angiospermae. An additional four angiosperms are possibly alien to the reserve. Of the 19 definitely alien monocotyledonous species seven are not known to grow in areas of natural vegetation, being confined to areas of intense human disturbance such as picnic sites. None of the monocotyledons were considered to be posing major problems in the reserve whereas one gymnosperm and six dicotyledons were. All of these were trees.

The life-form distribution of the alien flora is markedly different from that of the reserve's indigenous flora (Table 1). Even when we combined all tree and shrub categories (but not dwarf shrubs which are distinctive, being defined as species never exceeding 1 m in height), the shrub/climbers with the climbers, and the biennial and variable herbs with the annual herbs, the Chi-squared test for heterogeneity of the indigenous and alien flora distributions was highly significant ($X^2_{5DF} = 113, P < 0,001$).

Table 1 The number and percentage of species in different life-form categories in the indigenous and alien vascular floras of the Cape of Good Hope Nature Reserve (indigenous flora from Taylor 1985, life forms taken from Bond & Goldblatt 1984)

		Life-form categories (after Wells <i>et al.</i> 1986)											
Flora		Tree	Tree/ shrub	Shrub	Dwarf shrub	Shrub/ climber	Climber	Perennial herb	Biennial/ variable herb	Annual herb	Root parasite	Other parasites	Total
Indigenous	No.	4	24	217	213	0	34	457	13	79	6	5	1052
	%	0,4	2,3	20,6	20,2	0	3,2	43,4	1,2	7,5	0,6	0,5	100
Alien	No.	12	15(?16)	1	0	2	1	9(?10)	3	29(?31)	1	0	73
	%	16,4	20,5	1,4	0	2,7	1,4	12,9	4,1	39,7	1,4	0	100

Tree and tree/shrub species are much more frequent in the alien flora whereas the shrub and dwarf shrub element, which dominates the indigenous flora, is almost totally absent from the alien flora. These results are in accord with the general observation that alien trees appear to have filled an 'empty niche' in the fynbos (Campbell *et al.* 1979; Moll *et al.* 1980; Macdonald 1984). Comparison of ecosystems in matched environments in the Mediterranean-type regions of Australia (whence 18 of the reserve's invasive tree and shrub species emanated) and South Africa, has identified the absence of tall trees in the fynbos as one of the important anomalies requiring explanation (Milewski & Cowling 1985). That all six of the angiosperm tree species causing major problems in the reserve are from Australia reinforces the contention that this continent has given rise to a suite of tree species especially well adapted to invading fynbos vegetation (Macdonald 1985).

The other life form which is much more frequent in the alien flora than in the indigenous flora is that of the annual herbs (Table 1). However, of the 29 definitely alien annuals, 10 are apparently confined to sites of intense human disturbance. Most of the remainder occur most commonly in such sites. These species are found in natural vegetation only where this is very open, e.g. *Briza minor* on stream banks, *Medicago polymorpha* on the edge of Sirkelsvlei, and *Melilotus indica* next to the sea and on the rocky hills near Ribboksdam. Raitt (1983) has shown that where fynbos is subjected to a long history of frequent and intense human disturbance, the alien flora is totally dominated by this life form (69% of introduced genera being annuals alongside a railway on the Cape Flats).

It is also of note that 24 of the 29 naturalized annuals originate from Europe and Asia, many of them from the Mediterranean Basin. The ability of plants from this region to invade areas of human disturbance in the relatively recently colonized Mediterranean-type regions of the world has been attributed to the long history of human disturbance that the Mediterranean Basin has experienced (Groves 1986).

Small perennial plants are only a minor component of the reserve's alien flora. The few dwarf shrubs and perennial herbs that have successfully invaded within the reserve are, like the annuals, almost entirely restricted to sites of human disturbance. Where they are present in fynbos they are once again found in areas of relatively open plant canopies, e.g. *Ammophila arenaria* on littoral dunes and *Spergularia media* on rocky littoral sites. The inability of low-growing alien plants to successfully invade fynbos within the reserve is in accord with the hypothesis that there is intense competition for light between alien and native species in fynbos communities (Macdonald & Richardson 1986). Successful alien invaders

tend to be those which can overtop the indigenous plant canopy.

Another factor that might be limiting successful invasion by plants of these growth forms is herbivory. Several herbaceous alien species have been observed to be heavily grazed by ungulates within the reserve, e.g. *Avena barbata*, *Cortaderia selloana* and *Pennisetum clandestinum*. The intentional introduction of forage legumes and pasture grasses to ploughed strips along the reserve's roads in the late 1950s and 1960s failed, at least partly, as a result of excessive defoliation of the young plants (Opie 1967; Millar 1970). Grazing has been suggested to be an important selective pressure in shaping the alien flora of southern Africa (Macdonald 1984, 1985). That no geophytes have successfully invaded the reserve is possibly a further reflection of this type of selective pressure. The reserve has a high density of mole rats which feed mainly on geophytes. The large number of geophyte species in the indigenous flora presumably have adaptations that enable them to survive this predation pressure. However, geophytes from other mediterranean-type regions have not been subjected to such pressures (Milewski & Cowling 1985).

The role of ungulate herbivores in alien plant invasions in the reserve needs to be researched: on one hand, the introduction of these ungulates, most of which are alien to the reserve, is suspected to have led to the over-utilization of certain of the reserve's indigenous plants (Macdonald *et al.* in press). This might favour the establishment of alien plants, particularly where over-utilization leads to an opening-up of the plant canopy. On the other hand, the observations reported above indicate that ungulates might be limiting successful invasions. The interaction is complicated by two further considerations: the first of these is that the presence of these ungulates has been the stimulus for several intentional plant introductions to the reserve. The second is that alien plants might also have been unintentionally introduced in fodder imported to supplement the nutrition of these ungulates.

Although the collection of data on the alien flora of the reserve has been intermittent it appears that at least 8 species have been recorded from the reserve for the first time in the 1980s (*Bromus molliformis*, *Cortaderia selloana*, *Sesbania punicea*, *Vicia benghalensis*, *Tropaeolum majus*, *Callistemon rigidus*, *Nicotiana glauca*, *Orobancha ramosa*). If these were all new additions to the reserve's alien flora this would give an invasion rate of at least one species per year. On the currently observed ratio of problem species to total alien species (7:73) this rate of invasion can be expected to give rise to about one new problem species per decade.

Two important management considerations arise from the above analyses. Firstly, no more tree species should be

introduced to the reserve. Secondly, sites of human disturbance should be severely limited. Obviously, every effort should be made to prevent the inadvertent introduction of new alien species to the reserve, e.g. in fodder imports or during the movement of soil for roadbuilding and erosion-control purposes. A system of regular monitoring around sites of human disturbance should be initiated to enable the early detection of new invasions.

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The history and effects of alien plant control in the Cape of Good Hope Nature Reserve, 1941-1987

I.A.W. Macdonald*, D.L. Clark¹ and H.C. Taylor

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700 Republic of South Africa; Cape of Good Hope Nature Reserve, Divisional Council of the Cape, P.O. Box 1035, Cape Town, 8000 Republic of South Africa and Botanical Research Institute, P.O. Box 13, Clanwilliam, 8135 Republic of South Africa

Present address: ¹Department of Agriculture and Nature Conservation, Private Bag 2050, Keetmanshoop, 9000 South West Africa/Namibia

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Concern about the invasion of this reserve by alien trees and shrubs, principally *Acacia cyclops*, *A. saligna*, *A. longifolia*, *Eucalyptus lehmannii* and *Pinus pinaster*, was first expressed in 1941, 2 years after its proclamation. Control operations were started by 1943 and were almost totally ineffective for at least the first 35 years; no systematic control strategy was implemented, follow-up control work was inadequate to prevent re-establishment of felled thickets and the supervision of control teams was deficient. Linkage of control operations to firewood production was a significant factor in this failure. In 1974 a 10-year control strategy was drawn up and in the late 1970's began to be effectively implemented. Surveys of 40 plots in the centre of the reserve in 1966, 1976-80 and 1986 showed increasing densities of species other than the easily controlled *P. pinaster* up to 1976-80. Since then almost all individuals > 1,8 m in height have been eliminated and indications from smaller height classes are that seed banks are being depleted. Explanations are advanced for the successes and failures experienced during the 47 years of control. Some of the side-effects of these invasions and their control are discussed. One conclusion is that this reserve requires a qualified ecologist on its staff.

Bekommernis oor die indringing van uitheemse bome en struik, veral *Acacia cyclops*, *A. saligna*, *A. longifolia*, *Eucalyptus lehmannii* en *Pinus pinaster*, was reeds in 1941 uitgespreek, 2 jaar na die proklamasie van die reservaat. Beheeroperasies was in 1943 begin en was heeltemal onsuksesvol vir 35 jaar; daar was geen sistematiese beheerplan nie, opvolgwerk was onvoldoende en gevolglik het afgekapte bome weer gegroei. Die toesighouding oor die beheerspanne was ook onvoldoende. Die besluit om die beheeroperasies te gebruik om brandhout te kry was skynbaar een rede vir die mislukking van die vroeë pogings. Gedurende 1974 was 'n 10-jaar-beheerstrategie geformuleer en dit was uiteindelik in die laaste jare van die dekade doeltreffend geïmplementeer. Opnames van 40 persele in die middel van die reservaat was in 1966, 1976-80 en 1986 uitgevoer. Die digtheid van al die spesies behalwe *P. pinaster* het tot 1976-80 vermeerder. Sedertdien was amper al die plante met hoogte > 1,8 m uitgeroei en dit lyk asof die saadbank verminder het. Redes vir die suksesse en mislukkings van die program word voorgestel. Sommige van die ekologiese gevolge van die indringings en hulle beheer word bespreek. Die aanstelling van 'n vakkundige ekoloog as lid van die reservaat se personeel word aanbeveel.

Keywords: Alien plants, Cape, control strategies, fynbos, reserve management

*To whom correspondence should be addressed

Introduction

The invasion of fynbos vegetation by alien trees and shrubs is considered by several authorities to pose a serious threat to the long-term survival of its constituent species (Wicht 1945; Adamson 1953; Taylor 1977a; Hall 1978). Much has now been published on the extent of the problem (see references in Macdonald 1984) and on control measures for individual alien species, e.g. *Hakea sericea* (Fenn 1980; Fugler 1983; Kluge & Richardson 1983), *Pinus pinaster* (Kruger 1977; Donald 1982) and *Acacia longifolia* (Dennill 1985; Pieterse & Cairns 1986). Little published information is available on the results of field-scale control operations; quantitative data being available only for repeat surveys of sample plots in the northern Cape Peninsula mountains (McLachlan *et al.* 1980) and the Cape of Good Hope Nature Reserve (Taylor *et al.* 1985). The extensive field experience that

has been accumulated by fynbos managers has recently been drawn together in the report of a workshop meeting (Macdonald *et al.* 1985).

This paper describes the history of alien plant control operations in the Cape of Good Hope Nature Reserve and attempts to quantify their successes and failures.

The study area

The Cape of Good Hope Nature Reserve, 7 750 ha, is situated at 34°15'S 18°25'E and comprises the southern tip of the Cape Peninsula. The reserve's main topographic feature is a low plateau of sandstone rising from 60 m a.s.l. on the west to peaks up to 360 m on the east, from where the terrain falls steeply to the sea. Mean annual rainfall in the reserve ranges from 330 mm in the south to 660 mm in the north-east. Soils in the reserve range from the deep calcareous sands of recent

sand dunes to well-drained, highly leached, shallow, sandy lithosols on hillslopes. Much of the central plateau has marshy humic soils with impeded drainage. The vegetation is mainly Mesic Mountain Fynbos (*sensu* Moll *et al.* 1984) with small intrusions of elements from the West Coast Strandveld and Kaffrarian Thicket along the coastal strip. The vegetation is described in detail by Taylor (1983, 1984). The reserve has a vascular plant flora of exceptional diversity (1 052 species) and unusually high endemism with 12 species being restricted to the reserve (Taylor 1985). In 1939 the southern area was proclaimed a local authority nature reserve under the control of the then Divisional Council of the Cape (now the Western Cape Regional Services Council). By 1965 all the farms comprising the current reserve had been acquired. For about 120 years prior to proclamation, the area had been subjected to domestic livestock grazing and frequent burning while small areas had been cultivated or intensively disturbed around the scattered homesteads and military installations (Opie 1967; Taylor 1969; Clark 1985).

The intentional and unintentional introduction of a range of alien plant species has resulted in certain of these species invading areas of natural vegetation within the reserve (Macdonald *et al.* 1987). The most important alien species in the reserve are Rooikrans *Acacia cyclops* A. Cunn. ex G. Don, Port Jackson *Acacia saligna* (Labill.) Wendl., Cluster pine *Pinus pinaster* Ait., Long-leaved wattle *Acacia longifolia* (Andr.) Willd. and Spider gum *Eucalyptus lehmannii* (Schau.) Benth.

The management of the reserve is planned and implemented by the reserve's full-time staff. Management policies and strategies are evaluated prior to implementation by an advisory board which comprises representatives of natural resource management agencies, research bodies and special interest groups.

Methods

The early history of alien plant control in the reserve was mainly determined from the reserve's files and, in particular, from the minutes of meetings of the reserve's advisory board. A detailed history of control operations was extracted from the files, rangers reports and Chief Warden's reports for the period 1966 to 1983 by Dr S.A. Macdonald (Macdonald 1983).

The area of mapped control operations and infestations was measured by clipping and weighing the different mapped categories on photostat copies of the relevant maps. Corrections were made for different densities of photocopy ink on the various mapped categories. No corrections were made for angle of slope, all 'areas' being simple vertical projections. This will result in underestimations of the actual ground surface area infested, as many of the dense infestations, particularly of *A. cyclops*, occur on steep slopes.

The quantitative evaluation of the effects of recent control operations was based on a third survey, carried out from March to June 1986, of 40 of the 99 permanently marked monitoring plots (Figure 1) located on a 1 000-yard (914-m) grid throughout the reserve by

Taylor (Taylor & Macdonald 1985). The first and second surveys were conducted in 1966 and 1976–80 respectively (Taylor *et al.* 1985). Each of these 10.5-ha plots is circular with a 200-yard (183-m) radius centred on a permanent marker peg. (Plot relocation forms and original survey data are archived in the library of the Percy FitzPatrick Institute of African Ornithology). These plots fell in that portion of the reserve systematically cleared of alien plants since 1975 that had not been accidentally burned in early 1986. Of the 3 200-ha central section of the reserve covered by these 40 plots, approximately 404 ha (i.e. 12.6%) were included within the survey plots (not all of them were full circles due to topographic features, e.g. coastlines and sheer cliffs).

On each plot alien trees were classified by species and height class (0 to 0.3 m, > 0.3 m to 1.8 m and > 1.8 m) and counted until the number of individuals of a particular species in a height class exceeded 400; above this the density was given as > 400 plants plot⁻¹ (Taylor & Macdonald 1985). The time taken to search an area was related to the density of the native vegetation and the alien plants. Search times ranged from 10.4 man min ha⁻¹ in low, open vegetation to 52.6 man min ha⁻¹ in densely infested, tall, closed-canopy, marshy fynbos. The mean search time over all 40 plots was 19.7 man min ha⁻¹.

Differences between surveys were tested for using Chi-squared tests of the number of the 40 plots in the different density classes as defined by Taylor *et al.* (1985). Wherever possible, these analyses were carried out separately for each of the alien plant control blocks to see whether those blocks cleared earlier in the programme, and which had therefore received more follow-up clearings, showed greater reductions in alien plant populations.

The history of alien vegetation control

The early period: 1941–1959

The earliest documented evidence of the recognition of the alien vegetation problem by the reserve authorities dates from an advisory board meeting in January 1941 during which a member, P. Hare, advised that *Acacia cyclops* should be controlled (Anonymous 1941). Official attempts at eradication appear to have started between 1941 and 1943. Virtually all these initial efforts at control were made in the southern section of the reserve which, at that time, was designated a 'fauna reserve' as opposed to the northern area which was a 'flora reserve'.

The meagre resources of both funds and labour were ill spent. Most of the initial clearing was done in order to make fire breaks, to supply firewood, or for 'cosmetic' purposes (e.g. to reduce the visual impact of invasions along roads) and concentrated on the dense stands of mature *A. cyclops*. Follow-up work was ignored. This is demonstrated by the Buffels Bay infestation which was reported by the Divisional Council's engineer to have been completely cleared in both 1945 and 1959 (Anonymous 1945, 1959a). However, in 1981, before clearing operations had started there again, the area had reverted

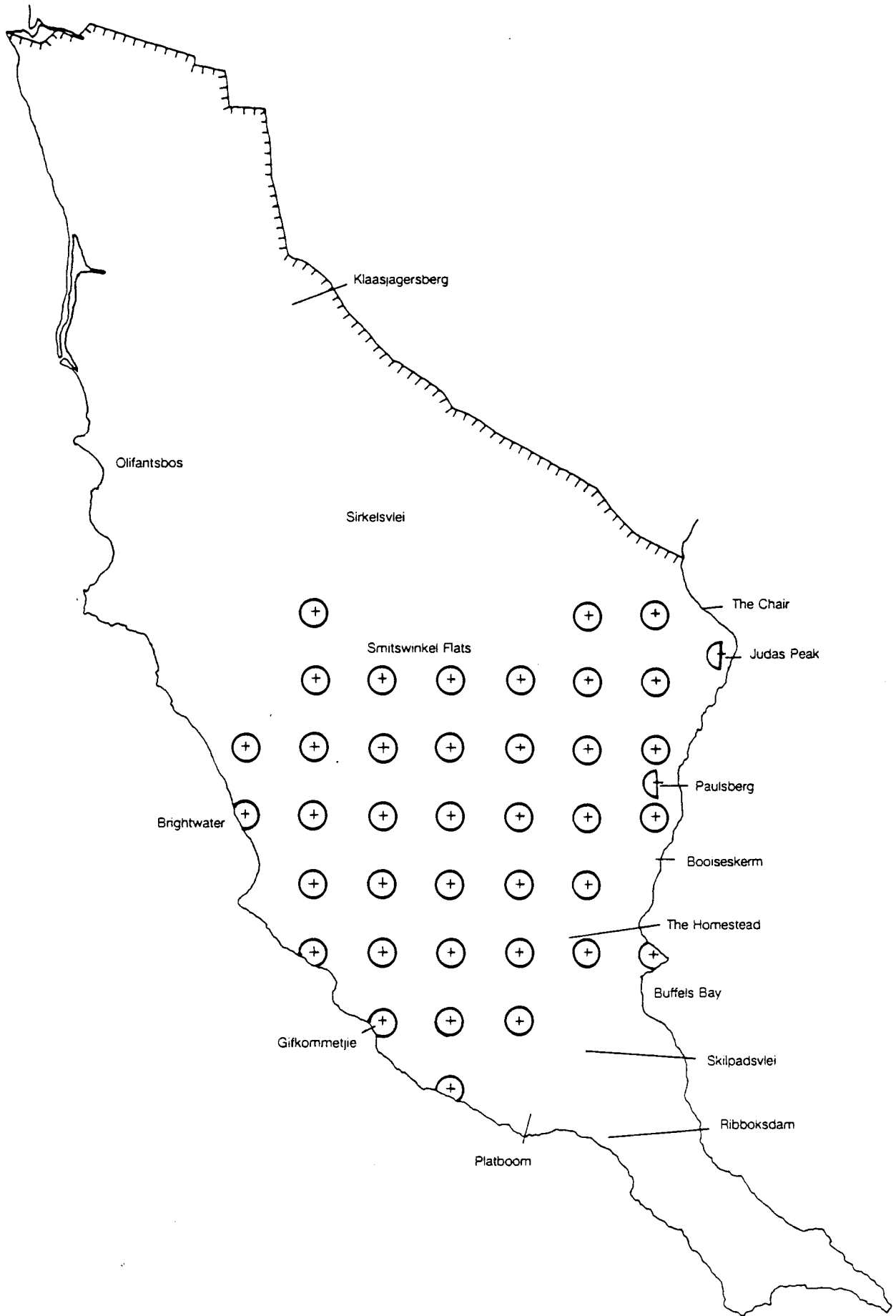


Figure 1 A map of the Cape of Good Hope Nature Reserve showing the locations of the sample plots resurveyed in 1986 and of places named in the text.

to a 100% infestation of adult trees. Piles of cut trees were found in the centre of this dense thicket, mute evidence of these earlier, wasted efforts at control. Another such example is provided by Coke (1961) who states that *A. cyclops* was almost eradicated from the area between Skilpadsvlei and Ribboksdam between 1952 and 1958. Currently this is one of the most densely infested areas in the reserve.

Possibly the major achievement of this phase was the gradual and, occasionally, reluctant acceptance by the Divisional Council of the Cape and by the reserve's advisory board and managers, that alien vegetation encroachment was in fact a major problem. This reached the point where, in September 1957, the advisory board recommended to the Council that a definite programme for the eradication of *A. cyclops* be prepared and implemented (Anonymous 1957a). Unfortunately no action was taken on this recommendation (Anonymous 1957b).

The second period: 1960–1974

From 1960 to 1974 more effort began to be put into the control of alien vegetation. Most of this was still aimed at the large, dense infestations in the south, although a large number of pine trees (mostly *Pinus pinaster*) were also felled throughout the reserve during this period.

Coke (1961), in a report which should have alerted the reserve authorities to the problem posed by *A. cyclops*, showed that it had spread dramatically between 1952 and 1961 (Figures 2 & 3). Although his aerial photographic interpretation was not perfect (Coke 1961), his maps allow for rough estimates to be made of the extent of *A. cyclops* infestations at these two dates (Table 1). There was also an increasing awareness that species other than *A. cyclops* were important, following Taylor's first survey of alien plant infestations in the reserve (Taylor 1967). Of the 99 plots he surveyed, only eight were free of aliens and these were all in areas which had not previously been cleared. It appears, therefore, that 24 years of control operations had failed to eradicate aliens from any area. However, these early control operations may have had value in that they possibly slowed down the rate of spread of the infestations.

Funds, labour and time spent on control operations were still inadequate despite having improved. The supply of firewood to picnic sites and 'cosmetic' considerations were still determining where clearing activities were carried out. This made adequate follow-up work impossible, and many infestations actually increased in density, while in only a few areas, for example the dune veld inland from Smith's farm (currently the Homestead Restaurant, see Figure 1) to near Brightwater, was there any marked improvement. The vegetation map drawn up by Taylor in 1969 based on his 1966 field work (Taylor 1969, 1984), showed only the larger and denser alien plant infestations (Figure 4). However, even these covered some 6.8% of the reserve's total area (Table 1). The 1966 plot survey showed that 13% of the 5-m × 10-m quadrats and 92% of the 10.5-ha plots had at least one alien plant in them

(Taylor & Macdonald 1985). These figures indicate the widespread occurrence of low-density stands of alien trees and shrubs in the reserve at this time.

Taylor (1967) urged the authorities to adopt a systematic approach to the problem. He stressed the importance of establishing priorities (the control of outlying thickets and lightly infested areas to be accorded high priority), of sustaining the control operations and of maintaining constant vigilance to prevent the reinvasion of cleared areas. He suggested that a control team of 15 labourers working 2 or 3 days a month could clear the lightly infested areas within 5 years. He subsequently amended this to 4 days a month and calculated that this would entail a recurrent expenditure of R2 500 per annum (=R12 750 in 1984 rands). He concluded that the slow removal of dense infestations would require larger resources of labour and funds and suggested numerous approaches for obtaining these resources (e.g. use of military trainees, voluntary groups, etc.). Later in 1967, Opie (1967) submitted his report on the reserve's history. In it he once again highlighted poor definition of priorities, the failure to sustain control programmes and the lack of follow-up operations as the reasons for the overwhelming failure of past control efforts.

For several years after these two reports were written, little improvement in the *modus operandi* of the reserve managers was apparent (Macdonald 1983). One of the factors militating against the effective implementation of any control programme during this period was the low level of motivation amongst the members of the clearing team and their inadequate supervision. For example, one of the rangers reported that on three occasions during the month of April 1970 he carried out spot checks on the team in the field and found them 'either fast asleep or sitting talking' (Tomkinson 1970). It is

Table 1 The area of dense alien woody plant infestations in the Cape of Good Hope Nature Reserve as determined from maps created by researchers and reserve staff

Year	Species	Area (ha)	As % of total reserve (7 750 ha)	Source
1952	<i>Acacia cyclops</i>	105	1.4	Coke (1961)
1961	<i>Acacia cyclops</i>	292	3.8	Coke (1961)
1969	All species	462	6.8	Taylor (1984)
1977–78	<i>Acacia cyclops</i>	908	11.7	Naude (1978)
1977–78	All species	1 633	21.1	Naude (1978)
1984	All species	592*	7.6	Clark (1985)
1987 (July)	All species (= <i>A. cyclops</i>)	422	5.4	Clark (this study)

*This estimate includes all 'medium to 100% infestation' densities and is thought to be more closely equivalent to Naude's (1978) 'dense' infestation than to Taylor's (1984) mapping unit. The statement that 'approximately 900 ha is 100% infested' at the end of 1985 (Anonymous 1986) is, presumably, an error

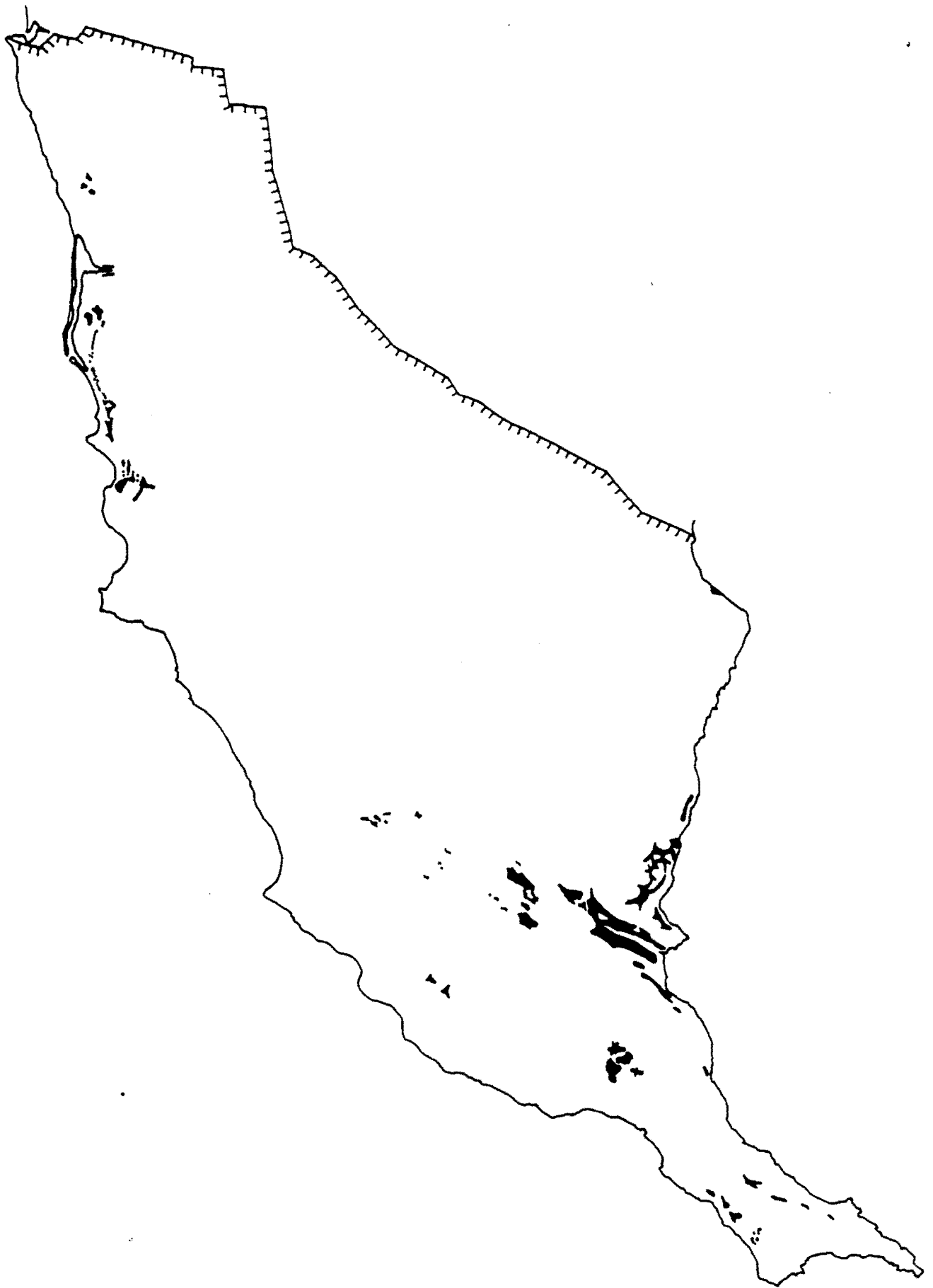


Figure 2 The distribution of dense stands of *Acacia cyclops* in 1952 as mapped from aerial photographs (after Coke 1961).

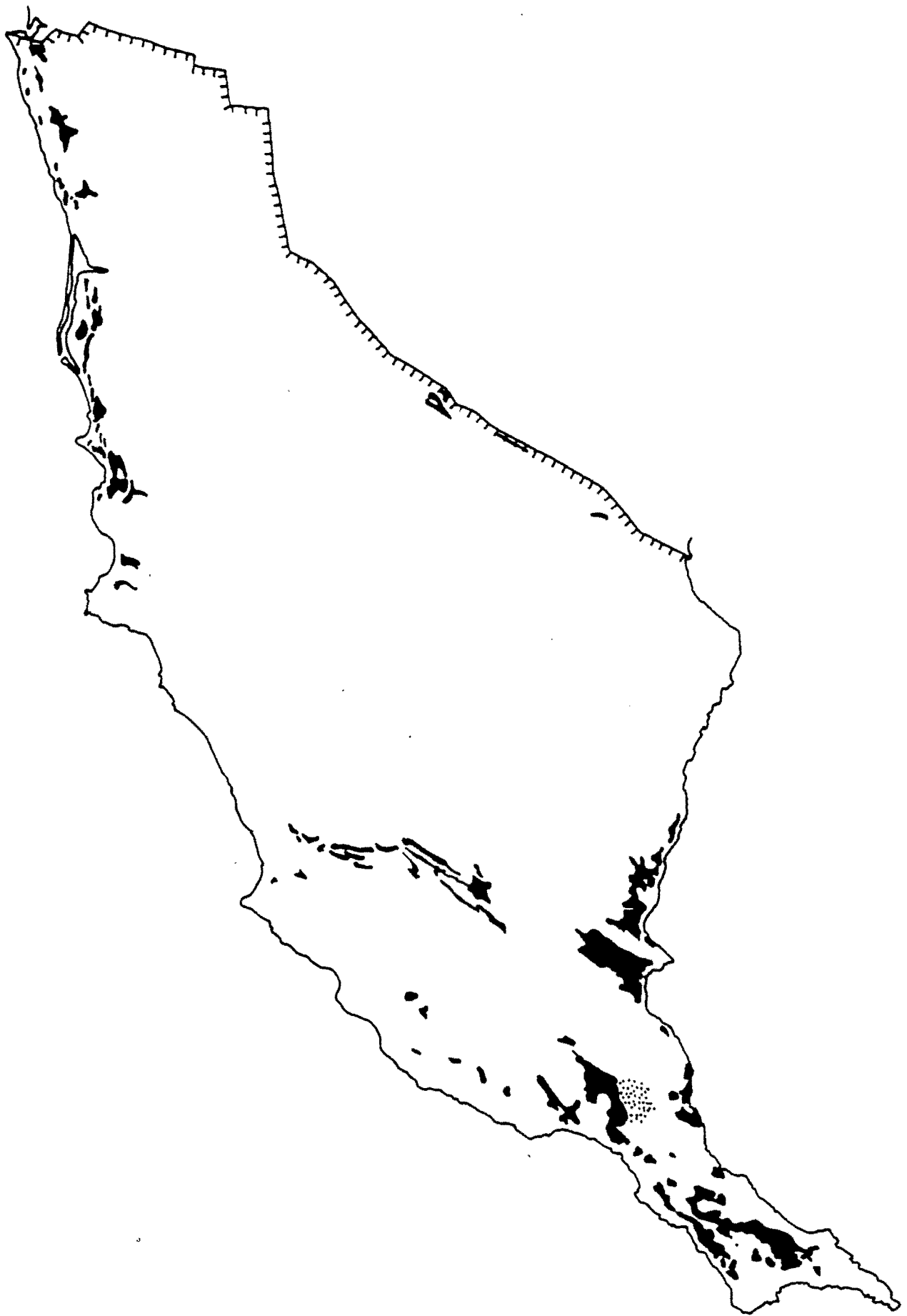


Figure 3 The distribution of dense stands of *Acacia cyclops* in 1961 as mapped from aerial photographs (after Coke 1961).

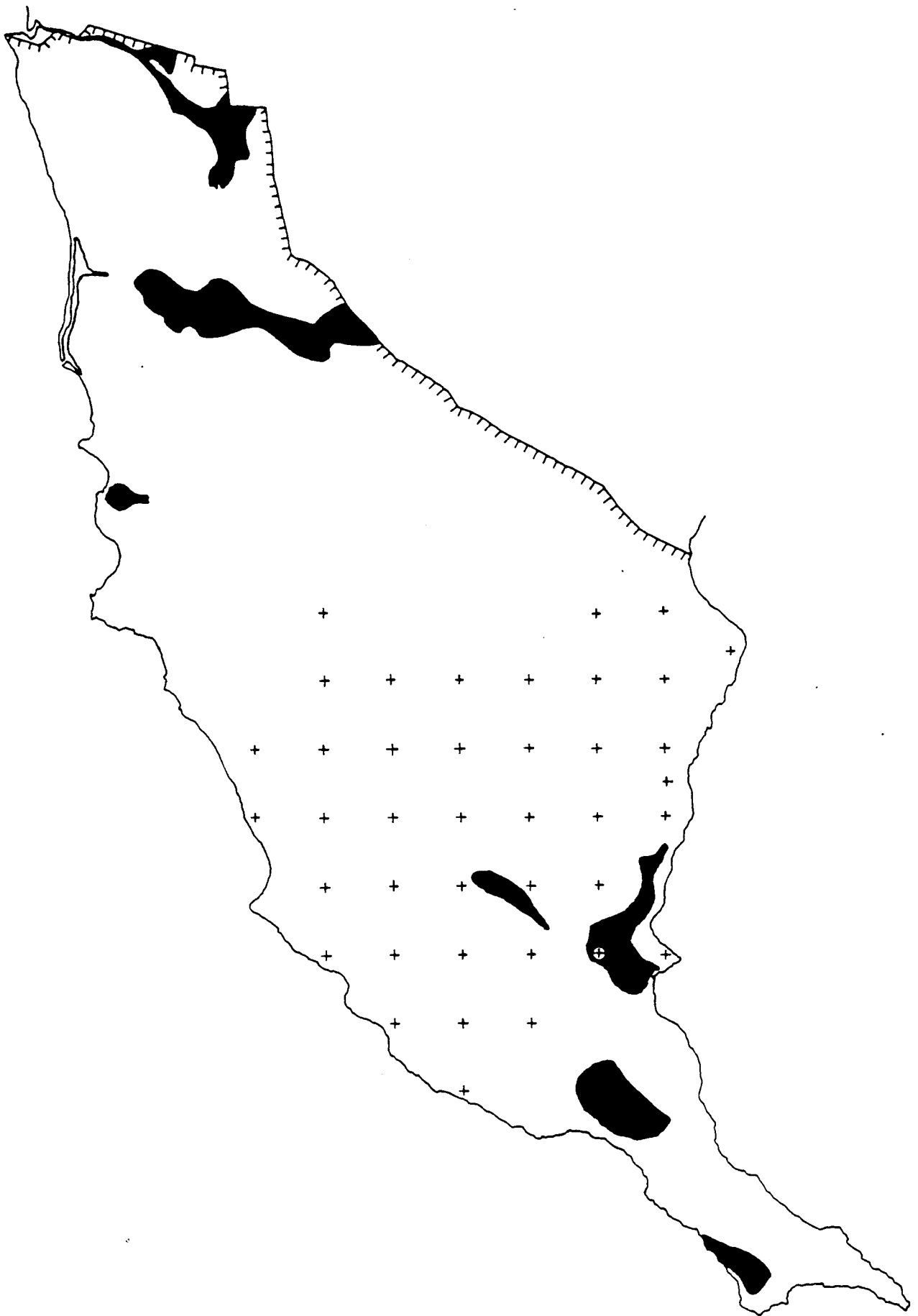


Figure 4 The distribution of the main thickets of alien woody plants in 1969 (after Taylor 1984) showing how the plots resurveyed in 1986 fell mainly in lightly infested areas of the reserve.

little wonder that during this period the reserve staff's reports began to take on a note of pessimism. For example, the Chief Warden reported in October 1969 that 'the labourers have been working full-time but little progress has been made' (Chief Warden 1969) and another of the rangers noted that 'the only way to make any impression on the dense growth of Rooikrantz and Port Jackson is to allow woodcutters to enter the reserve and to cart off as much as they can cut' (Langley 1969). This same ranger, reporting on a month's progress, went so far as to state that 'the gang of labourers continued to make their futile efforts to combat the ever-reaching *Acacia*' (Langley 1970). A year later the same sentiment was still being expressed; 'I sincerely do not think that we are going forward with the eradication of alien vegetation.....There are not more than 10 labourers working on the eradication of alien vegetation. It appears as if we are actually going forward but I think we are not even on neutral ground as the Rooikrantz and Port Jackson seeds are germinating all over the reserve and, while we are concentrating on certain basic areas, the total amount.....cut down does not equal the amount growing throughout the reserve' (Gubb 1971). This ranger then highlighted the inability of the control team to carry out follow-up weeding on all the small patches of initial clearing that were occurring scattered throughout the reserve and concluded that 'if something definite is not done in the near future, who can count the number of years.....it will take before the reserve is overgrown with alien vegetation' (Gubb 1971).

In April 1970 the first management plan for the reserve was produced by the professional staff of the Cape Department of Nature and Environmental Conservation (at that time called the Department of Nature Conservation of the Cape) which subsidizes the running of the reserve (Millar 1970). This plan drew attention to the 'haphazard approach' being used for alien plant control, the fallacy that firewood production resulted in alien plant control and the fact that approximately 45% of the working time of the team of 13 labourers responsible for veld management was actually being spent in chopping firewood, cleaning picnic sites and tidal pools and in other activities unrelated to alien plant control. The report recommended the drawing up of a 'predetermined plan' of alien plant control and that at least five and preferably 10 labourers should be allocated full-time to its implementation. It was predicted that unless such 'drastic action' was taken, these plants 'will take over the reserve completely within about 20 years' (Millar 1970). Finally, in 1974, a '10-year' plan for the systematic clearance of alien infestations in the central portion of the reserve was drawn up (Anonymous 1974), approved and, in 1975, implementation began.

The third period: 1975–1980

The introduction of this plan should, by rights, have heralded a new era of effective alien plant control in the reserve. The area was divided up into eight compartments (Figure 5). Each block was to be burned and then cleared, and follow-up work would be done on a regular

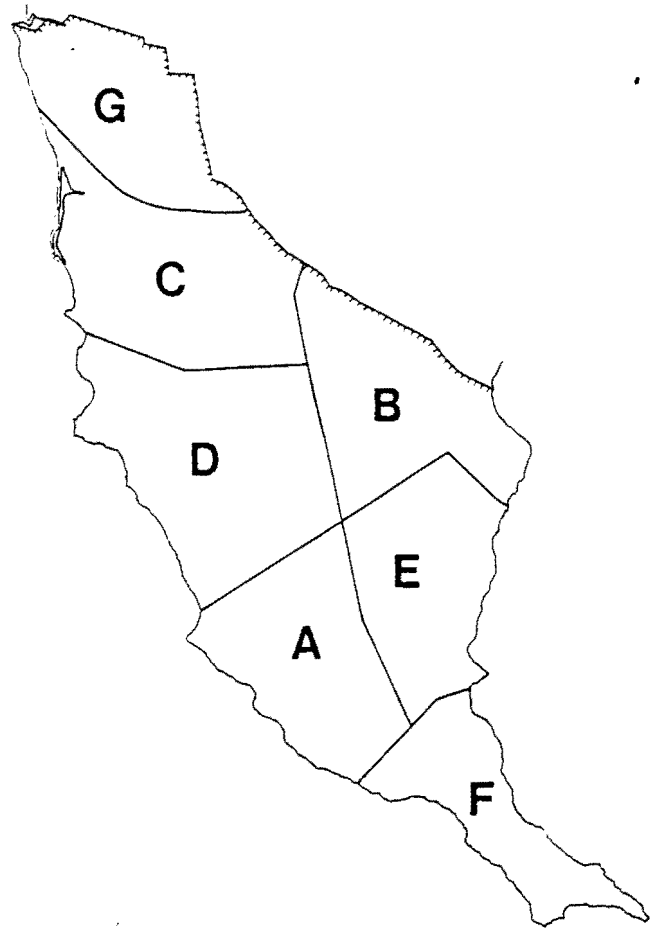


Figure 5 The layout of the blocks as given in the 1974 proposal for a systematic control plan. Blocks were scheduled to be burnt in alphabetical order at 2-year intervals with most of the clearing effort occurring after the fire and follow-up weeding to be repeated annually in each cleared block for at least a decade thereafter (after Anonymous 1974).

basis. Due to an unplanned fire in February 1975, the boundaries and the order of treatment of these blocks was changed and clearing was started in the compartment with the least aliens (see Figure 6). A substantial modification of the original proposal was the decision to fell all the alien trees in a block prior to burning. No documented reason for this highly significant modification is given but it appears that the provision of the maximum amount of firewood from the clearing operations was a factor. In later years it transpired that this decision might have been a wise one: where dense alien infestations were burned standing, subsequent follow-up weeding was made difficult by the lattice of burned and fallen stems. The ecological effects of the alternative clearing and burning strategies were apparently not taken into account when this decision was taken (see Discussion). Although the plan was drawn up in 1974, the system was not effectively implemented until 1980/81.

Just how haphazard the control operations continued to be, is illustrated by a series of monthly maps drawn by the ranger in charge of this activity for the period July 1974 to November 1976. Although these maps were

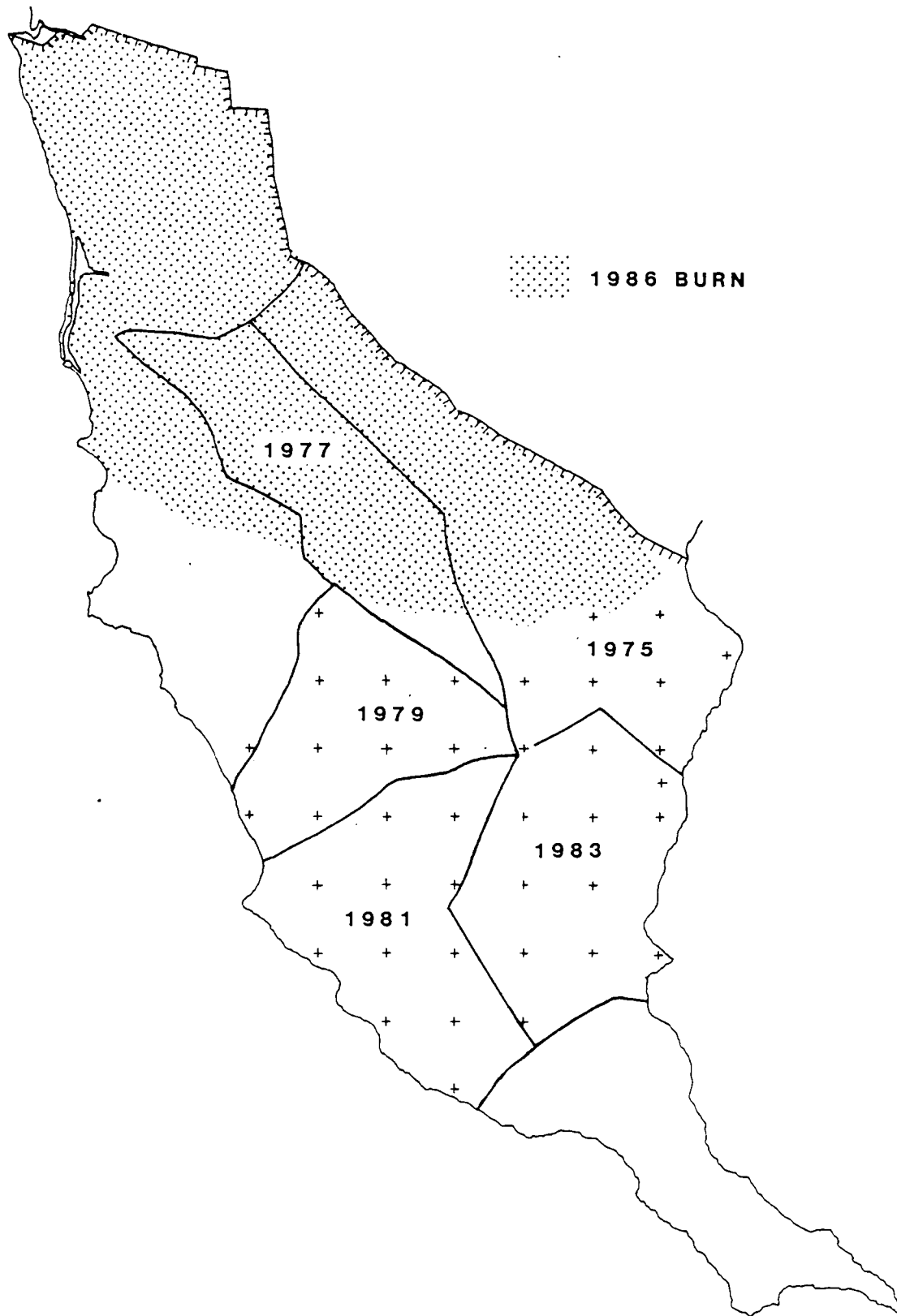


Figure 6 The layout of the alien plant control blocks as implemented in the systematic control programme 1975 to 1986. The extent of the February 1986 wildfire and the location of the plots resurveyed in 1986 are also shown.

drawn on too small a scale for accurate plotting of the operations, they do illustrate the chaotic dispersion of effort and the low level of compliance with the plan over this period (Figure 7). These maps do not show the recurrent clearing of alien plants along roads which served to dissipate further the energies of the control team.

Due to this haphazard initial clearing, a systematic follow-up programme could not be maintained. After the first clearing of alien *Acacia* species, follow-ups must be repeated for more than 10 years to ensure that the stand does not become re-established from the soil-stored seed bank (Milton & Hall 1981; Macdonald & Jarman 1984; Macdonald *et al.* 1985). Consequently, in the Cape Point reserve where clearing of *Acacia* species had been in progress for a considerable time by the mid 1970's, the area of follow-ups should have greatly exceeded the area of initial clearing. In reality this was only the case during the last 5 months of the 29-month period and, for the period as a whole, the total area of follow-up operations was only slightly more than half the area initially cleared (Table 2). The maps for this period (Figure 8) show that although mature trees were removed from 642 ha, only 117 ha of this area were subjected to follow-up weeding. Comparison of Figure 8 with Figure 7a shows that most of the area cleared in the south of the reserve in 1974-75 had been re-cleared at least once by November 1976. However, several of the

Table 2 The extent of initial clearing and follow-up operations as determined from the monthly maps of the alien plant control team's activities

Period	Area of initial clearing operations		Area of follow-up operations	
	(ha)	% of reserve's area	(ha)	% of reserve's area
July 1974 to June 1975	158	2.0	148	2.0
July 1975 to June 1976*	418	5.4	158	2.0
July 1976 to November 1976	113	1.5	224	3.0
July 1974 to November 1976	642	8.3	363	4.7

*No reports could be located for the months of May and June 1976 so this period is effectively July 1975 to April 1976. It is not certain that any control work did actually take place in these two missing months as sometimes the entire control team were used on other projects (Macdonald 1983)

scattered smaller areas had apparently not been re-cleared for at least 17 months following initial clearing. Thus this basic flaw in the reserve's approach to alien plant control, pinpointed a decade earlier by Taylor (1967) and recognized by reserve staff at least 5 years

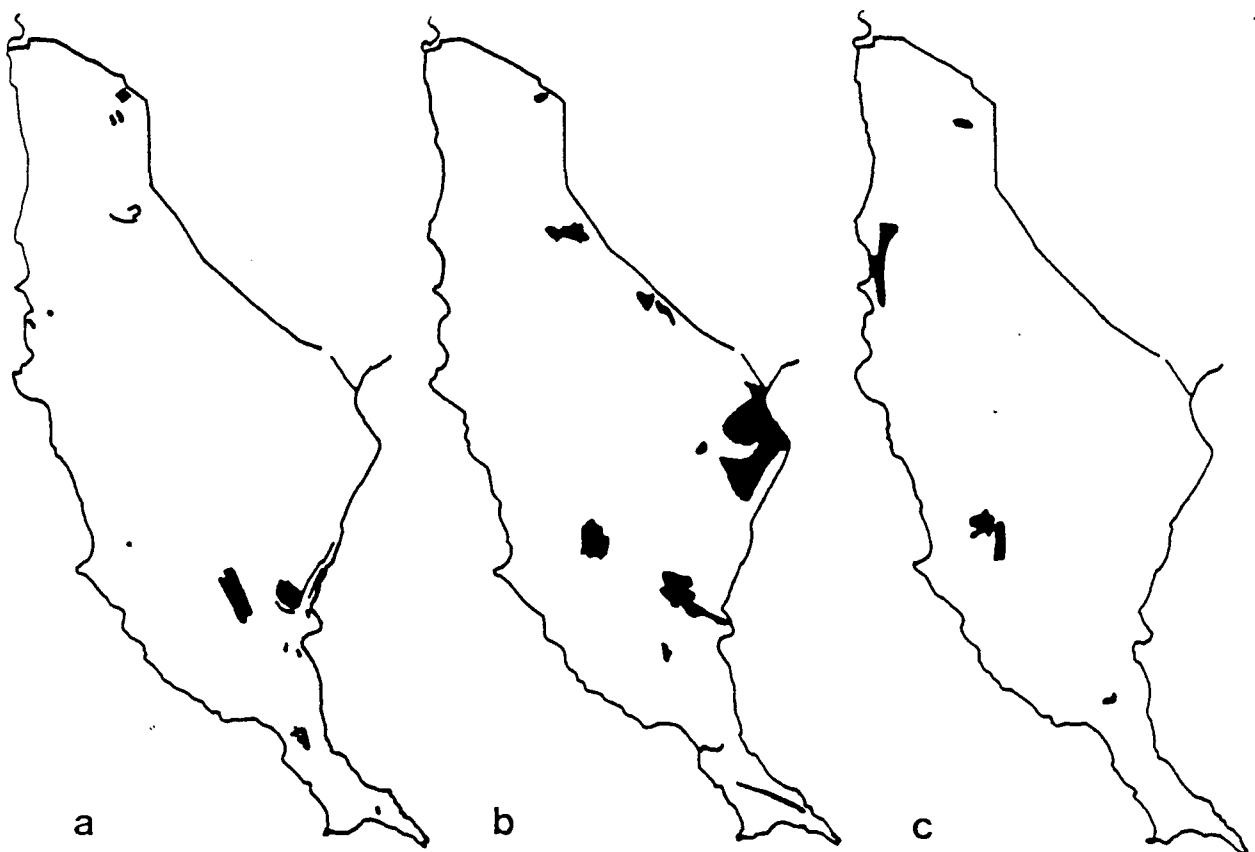


Figure 7 The location of initial clearing operations in the periods (a) July 1974 to June 1975, (b) July 1975 to June 1976 and (c) July 1976 to November 1976. [After maps included in Macdonald (1983), see footnote to Table 2].



Figure 8 The areas subjected to initial clearing and follow-up weeding over the period July 1974 to November 1976 showing the extent of overlap of these two operations (source as for Figure 7). Key: Black = initial clearing only; stipple = follow-up weeding only; crosshatching = initial clearing and follow-up.

earlier (Gubb 1971), was still being allowed to occur, in direct opposition to the provisions of the agreed systematic control plan.

From October 1977 to July 1978 one of the reserve's rangers mapped the infestations of all the major alien woody plants in the reserve (Naude 1978). Once again the mapping was carried out at a scale too small for the results of these ground surveys to be precise but it is apparent from these maps that little, if any, progress had been made in the elimination of even the dense infestations by this date (Figure 9; Table 1). If the 1952 and 1961 *Acacia cyclops* maps (Figures 2 & 3) are compared with the analogous 1977-78 map (Figure 10), it is apparent that the only important dense infestation of this species that had been removed was that on the inland dune in the south centre of the reserve. During this period several new areas of dense *A. cyclops* had arisen within the reserve, e.g. northwards along the eastern coastal shelf from Booiseskerm to The Chair and on the western coastal shelf around Gifkommetjie. Obviously there were subjective differences in the definition of a 'dense infestation'. Nevertheless, in view of the small percentage of the reserve's total area cleared each year (Table 2) relative to the rate of increase in dense infestations (Table 1), it seems likely that by 1977-78 the area densely infested had actually increased since 1961 — regardless of the fact that Taylor's (1967) advice on clearing low density infestations first had still not been heeded.

However imperfect this alien plant-mapping exercise might have been, it was apparently the first time the staff had ever attempted to draw up an holistic account of the extent of the problem within the reserve. As this is one of the most important steps in the planning and execution of any control programme (Macdonald, in press), it might well have been a turning point in this reserve's control history. From 1978 the implementation of the control programme improved (Macdonald 1983). Other factors which might have influenced this were the launching of a major public awareness campaign on alien plant invasions by the Cape Department of Nature and Environmental Conservation (Stirton 1978) and the appointment of several rangers who began to take a keen interest in the control programme. Although previously a few rangers had been highly motivated in this regard, this was the first time that a whole cohort of rangers became fully committed to the task. It was also the first time that they had a meaningful control strategy to direct their enthusiasm. Two other factors which improved the staff's attitude towards alien plant control were the initiation of a voluntary alien plant 'hack' within the reserve by members of the Wildlife Society of Southern Africa (Chief Warden 1980) and the increased interaction between reserve staff and outside scientists arising out of the Fynbos Biome Project (Kruger 1978). Although the amount of work contributed by volunteers was small, it provided a morale booster to the staff in their pursuance of this otherwise unrewarding task. 'Hacks' by school groups and army units were to become recurrent features in addition to the regular work-meets of the Wildlife Society (Macdonald 1983). Information

and encouragement from several Fynbos Biome Project researchers provided a more tangible contribution to this improved attitude and performance. The close interaction between the local research community and the reserve's staff culminated in the reserve playing an important role in the South African contribution to the international SCOPE Project on the Ecology of Biological Invasions (Macdonald & Jarman 1984; Macdonald *et al.* 1985, 1988).

However, labour was still inadequate. By February 1980 there were only 36 men employed full-time on 'veld management' as compared to the 50 that had been agreed to in the 1975 plan for the period up to 1979 and the 70 for the period 1980 to 1985 (Wright 1980). Overall the alien plant problem continued to worsen during this period. The results of the second survey of the monitoring plots (Taylor *et al.* 1985), carried out between 1976 and 1980, showed that since the first survey in 1966 all but three species had increased their ranges within the reserve. Of these, *Cupressus macrocarpa* Hartweg and *Lantana camara* L. were only marginally invasive. The other species, *Pinus pinaster*, generally present at low densities in the reserve, was relatively easy to control as it does not build up a soil-stored seed bank and can be killed by felling (Kruger 1977; Macdonald *et al.* 1985).

Five new species had made an appearance on the 10,5-ha plots and still only 8% of the plots were free of woody aliens. Of these plots free of aliens, some had been cleared but new infestations balanced out these minor advances (Taylor *et al.* 1985).

The fourth period: 1981-1987

By 1981 alien vegetation control had at last received the high priority it deserved in the reserve's management activities. By the 1984/85 financial year the budget for the control programme was approximately R150 000 (Clark 1985). Initial clearing was being carried out by a team of 14 men while follow-up operations were done by 32 men, although this team was still having its crucially important work interfered with by the demands of numerous lesser tasks (Clark 1985). The introduction of private woodcutters in 1982 removed most of the burden of firewood production from the reserve staff. For the first time in the history of control operations these could now be located entirely independent of the need to produce high yields of readily retrievable firewood. The training, motivation and supervision of labourers in the control teams were all greatly improved as were the day-to-day planning and organization of control operations. Advances were also made in control technology. For example, in March 1982, it was reported that 'two new chainsaws saw an encouraging increase in rate. In one week the work done in 5 previous weeks, done when using only axes and slashers....' (Chief Warden 1982). [The time lag in the adoption of this new technology appears remarkable as it was reported that the staff had attended a chainsaw demonstration in July 1977 (Clark

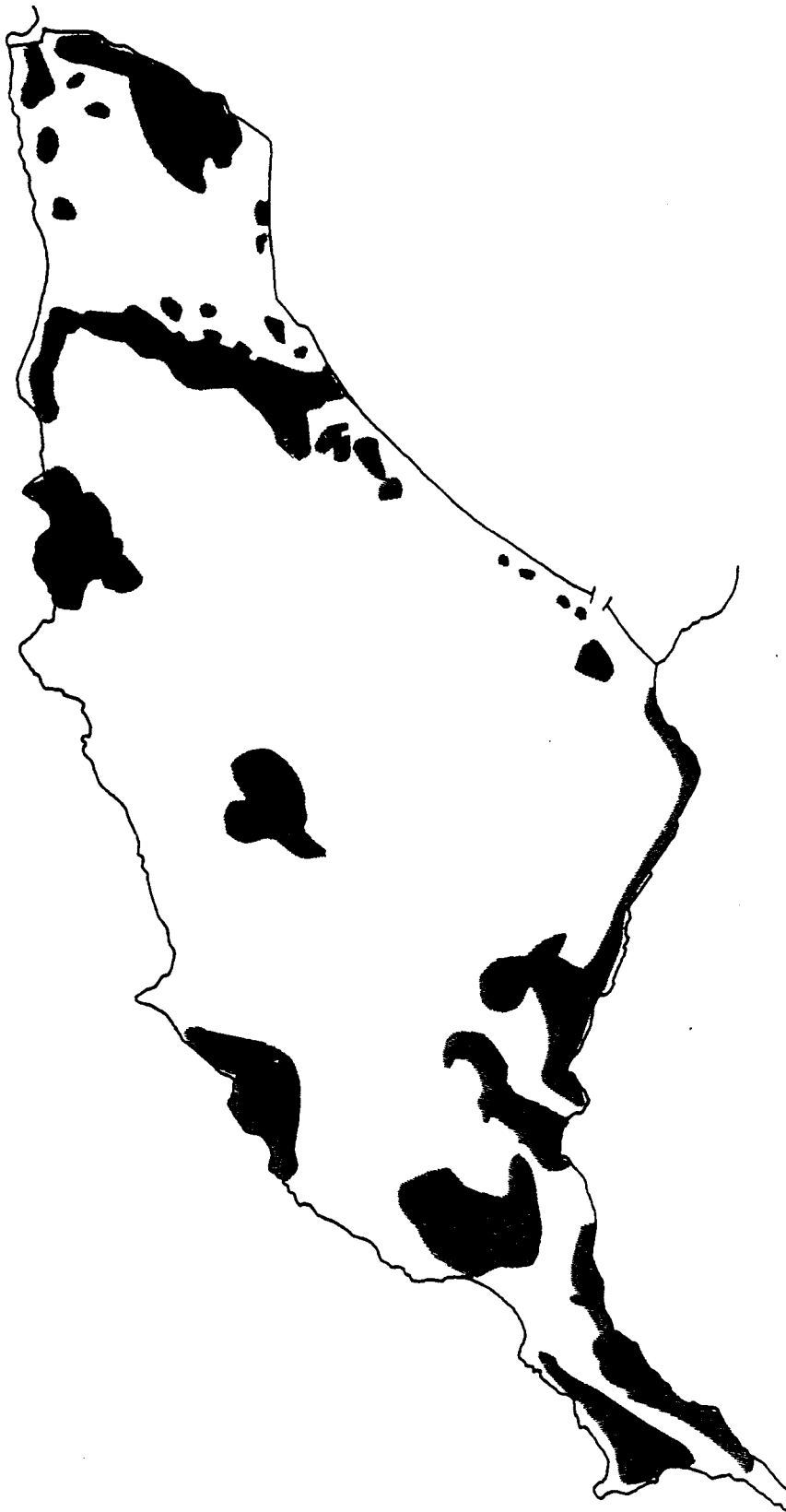


Figure 9 The areas mapped as being densely infested by alien trees and shrubs in 1977-78 (after Naude 1978). The same map projection as in Figures 7 and 8 is used here to enable comparisons to be made with the control operations over the preceding 3 years.



Figure 10 The areas mapped as being densely infested by *Acacia cyclops* in 1977-78 (after Naude 1978). The same map projection as in Figures 2 and 3 is used here to enable direct comparisons to be made with the earlier maps of this species.

1977)]. Control methods employed during this period have been described in detail by Clark (1985).

By 1986 the initial clearing of all the central control blocks had been completed except for some dense infestations of *A. cyclops* in the 1983 block south and

east of a line drawn from Paulsberg to the Homestead Restaurant and across the Peninsula to Platboom (Figure 1). Follow-up operations were being conducted on a 2-year rotation over the entire central portion of the reserve. With the aid of additional labourers employed under the government's Work Creation Scheme, the removal of the alien thickets in the northern area was started in 1984. The February 1986 fire (Figure 6) burned virtually the whole of this area and, in the following year, the standing dead trees were felled or, where there was no regeneration of native vegetation, bulldozed. By mid 1987 all the infestations in this northern area had been cleared and follow-up work had been started.

By July 1987 the control programme had eliminated seed production of alien trees and shrubs on 88% of the reserve's area. A sketch map of the remaining alien plant infestations compiled from field knowledge, indicated that dense infestations covered approximately 422 ha in the south of the reserve (Table 1). These were almost entirely *Acacia cyclops*. The Klaasjagersberg complex of about 16 ha held the only remaining stands of mature alien plants in the north of the reserve. The smaller individuals of invasive species had been removed from this area. Approximately 285 ha in the northern area held dense stands of alien regeneration at this date.

Results of the 1986 third survey

The frequencies of occurrence at each survey of the major alien plant species on the plots resurveyed in 1986 are presented in Table 3. *Acacia longifolia* was recorded on single plots in the 1979 control block in the second and third surveys. In 1986 this species was only present as a single small plant in an eroded area of plot 56 on the Smitswinkel Flats. Small individuals of *Eucalyptus lehmannii* and *Myoporum serratum* R. Br. as well as several plants of the herbaceous alien species, *Ricinus communis* L., *Tropaeolum majus* L. and *Pennisetum clandestinum* Chiov., were also growing on this eroded area. Since none of these species had been recorded on

Table 3 The number of those plots surveyed for the third time in 1986 which had plants of the major invasive species in them at each of the three surveys (for location of the control burn blocks see Figure 6)

Year of control burn in block	Surveyed in 1986	Number of plots											
		Having alien plants in them at surveys 1, 2 & 3											
		<i>Acacia cyclops</i>			<i>A. saligna</i>			<i>Eucalyptus lehmannii</i>			<i>Pinus pinaster</i>		
		1*	2*	3*	1	2	3	1	2	3	1	2	3
1975	8	7	6	6	1	1	1	0	0	0	3	0	0
1979	10	7	7	6	4	4	3	1	1	1	1	1	1
1981	11	9	11	10	4	6	4	0	1	1	1	0	0
1983	11	10	11	9	3	5	3	1	1	2	2	1	0
All blocks combined	40	33	35	31	12	16	11	2	3	4	7	2	1

*Survey dates: 1=1966, 2=1976-80, 3=1986

the plot during previous surveys it appears likely that they had been unintentionally introduced in plant material that had been used for mulching the eroded area.

Of the more common invasive species, *Acacia cyclops*, *A. saligna* and *Eucalyptus lehmannii* showed no significant changes in frequency of occurrence within individual blocks or over the whole area. In the case of *Pinus pinaster* there were significant reductions in frequency in the 1975 control block (χ^2 with 2 DF=6,86; $P<0,05$) and over the whole area (χ^2 with 2 DF=6,76; $P<0,05$). Using 2×2 contingency tables and Yates' Correction to compare the frequencies of the individual surveys with each other, it was apparent that the only possibly significant reduction in *P. pinaster* was that between the 1966 and 1986 surveys (χ^2 with 1 DF=3,47; $P=0,06$). In absolute terms the reduction in density of *P. pinaster* over all plots had been from one individual per 19,2 ha in 1966 to one per 36,7 ha in 1976-80 to one per 202 ha in 1986.

The distribution of plots according to density classes for the two important *Acacia* species (Table 4) showed no significant changes within individual control blocks or over the whole area. However, where the distribution of plots according to the density of plants in the different height classes was analysed there were several statistically significant changes (Table 5).

Table 4 Number of plots falling in the different density classes of the two major alien plant species at each survey (for location of the control burn blocks see Figure 6)

Year of control burn in block	Density class (plants 10,5 ha ⁻¹)	Number of plots at each survey					
		<i>Acacia cyclops</i>			<i>Acacia saligna</i>		
		1*	2*	3*	1	2	3
1975	>400	0	0	0	0	0	0
	101-400	0	0	2	0	0	0
	1-100	7	6	4	1	1	1
	0	1	2	2	7	7	7
1979	>400	0	2	1	0	0	0
	101-400	3	1	0	0	0	0
	1-100	4	4	5	4	4	3
	0	3	3	4	6	6	7
1981	>400	3	5	3	0	1	0
	101-400	2	1	0	1	0	1
	1-100	4	5	7	3	5	3
	0	2	0	1	7	5	7
1983	>400	1	2	3	0	0	0
	101-400	3	3	2	0	0	0
	1-100	6	6	4	3	5	3
	0	1	0	2	8	6	8
All blocks combined	>400	4	9	7	0	1	0
	101-400	8	5	4	1	0	1
	1-100	21	21	20	11	15	10
	0	7	5	9	28	24	29

*Survey dates: 1=1966, 2=1976-80, 3=1986

In both *A. cyclops* and *A. saligna* the frequency of plots having high densities of established trees (height >1,8 m) decreased significantly by 1986. For *A. cyclops* there were sufficient plots in the higher density classes to allow for the calculation of χ^2 over all these classes. The Chi-squared value obtained was 33,22 which, with 6 DF, gave $P < 0,01$. For *A. saligna* there were so few plots in the higher density classes that the plots had to be classified as either having plants greater than 1,8 m in height or not having such plants. The change over time was significant (χ^2 with 2 DF=7,07; $P<0,05$).

In *A. saligna* the mean density of trees on the plots was one plant per 4,9 ha in 1966 and this had been reduced to one per 202 ha in 1986. In 1976-80 one plot (plot 75 near Brightwater, see Figure 1 and Taylor *et al.* 1985) had more than 400 plants and was therefore not fully enumerated. The mean density of *A. saligna* trees on all the other plots at this survey was one plant per 5,6 ha. The comparable densities in 1966 and 1986 (i.e. excluding plot 75) were one plant per 8,4 ha and no plants per 393,5 ha. The mean densities of *A. cyclops* trees on the plots, excluding the six which had >400 individuals at any survey, were one plant per 0,7 ha, one per 0,3 ha and one per 341 ha in 1966, 1976-80 and 1986 respectively.

In *A. cyclops* there were also significant changes in the frequency of plots in the different density classes for saplings (height 0,3 to 1,8 m) (χ^2 with 6 DF=15,83; $P<0,02$). The number of plots with high densities of saplings increased by the second survey. This number had decreased by the third survey as had the number of plots with low densities of saplings. In *A. saligna* which, unlike *A. cyclops*, coppices readily once plants have become established, the reduction in the frequency of plots having saplings was not statistically significant. However, the absolute densities of *A. saligna* plants in this height class, meaned over all plots except plot 75,

Table 5 The distribution of plots at each survey according to the densities of plants in each height class for the two major alien plant species

Category and height class	Density class (plants 10,5 ha ⁻¹)	Number of plots at each survey					
		<i>Acacia cyclops</i>			<i>Acacia saligna</i>		
		1*	2*	3*	1	2	3
Trees >1,8 m	>400	1	5	3	0	1	0
	101-400	3	1	0	0	0	0
	1-100	23	18	3	9	5	1
	0	13	16	34	31	34	39
Saplings 0,3-1,8 m	>400	2	7	4	0	1	0
	101-400	8	3	2	1	0	0
	1-100	22	23	16	9	13	10
	0	8	7	18	30	26	30
Seedlings <0,3 m	>400	2	6	4	0	1	0
	101-400	3	3	6	0	0	0
	1-100	11	16	20	3	11	5
	0	24	15	10	37	28	35

*Survey dates: 1=1966, 2=1976-80, 3=1986

were one plant per 4,0 ha in 1966, one per 3,6 ha in 1976–80 and only one per 24,6 ha in 1986. (Plot 75 had a density of one sapling per 0,1 ha in 1966 and one per 0,15 ha in 1986). Therefore, by 1986, the control programme had begun to reduce the density of established individuals of even this 'difficult to kill' species.

Of possibly greater long-term importance was the significant reduction in the frequency of plots having 'seedlings' (<0,3 m in height) of *A. saligna* (χ^2 with 2 DF=8,04; $P<0,02$). The situation in 1986 was in fact worse than in 1966 (5 plots had seedlings in 1986 as against 3 in 1966) but there had been a marked improvement since 1976–80. The absolute densities of seedlings in all plots other than plot 75 at the first, second and third surveys were one plant per 43,7 ha, 5,1 ha and 20,7 ha respectively. (Plot 75 had one seedling per 0,3 ha in both 1966 and 1986). By contrast, *A. cyclops*, the seeds of which are more readily dispersed by birds and mammals than are those of *A. saligna* and which had much higher densities of fruiting trees in and adjacent to the survey area at the beginning of the control programme, showed a possibly significant increase in plots having high density stands of seedlings over the survey period (χ^2 with 6 DF=12,26; $P=0,056$). Excluding the six plots on which there were more than 400 plants at any survey, the mean densities of *A. cyclops* seedlings at the first, second and third surveys were one plant per 1,4 ha; 0,2 ha and 0,3 ha respectively. It appears that even in this relatively well-established species, the recent period of control had begun to reduce seedling densities. With continued follow-ups preventing plants from setting seed in this area and with the destruction of the last remaining large infestations in the south of the reserve, it appears feasible that even *A. cyclops* can be eradicated from the reserve.

Discussion

The main points arising from the study

The history of alien plant control in the reserve clearly indicates the importance of understanding the ecology of the target species. Virtually all the early efforts at controlling the alien *Acacia* species were totally wasted because of a lack of appreciation of the significance of the persistent seed bank in the soil. Another equally important consideration that emerges is the need for a systematic approach to these control operations. It was only when such an approach was adopted and effectively implemented in the late 1970's that the level of infestation began to decline.

The cardinal importance of controlling alien plants before they achieve high densities is illustrated by the almost total elimination of *Pinus pinaster* from the central portion of the reserve and the greater success in controlling *Acacia saligna* in this area than has been the case with *A. cyclops*. This has been achieved even though it is more difficult to kill established *A. saligna* plants than *A. cyclops* plants and despite the fact that *A. saligna* gives rise to a denser and longer-lived seed bank in the soil (Holmes *et al.* 1987). The rather obvious point that it is essential to find a technique that will kill the

target species is illustrated by *Eucalyptus lehmannii*. Even though this species was present only at low densities on a few of the plots, it had not been eliminated from any of these by 1986 (Table 3). The individuals survive as coppice growth and will presumably continue to do so until an effective control technique for coppicing plants is developed.

Another point which emerges from this review is the fundamental role played by managers in determining whether a control programme will be effective. Nothing that was done in the late 1970's was fundamentally different from what had been tried in the preceding 30 years. If anything, the alien plant situation in 1978 was worse than at any time in the reserve's history (Taylor *et al.* 1985). The major difference was that the new cohort of young rangers adopted alien plant control as one of their main endeavours. Their enthusiasm became infectious and spread to all levels in the management hierarchy. If it had not been for the generally high level of motivation amongst the reserve staff during this period, it is uncertain whether the initial clearing cycle of the '10-year plan' would ever have been completed and it is highly unlikely that it would have been done within 10 years. The recent heightened public awareness of the threat of alien plant invasions as a conservation issue probably played a role in improving the 'status' of this often thankless and apparently unrewarding task.

The final general point that needs to be emphasized is the deleterious consequence of the decision to link alien plant control to the production of firewood. This policy prevented the adoption of an effective control programme for some 35 years and diverted much of the energy of the control team from their main task of killing established trees and controlling regeneration. This diversion of labour at a time when the team was very small was probably critical in allowing the infestations to spread faster than they could be controlled. As a result it is highly likely that the authorities have in effect had to pay very dearly for this allegedly 'cheap' firewood.

Side-effects of the alien plant control operations

The side-effects of alien plant control operations have never been adequately assessed. One of the obviously significant side-effects has been the alteration of fuel loads. Where the cut branches have been stacked in huge piles, allowed to dry out and then burned, the fires have been of unnaturally high intensity and long duration. This has resulted in the formation of circular patches up to 5 m in diameter of bare soil, often completely devoid of vegetation. Some of these scalded areas are still bare 10 years after they were burned. Areas that have been cleared of dense alien thickets appear 'pock-marked' by these bare patches when viewed from the air. It is uncertain whether these soils will ever regain their original characteristics. Currently they provide foci for the re-establishment of alien vegetation since most native species are apparently unable to colonize this 'new' habitat.

Another important side-effect of control operations has been the creation of an extensive network of roads

and tracks to facilitate access to the infestations. These tracks were not sited according to normal road-engineering standards and several have become deep erosion gulleys, threatening to alter irreversibly the local geomorphology and soil hydrology. So serious has this problem become that, even though labour is always in short supply for control operations, five men were removed from the veld-management team in July 1981 and put onto erosion-reclamation work full-time (Von Kaschke 1981 *contra* Anonymous 1986). During 1984 this team was disbanded 'in favour of using all available labour [on erosion control] for two months (December/January) every year' (Anonymous 1986). Finally, in 1986-87 a team of approximately 10 labourers were taken off alien control work and put onto erosion control full-time. The creation of tracks and the associated accelerated soil erosion also has a negative influence on alien plant control because tracks and eroded areas often provide sites for the successful establishment of these plants in areas otherwise free of alien vegetation.

The side-effects on the native vegetation and fauna of the large quantities of herbicides used in control operations have never been assessed. In recent years where dense infestations of *Acacia* have been cleared and the area burned, the mass seedling regeneration has been treated with blanket herbicide applications, mostly using hand-held mistblowers but to a limited extent also by aerial application. Under these conditions, the unintentional mortality of native plants is of course unavoidable. No quantitative evaluation of such effects has been made. In some cases spray drift has been found to have killed indigenous plants in adjacent uninfested areas. (In this connection the recent reserve policies of only using the 'safest' herbicides and never conducting blanket spraying within drift range of known populations of rare plant species are to be commended). Although the use of pesticides in nature reserves is justified where the loss to conservation will be greater if they are not employed, it is highly undesirable that they should be used on this scale in a reserve renowned for its small-scale differentiation of plant communities (Taylor 1984) and highly localized endemics (Taylor 1977b) without careful scientific evaluation of each operation.

A possible deleterious side-effect of these operations is the inadvertent spread of pathogenic soil fungi. In particular the possibility exists that either an alien species or alien mating strain of the plant pathogen *Phytophthora cinnamomi* has been spread throughout the reserve on the mattocks used to remove individuals of coppicing species [see Macdonald & Richardson (1986) for a discussion of, and references on, the possible alien status of *P. cinnamomi* in the south-western Cape]. The high level of mortality amongst native Proteaceae within the reserve as a result of *P. cinnamomi* infestations appears unusually high for a nature reserve (Von Broembsen & Kruger 1985; Von Broembsen pers. comm.) It is known that *P. cinnamomi* can be carried on digging tools (Brits & Von Broembsen 1978) and, at least on one occasion, such dispersion is thought to have resulted in abnormal mortality of a

native Proteaceae within a fynbos nature reserve (Van der Merwe 1975).

Side-effects of the ineffectiveness of early control

That the alien plant infestations were allowed to become so widespread and dense before they were finally subjected to an effective control programme, has had several other potentially serious effects on the reserve's native biota. As has been stressed on numerous occasions, the reserve's primary conservation priority should be the preservation of its highly diverse and unique flora (e.g. Taylor 1967, 1977b; Millar 1970). In 1977 Taylor (1977b) estimated the reserve to contain 'at least 39 species of plants that are either endemic to it or so rare and localized that their existence elsewhere is threatened'. In 1985 the local Red Data Book included 52 species of plants that occur in the reserve; six were listed as endangered, seven vulnerable, 29 rare, three indeterminate and seven uncertain (Hall & Veldhuis 1985; Taylor 1985). The spread of alien trees has threatened the survival of populations of several of these species (Taylor 1977b; Macdonald 1983). The edaphic changes resulting both from the litter of dense alien thickets and from the burning of felled stands might have reduced the long-term suitability of these habitats for rare species (cf. Macdonald & Richardson 1986). How long such effects persist is uncertain.

The deleterious effect of alien plants on endangered species may not be restricted to plants: Picker (1985) has shown that within the reserve the survival of the Red Data Book frog, *Xenopus gilli* Rose & Hewitt is threatened through hybridization with its common congener *X. laevis* Daudin. This hybridization only occurs in those water bodies which no longer have the characteristic high humic acid content derived from fynbos vegetation in their catchments. The formation of dense alien thickets has been a significant factor in modifying catchment characteristics.

The formation of extensive, dense thickets of alien trees has also had marked effects on the occurrence, relative abundance and ecology of other vertebrate species within the reserve. By 1975-76 the reserve's chacma baboons *Papio ursinus* were estimated to be spending a third of their annual foraging time eating the seeds of alien *Acacia* and *Pinus* species (Davidge 1978). Several bird species are present in the reserve only as a consequence of these thickets, a notable example being the pied barbet *Lybius leucomelas* which colonized the area in 1970 and which nests only in the stems of alien tree species within the reserve (Langley 1976; Macdonald 1986). The effects of these and other similar changes on the functioning of native communities are mostly unknown, but recent studies indicate that at least avian nectarivory is severely impacted (M.W. Fraser pers. comm.).

The need for professional scientific staff

This analysis indicates that much damage has been done to the reserve's natural ecosystems and that time, effort and money has been wasted as a result of poorly planned

and poorly implemented control operations. In 1957 the reserve's advisory board, which in those days contained several natural scientists of standing, recommended the appointment of an academically trained professional ecologist to supervise research and biological management in the reserve (Anonymous 1958). This recommendation was never implemented, ostensibly because of a lack of funds, but correspondence on file indicates that the fear that such an appointee would dictate management to the reserve's untrained staff and to the Council itself was also a significant factor (Anonymous 1959b). A decade later Taylor (1967) reiterated this recommendation in his report to the advisory board on the alien plant problem. In the first management plan drawn up for the reserve (Millar 1970), the appointment of a trained ecologist to the reserve's staff was once again recommended. By this stage the complexity of managing the reserve was so apparent that it was further recommended that a professionally qualified person also be appointed to head the reserve's management staff. To date, neither of these recommendations has been implemented. It is our considered opinion, based on the detailed analysis of this one management activity (and it is but one component of an extraordinarily complex set of interconnected and sometimes conflicting management activities occurring within this important reserve), that the appointment of full-time professionals to the reserve's staff is long overdue. Had such an appointment been made in the late 1950's it is likely that this paper need never have been written.

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Introduced Species in Nature Reserves in Mediterranean-type Climatic Regions of the World

I. A. W. Macdonald

Percy FitzPatrick Institute of African Ornithology, University of Cape Town,
Rondebosch 7700, Republic of South Africa

D. M. Graber

Sequoia and Kings Canyon National Parks, Three Rivers,
California 93271, USA

S. DeBenedetti

Pinnacles National Monument, Paicines, California 95043, USA

R. H. Groves

CSIRO Division of Plant Industry, GPO Box 1600, Canberra,
ACT 2601, Australia

&

E. R. Fuentes

Facultad de Ciencias Biologicas, Pontificia Universidad Catolica de Chile,
Cassilla 114-D, Santiago, Chile

(Received 29 July 1987; accepted 31 July 1987)

ABSTRACT

The invasions of introduced species into three nature reserves in California, two in Australia, one in Chile and one in South Africa are described. In most reserves the major invasion has been by herbs, primarily annual grasses from Europe and the Mediterranean Basin. It appears likely that fire regimes have been altered and the density of some native plant populations reduced. In the South African reserve, invasions by introduced trees threaten certain native plant species with extinction. Over all regions smaller reserves tend to show

37

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higher proportions of invasive introduced species in their vascular plant floras, and both freshwater fish and mammalian faunas, than do larger reserves. Few vertebrates are thought to pose significant conservation problems. These reserves tend to be susceptible to invasion of non-native species from elsewhere on their own continents. The intentional or accidental introduction of species to these reserves should be avoided.

INTRODUCTION

The regions of the world experiencing Mediterranean-type climates (winter rainfall and summer drought) contain biotas that are distinct from those of the continents on which they occur. These biotas are often rich in species, particularly plant species, and have come to contain a disproportionately high number of taxa threatened with extinction (Ayensu & DeFilipps, 1978; Leigh *et al.*, 1981; Hall & Veldhuis, 1985). This situation has arisen mainly through extensive agricultural and urban transformation (e.g. Moll & Bossi, 1984; Mooney *et al.*, 1986), but it has also been postulated that these quasi-insular Mediterranean-type regions are also especially susceptible to invasions by introduced species (Ferrar & Kruger, 1983). Although rigorous tests of this hypothesis have not yet been carried out, the extent of plant invasions (Macdonald, 1984), and the number of introduced bird and mammal species established in nature reserves (Macdonald *et al.*, 1986) support this contention for the fynbos biome of southern Africa.

- The nature reserves that have been created to protect these regions' biotas are often small and surrounded by transformed ecosystems in which introduced species are common. They have often been established, only recently, following a period of extensive human modification. This paper documents the role introduced species are playing in selected nature reserves in the Mediterranean-type regions which have been settled by Europeans, i.e. California, Chile, South Africa, south-western and south-eastern Australia. The approach, definitions and terminology used in this study are described in Usher *et al.* (1988—this issue).

Reserves from the various regions were chosen on the basis that they were relatively well-known as regards both abiotic and biotic components and their history of land-use and reserve management. The amount of information available for each reserve varied markedly and the case study reports are thus of different lengths. The reserves were not chosen as being particularly heavily invaded by, or free from, introduced organisms. Wherever possible, reserves that had been relatively long-established were chosen in order to minimise the influence of non-conservation land-use practices on the site's invasion by introduced species. The details of the reserves are presented in Table 1.

TABLE I
Details of the Reserves Studied

<i>Reserve name</i>	<i>Country</i>	<i>Coordinates</i>	<i>Altitude (m, a.s.l.)</i>	<i>Rainfall (mm)</i>	<i>Size (ha)</i>	<i>Year of establishment</i>
Jasper Ridge Biological Preserve	California, USA	37°24'N 122°13'W	66-209	c. 700	525	1956
Sequoia and Kings Canyon National Parks	California, USA	36°45'N 118°45'W	400-4 418	660-1 120	349 811	1890
Pinnacles National Monument	California, USA	36°30'N 121°11'W	244-1 007	418	6 600	1908
Kings Park Nature Reserve	Western Australia	32°00'S 115°50'E	5-30	889	c. 300	1872
Myall Lakes National Park	New South Wales, Australia	32°30'S 152°25'E	0-110	1 390	28 000	1972
La Campana National Park	Chile	32°57'S 71°05'E	400-2 200	c. 800	8 000	1967
Cape of Good Hope Nature Reserve	South Africa	34°15'S 18°25'E	0-360	330-660	7 750	1939

THE JASPER RIDGE BIOLOGICAL PRESERVE

The reserve is situated in the eastern foothills of the Santa Cruz Mountains and is surrounded by urban and agricultural development. Cattle grazed the area of the reserve from the early 1800s to 1960 and some of the indigenous timber (mainly *Sequoia sempervirens*) was logged in the mid 1800s. The San Francisquito Creek was impounded within the reserve in 1892, resulting in the formation of 120 ha of aquatic and semi-aquatic habitats including 30 ha of open lake. The vegetation on the reserve is exceptionally diverse, ranging from mixed evergreen forest (c. 100 ha), oak woodlands (c. 60 ha), chaparral (100 ha) to open grasslands on greenstones and serpentine.

In terms of both the absolute number of invasive introduced species (I) and the relative index of invasion,

$$V = 100 I/S\%$$

where S is the total number of native and introduced species, fish (I = 6 and V = 86%) and angiosperms (I = 173 and V = 27%) are the groups most severely invaded (Table 2).

The number and proportion of introduced vascular plant species shows a progressive increase over time. In 1962 a list showed I = 89 and V = 20% (Porter, 1962), by 1971 it was I = 108 and V = 22% (Thomas, 1971) while more recent lists of H. Dengler (pers. comm.) gave I = 161 and V = 25% by 1973 and I = 175 and V = 27% by 1986. The latter listing includes several species which have been represented only by a single individual, e.g. the southern Californian shrub *Penstemon antirrhinoides* established on the edge of a trail by 1953, the pampas grass *Cortaderia selloana*, one plant of which was found and removed in 1969, and a lone *Nicotiana acuminata* recorded at a stream crossing in 1982. The invasion rates are approximately 1 to 2 new introduced vascular plant species per annum in recent decades. Averaged over the period since the beginning of the Spanish colonisation in 1769 (when introductions to California are thought to have begun; Mooney et al., 1986), the rate of introduction has been 0.78 species per annum.

Although most of the introduced angiosperm species are dicotyledons (I = 125, V = 26%), the monocotyledons show a slightly higher invasion index (I = 41, V = 28%). The majority of introduced plant species are herbaceous, only 16 being trees or shrubs. A few of the bird-dispersed shrubs and trees are becoming more abundant, e.g. *Rubus procerus*, *Crataegus monogyna*, *Cotoneaster pannosa* and *Olea europea*, but, except for some dense stands of *Acacia decurrens* and *Ailanthus altissima* along the lower reaches of San Francisquito Creek, woody plants are not a major problem in the reserve (H. Dengler, pers. comm.).

The habitats invaded by the introduced species of flowering plants were

TABLE 2
 Numbers of Native and Introduced Species, Recorded from Jasper Ridge Biological Preserve, by Taxonomic Groups

Taxonomic group	Number of species						Sources of data		
	Native					Introduced			
	Endemic to:			Not endemic	Total	Total	Invasive		
	Reserve 3548 km ²	Californian province	Nearctic realm						
Vascular plants	0	1	(48%	43%	9%)	486	?		
			from Thomas (1961) for Santa Cruz Mountains						
Ferns and allies						15	1	1	
Gymnosperms						2	?	1	
Angiosperms						469	?	173	
Orthoptera						35	1	1	Weissman & Rentz (1978)
Amphibians	0	0	4	5	0	9	1	1	Harvey (1982a)
Fish (freshwater)						1	6	6	Aris & FitzPatrick (1980)
Reptiles	0	0	0	10	4	14	0	0	Harvey (1982a)
Birds	0	0	1	?	?	164	4	1	Clark & Clark (1986)
Mammals	0	0	4	15	5	24	5	3	Harvey (1982b)

determined from the annotated checklists (Porter, 1962; Thomas, 1971). Of the 108 species, 38 were restricted to disturbed areas (e.g. road verges), 11 were found in these areas as well as in areas of 'natural' vegetation, 18 were restricted to sites of artificially high moisture availability (near drinking troughs, the verge of the impoundment and below its wall) and 14 were found only in the riparian habitat. Of the species that were recorded in 'natural' vegetation, 36 were in grassland, 18 were in open oak woodland, 3 were in closed oak woodland/oak-madrone forest and only 1 species, *Galium murale*, was recorded from chaparral (apparently in a disturbed area, H. Dengler, pers. comm.). The communities with more complete woody plant canopies thus appear less susceptible to invasion by these introduced plant species, as found by Frankel (1977), who studied the roadside vegetation of California.

The habitat most severely invaded by introduced plants is the grassland occurring on soils other than those derived from serpentine. Annual herbs, mostly grasses of European or Mediterranean origin (e.g. *Avena barbata*, *A. fatua*, *Bromus mollis* and *B. rigidus*), made up an average of 89% (range 73–99%, $n = 4$) of the above-ground phytomass in this grassland in 1966, five years after the cessation of cattle grazing. By contrast, introduced plant species made up only 28% on average of the phytomass of grassland on serpentine soils (range 10–53%, $n = 4$) (McNaughton, 1968). Introduced grasses, other than *Bromus mollis* and *Gastridium ventricosum*, tend to be excluded from serpentine soils. Turitzin (1978) has shown that on soils derived from sandstone, introduced grasses grow to a height and density such that competition for light would be significant for shorter plant species. No plant species are known to have become locally extinct in the reserve as a result of this invasion, although the invasion is thought to have occurred prior to any botanical collecting in the region. The serpentine soils now hold virtually all the Californian endemic herbaceous plants, possibly indicating earlier elimination of the endemics from the more heavily invaded soil types derived from sedimentary rocks.

The introduced fish species all inhabit the artificial impoundment where they dominate the biomass of the fish community (Wohlschlag, 1952). The composition of the fish community changes after the dam dries out in drought periods, e.g. the formerly abundant *Cyprinus carpio* disappeared following the dam drainage in 1924 (Wohlschlag, 1952).

The only introduced amphibian is the bullfrog *Rana catesbiana*, which possibly displaced the native *Rana aurora* in the impoundment (Storer, 1925; Harvey, 1982a). *R. aurora* still occurs in the creeks on the reserve (H. Dengler, pers. comm.). The only introduced bird considered invasive, i.e. breeding in the reserve, is the European starling *Sturnus vulgaris*, which first arrived in the area in 1961 (H. Dengler, pers. comm.). Of the three invasive mammals

only the squirrels *Sciurus niger* and *S. carolinensis* are thought to be having any detectable effect on the reserve's biota. They have become more widespread in recent years, during which period the range of the indigenous *S. griseus* has contracted (Harvey, 1982b). Although not becoming truly feral, domestic dogs *Canis familiaris* enter the reserve and possibly affect the reserve's vertebrate fauna through predation. Cats *Felis catus* are rarely seen, even on the reserve's boundaries (H. Dengler, pers. comm.). Cattle *Bos taurus* probably had the greatest impact on the reserve; since their removal the populations of several indigenous plant species have increased (H. Dengler, pers. comm.).

The rapid sedimentation of the impoundment on San Francisquito Creek probably indicates accelerated erosion in its catchment (cf. maps in Wohlschlag (1952) and Aris & FitzPatrick (1980)). Whether this resulted from agricultural soil disturbance outside the reserve, or from the effects of overgrazing by cattle, or from the replacement of the native herbaceous ground layer by introduced grasses, cannot now be determined. The alteration of the fire regime as a consequence of the lush growth of these grasses is possibly another important ecological impact. Although several fires have entered the reserve's grasslands, no major fires have been allowed to spread into the wooded communities this century.

The most important control operations in the reserve are those aimed at limiting the extent of *Myriophyllum brasiliense* beds in the impoundment. This has been achieved by water level manipulation and mechanical removal using floating plant cutters. Currently, the latter approach is being followed, the cost being \$5000–6000 per annum for salaries and maintenance of the equipment, only about 4% of the reserve's total management budget. The operations are primarily aimed at reducing mosquito breeding sites in the lake and are carried out for public health rather than conservation reasons (A. Grundmann, pers. comm.).

Low density volunteer stands of introduced tree species (e.g. *Acacia baileyana* and *A. decurrens*) appearing on the San Francisquito Creek have been routinely ringbarked on discovery.

SEQUOIA AND KINGS CANYON NATIONAL PARKS

These contiguous national parks form a single international Biosphere Reserve. The reserve constitutes a portion of the western slope of the Sierra Nevada range, which rises to the Pacific crest on the reserve's eastern boundary. The reserve is bounded on the north, east and south by National Forest land, little modified and used for timber harvesting, grazing and

recreation. To the west are largely privately owned ranchlands with agricultural land and small villages. Three major river systems, the Kings, Kern and Kaweah, flow westwards through the reserve.

The climate is characterised by warm dry summers with precipitation uncommon except for thundershowers above 2000 m. Winters are cool and moist with most precipitation occurring as snow above 1800 m. Average daily temperature extremes at Ash Mountain (518 m) are 0.5°C and 8.3°C in January, and 20.5°C and 36.6°C in August; at Giant Forest (1954 m) they are -6.1°C and 3.3°C in January and 11.6°C and 27.2°C in August. The reserve is relatively 'natural', with 85.3% of its area classified as wilderness in 1984, although there are 1270 km of developed trails and 300 km of paved roads.

The area had been used by humans prior to its designation as National Parks, a process which began in 1890 but which was only finally completed in 1984. The most recent settlement by aboriginal people occurred about 500 years ago (Whistler, 1984). Villages were located in the foothills, with mid-elevation sites used seasonally and high elevations used primarily as trade routes. Prehistoric occupation of the area is thought to have begun three to four thousand years ago (Wickstrom, 1987). When Europeans arrived in the area about 1850, the local Western Mono Indians were using fire on a regular basis, apparently to clear brush and improve forage for game animals such as deer *Odocoileus hemionus*, and possibly to favour certain wild food crops (Lewis, 1973). Although by the mid-1860s many Indians had been extirpated or had abandoned the area, the practice of burning was continued until establishment of the reserve. Virtually all of the parks was subjected to livestock grazing by the 1860s, much of it extreme in intensity. It was during this period that Mediterranean annual grass species became established. Grazing largely ceased at the mid and lower elevations with park establishment in 1890, but continued in the subalpine and alpine zones for at least another decade. Fire suppression replaced light burning as policy by 1900, and was successfully effected by 1930. Beginning in the late 1960s, fire suppression was gradually replaced by the policy of prescribed burning, and has been evolving towards the practice of permitting natural ignitions (by lightning) to burn freely in most areas, augmented or replaced by prescribed fire in some locations.

The most important invasion is again that of European and Mediterranean grass species (Table 3). Generally this is only a problem in the oak woodland at altitudes less than 1300 m. Trials of different seasons and frequencies of fire were carried out in the 1970s to see if manipulation of the fire regime could be used to reverse the invasion. Although certain extreme regimes did tend to disadvantage the introduced annual grasses, the side effects of these regimes were likely to be undesirable (faunal and soil impacts) and it was observed that the dominance of introduced grasses was soon re-

TABLE 3
 Numbers of Native and Introduced Species, Recorded from Sequoia and Kings Canyon National Parks, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>							
	<i>Native</i>					<i>Introduced</i>		
	<i>Endemic to:</i>				<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>
	<i>Reserve</i>	<i>1000 km²</i>	<i>Sierra-Cascades province</i>	<i>Nearctic realm</i>				
Pathogenic micro-organisms						?	?	1
Vascular plants	0	0	?	?	?	1148	89	89
Ferns and allies	0	0	3	29	4	36	0	0
Gymnosperms	0	0	5	11	0	16	0	0
Angiosperms	0	0	?	?	?	1096	89	89
Amphibians	0	2	3	5	0	10	1	1
Fish (freshwater)	0	1	2	2	0	5	3	3
Reptiles	0	0	3	21	0	24	0	0
Birds	0	0	0	?	?	194*	5	5
Mammals	0	0	3	50	18	71	7	3

* Only 155 of these species are regularly recorded.

established. Field scale implementation of this control measure was never attempted and no other techniques have been tried.

Amongst the vertebrate invaders, only the intentionally introduced fish are widespread and might be having undesirable effects on the reserve's aquatic systems. The introduced beaver *Castor canadensis* was thought to pose a potential conservation problem in the reserve. However, the species has apparently failed to expand its population or range within the reserve and thus is currently not a major cause for concern. Most of the introduced birds and mammals tend to be localised around sites of habitation or to penetrate the reserve on its lower boundary only marginally.

Introduced species do not currently command a significant proportion of the reserve's research and management budget, but surveys are being carried out to determine the status of introduced plants and vertebrates.

PINNACLES NATIONAL MONUMENT

This reserve is situated in a north-south trending inner coastal mountain range which is flanked by transformed agricultural habitats. The park had been subjected to cattle grazing prior to proclamation. The reserve's boundary has been expanded over time such that its total area was 810 ha in 1908, 1930 ha in 1931, 5780 ha in 1941 and 6600 ha in 1978.

The vegetation is mainly chaparral with open woodland of oak *Quercus kelloggii* and digger pine *Pinus sabiniana* on the deeper soils. Well-developed riparian woodland flanks the seasonal river courses which rise in the reserve and drain to the east and west.

Once again the major invasion of introduced species has been that of European grasses (Table 4). No management of these grass invasions has been attempted locally. Although a policy of total fire suppression has been followed for the last 50 years, arson and accidental fires are so frequent that fire frequency is considered to have increased relative to the 'natural' fire regime in certain portions of the reserve. The flammability and continuity of the vigorous introduced grass layer has probably contributed to this situation. The seasonal incidence of fire might also have been significantly affected as the non-native grasses grow and dry out earlier in the year. Spring and early summer fires have probably become more frequent.

As in the case studies of Jasper Ridge and Sequoia and Kings Canyon, the paucity and almost total failure of introduced woody plant species is noteworthy. *Ailanthus altissima*, the only invasive tree recorded, is known only from an early homesite. A single walnut tree *Juglans regia* is known to persist in one of the reserve's riparian zones.

In this reserve, introduced vertebrates pose several management

TABLE 4
Numbers of Native and Introduced Species, Recorded from Pinnacles National Monument, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>								<i>Sources of data</i>
	<i>Native</i>					<i>Introduced</i>			
	<i>Endemic to:</i>			<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>		
	<i>Reserve 1000 km²</i>	<i>Californian province</i>	<i>Nearctic realm</i>						
Vascular plants	0	0	158	230	30	418	79	77	Halvorson (1985); Bjornerud (1986)
Ferns and allies	0	0	2	6	0	8	0	0	
Gymnosperms	0	0	1	1	0	2	0	0	
Angiosperms	0	0	155	223	30	408	79	77	
Amphibians	0	0	0	8	0	8	0	0	Fellers (1986)
Fish (freshwater)	0	0	0	1	0	1	1	1	
Reptiles	0	0	4	13	5	22	0	0	Fellers (1986)
Birds	0	0	3	33	98	134	5	4	Avery & van Riper (1986)
Mammals	0	0	8	6	23	37	5	4	Fellers & Arnold (in press)

problems. Trespass cattle, although not becoming feral, are a problem in certain of the unfenced boundary zones of the park. A small population of feral goats *Capra hircus*, numbering approximately 30 individuals, was eliminated by 1983. Feral pigs *Sus scrofa* are by far the greatest problem (DeBenedetti, in press). These have penetrated the reserve for several decades, remaining at low densities until some 10 to 20 years ago. It is postulated that survival has improved as the population's domestic traits have regressed and the population is now estimated at 200 to 400 individuals. Their effects are unquantified but appear to be severe. The soil disturbance resulting from their feeding activities is extremely widespread, present in all plant associations, is increasing in extent and is thought to be accelerating soil erosion rates. Pigs compete with native fauna for the acorn mast and jeopardise the re-establishment of native plant species, particularly *Quercus* species. They are also thought to be adversely affecting the populations of certain native animal species, particularly amphibians and ground-nesting birds, through predation.

Control of feral pigs in Pinnacles National Monument began in 1970 and is currently the top priority for resource management. A budget of \$500 000 has been approved for the erection of a pig-proof boundary fence over the five years, 1986 to 1990. An additional recurrent annual budget of \$25 000 has been proposed for fence maintenance and pig control operations. The current annual resource management budget for the reserve is c. \$50 000, so that the planned expenditure on feral pig control amounts to a large proportional increase.

The other vertebrate species considered a potential problem is the European starling. Having only colonised the reserve within the last decade, it was found to be the sixth most numerous bird in one of the oak savanna communities during 1984–85 (Avery & van Riper, 1986). By analogy with its known behaviour elsewhere it has been postulated that its invasion might limit the populations of native, hole-nesting bird species. Monitoring and possible remedial action (placement of starling-proof nest boxes in the affected community) has been advocated (Avery & van Riper, 1986).

Two gamebirds, chukar *Alectoris chukar* and the eastern American wild turkey *Meleagris gallopavo*, have been recorded on the reserve. Both are established in nearby agricultural land, but are not known to have bred successfully in the reserve (Avery & van Riper, 1986).

KINGS PARK NATURE RESERVE

This small nature reserve is located within the city of Perth and is surrounded on three sides by urban areas and on its south side by the Swan

River. About 300 ha can be considered a nature reserve as the remaining 100 ha have been developed as a semi-natural botanical garden and recreation area. The land rises steeply from the Swan River in the south and east, but is otherwise of gently undulating relief.

The area has a history of aboriginal use, but was apparently little affected by this usage. Most of the large jarrah *Eucalyptus marginata* trees on the area had been felled for timber post-European colonisation in the 1800s and prior to its proclamation as a reserve. Set aside initially in 1872, it was increased in area in 1890 and has remained unaltered since 1903. An attempt was made in the 1950s to rectify what was thought to be an unnaturally high incidence of high intensity wildfires by prescribed rotational burning using low intensity fires. Currently the policy is one of containment of wildfires.

The major invasion has been that of herbaceous plant species (Table 5). These include grasses such as *Ehrharta calycina*, *Eragrostis curvula*, *Rhynchelytrum repens* and *Pennisetum villosum* (the first three from South Africa, the last from South America), geophytes such as *Homeria flaccida*, *Romulea rosea*, *Gladiolus caryophyllaceus* and *Freesia leichtlinii* (from South Africa) and dicotyledonous forbs such as *Trifolium campestre* (from Europe) and *Arctotheca calendula* (from South Africa). The most important species is *E. calycina*, which occupied 0.1 ha in Kings Park by 1924. It spread rapidly following fires and the clearing of fire breaks (Main & Serventy, 1957; Baird, 1977) and is still spreading within the reserve, notwithstanding an attempt to limit its spread using cattle grazing in the period 1949–51. It is not a significant problem in areas having a dense canopy of native shrubs or trees, or in areas of natural vegetation far from sites of artificial disturbance such as fire breaks and paths. It has undesirable effects through preventing the establishment of native herbs, shrubs and trees and through increasing fuel loads and combustibility of the herb layer. It is being controlled by sowing the seed of native shrub species and, in other areas, by heavy grazing. The latter approach has undesirable side effects on the native flora of a reserve. Selective herbicides have been used to treat dense stands of the species.

The Eurasian clover *T. campestre* is widespread, particularly after fire. It is considered a major problem as it elevates the soil nitrogen status, which is thought to favour the introduced grass species which are more difficult to control. The only introduced woody plant that is invading is *Brachychiton populneus*, a native of south eastern Australia. It is already widespread in the park and is increasing, apparently following seed distribution by birds.

The only introduced vertebrates recorded are birds and mammals (Table 5). The mallard *Anas platyrhynchos* is found on the reserve's man-made lakes. It is known to hybridise with the native black duck *A. superciliosa* in Western Australia and its presence is therefore considered inimical to the interests of nature conservation in the region (Frith, 1967). The two

TABLE 5
Numbers of Native and Introduced Species, Recorded from Kings Park Nature Reserve, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>						<i>Sources of data</i>				
	<i>Native</i>			<i>Introduced</i>							
	<i>Endemic to:</i>			<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>				
	<i>Reserve 1000 km²</i>	<i>Western Sclerophyll province</i>	<i>Australian realm</i>								
Vascular plants	?	?	?	?	?	268	102	102	Baird (1977); Main & Serventy (1957)		
Amphibians	?	?	?	?	?	>2	0	0	Tingay & Tingay (1982); Browne-Cooper (1986)		
Reptiles	?	?	?	?	?	>15	0	0			
Birds	0	0	5	30	30	65	6	6	E. Bennett (pers. comm.)		
Mammals	0	0	?	?	?	>1	5	5			

introduced doves, *Streptopelia chinensis* and *S. senegalensis*, feed mainly on leftover food scraps and the seeds of garden and road verge weeds (Frith *et al.*, 1976). They are not considered to have displaced any native bird species (Frith, 1982). The European goldfinch *Carduelis carduelis*, although formerly recorded as breeding in Kings Park, is no longer present in the reserve, possibly a result of an eradication campaign carried out by the Department of Agriculture in the 1950s (E. McCrum, pers. comm.).

The kookaburra *Dacelo gigas*, introduced from south eastern Australia, has established a breeding population in the reserve. It possibly competes for nesting holes with the native Port Lincoln ringneck parrot *Barnardius zonarius*, tree martin *Cecropis nigricans* and sacred kingfisher *Halcyon sancta*. It preys on invertebrates, small birds and reptiles and is possibly competing with the smaller native kingfisher species for food. Although it is widely held by laymen to cause the disappearance of small bird species from Western Australian gardens, this has been disputed (Garstone, 1974). The only small native bird species known to have disappeared from Kings Park is the splendid wren *Malurus splendens*, although this is possibly attributable to habitat changes following controlled burning (Tingay & Tingay, 1982). Another eastern Australian species, the rainbow lorikeet *Trichoglossus moluccanus*, has also recently established a breeding population in the reserve.

The introduced mammals known from Kings Park are feral domestic cats, European rabbits *Oryctolagus cuniculus*, black rats *Rattus rattus*, house mice *Mus musculus* and, occasionally, red foxes *Vulpes vulpes* (E. Bennett, pers. comm.). The cat and the fox are considered to have effectively eliminated most of the small native mammals from the reserve, e.g. the quenda *Isoodon obesulus*, which is now locally extinct (Tingay & Tingay, 1982). In 1985 and 1986 nesting burrows within the reserve of the native bee-eater, *Merops ornatus*, have been destroyed by an introduced predator, thought to have been the fox (W. J. M. Miller, pers. comm.). Rabbits are considered to damage native vegetation through their burrowing and feeding activities (E. Bennett, pers. comm.). None of the impacts of introduced vertebrates has been quantified within Kings Park and the managing authority has not initiated any control measures for these species.

MYALL LAKES NATIONAL PARK

This reserve comprises a coastal barrier system with a chain of brackish lakes separated from the sea by sand dunes. The Myall River runs into the southern section of the park. Rainfall is fairly evenly distributed throughout the year with a slight increase in late autumn to early winter. Monthly mean temperatures range from 6°C to 28°C.

TABLE 6
 Numbers of Native and Introduced Species, Recorded from Myall Lakes National Park, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>						<i>Sources of data</i>			
	<i>Native</i>			<i>Introduced</i>						
	<i>Endemic to:</i>			<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>			
	<i>Reserve 1000 km²</i>	<i>Eastern Sclerophyll province</i>	<i>Australian realm</i>							
Vascular plants	0	?	?	?	?	469	42		42	Myerscough & Carolin (1986)
Birds	0	0	?	103	134	244	7		3	Recher (1975)
Mammals	0	?	?	?	?	38	7	7	B. Fox (pers. comm.)	

Most of the park area is natural although aboriginal use of the area was extensive. The forested areas were subjected to limited selective logging by the early European settlers since their arrival in 1816. Mining for heavy minerals began in 1956 and continued until 1984 (Fox & Fox, 1984). The area was used for low intensity cattle grazing, which entailed annual patch burning, for a period of approximately 150 years prior to its proclamation as a national park in 1972. Major additions to the park were made in 1979 and 1981.

The only known invasions in the park are those of vascular plants, birds and mammals (Table 6). Of the 42 introduced plant species recorded only three are woody plants; *Pinus elliottii*, *Chrysanthemoides monilifera* and *Lantana camara*. It is only these three species that are considered to be posing any threat to the reserve. The most important is the southern African shrub *C. monilifera*. The species was deliberately planted for dune stabilisation in the 1950s and 1960s and has now invaded extensive areas on the coastline of New South Wales and southern Queensland (Love, 1985). In the park it is principally invading the sand-mining paths and dunes where it prevents the establishment of native shrubs and trees, especially *Acacia longifolia* (Weiss & Noble, 1984). Attempts to control *C. monilifera* using herbicides were initiated in the park in 1981 (M. Dodkin, pers. comm.). This control has been only partly successful and a control strategy in which invaded areas are burnt and then reburnt before *C. monilifera* seedlings have begun flowering, is being considered.

Of the seven introduced bird species recorded for the area by Recher (1975), the domestic pigeon *Columba livia*, spotted turtle-dove *Streptopelia chinensis*, house sparrow *Passer domesticus* and European goldfinch are mainly confined to gardens and other transformed areas in Australia (Blakers *et al.*, 1984). The Eurasian skylark *Alauda arvensis* and spice finch *Lonchura punctulata* are generally only found in modified ecosystems, the former favouring grazed pastures and the latter thickets of the introduced *Lantana camara* (Blakers *et al.*, 1984). Only the European starling is considered likely to have any major conservation impact in the park as this species penetrates areas of native vegetation where it competes for nest holes with indigenous hole-nesting birds (Blakers *et al.*, 1984).

The introduced mammal species recorded on the reserve comprise three carnivores, the domestic dog, red fox and cat, two leporids, the European brown hare *Lepus capensis* and European rabbit, and two rodents, the black rat and house mouse (B. Fox, pers. comm.). The house mouse is probably the most numerous introduced mammal with recorded densities of 35 ha^{-1} after fire on areas previously disturbed by mining. However, it is an early successional species in the post-fire succession, where it precedes and is replaced by the native mouse *Pseudomys novaehollandiae* (Fox & Fox, 1984).

It does not outcompete *P. novaehollandiae* (Fox & Pople, 1984), although it has certainly been a successful invader of native ecosystems virtually throughout Australia (Strahan, 1983). No control of *M. musculus* has been attempted in the park. Control elsewhere, using poison baits, has usually been unsuccessful.

Cats are considered to pose a problem in the park. Elsewhere in Australia they have been shown to establish completely feral populations that are significant predators on native species, particularly small mammals, birds and lizards. They are thought to have been a contributory factor in the local extinction of the eastern native cat *Dasyurus viverrinus* on the Australian mainland generally, including in the Myall Lakes area. No control of feral cats has been attempted in this park, although elsewhere in Australia trapping and the use of poison baits have had some success.

Species which may constitute a problem in other areas, such as the rabbit and fox, are only present in areas of the park where there has been grazing and on less infertile soils. They are not regarded as significant problem species.

LA CAMPANA NATIONAL PARK

Situated in the coastal ranges of Chile, this reserve is c. 100 km from Santiago and c. 80 km from Valparaiso within the most densely populated area in the country. The reserve is the core of an international Biosphere Reserve which also includes the Penuelas Reserve. The reserve is surrounded by agricultural land and areas where man's impact is at least 400 years old and varied (grazing, wood-cutting, fires, small-scale agriculture). Its boundaries were legalised only in 1985, although the park was established by a law passed in 1967 (Rundel & Weisser, 1975). Prehispanic use of the area has not been documented. Since the Conquistadores arrived, the land has been used for mining purposes, grazing, wood-cutting, palm-cutting (to extract the sap and make palm-honey) and bark-stripping of the soap-tree *Quillaia saponaria*. Mining still occurs (according to Chilean law it has priority over other uses). Grazing and wood-cutting have decreased, but not stopped. The felling of palms was stopped in 1983. In 1986 the park is still not fenced in its entirety and trespassers (people and grazing animals) cannot always be kept out.

The terrain is extremely rugged, with less than 10% having moderate slopes. The reserve forms part of the catchment of the Aconcagua River. The vegetation is diverse ranging from stands of the palm *Jubea chilensis* to sclerophyllous forests and shrublands, hygrophyllous and winter-deciduous forests and thorn scrub (Rundel & Weisser, 1975).

The rugged topography has not allowed the cultivation of introduced

TABLE 7
 Numbers of Native and Introduced Species, Recorded from La Campana National Park, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>						<i>Sources of data</i>		
	<i>Native</i>			<i>Introduced</i>					
	<i>Endemic to:</i>		<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>			
	<i>Reserve 1000 km²</i>	<i>Chilean Sclerophyll province</i>					<i>Neotropical realm</i>		
Vascular plants	?	?	?	?	?	> 100	††	††	Redon & Walkowiak (1978); Villasenor & Serey (1980/81)
Amphibians	0	0	3	0	0	3	0	0	
Reptiles	0	0	?	13	0	13	0	0	See references in Rundel & Weisser (1975)
Birds	0	0	0	46	3	49	1	1	
Mammals	0	0	?	16	0	16	24	2	

†† = Numerous species, exact number unknown.

plants. Since the park was established attempts have been made to reduce man's impact upon the landscape, but the extent to which these have been successful is unknown. Fire is actively controlled by the forestry service (Corporación Nacional Forestal) that administers the park. In 1982 a management plan was drawn up for the park, but there are no plans regarding introduced species.

The major invasion that is known to have occurred is that of an unquantified, but large, number of species of European and Mediterranean grasses and herbs (Table 7). There are no known woody plant invaders.

The only introduced bird species present is the Californian quail *Lophortyx californica*. There is no information on the extent of its invasion or its effect. Two European leporids have invaded the park, the rabbit and brown hare. The rabbit is thought to have spread in response to the man-induced opening of the canopy of indigenous vegetation communities and the lack of predation pressure from native predators (Jaksic *et al.*, 1979; Simonetti & Fuentes, 1982). Chile has no native leporids and there is no indication that rabbits compete with any native mammal. They do, however, have a significant effect on the distribution patterns of perennial herbs and may be detrimentally affecting shrub recruitment (Fuentes & Etchegaray, 1983; Fuentes *et al.*, 1983).

Analysis of an extensive series of pellets of the barn owl *Tyto alba* in central Chile, which included a sample from the nearby Penuelas Reserve, showed the black rat and house mouse to be relatively common in this region (Jaksic & Yanez, 1979). Although it is uncertain whether these species have invaded La Campana, this appears likely.

There have been no attempts to manage any introduced species in this recently established and, as yet, poorly researched reserve.

CAPE OF GOOD HOPE NATURE RESERVE

Situated at the southern tip of the Cape Peninsula, this reserve has long been one of the most visited tourist spots in South Africa. It was proclaimed a local authority nature reserve in 1939 and its current extent was finally secured through land purchase by 1965.

Surrounded by ocean on two sides, it has a northern land boundary c. 16 km long adjacent to privately owned farmland, a small village and mountain land owned by the state. The Klaasjagers River enters the reserve as a small stream on its northern boundary and another stream runs out of the reserve at its northwesternmost point. The reserve is surrounded by a coastal shelf which is widest along the western coastline. Most of the reserve is a low plateau of sandstone rising from 60 m a.s.l. on the west to peaks up to

360 m on the east of the peninsula, where the terrain falls steeply to the sea. There are recent and fossil sand dunes, well-drained nutrient-poor soils and extensive areas of impeded drainage on the flatter areas of the central plateau. Vegetation ranges in structure from low, closed-canopy forest, dune scrub through a variety of heathlands, to marshes dominated by low sedges and Cape reeds (*Restionaceae*). The flora is exceptionally diverse, with much higher levels of local endemism than are found in the other reserves in this study (cf. Tables 2–8).

The most important invasion is that of 18 species of introduced woody trees and shrubs (Macdonald *et al.*, 1987). The extent of these and their change through time, and in response to control operations, have been documented by Taylor & Macdonald (1985) and Taylor *et al.* (1985). The Australian wattle *Acacia cyclops* is the most important species. It was first introduced to the area of the present reserve in the mid-1880s, at which time the area was used for livestock grazing and some crop production. By 1966 *A. cyclops* was present in 79% of a series of 10.5 ha circular quadrats systematically placed throughout the reserve (Taylor & Macdonald, 1985). 'High density' (> 400 plants per quadrat) infestations were found in 13% of the quadrats, mainly those in the lower rainfall south of the reserve, in which area the species had initially been introduced. By 1980 the frequency of occurrence had increased to 86% with 'high density' stands being present in 26% of quadrats (Taylor *et al.*, 1985). A decade of intensive control operations (1976–85), in that portion of the reserve where its initial density was lowest, failed to reduce significantly the frequency of occurrence of *A. cyclops* or its density distribution within quadrats. The problem arises from the immense buried seed bank that *A. cyclops* generates in South Africa, and the wide dispersal of its seeds by vertebrates (mainly birds).

The heavy grazing of the area by domestic livestock, and the frequent burning of the fynbos prior to proclamation, are thought to have facilitated the woody plant invasions. Certainly, frequent fires speed up the invasion process under current conditions (Taylor, 1977; Clark, 1985). The effects of the woody plant invaders are severe with the total replacement of native species by dense stands of these species being a common phenomenon. Some of the rare native plant species on the reserve are threatened with local extinction (which in several cases would be total extinction) if these stands of introduced trees are not prevented from spreading (Taylor, 1977). By contrast, introduced grasses and forbs, although present, are generally restricted to disturbed sites and are not considered to pose any threat to native species or ecosystem function within the reserve (Macdonald *et al.*, 1987).

Amongst the vertebrates numerous introductions of sport fish have been made to the naturally fish-free lakelets of the reserve. These fish normally

TABLE 8
 Numbers of Native and Introduced Species, Recorded from The Cape of Good Hope Nature Reserve, by Taxonomic Groups

Taxonomic group	Number of species							Sources of data	
	Native					Introduced			
	Endemic to:			Not endemic	Total	Total	Invasive		
	Reserve	471 km ²	Cape Sclerophyll province						Africo-tropical realm
Vascular plants	12	72	(c. 83% of flora)	?	?	1 052	80	73	Oliver (1977); Taylor (1985)
Ferns and allies	0	0	1	4	3	8	0	0	Taylor (1985)
Gymnosperms	0	0	0	0	0	0	5	5	Taylor <i>et al.</i> (1985)
Angiosperms	12	72	?	?	?	1 044	76	68	Taylor (1985); Macdonald <i>et al.</i> (1987)
Amphibians	0	0	7	5	0	12	1	1	de Villiers (1986)
Fish (freshwater)	0	0	1	0	0	1	75	71	D. Clark (pers. comm.)
Reptiles	0	0	5	25	2	32	1	1	de Villiers (1986)
Birds	0	0	3	99	58	160	8	4	M. Fraser (pers. comm.)
Mammals	0	0	4	17	2	23	10	8	Anon. (1983)

perish during the next drying cycle in a low-rainfall year. One introduced *Tilapia* sp. is known to occur in a small impoundment on a perennial stream. The only native freshwater fish, the minnow *Galaxias zebratus*, occurs in ephemeral streams and is not considered to be threatened by introduced fish species.

The introduced amphibian is more interesting; it is the African platanna *Xenopus laevis*. Although it is disputed whether it is native to the reserve, it is known to have been introduced along with fish to lakelets in the reserve in the 1970s. In the 1980s it was found to be hybridising with its rare congener *X. gillii* (Picker, 1985). Remedial action was taken in 1984 in the form of a platanna-proof wall being built around a lakelet containing pure *X. gillii* stocks.

The invasive reptile is a large southern African land tortoise, *Geochelone pardalis*, intentionally introduced to the reserve. Ostriches *Struthio camellus*, which are not native to the Cape Peninsula, were also introduced and are thriving. Similarly, most of the invasive mammals are African ungulates introduced to the reserve by the managing authority. None of these species is known to be having a deleterious effect, although it has been suggested that overgrazing of palatable native plant species is occurring.

Most of the self-introduced vertebrate species, e.g. feral pigeon, house sparrow, chaffinch *Fringilla coelebs* and grey squirrel *Sciurus carolinensis*, remain confined to areas of human habitation and other transformed sites. They are thus not listed as being invasive in this reserve. The intentionally introduced peacock *Pavo cristatus* has a small feral population breeding in the natural vegetation around the reserve's administrative headquarters. As with the introduced tortoises, peacocks feed mainly in man-modified habitats. *Rattus rattus*, *R. norvegicus* and European starlings are known to feed along the intertidal and coastal scrub zones away from transformed habitats. The southern African guineafowl *Numida meleagris*, introduced into the southwestern Cape for sport hunting, has a self-established population in the reserve.

The only active management of introduced species is that of the woody plant invaders. The control operations were initiated in 1943 and have continued ever since. Currently this management is the single most important facet of the reserve's resource management programme. A team of 14 men work full time on clearing stands of these trees, while a further team of 32 men work virtually full time on the follow-up weeding programme. In 1984/85 the expenditure on this operation was in excess of R154 000 (c. US \$100 000) (excluding transport costs and equipment depreciation), which is some 38.5% of the reserve's total budget. The operation will have to be maintained at its present level for at least another decade if it is to be successful.

DISCUSSION

In so far as this study covered only a small sample of reserves, any synthesis must take the form of a series of initial postulates rather than firm conclusions. The first of these relates to the influence of reserve size on the proportion of species in the various taxonomic groups made up by introduced forms (Fig. 1). The proportion of introduced species tends to be smaller the larger the reserve. This is not purely the result of larger reserves having more native species, although this is responsible for the difference in this proportion for vascular plants between Sequoia/Kings Canyon and Pinnacles National Monument (Tables 3 and 4). The smaller reserves often have higher absolute numbers of introduced species. It is not only the smallness of a reserve that is important. It appears likely that the location of both the small reserves in urban areas was important in giving rise to the

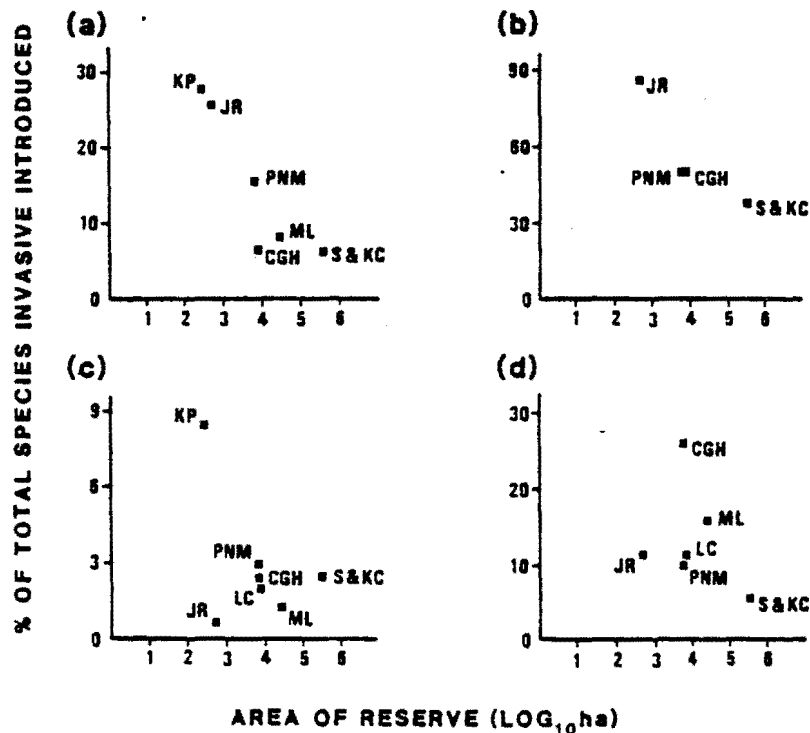


Fig. 1. The percentage of the total number of species recorded from the reserve that are invasive introduced species plotted against the log of reserve area. The individual diagrams show (a) vascular plants, (b) freshwater fishes, (c) birds and (d) mammals. The points indicate the following case history reserves: CGH, Cape of Good Hope Nature Reserve; JR, Jasper Ridge Biological Preserve; KP, Kings Park Nature Reserve; LC, La Campana National Park; ML, Myall Lakes National Monument; PNM, Pinnacles National Monument; S & KC, Sequoia and Kings Canyon National Parks.

high proportions of introduced vascular plants. Small reserves in urban areas appear to be especially at risk to invasion, particularly by introduced plants.

Invasion by herbaceous plants, mainly annual grasses, appears to be the most significant invasion of Mediterranean-type reserves on a global scale. The reduction of the woody plant canopy cover appears to have favoured this invasion in all areas. The nature conservation implications of this invasion are generally imperfectly understood. Current evidence does not indicate that a massive decrease in native species diversity has resulted, and altered fire regimes are possibly the most serious ecosystem-level effect of these invasions. Accelerated soil erosion might have resulted from this invasion in California, c.f. the Jasper Ridge account. In the long term this invasion could seriously destabilise the native ecosystem's communities, both plant and animal. However, from the viewpoint of the potential loss of native species diversity, the invasion of South African fynbos reserves by introduced woody plants appears to be the most serious invasion occurring in this biome.

Changes in the natural fire regime and plant/herbivore relationships seem to have been involved in almost all the major invasions by introduced plant species. In some cases, e.g. in the Myall Lakes reserve, these changes have apparently also influenced vertebrate invasions.

In general, freshwater fish, which have almost invariably been intentionally introduced, have been the vertebrate group showing most invasion. Few introduced birds have successfully invaded. Among the successful species have been the European starling (now in all reserves other than that in southwestern Australia, into which region they are being actively prevented from spreading (Blakers *et al.*, 1984) and that in Chile where they have not been introduced), and a variety of gamebirds that have been introduced into the regions for sport hunting, but have subsequently spread unaided into the reserves. In several cases species from elsewhere on the same continent have been able to establish populations in the reserves. Only the starling, through competition for nest sites with indigenous hole-nesting bird species, is thought to pose any major conservation problem. Introduced mammals, particularly cattle, feral pigs and European rabbits, are thought to have had deleterious impacts on the reserves' vegetation. Introduced mammalian carnivores are thought to pose a problem only in the two Australian reserves. However, although suspected of causing the local extinction of susceptible native mammals in both these reserves, their impacts are poorly quantified. The southern African reserve has an unusually high proportion of introduced mammal species as a result of an active policy of introducing non-native game species. Their impact is uncertain.

Invasions by introduced animals other than vertebrates have hardly been studied in these reserves. Where any information on invertebrates is available, e.g. Orthoptera in Jasper Ridge (Table 2) and Mollusca and Hymenoptera in the Cape of Good Hope reserve (D. L. Clark, pers. comm.), introduced species are known to be present. In the case of the Argentine ant *Iridomyrmex humilis* the ecological impact on fynbos reserves is thought to be serious (Bond & Slingsby, 1984). Rectifying the current situation where little or nothing is known about introduced invertebrates and micro-organisms should be a high priority for research in these reserves.

In so far as these reserves all tend to be susceptible to invasions by introduced species, management policies should be aimed at minimising accidental introductions. Care should be taken to avoid practices which alter the regimes of fire and herbivory under which the native biota have evolved, because altered regimes appear to favour introduced species. Intentional introduction of non-native species, even from areas on the same continent, should never be undertaken in the nature reserves of Mediterranean-type regions. The conservation of these regions' unique biotas should in all cases be their primary management objective.

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A List of Alien Plants in the Kruger National Park

I.A.W. MACDONALD and W.P.D. GERTENBACH

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The alien vascular plant flora of the Kruger National Park is listed. Annotations cover the invasive status, modes of introduction and dispersal, dates of first recording, ecological impacts and control status of each species. The list comprises 156 species of which 113 are considered invasive within the park. Most of the species have been accidentally introduced to the park. The ecological impacts of 27 species (of which 11 are trees and shrubs) were rated as moderate or high. By 1985 only 10 species are thought to have been eradicated from the park. Most of the invasive species are herbaceous weeds of man-disturbed sites and the eradication of these is generally considered impossible.

Most of the important species are dispersed by water and animals. The significance of limiting reinvasion of the park down the rivers flowing into the park, is stressed.

Key words: Plants, alien, exotic, check list, ecological impacts, control.

I.A.W. Macdonald, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700 Republic of South Africa; W.P.D. Gertenbach, National Parks Board, Kruger National Park, Private Bag X402, Skukuza, 1350 Republic of South Africa.

Introduction

This list has been compiled, in main, from a computerised listing of the Skukuza herbarium collection of the park's flora (Gertenbach 1985). This list was compared with a comprehensive listing of the invasive alien flora of southern Africa (Powrie & Macdonald 1985) and the alien taxa were extracted. Additional information on alien plants was extracted from the questionnaire survey of alien plants in the reserve (Gertenbach 1984), from a rapid survey carried out in June 1984 (Macdonald & Macdonald 1984) and from a review of the annual reports of the park and of the files relating to alien plants (Macdonald *in press*). In several cases the alien status of a species occurring in the park is uncertain. In such cases we have had to be guided by the available literature and, in a few cases, by reference to the staff of the Botanical Research Institute, Pretoria.

A total of 156 plant species alien to Kruger National Park are listed. Of these 113 are considered to be "invasive" in so far as they have established self-sustaining populations within the park in the absence of active human assistance.

Presentation of the list

Each genus of alien plant mentioned is given the De Dalla Torre and Harms number as reflected in Gibbs Russell & the Staff of the National Herbarium (1984). The species are numbered using the same system where these species are included in the list of Southern African plants (Gibbs Russell *et al.*, *op. cit.*).

After the species name the first column INTRO gives the known method of introduction to the park of each invasive species (C = intentionally brought in for the purposes of cultivation, N = brought in accidentally or invaded "naturally"). The second column CULT marked with an asterisk (*) indicates those species which are thought to be present only in cultivation within the park, i.e. the non-invasive introduced species.

In the First Records column are given the earliest year in which the plant was recorded from the park according to a particular data source. There are often several "first records". Where the date is unqualified this is the earliest collection represented in the Skukuza herbarium. Where the date has an F-prefix this is the date given for the earliest collection in Obermeijer (1937). An A-prefix signifies the first date of recording in either an Annual Report of the Park Warden or in a National Parks Board file. A Q-prefix indicates the year of first recording given in the questionnaire returned from the park (Gertenbach 1984). A P-prefix indicates the earliest collection date in the PRECIS databank of the National Herbarium, Pretoria.

A "+" sign in the F1 column indicates that the species was included in the first published list of the park's flora (Obermeijer 1937), while an X in the F2 column indicates inclusion in the second published checklist (Van der Schijff 1969).

The remaining columns classify the species firstly, into, Trees and Shrubs and Other Growth Forms and, secondly, into species having slight (S), moderate (M) or high (H) ecological impacts. In these columns, those species rated as having a slight impact are all shown as "1", while those with moderate or high impacts are listed with a letter denoting their main means of dispersal within the park (excluding human distribution). The means of dispersal listed are: water (W), mechanical (M), animals (A) and wind (Z). The lower case letter adjacent to the symbol in these columns indicates those species which have been eliminated (e), those for which control is considered possible given available technologies (p) and those where control is impossible at present (i).

The approach adopted in the classification of species by their ecological impacts warrants elaboration. A species was regarded as having a *slight impact* when, at current infestation levels, which are not being maintained by active control measures, the species is thought not to be significantly reducing the populations of any of the park's native species and not to be influencing ecosystem functioning. A *high impact* was attributed to species where it was considered that uncontrolled infestations have reduced or could reduce significantly the populations of native species or markedly alter some aspect of ecosystem functioning. In the absence of detailed ecological studies of alien plants in the park these ratings have had to be made subjectively based on the authors' experience with the species in the park and elsewhere in southern Africa. In addition the relevant published literature (Moran & Moran 1982) has been extensively reviewed. A *moderate impact* was allocated to species which were possible candidates for a high impact rating but where there was considerable uncertainty as to the severity of these impacts under local park conditions. These impact ratings should thus be regarded as providing a preliminary and highly tentative estimate of this extremely important but difficult to quantify component of the invasion process.

Discussion

Obermeijer (1937) listed six alien species for the Kruger National Park. The list of alien plants increased rapidly, partly as a result of increased plant collecting, but also because of new invasions and Codd (1951) listed 32 alien plant

		Species list									
I N T R O	C U L T O	First Records	Trees and Shrubs			Other Growth Forms					
			F 1	F 2	S M H	S M H	S M H	S M H			
Pteridophyta											
Salviniaceae											
0000210	<i>Salvinia</i>										
00100	<i>S. molesta</i>	N	Q1975 A1975								Wp
Angiospermae											
Monocotyledonae											
Poaceae											
9901070	<i>Paspalum</i>										
00600	<i>P. urvillei</i>	N									li
9901120	<i>Echinochloa</i>										
00200	<i>E. crus-galli</i>	N	1949	X							li
9901390	<i>Pennisetum</i>										
01100	<i>P. purpureum</i>		1958								
01200	<i>P. setaceum</i>	N	1953 P1953	X							li
9901400	<i>Cenchrus</i>										
00200	<i>C. brownii</i>	N		X							li
9902130	<i>Arundo</i>										
00100	<i>A. donax</i>	N	P1950	X							Wi
9902860	<i>Eragrostis</i>										
00900	<i>E. barrelieri</i>	N	1971 P1971								li
9904710	<i>Bambusa</i>										
00100	<i>B. balcooa</i>										
Cyperaceae											
0459000	<i>Cyperus</i>										
00800	<i>C. compressus</i>	N	1953 P1950	X							li
Araceae											
0791000	<i>Pistia</i>										
00100	<i>P. stratiotes</i>	N	Q1950 P1953								Wp
Commelinaceae											
0896000	<i>Commelina</i>										
00300	<i>C. benghalensis</i>	N	P1953	X							li
Pontederiaceae											
0921000	<i>Eichhornia</i>										
00100	<i>E. crassipes</i>	N	1975 Q1975 A1977								Wi
Liliaceae											
1026000	<i>Aloe</i>										
00100	<i>A. longibracteata</i>										
1050000	<i>Nothoscordum</i>										
00100	<i>N. inodorum</i>	N	1959 P1959								li

Species list (Continued)

	I N T R O	C U L T	First Records	Trees and Shrubs			Other Growth Forms		
				F 1	F 2	S M H	S M H		
2335000 <i>Alternanthera</i>									
00300 <i>A. pungens</i>	N		1950 P1952	X			li		
00400 <i>A. sessilis</i>	N		1949	X			li		
2338000 <i>Gomphrena</i>									
00100 <i>G. celosioides</i>	N		F1932 P1949	+ X			li		
Nyctaginaceae									
2347000 <i>Mirabilis</i>									
00100 <i>M. jalapa</i>		*							
2349000 <i>Boerhavia</i>									
<i>B. diffusa</i>	N		F1932 P1949	+ X			li		
2350000 <i>Bougainvillea</i>									
<i>B. glabra</i>		*							
<i>B. spectabilis</i>		*							
Phytolaccaceae									
2380000 <i>Phytolacca</i>									
00200 <i>P. dioica</i>		*							
Aizoaceae									
2387000 <i>Mollugo</i>									
00300 <i>M. nudicaulis</i>	N		1949 P1953				li		
2395010 <i>Zaleya</i>									
00100 <i>Z. pentandra</i>	N		1950 P1950	X			li		
Portulacaceae									
2421000 <i>Portulaca</i>									
00700 <i>P. oleracea</i>	N		1954 P1950	X			li		
01000 <i>P. quadrifida</i>	N		P1952	X			li		
Basellaceae									
2424000 <i>Basella</i>									
00100 <i>B. paniculata</i>	N		1959 P1959				li		
2428000 <i>Anredera</i>									
00100 <i>A. baselloides</i>	N		1954				li		
Caryophyllaceae									
2455000 <i>Polycarphaea</i>									
00100 <i>P. corymbosa</i>	N		1949 P1949	X			li		
Menispermaceae									
2570000 <i>Cocculus</i>									
00100 <i>C. hirsutus</i>	N		F1930 P1930	+			li		

Species list (Continued)

	I N T R O	C U L T	First Records		Trees and Shrubs			Other Growth Forms		
			F 1	F 2	S	M	H	S	M	H
Lauraceae										
2783000										
2825000										
00100		N		1953						Ai
Papaveraceae										
2852000										
00300		N		1932	+					Wi
Brassicaceae										
2883000										
00400		N		1954						li
				P1954						
2946000										
00100		N		1953						li
Capparaceae										
3082000										
00900		N		1953		X				li
Moringaceae										
3128000										
		C		1977			1p			
Crassulaceae										
3166000										
Rosaceae										
3340000										
Fabaceae										
3446000										
		N				X		We		
3520000										
00800						X				
3536000										
01500										
01600		C		P1961				1e		
03200		N		P1953				1p		
03300		N		P1949		X		1p		
04700		N						1p		
3556000										
00100										
3559000										
00100		N		1961						Wp
				A1948						
				P1953						
00500		C		1949		X		1e		
				P1950						

Species list (Continued)

	I N T R O	C U L T O	First Records	Trees and Shrubs			Other Growth Forms		
				F 1	F 2	S M H	S M H		
3669000									
06800			1966 P1949				li		
3734000					X				
3747000									
00100			1949 P1953	X	lp				
			1980			Wp			
3793000									
00300			1949 P1953	X			li		
3804000									
00100			1949				li		
3825000									
3857000									
00100				X			li		
3905000									
01200			1949 P1949				li		
Oxalidaceae									
3936000									
04500			1952 P1952	X			li		
11500			1978 P1962				li		
Rutaceae									
4100000									
Meliaceae									
4156000									
4175000									
00100			Q1940 A1948 1954 P1954	X		Wi			
Euphorbiaceae									
4407000									
00100									
4424000									
00100			1949	X	li				
4498000									
03800				X					

Species list (Continued)

	I N T R O	C U L T	First Records	Trees and Shrubs			Other Growth Forms		
				F 1	F 2	S M H	S M H		
12500	<i>E. heterophylla</i>	N	1950 P1950	X			li		
	<i>E. pulcherrima</i>	*		X					
24050	<i>E. splendens</i>	N	1952	X			li		
Anacardiaceae									
4545000	<i>Mangifera</i>								
00100	<i>M. indica</i>	*							
4562000	<i>Harppephyllum</i>								
00100	<i>H. caffrum</i>	*							
4594000	<i>Rhus</i>								
	<i>R. lancea</i>	*							
Sapindaceae									
4831000	<i>Dodonaea</i>								
	<i>D. viscosa</i>	C	1950		lp				
Tiliaceae									
4953000	<i>Corchorus</i>								
01200	<i>C. tridens</i>	N	1949 P1949	X			li		
01300	<i>C. trilocularis</i>	N	1949 P1933	X			li		
4975000	<i>Triumfetta</i>								
00600	<i>T. pentandra</i>	N	1949 P1953				li		
01000	<i>T. rhomboidea</i>	N	1953 P1933				li		
Malvaceae									
4995000	<i>Malvastrum</i>								
00100	<i>M. coromandelianum</i>	N	1954 P1954				li		
4998000	<i>Sida</i>								
00250	<i>S. alba</i>	N	1973 P1953				li		
00400	<i>S. cordifolia</i>	N	P1933	X			li		
5013000	<i>Hibiscus</i>								
01300	<i>H. cannabinus</i>	N	1953 P1950	X			li		
Bombacaceae									
5024000	<i>Bombax</i>								
	<i>B. spp.</i>	*							
5024010	<i>Pochota</i>								
	<i>P. glabra</i>	*							
Sterculiaceae									
5059000	<i>Waltheria</i>								
00100	<i>W. indica</i>	N	P1949	X			li		
Passifloraceae									
5372000	<i>Passiflora</i>								
00200	<i>P. edulis</i>	*							

Species list (Continued)

	I N T R O	C U L T	First Records	Trees and Shrubs			Other Growth Forms		
				F 1	F 2	S M H	S M H		
Caricaceae									
5377000									
Cactaceae									
5417000									
00100	N		1952						Ae
01000	C			X		Ap			
Myrtaceae									
5559000									
00200	C		1949	X		Ai			
5598000									
5603000									
Apiaceae									
5894000									
00350	N		P1954						li
Oleaceae									
6420000									
6436000									
Loganiaceae									
6473000									
Apocynaceae									
6560000									
6582000									
6597000									
00100	N		1952 P1951						Wi
6687000									
0000000									
Convolvulaceae									
6968000									
7003000									
04200	C								Me
Boraginaceae									
7052000									
01100	N		P1959						li

Species list (Continued)

	I N T R O	C U L T O	First Records	Trees and Shrubs			Other Growth Forms		
				F 1	F 2	S M H	S M H		
7056000 <i>Trichodesma</i> 00400 <i>T. zeylanicum</i>	N		1952 P1932	X				li	
Verbenaceae									
7138000 <i>Verbena</i> 00100 <i>V. bonariensis</i>	N		1952 P1952	X				li	
7144000 <i>Lantana</i> 00200 <i>L. camara</i>	C		Q1940 P1950	X			Ai		
7162000 <i>Duranta</i> 00100 <i>D. repens</i>	N		1953 P1953	X	li				
Labiatae									
7366000 <i>Ocimum</i> 00100 <i>O. canum</i>	N		P1950					li	
Solanaceae									
7400000 <i>Withania</i> <i>W. somnifera</i>	N		1949 P1949	X				li	
7401000 <i>Physalis</i> 00100 <i>P. angulata</i>	N		1952 P1952	X				li	
00500 <i>P. peruviana</i>	N		1949	X	li				
7407000 <i>Solanum</i> 04000 <i>S. mauritianum</i>	C		A1985 P1952	X			Ap		
7415000 <i>Datura</i> 00600 <i>D. stramonium</i>	N		P1953	X				Ai	
7434000 <i>Nicotiana</i> 00200 <i>N. glauca</i>	N		A1958 P1948	X			We		
Scrophulariaceae									
7625000 <i>Striga</i> 00100 <i>S. asiatica</i>	N		P1953	X				li	
Bignoniaceae									
7705000 <i>Arrabidaea</i> <i>A. mollis</i>									
7725000 <i>Jacaranda</i> <i>J. mimosifolia</i>	C		Q1953	X			Zp		
7733000 <i>Tecoma</i> <i>T. stans</i>	C						le		
7742000 <i>Spathodea</i> <i>S. campanulata</i>									
Rubiaceae									
8464000 <i>Richardia</i> 00100 <i>R. brasiliensis</i>	N			X				li	

Species list (Continued)

	I N T R O	C U L T	First Records	Trees and Shrubs			Other Growth Forms		
				F 1	F 2	S M H	S M H		
Asteraceae									
8795000									
00100									
8926000									
9130000									
00100									
00300									
9148000									
00200									
9155000									
00200									
9166000									
00100									
9196000									
00100									
9237000									
00200									
00300									
00500									
9245000									
00100									
9282000									
00200									
9291000									
00100									
9311000									
00200									
9595000									
00100									
01000									

species. Van der Schijff (1957) conducted a detailed survey of the park's flora and classified 43 species as aliens. The number of species had increased to 76 by 1969 (Van der Schijff 1969). This study shows there to be at least 156 plant species alien to the park of which 113 are considered "invasive". The increase in alien plant species over time is presented graphically in Figure 1.

The earliest record for each alien plant species within the park often varies between the different sources. Of the 52 species for which two or more records

exist only 22 had first been recorded in the same year from each source. Fifteen species had all their first records from different sources within five years of one another, 13 species within ten to twenty years, one species had 27 years between records and another had 33 years. In the latter case, which was *Solanum mauritianum*, it appears that an initial invasion along the Crocodile River at Crocodile Bridge (Van der Schijff 1969) either failed or was eliminated and that the plants first reported in 1985 from Skukuza by park authorities were from a totally new introduction. The long interval between the first records of 15 of the species as recorded from different data sources, indicates how little reliance can be placed on these first records when there is no systematic monitoring system in operation.

Of the 113 invasive alien plant species recorded, only 13 are known to have been intentionally cultivated within the park. Of these 13 species (almost all

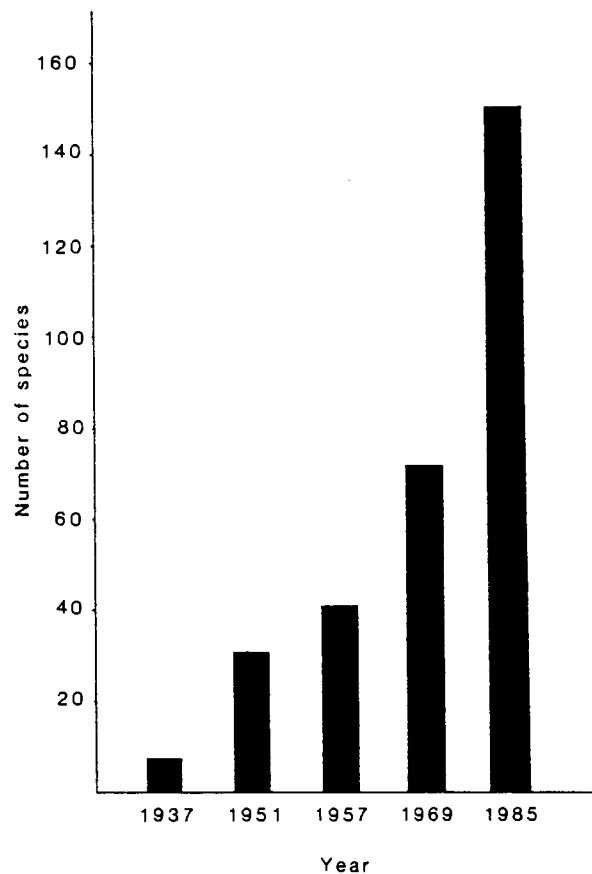


Fig. 1. The number of alien plant species recorded from the Kruger National Park as recorded in successive published floras.

perennial trees, shrubs or creepers) six are considered to have moderate ecological impacts while two, *Lantana camara* and *Melia azedarach*, have high impacts and are currently the two major problem species in the park.

The ecological impacts of 11 of the 25 invasive tree and shrub species were rated as moderate or high, whereas only 16 of the 88 species of other growth forms were so rated. All three of the floating aquatic macrophytes (*Salvinia molesta*, *Pistia stratiotes* and *Eichhornia crassipes*) were rated as having high ecological impacts. The high proportion of trees and shrubs and of floating aquatic macrophytes that were considered to have potentially significant ecological impacts can be attributed to the observation that alien species in both these growth forms can form dense, virtually monospecific stands. These stands have been observed to reduce the densities of native plant species and, in the case of the aquatic macrophytes, to shade out native submerged macrophytes entirely.

By July 1985, when this list was compiled, 10 species are thought to have been successfully eradicated from the park. In addition it was likely that *S. molesta* had also been eliminated. Of the 10 species eliminated, seven were trees and shrubs and six were species rated as having only slight ecological impacts. Excluding *S. molesta*, only one species rated as having a high impact, *Opuntia aurantiaca*, was thought to have been entirely eradicated. Certainly, none of the park staff in 1985 knew of the occurrence of any plants of this species within the park, although it had apparently been collected there in 1952. Most of the invasive alien plant species are herbaceous species which are often associated with man-disturbed areas. In general it is considered impossible to eradicate these herbaceous alien weeds given current control technology. Most of the species are persistent annual weeds of cultivated areas where they survive notwithstanding cultivation and chemical control methods which are far more drastic than would be possible within a national park. A total of 89 species belong to this category. The eradication of 14 species is considered possible. In almost all cases these are large perennial plants which require several years to grow to reproductive size. In most cases they are confined to localised areas around the sites of introduction. In the case of the aquatic macrophytes practical experience within the park indicates that chemical control is possible in localised infestations.

Of the 27 species having moderate or high ecological impacts, 14 are dispersed primarily by water, 10 by animals, two (*Agave sisalana* and *Ipomoea purpurea*) mechanically over short distances and only *Jacaranda mimosifolia* by wind. Several of the animal-dispersed species are known or are considered to be dispersed also by water (e.g. *Opuntia aurantiaca*, *O. vulgaris* and *Lantana camara*). It is of cardinal importance to limit the infestations of all these water-dispersed species outside the park's boundaries on rivers flowing into the park. This will only become possible when the authorities responsible for these upstream areas recognise their responsibility to control these problem species and then launch carefully planned and adequately funded control programmes. Once the initial clearance operations have been conducted it is essential that there be continual vigilance to ensure that new infestations do not build up again in these headwater regions. Similarly, routine monitoring of these rivercourses within the park should be undertaken to enable the early detection and removal of new invasions.

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THE HISTORY, IMPACTS AND CONTROL OF INTRODUCED SPECIES IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

By

I. A. W. MACDONALD

Percy FitzPatrick Institute of African Ornithology,
University of Cape Town

SUMMARY

The environment and history of this 19 485 km² tropical and subtropical savanna national park are described. The growth in awareness of the problems posed by alien organisms is documented: protected since 1898 and proclaimed as a national park in 1926, the first major policy decisions and control programmes for introduced species were initiated in the 1950s. Eight introduced pathogenic micro-organisms, 113 higher plants, two molluscs, one ant, one fish, one bird and two mammals have become 'invasive' in the Park. Only the micro-organisms and seven of the higher plants (comprising three floating aquatic macrophytes, one tree, one shrub, one cactus and one herb) are considered to have serious ecological impacts on the Park. The control programmes that have been carried out are described: seven of 25 invasive species of trees and shrubs and three of 88 plant species of other growth forms have been eliminated. With current technology, control is considered feasible for a further 13 and one species respectively. Intentional and accidental introduction by man and water-borne dispersal into the Park down the major influent rivers are all of major importance. Infestations of introduced plants are negligible in the frequently fired savanna vegetation while the rivers, riverbeds and riverine fringe have heavy infestations. Fire and ungulate herbivory are considered important factors limiting plant invasions. Control of certain introduced plant species along these rivers has proven to be difficult if not impossible, and the growth in the allocation of manpower and funds to these control programmes is documented. The importance of devising effective control strategies for these water-dispersed species is stressed.

INTRODUCTION

The Kruger National Park lies in the north-eastern lowveld of the Transvaal Province of the Republic of South Africa. Biogeographically, the Park is situated in the South African Savanna/Woodland Province of the Africotropical Region (Udvardy 1975)—in the south of the Sudano-Zambeian Region *sensu* Werger and Coetzee (1978). Situated between the latitudes 20°20'S and 25°31'S and longitudes 30°50'E and 32°02'E, the Park is currently 1 948 528 ha (19 485 km²) in extent (Pienaar 1982).

The environment of the Park

The Park is characterized by gently undulating topography with no high mountain ranges. Altitude above sea-level varies from 839 m at the highest point in the south to 122 m at the lowest point in the gorge of the Sabie River where it leaves the Park in the east. Much of the central portion of the Park is an extensive basalt plain at approximately 260 m. In the extreme north, hilly terrain occurs again with the highest point at 442 m. The landscapes of the Park together with their vegetation and mammalian faunal assemblages are described by Gertenbach (1983). The climate is warm and semi-arid with a unimodal summer rainfall peak—Köppen classification BSh (Macdonald 1982). Mean annual rainfall varies from approximately 750 mm in the

extreme south-east to 440 mm in the north-east, most of the Park receiving less than 550 mm. Mean monthly rainfall is highest from December to February and lowest in July and August (Gertenbach 1980). This seasonal rainfall cycle is an important factor in the biology of most of the Park's species (e.g. Kemp 1974). Annual rainfall totals have been observed to fluctuate according to a quasi-20-year oscillation, ten-year periods of generally above- and below-average rainfall alternating (Gertenbach 1980). This supra-annual rainfall cycle dominates much of the area's ecology at the population and community levels (Smuts 1978; Gertenbach 1980; Macdonald 1982).

Early history of the Park

Archaeological remains from the region indicate that hunter-gatherers had probably been present in the vicinity for the entire period of the evolution of *Homo sapiens*. However, the major impact of man on these areas seems to have occurred after the start of the Iron Age, since when population densities have increased sharply (Markers & Evers 1976). People with Iron Age technology are considered to have entered the eastern Transvaal during the first centuries A.D. (Rightmire & Van der Merwe 1976; Marker & Evers 1976). They are known to have been cultivating millet *Pennisetum americanum* in about A.D. 400 and to have added sorghums *Sorghum* spp. to their crops by the late Iron Age—after A.D. 1000 (Marker & Evers 1976). Although sheep are known to have been herded by Iron Age pastoralists in the region since the first century B.C. (Sandelowsky *et al.* 1979; Walker 1983) and cattle are known to have been here for several centuries, there is no indication of the length of time domestic livestock were present in the specific area of the present National Park. When the first European explorers entered this area in A.D. 1725 it was sparsely populated by isolated Bantu tribes. Endemic diseases and tribal wars kept human densities low, domestic stock were excluded by the presence of tsetse flies *Glossina* spp. and the associated trypanosomiasis of ungulates (Pienaar 1982). Following the rinderpest epizootic of 1896, domestic livestock were introduced to the area. Prior to this, in 1884, initial moves had begun to have a portion of the Transvaal lowveld made a game reserve to protect the dwindling wild ungulate herds from over-hunting. In 1898 the Sabie Game Reserve (4 600 km² of the southern section of the current Park) and, in 1903, the Shingwedzi Reserve (10 360 km² in the north) were proclaimed (Stevenson-Hamilton 1937). In 1904 these areas were increased to a total of 37 000 km². At this stage the reserve covered virtually the whole north-eastern lowveld from the foothills of the Transvaal Drakensberg in the west to the Lebombo mountain range in the east. To the east of the Lebombos stretched the Mozambique plain which was still virtually pristine. However, this 'ecosystem reserve' was markedly reduced in area and ecological completeness by the excision of most of the higher-rainfall savannas in the west prior to its proclamation as a National Park in 1926.

The low-density Bantu population which occupied the Park at the time of its proclamation was originally permitted to keep small herds of cattle, sheep and goats. They cultivated fields in the vicinity of their villages. In 1938 all domestic livestock within the Park's boundaries were destroyed by the State veterinary authorities in an effort to prevent the spread of foot-and-mouth disease. This marked the end of an

era, for crop cultivation by the villagers was now impossible as they had depended on draught animals for ploughing. The subsistence population within the reserve dwindled to zero as people emigrated to areas outside the Park (Pienaar 1982).

MANAGEMENT

History of the Park's management

The first official warden of the then Sabie Game Reserve was appointed in 1902. This marked the beginning of a long era of pragmatic management with policies based on a common-sense appraisal of the situation without any scientific input to this process. The combating of poaching and control of carnivores were immediately implemented as a means of increasing what were considered to be unnaturally depleted ungulate populations (Pienaar 1982). An attempt at controlled burning of the savannas within the Park was the other major management input at this time. Policies switched from burning areas in early winter to attract game, to one of complete protection of the whole area from fire (initiated in 1929—Anon. 1929) to one of burning all grass 'over one year old' (initiated in 1939—Anon. 1941). In reality these fire management policies were all largely ineffective as uncontrolled fires lit by poachers, subsistence inhabitants of the Park (and those in boundary communities) and later by tourists continued to dominate the fire regime throughout these years. Following the appointment of the Park's first research ecologist in 1950 and the establishment in 1953 of a series of fire experimental plots and of the first effective system of fire-breaks, a three-year rotational burning regime was introduced over most of the Park in 1955 (Pienaar 1982). Only the higher-rainfall savannas in the south-west of the Park were burnt biennially. This system with minor modifications is still in operation (Pienaar 1982). The intentional firing of most of the Park's area is the management input which has probably had the single greatest impact on the invasion of the reserve by alien plants.

The Park's boundaries were fenced as agricultural development outside the Park and the concomitant need for control of animal movement increased. In 1959 fencing of the southern boundary began; in 1960–61 the western boundary and by 1980 the eastern and northern boundary fences were completed. In 1933 the first boreholes were sunk to create artificial watering places for game, using pumped underground water supplies. By 1982 there were 365 productive boreholes scattered throughout the Park, 12 large impoundments on the major rivers and some 50 smaller impoundments on seasonal watercourses (Pienaar 1982). Thus the natural dispersion and movements of the area's ungulate populations have been radically altered. From the initiation of the first game reserve large carnivores have been heavily 'managed'. This started as a 'shoot on sight' policy and was gradually reduced as the ecological role of predators came to be appreciated. However, the already rare African hunting dog *Lycaon pictus* was last recorded as being shot within the Park in 1942 (Anon. 1942) and selective predator control was still being practised in 1960 (Smuts 1978). Lion *Panthera leo* and spotted hyaena *Crocuta crocuta* were once again subjected to control operations between 1974 and 1977 (Smuts 1978). Cropping of over-abundant ungulate popu-

lations within the Park began in 1964 when 104 hippos *Hippopotamus amphibius* were killed because they were judged to be faced with certain starvation during a low-rainfall period (Pienaar 1982). Over the period 1967 to 1982 a total of 9 456 elephant *Loxodonta africana*, 25 857 buffalo *Syncerus caffer* and 828 *H. amphibius* have been killed in order to keep these populations within the 'carrying capacity' of the Park (de Vos *et al.* 1983). The interactions between large ungulates, disease and predation are all now managed within the Park to greater or lesser degrees (Pienaar 1983). Given the control on water supplies, on movement of ungulates through fencing and the management of fire regimes within the Park, there is very little about the Park's ecological functioning that can today be considered strictly 'natural'.

One aspect of Park management that might have a considerable influence on the introduction and establishment of alien species is tourist utilization of the area. In 1923 the first visitors entered the Park by rail and in 1927 the first tourists in cars arrived (Pienaar 1982). In 1934 there were already 19 740 visitors and this number had roughly doubled by 1946 to 38 367 (Anon. 1935; Pienaar 1982). This number had increased fivefold to 216 680 by 1964, and tenfold to 428 840 (in 108 157 cars) by 1980 (Pienaar 1982). The growth in visitor numbers is possibly not the only aspect of significance for plant invasions. Associated with this increase were massive developments of roads, restcamps and services required by these visitors. The growth of tourism and management infrastructure has resulted in some 2 800 staff being employed in the Park by 1984 (Anon. 1984). These staff generally have their families living with them. Most of the goods required by this resident and transient population have to be imported from outside the Park, thus ensuring a continual supply of accidentally translocated plant seeds. Developments such as roads alter the regimes of soil moisture availability and herbivory (Pienaar 1983), alterations which might be critical for the establishment of introduced plants.

History of the management of introduced species

Awareness of the potential problems posed by alien organisms within the Park was not evident in the earliest years of its history. In 1930, for example, it was reported that a programme of intentional introduction and cultivation of the Kalahari tsama melon *Citrullus lanatus* in the arid areas of the Park had been unsuccessful. In the same year crested guineafowl *Guttera pucherani* were introduced (Anon. 1930). Both these species have subsequently been listed as occurring naturally in the Park (Van der Schijff 1969; Kemp 1974). However, it is apparent from the contemporary accounts, particularly in the case of *G. pucherani*, that this was unknown at the time of the attempted introduction. In the case of *C. lanatus* it is possible that the species is in fact alien as it has not been recorded in two independent analyses of the sandveld flora of the Park (Van der Schijff 1964; Van Rooyen *et al.* 1981). It still is only listed on the basis of a single collection made from the higher-rainfall Pretoriuskop area where it may have been introduced (Van der Schijff 1969; Botanical Research Institute, Pretoria, pers. comm.). That there was, at this time, no prohibition on the introduction of alien plant species into the Park's restcamp gardens is borne out by the account of Bigalke (1947).

Introduction programmes were considered or attempted (all without success) for four species of ungulates, two of which were definitely alien to the Park, lechwe *Kobus leche* from Zambia (Anon. 1930) and springbok *Antidorcas marsupialis* from western South Africa (Bigalke 1947), and two of which were at the time not considered to occur in the Park, oribi *Ourebia ourebi* (Anon. 1932) and red duiker *Cephalophus natalensis* (Anon. 1934).

Awareness of the desirability of excluding alien organisms from the Park apparently grew rapidly, as the warden, writing in 1937 on the characteristics of an 'ideal wild life sanctuary', stated 'All indigenous species of fauna and flora ought to be represented, but the introduction of exotic types of either should be religiously avoided; they introduce a discordant element, and, even should they succeed in assimilating themselves with the environment, they will generally appear incongruous, conferring an air of artificiality on the whole' (Stevenson-Hamilton 1937: 260). There is, however, no mention of the control of any introduced species in this book.

The article by Bigalke in 1947 appears to mark the beginning of a period of heightened awareness concerning introduced organisms in South Africa's national parks. In 1948 the warden initiated correspondence on the problem posed by infestations of *Xanthium strumarium* along the Park's rivers and the potential problem that could arise from the planting of the alien *Caesalpinia decapetala* as a hedge along the Park's boundary by the then Department of Native Affairs. For the control of the declared noxious weed *X. strumarium* within the Park he proposed that half the costs should be borne by the then Department of Agriculture. This was rejected in 1949 and to this day *X. strumarium* remains one of the Park's intractable alien plant problems. The threat posed by already established infestations of *Melia azedarach*, *Tagetes minuta* and *C. decapetala* were recognized at this time (National Parks Board files, unpublished). In line with this heightened awareness of invasive alien plants, the first removal of alien plants from the restcamps was initiated in 1950. As could be anticipated, these removals met with resistance: the Nelspruit and District Publicity Association, in protesting the proposed removal of flamboyant trees *Delonix regia* from the Pretoriuskop Camp, even went so far as to state that 'the flamboyant has definitely become indigenous to and associated with this area . . .' (National Parks Board files, unpublished).

During 1957, in what was the first meaningful attempt at alien control in the Park, the Board formally decided to launch major eradication programmes for *Melia azedarach* along the Sabie, Crocodile and Nsigazi rivers (National Parks Board files, unpublished). In December 1958 the Board passed a resolution prohibiting the cultivation of any of the known alien plant invaders of South Africa in staff gardens or rest-camp grounds (Brynard & Pienaar 1960). In the same publication the results of local trials of chemical methods for the control of *M. azedarach*, *Nicotiana glauca* and *Opuntia vulgaris* were reported (Brynard & Pienaar 1960).

INTRODUCED SPECIES

The numbers and types of introduced species invading the Park

No detailed field investigations have been carried out in the Park specifically aimed at surveying the occurrence of introduced taxa. The statistics that have been assembled (Table 1) have in the main been extracted from published and unpublished reports listing all the species of a particular taxonomic group that have been recorded within the Park up to July 1985. Introduced species were normally listed incidentally during surveys which were aimed at providing inventories of the native species. An introduced species is classed as 'invasive' if it is considered ever to have established a population within the Park which is or was self-sustaining in the absence of active human assistance.

Whether a particular species is native or introduced is sometimes uncertain. In these cases I have, wherever possible, consulted reference texts and been guided by the most up-to-date statement on the species' native range. The most difficult organisms to classify as either introduced or native are the pathogens and parasites associated with the Park's relatively well-studied fauna. In these decisions I have mainly followed Neitz (1965). However, in several cases (such as those of the rinderpest virus, the canine distemper virus, *Bacillus anthracis* and the causal organism of malignant canine rickettsiosis *Ehrlichia (Rickettsia) canis*) it is by no means certain that the species were introduced into the Park. In these cases the observation that the organism suddenly caused (or is thought to have caused) unprecedented levels of mortality in native mammals within the Park, often associated with outbreaks of the disease in domestic animals within or adjacent to the Park's boundaries, has led to the inference that the organism (or some strain thereof) was in fact introduced into the Park. In almost all cases the 'introduction' was only indirectly brought about by man. For example, the rinderpest virus swept down Africa and was probably aided in its advance through the movement of domestic livestock by man. In two cases it is especially unclear whether the organisms were introduced. These cases both relate to a report on cheetah *Acinonyx jubatus* in the Park (Young 1972). The mites responsible for cat mange *Notoedres cati* are recorded as having infected both the Park's cheetahs and those 'imported from other parts' and to have now been 'largely eliminated from the Kruger Park' (Young 1972). Whether the mites were brought in with cheetah being introduced into the Park from South West Africa is uncertain, but this was recorded for another mite species, *Sarcoptes scabiei*, introduced from the same area into the Umfolozi Game Reserve (M. E. Keep, pers. comm.). In the same article Young (1972) mentions cheetah being killed by 'cat flu' (presumably feline panleucopenia). It is, however, not clear whether these animals died in the Park or elsewhere. If they did so in the Park, then this is another introduced pathogen as the virus would almost certainly have been transmitted to the wild animals from domestic cats *Felis catus* (M. E. Keep, pers. comm.). Both these cases are considered uncertain and are listed with a '?' in Table 1.

The vast majority of known introduced species in the Park are higher plants. Flowering plants dominate (155 spp.), 112 of these being considered invasive. The

Table 1
The status of introduced species in the Kruger National Park

Taxonomic group	Total no. non-invasive species recorded	Total no. of species ever recorded	Total no. of species still present in Park	Invasive species									Sources of data Reference no.	
				Impact rating of species										
				Slight			Moderate			Severe				
e	★ p	i	e	p	i	e	p	i						
Pathogens & parasites of mammals	?	8(+72)	7								1(+?1)	1	6(+?1)	1, 6, 28, 66, & W. P. D. Gertenbach, pers. comm.
Vascular plants	43	113	103	6	7	75	3	5	10	1		2	4	1, 3, 4, 11, 12, 25, 30, 31, 59, 61
Ferns	0	1	1										1	
Trees & Shrubs	32	25	18	5	7	3	2	5	1				2	
Other Flowering Plants	11	87	84	1		72	1		9	1		1	2	
Molluscs	2	2	2			2								29, 49, 56, 57
Ants	3	1	1			1								44
Fishes	0	1	1						1					37, 38, 39
Reptiles	0	0	0											17, 42
Birds	0	1	1			1								19
Mammals	4	2(+?1)	2(+?1)		2									1, 2, 35, 36, 43, 45, 50

★ = Control status within Park
 e = currently eliminated
 p = available technology makes control practically possible
 i = impossible to control given available technology

majority of these species are 'weedy' herbs, mainly annuals. However, 25 species of woody trees and shrubs are invasive and several of these constitute significant management problems.

Of the four introduced mollusc species two are slugs restricted to gardens in Skukuza (Van Bruggen 1966, 1968), one is an aquatic snail *Limnaea columella* with isolated small infestations on some of the influent rivers (Oberholzer & Van Eeden 1967) and one is a terrestrial snail *Acanthinula aculeata* which is thought to have entered the Park via the railway line that traverses it (Sirigel 1979). The four introduced ant species are all human commensals, only one of which, *Camponotus rufoglaucus*, is considered to occur away from human habitation (Prins 1964 and pers. comm.).

The only introduced fish species recorded from the Park is the common carp *Cyprinus carpio* which has been found in two of the major influent rivers, the Olifants and Luvuvhu (W. P. D. Gertenbach, pers. comm.).

Amongst the reptiles only one species is pantropical. This is the tropical house gecko *Hemidactylus mabouia* which is found in South America, the West Indies, tropical Africa and the Indian Ocean islands. Where the species is truly 'indigenous' is uncertain but within the Park it lives both in human habitations and in natural situations (Pienaar *et al.* 1983).

The only introduced bird is the house sparrow *Passer domesticus* which is marginally 'invasive', being restricted to the vicinity of human habitations (Kemp 1974). Similarly the commensal rodents, *Mus musculus* and *Rattus rattus*, might be classed as invasive (Pienaar 1963, 1964 & Pienaar *et al.* 1980). Domestic cats, although known to have hybridized with the indigenous *Felis lybica* within the Park (Pienaar 1964), are not known to have established a feral population there. The small southern African antelope *Pelea capreolus*, which is unlikely to have occurred in the area of the Park (Smithers 1983), was intentionally introduced prior to 1979 (Rautenbach *et al.* 1979). This introduction has been successful, the species being seen regularly in the Malelane area (15 on one day recently) (P. van Wyk, pers. comm.). This species is listed with a '?' in Table 1 as its original distribution is debatable.

The history of invasions

Possibly the first invasive species to be introduced into the area of the present Park is *Rattus rattus* which was apparently introduced south of the Limpopo River by Bantu in approximately A.D. 800 (Plug *et al.* 1979). These early villagers might also have brought the palm *Borassus aethiopum* into the northern areas of the Park. This species is a highly favoured food and alcohol-producing plant further north in Africa and mature plants were present in the Shingwedzi area in 1903 (Stevenson-Hamilton 1937) although the validity of this record has been queried (Codd 1951) and none are still extant (Gertenbach 1985). Fire and, possibly, elephants might have prevented their re-establishing themselves once the villages were deserted (Wicht 1969). Certainly a few remnant adult specimens still survive in the eastern lowveld outside the Park (Wicht 1969) but these are dying out and are not being replaced (Palgrave 1977). *Moringa oleifera* is thought by some authorities to have been introduced into southern

Africa by the Arab slave traders (Palgrave 1977). The tree euphorbia *Euphorbia tirucalli*, which is generally recognized as being indigenous throughout its range in southern Africa, was widely used as a hedge plant by Bantu villagers and was possibly introduced to eastern Africa from Angola by the Portuguese (Leach 1973). *Ricinus communis*, a native of tropical Africa, is not indisputably alien to the Park (Macdonald & Macdonald 1984). It is another species which, if indeed not native, may well have been introduced during the early Bantu invasion of the area.

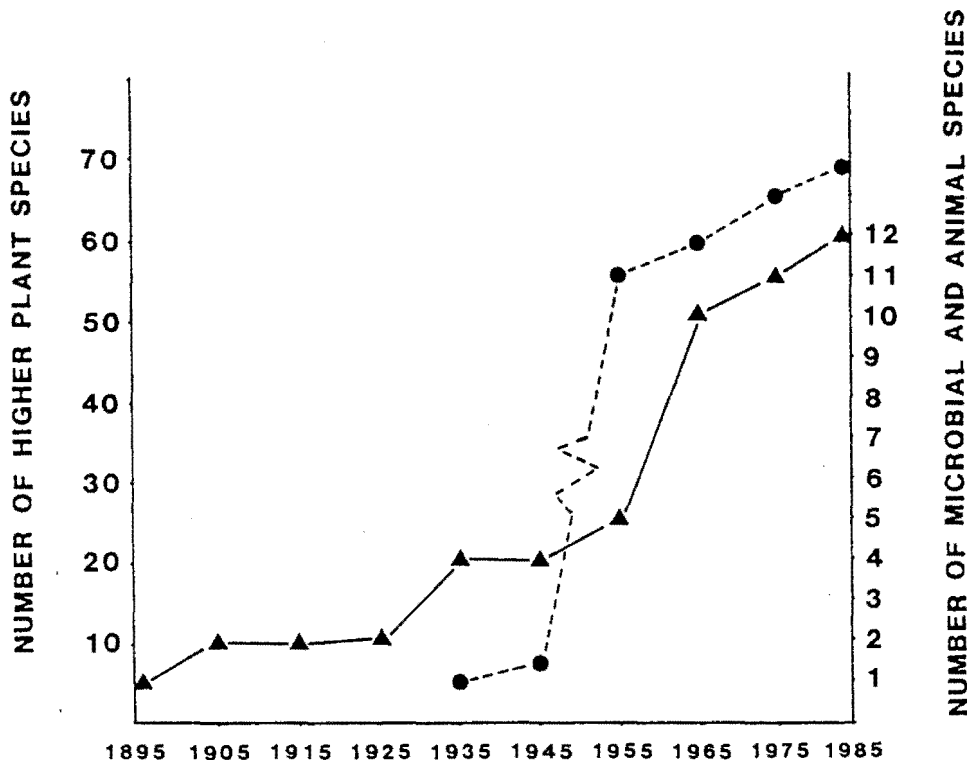


Fig. 1. The cumulative number of invasive introduced species known to be present in the Kruger National Park at ten-year intervals from 1895 to 1985: (▲—▲) Microbial and animal species, (●—●) Higher plants. About 42 spp. are omitted from the plant species graph as the dates of their first observation are unknown. They are listed by Van der Schijff (1969) who collected mainly in the early 1950s so the line between 1945 and 1955 is broken to indicate their probable first recording during this decade.

Most of the invasive introduced species have reached the area since the advent of European colonization (Fig. 1). Of the 15 faunal and microbial invaders six species are known to have been present in the first 50 years since 1895, with nine additional species being added in the next 40 years. Of the 113 invasive alien plants, 8 are known to have been present in 1945 with the remaining 105 species being recorded only since this date. However, this first figure is likely to be an underestimate as extensive botan-

ical collections were made in the area of the Park only from 1949 (Van der Schijff 1969).

What is known is that in the decade from 1975 to 1984 two new aquatic plants invaded the Park, *Salvinia molesta* in 1975 (Anon. 1975) and *Eichhornia crassipes* in 1977 (Anon. 1978), and one terrestrial species, *Solanum mauritianum*, was recorded as invading the Skukuza area of the Park for the first time in 1984 (W. P. D. Gertenbach, pers. comm.). *S. mauritianum* (*S. auriculatum*) had previously been known from the Malelane area of the Park (Van der Schijff 1969) but had apparently been eliminated from here by 1984 (Gertenbach 1984). This arrival rate of one new plant species every three to four years approximates that observed in the smaller Natal reserves (Macdonald & Jarman 1985).

The house sparrow *Passer domesticus* is the only introduced animal species for which the invasion has been reasonably well documented. First recorded at Skukuza restcamp in July 1957 (Wetmore 1957), it was present at the Letaba restcamp by September 1959 (Van Bruggen 1960) and at Shingwedzi by May 1961 (Harwin & Irwin 1966). By 1969 Kemp (1969) could state 'recorded at all the camps in the Park. A very common breeding resident around human habitation.' Its status in July 1984 was the same as in 1969 (Macdonald, unpublished observations).

The pattern of invasions

There are two main means of entry of introduced species into the Park. Either they are brought in, sometimes intentionally, by man or they invade down the influent rivers. Most of the pathogens were presumably brought in with domesticated animals, in particular those associated with the canids. In the case of anthrax, Pienaar (1960) postulates that infected carcasses were washed into the Park by floodwaters as an outbreak had occurred outside the north-western boundary the year before the first observed outbreak in the Park.

The introduced fish and aquatic molluscs were presumably brought in by influent waters. Most of the introduced plants causing serious problems were possibly also brought in by these rivers. However, several of the invasive introduced plants were originally introduced intentionally into restcamp and staff gardens. By 1951 Codd could already list 17 tree and shrub species that had been so introduced. It is noteworthy that *Melia azedarach*, whose presence in the Park has in recent years mainly been ascribed to waterborne seed dispersal down the influent rivers (Van Wyk 1967), was recorded as being cultivated in Skukuza, Malelane and Crocodile Bridge restcamps in 1951. The species was known to be established only in areas of natural vegetation along the banks of the Crocodile River at Malelane at this date (Codd 1951).

Once in the Park most of the serious spread continues to be by water although man-assisted spread can be important. An example of this is *Xanthium strumarium* which is spread mainly by water-flow along several of the major rivers. However, riversand is used for road-building operations and this has resulted in the much wider distribution of the species within the Park (Gertenbach 1984). Similarly the aquatic plant *Pistia stratiotes* has been cultivated in restcamp ponds and this practice has possibly led to the species invading the Sabie River. It might not simply be coincidental

that the invasion of the isolated Mtshawu Dam by *Salvinia molesta* was noted 'a few years' after the rare fish species *Serranochromis intermedius* had been translocated to this dam from elsewhere in the Park (Anon. 1975). The possibility exists that a fragment of *S. molesta* was introduced into the dam during this translocation. An alternative explanation for the invasion of this vegetatively reproducing species is that it was brought in by waterfowl (P. van Wyk, pers. comm.).

If each of the 26 invasive plant species rated as having a moderate or severe impact within the Park is classified according to its *main* means of dispersal (deduced from the pattern of its distribution and observations on dispersal both in the Park and elsewhere in the region), the following results emerge: Thirteen of the species are primarily dispersed by water, ten by animals (taking biotic dispersal of *Lantana camara*, *Opuntia* spp. and *Datura stramonium* to be more significant than water dispersal), one by wind (*Jacaranda mimosifolia*) and two by mechanical dispersal (*Agave sisalana* and *Ipomoea purpurea*). This analysis relates only to that part of the dispersal process *after* human translocation. In many cases, e.g. *A. sisalana*, *M. azedarach*, *L. camara*, *X. strumarium*, and *P. stratiotes*, long-distance intercatchment dispersal is almost entirely due to man.

The densities of introduced species within the Park are generally low. Most of the faunal invaders have been recorded at only a few localities, e.g. *Mus musculus* at one ranger's outpost (Pienaar *et al.* 1980) and the aquatic mollusc *Limnaea columella* at only three of the 128 localities searched (Oberholzer & Van Eeden 1967). Densities of most introduced plant species within the Park are much lower than is currently the case in comparable environments elsewhere in southern Africa (Macdonald & Macdonald 1984 & unpublished data). Exceptions are the floating hydrophyte species which have formed complete mats over certain of the rivers for short periods in the recent past (Anon. 1980, 1983) and *Xanthium strumarium* and *Lantana camara* which have formed extensive, dense stands along several of the rivers (National Parks Board files; Anon. 1978; Macdonald & Macdonald 1984). The total absence of introduced plants, at least of conspicuous tree and shrub species, from large tracts of the frequently-fired savanna vegetation that covers most of the Park is considered to be due, at least in part, to the absence of introduced species adapted to this fire regime. The conspicuous herbaceous species are similarly most frequent in fire-protected habitats, such as riverine strips, although several species are also found along road verges (Macdonald & Macdonald 1984).

Impacts of invasive species

The invasive species were categorized as giving rise to slight, moderate or severe impacts (Table 2). A slight impact is one where the species, at current infestation levels, is considered to influence seriously either populations of native species or ecosystems functioning within the Park. A severe impact is one where it is considered that *uncontrolled* infestations have reduced or could seriously reduce the densities of native species or markedly alter some aspect of ecosystem functioning within the Park. Moderate impacts were allocated to intermediate cases. In the absence of quantitative data these impacts were rated subjectively. Information recorded by the Park author-

Table 2
Annual expenditure on alien plant control operations
in the Kruger National Park

Year	Actual Rands	Inflation corrected 1983 Rands	Main species controlled	Total no. of individuals removed	Source reference no.
59/60	298	1 637	Lantana, Melia	12 671	61
60/61	637	3 461	Lantana, Melia	19 675	61
61/62	882	4 700	Others, Lantana	16 206 +	61
62	455	2 390	Lantana, Melia	1 882	61
62/63	489	2 569	Lantana, Melia	22 357	61
63/64	387	1 998	Lantana, Melia	6 703	61
64/65	180	900	Lantana, Melia	17 282	61
65/66	(?)5	()	Lantana, Melia	38 214	61
66/67	224	1 053	Melia	43 616	61
1981	57 000	74 015	Lantana, Salvinia	N/R	11
1982	58 000	65 791	Lantana, Salvinia	N/R	11
1983	58 000	58 000	Lantana, Salvinia	N/R	11

ities and by myself from within the Park and information on these species' behaviour elsewhere in southern Africa was used to make the ratings.

The introduced pathogens were all rated as having severe impacts. The rinderpest virus caused large reductions in the density of susceptible native ungulates (Stevenson-Hamilton 1937). These reductions are thought to have resulted in tsetse flies, *Glossina* spp., disappearing from the area of the Park. This virus has apparently died out in southern Africa (Neitz 1965). *Bacillus anthracis* is considered an important introduced organism within the Park (W. P. D. Gertenbach, pers. comm.). The massive effect that this organism can have on indigenous ungulate populations has been documented for the first (1959) and second (1960) outbreaks recorded in the Park (Pienaar 1960, 1961). The effects are so severe that costly immunization campaigns for the rare and highly susceptible roan antelope *Hippotragus equinus* are now undertaken annually in the northern portions of the Park where anthrax is now considered 'endemic' (Pienaar 1983).

The introduction of four pathogens of the domestic dog *Canis familiaris* is considered to have given rise to the marked reductions in the densities in the Park's indigenous canids, *Lycaon pictus*, *Canis adustus* and *C. mesomelas* (Anon. 1937 to 1945, Neitz 1965, Pienaar *et al.* 1980). The pathogens involved are the European variant of the rabies virus, the canine distemper virus, *Ehrlichia (Rickettsia) canis* and *Babesia canis* (Neitz 1965). Two other organisms which are thought to have been introduced into the Park are those responsible for brucellosis, *Brucella abortus* and bovine tuberculosis, *Mycobacterium bovis* (W. P. D. Gertenbach, pers. comm.). The impacts of these last two pathogens are uncertain but likely to be severe.

The floating aquatic fern *Salvinia molesta*, the tree *Melia azedarach*, the shrub *Lantana camara*, the two floating aquatic flowering plants *Eichhornea crassipes* and

Pistia stratiotes, the jointed cactus *Opuntia aurantiaca* and the herbaceous annual *Xanthium strumarium* are the only other introduced species rated as having a severe impact. Eight species of trees and shrubs and ten other flowering plant species were rated as having moderate impacts.

The only faunal invader considered likely to have a moderate impact was the fish *Cyprinus carpio*. However, it should be stressed that no information is available as to the density of the species within the Park and this rating is made on the basis of the species' environmental impact elsewhere in southern Africa (Harrison 1954). All the other invasive species are considered to have only slight impacts.

With the exception of rinderpest and the tsetse fly there is as yet no indication that any introduced species has resulted in the local extinction of an indigenous species within the Park. Indeed, if the floating hydrophyte *Pistia stratiotes* is in fact introduced to the northern rivers of the Park and not indigenous to them, there is the possibility that introduced plants have in fact been responsible for the addition of a new species to the Park's avifauna. The species involved is a tropical plover *Vanellus crassirostris* which feeds on floating hydrophyte mats (Maclean 1985) and which was first recorded from the Luvuvhu River in the Park in 1969 (Kemp 1974). This plover has recently expanded its breeding range in Zimbabwe in response to infestations of another introduced hydrophyte, *Salvinia molesta* (Hancock 1985; Hustler 1985). The introduced floating hydrophytes have certainly given rise to a new habitat within the Park and another bird species, the jacana *Actophilornis africanus*, has also expanded its population, in this case in response to the infestation of *Eichhornea crassipes* on the Crocodile River (Macdonald & Macdonald 1984).

Of all the introduced organisms it would appear that pathogens have come closest to eliminating a vertebrate species from the area, with the eland *Taurotragus oryx* apparently being totally eliminated from the northern portion of the Park until 1931, following the rinderpest epizootic of 1896 (Anon. 1931) and all three indigenous canids being reduced to critically low densities over the period 1937 to 1945 (Anon. 1937 to 1945). Although the causal organism or organisms in the latter decline were not rigorously determined, 'The type of sickness to which they [*Lycaon pictus*] have certainly fallen victim during the last six or seven years . . . is probably akin or identical with the very fatal and novel type of dog disease which killed all the domestic dogs [*Canis familiaris*] some ten years ago. . . . I have not personally seen a wild dog dead of sickness but natives who say they have describe the symptoms as similar to those which the domestic dogs showed' (Anon. 1937). Later the mortality in *L. pictus* was attributed to *Ehrlichia canis* (Anon. 1938) and that in the two jackals to the canine distemper virus (Anon. 1943). All three populations have subsequently recovered in numbers, presumably as a result of a build-up of immunity to these pathogens (Reich 1977; Pienaar *et al.* 1980).

The only known genetic or evolutionary effect of an introduced species in the Park is the hybridizing of the domestic cat *Felis catus* with the indigenous *F. lybica* (Pienaar 1964). This is occurring throughout southern Africa and poses a severe threat to the genetic integrity of *F. lybica* (Smithers 1983). How extensive the genetic pollution of the Park's *F. lybica* gene pool has been is uncertain.

THE CONTROL OF INTRODUCED SPECIES

The invasive species were rated as to whether they had already been eliminated from the Park or, where this has not been achieved, whether or not available technology made their control feasible (Table 1).

Of the introduced pathogens only *B. anthracis* is currently being 'controlled' through the inoculation of highly susceptible species (De Vos *et al.* 1973), and, in the past at least, through the burning of infected carcasses during epizootics (Pienaar 1960, 1961). This latter approach seems to have failed and to have been abandoned in the Park in recent years although it has been adopted in other savanna reserves in southern Africa (Ebedes 1977). If the rinderpest virus once again reaches the Park plans have been made to inoculate 'breeding nuclei' of each of the susceptible ungulate species within the Park (Pienaar 1983). Most of the 'control' of introduced pathogens is being exercised by veterinary authorities outside the parks in southern Africa. The prophylactic vaccination of domestic cats *Felis catus*, to prevent the transfer of feline panleucopenia, is one of the few preventative measures being taken within the Park itself (De Vos & Lamprechts 1971; Young 1972). If the organism causing cat mange is in fact not native to the Park then this is an introduced parasite that has been 'largely eliminated' by capturing infected animals and treating them individually with 'parasite-destroying preparations' (Young 1972).

Salvinia molesta was first recorded from the small Mtsawu Dam within the Park in 1975 (Anon. 1975). Aerial spraying of the infestation using a range of herbicides was carried out annually until 1983 when two applications of Clarason appeared to have finally eliminated the species (Anon. 1984). As earlier annual reports contained statements to the effect that the species had been successfully controlled (Anon. 1976, 1978) only for subsequent reports to state that it had not (Anon. 1979 to 1982), this species is not rated as having been eliminated (Table 1). Dense infestations of this species on the influent Letaba River west of the Park's boundary (Gertenbach 1984; Macdonald unpublished observations) indicate that reinfestation of the Park is likely, even if the Mtshawu Dam infestation is successfully eradicated.

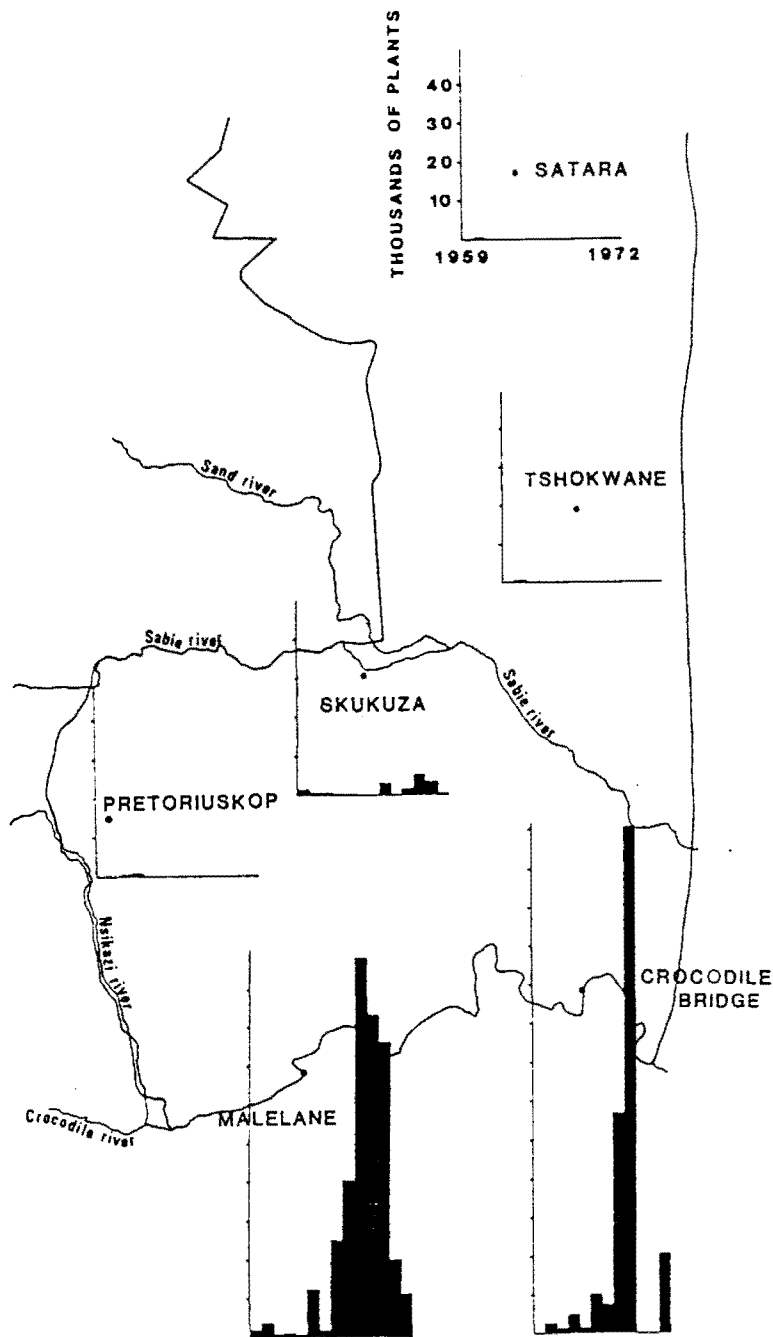
Pistia stratiotes, although present on the northern tropical rivers within the Park (Macdonald & Macdonald 1984), appears to cause no major problems, is not indisputably introduced and has never been controlled on these rivers. Although 'negative records' of aquatic plants are not strong evidence that the species was absent (as many botanists fail to collect them), it is possible that even in the tropical north of the Park the species is a recent introduction as it was not listed in either of the early Park floras (Obermeijer 1937; Van der Schijff 1969). However, in the subtropical south of the Park, the species 'appeared in the Sabie River' in 1982 (Anon. 1983), possibly as a result of its cultivation in a garden pond at Skukuza. In 1983 aerial applications of herbicides were carried out as the species was considered to pose 'a threat to the proposed series of weirs in the river and to the whole riverine ecology' (Anon. 1983). By July 1984 the species was still present in the Sabie albeit at low densities (Macdonald & Macdonald 1984).

The other introduced hydrophyte, *Eichhornea crassipes*, which first invaded the Crocodile River within the Park in 1977 (Anon. 1978) had not yet been subjected to

control by 1984 (Anon. 1984) as any action was considered futile as long as the headwaters outside the Park's boundaries remained infested (Anon. 1978, 1979, 1981).

Agave sisalana was initially cultivated within the Park (Gertenbach 1984). Fortunately, dispersal of the species is limited; infestations generally being found only in the immediate vicinity of initial plantings (Macdonald, unpublished observations). Control was first recorded in 1965 in the Crocodile Bridge area (Van Wyk 1967; Anon. 1967). By April 1973 a total of 302 plants were recorded as having been removed from this area, 8 000 plants from the Malelane area, 324 from the Skukuza area, 280 from Kingfisherspruit and 131 from the Satara area. By April 1975 only a further 250 plants were recorded as having been removed throughout the Park (Anon. 1968 to 1975). The species is not mentioned in subsequent annual reports, although in 1984 it was recorded as still being present in cultivation and as uncontrolled infestations within the Park (Gertenbach 1984).

The tree *Melia azedarach* was first recorded as being controlled in 1959 (Van Wyk 1967). This species had spread into the Park along the banks of influent rivers prior to 1948 (National Parks Board files). Infestations along the Crocodile River are thought to have originated from two trees planted in the late nineteenth century on the Kaap River tributary at Noordkaap Station, approximately 30 km west of the boundary (Van Wyk 1967). The numbers of individuals recorded as being removed annually from various districts within the Park are presented in Fig. 2. It is apparent that the control of small infestations away from the major influent rivers of the Park proved simple and in most cases a single operation sufficed to eradicate the entire infestation (Satara, Tshokwane and possibly Kingfisherspruit). At Pretoriuskop where the infestation was presumably on the upper Nsigazi catchment—which river is almost all within the Park—complete control was apparently achieved by 1962. However, along the Sabie (controlled from Skukuza) and Crocodile rivers (controlled from Malelane and Crocodile Bridge), which have extensive river lengths outside the Park, the number of plants removed tended to increase with time and eradication had not been achieved by 1973. Following the above-average rainfall of the mid-1970s *Melia*, along with other alien species, was recorded as having once again 'got the upper hand' in 1977–1978 (Anon. 1978). A five-year plan to clear both these rivers was then drawn up and additional labour was budgeted for this purpose. However, in 1979 it was reported that control had been initiated along the lowest stretch of the Sabie within the Park and that it was 'now relatively clean from the gorge to the highwater bridge' (Anon. 1979). In 1980–1981 it was reported that the Sabie River had been cleared between Skukuza and the eastern boundary (Anon. 1981). In 1981 a permanent post was created for a senior official who would oversee pollution and alien plant control operations (Anon. 1982). It was only in 1983–1984 that a start was made with a systematic clearance of aliens from the Park's western boundary (Anon. 1984). In this year it was reported that the upper 6 km of river-course had been cleared, although most of the infestations here were presumably of *Lantana camara*, with only 47 *M. azedarach* plants recorded as having been removed (Anon. 1984). Control of *Melia* along the Sabie below Skukuza was virtually complete by July 1984 while infestations were still considerable along the Crocodile River (Macdonald & Macdonald 1984). A



• Fig. 2. The annual number of *Melia azedarach* plants recorded as being removed from different districts within the Kruger National Park from 1959 to 1972: (■) annual number removed. The axes on all graphs are at the same scale as for Satara.

satisfactory level of control on the Crocodile River is made virtually unattainable by the fact that the river's southern bank is owned by private farmers who, in most cases, are doing nothing to control *M. azedarach* infestations. The possibility of new infestations arising within the Park has to be continuously watched for: in July 1984 it was observed that an individual of this species had been planted in a picnic-spot garden in the north of the Park. Although it had been allowed to grow to reproductive size it had subsequently been detected, ringbarked and killed by Park officials (Macdonald & Macdonald 1984).

The control of the Park's other major woody plant invader, the shrub *Lantana camara*, has followed an almost identical course to that of *M. azedarach*. However, unlike *M. azedarach*, most of the infestations within the Park are considered to have originated from plantings in restcamp gardens (Brynard & Pienaar 1960). Whether this is so or not cannot now be determined; what is apparent is that the problem is undoubtedly most serious along the major influent rivers (Fig. 3). There are extensive infestations west of the Park and these are thought to provide a source of seed for the reinvasion of these rivers (P. van Wyk, pers. comm.). The Shingwedzi infestation provides an example of one that undoubtedly arose from an intentional planting: in 1971 it was discovered that 90 plants had been cultivated in the labourers' gardens at Shingwedzi in the north-east of the Park (Anon. 1972). In 1973-1974 a campaign had to be launched in this area and it was recorded that 10 924 individuals had been removed (Anon. 1974). No specific mention of this infestation is made between 1974 and 1984 (Anon. 1975 to 1984). By contrast, on the major influent rivers the problem has tended to increase with time (Fig. 3) and effective control had still not been achieved on any of these rivers by 1984 (Anon. 1984; Macdonald & Macdonald 1984).

The control of *L. camara* is even more difficult than that of *M. azedarach*, as it is more effectively dispersed by birds and as a result has a more diffuse infestation along the rivers, i.e. it is not so strictly confined to the river banks (Van Wyk 1967, Macdonald & Macdonald 1984). Control operations have thus to be carried out in a wider strip along both sides of infested rivers. In addition, the species is not as easily differentiated from native species of similar growth form as is *M. azedarach*. Detection of individual plants, in particular of small individuals, is thus less likely during sweep operations.

The two cactus species *Opuntia aurantiaca* and *O. vulgaris* have both been effectively controlled within the Park. It is not known how extensive the infestations of *O. aurantiaca* were, but the species is mentioned as being present by Van Wyk (1967). By 1984 it is stated to have been totally eradicated (Gertenbach 1984). That the invasion of this species was checked at an early stage is probably the single greatest achievement in the control of introduced organisms within the Park, as this species has proven to be an intractable problem once infestations have become established in similar environments elsewhere in South Africa (Zimmerman & Moran 1982). Based on its performance elsewhere in the subcontinent, this is one of only two terrestrial flowering plants that is not a shrub or tree rated as having a potentially severe ecological impact (Table 1).

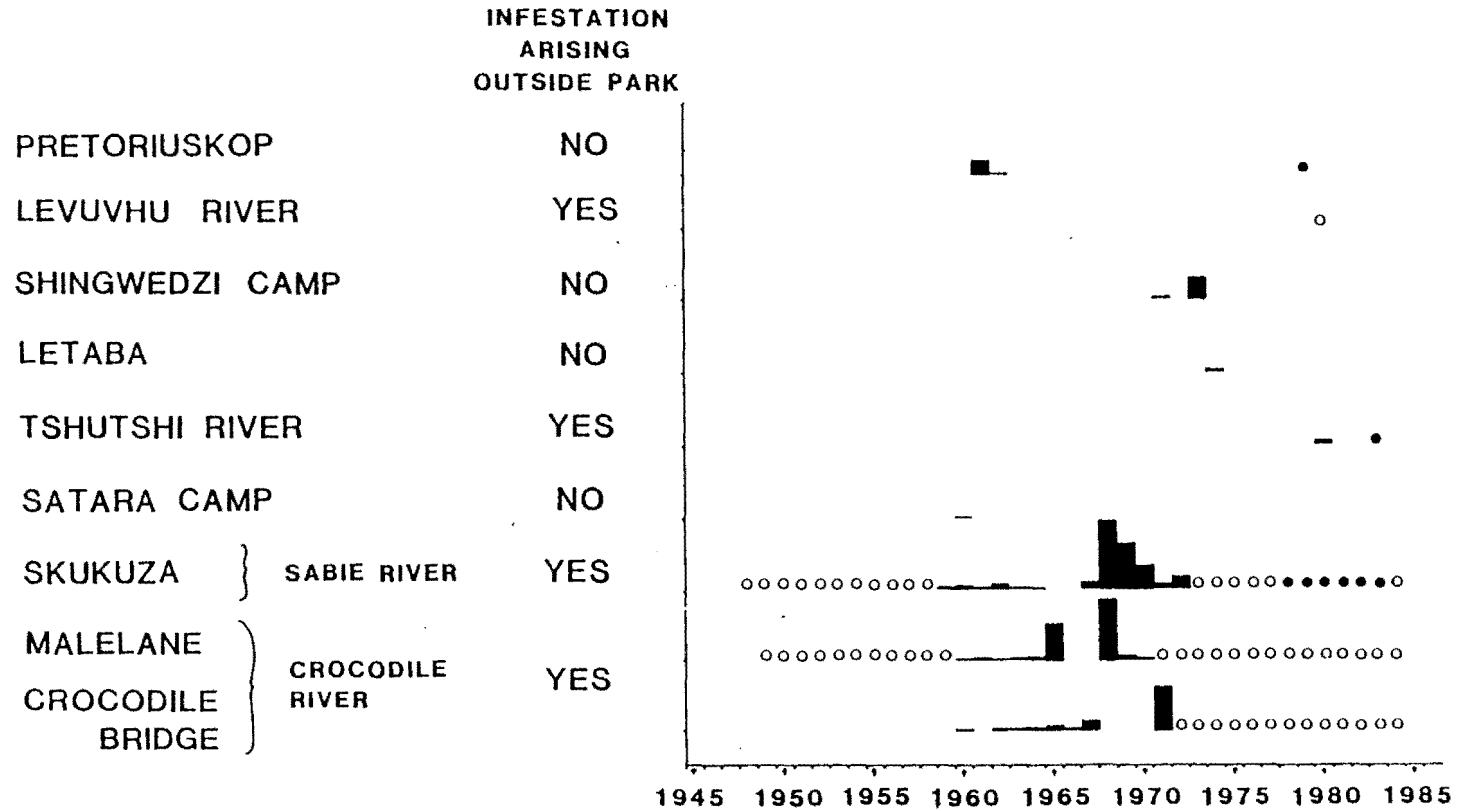


Fig. 3. The known occurrence of infestations of *Lantana camara* and the annual number of plants removed from the different districts of the Kruger National Park: (○) infestation present, (●) control operations known to be in progress, (■) annual number removed. Vertical scales for numbers of plants removed per annum differ between areas. Maximum numbers ($\times 10^3$) removed in any year were: Pretoriuskop—0,89; Shingwedzi Camp—10,9; Letaba—0,9; Tshutshi River—1,99; Satara Camp—0,005; Skukuza—391; Malelane—46,9; Crocodile Bridge—10,5.

The control of *O. vulgaris* has apparently been achieved using only physical removal and chemical treatments (Brynard & Pienaar 1960; Gertenbach 1984). Apparently the available biocontrol agent, *Dactylopius ceylonicus* (Zimmerman & Moran 1982) has not been intentionally introduced into the Park, although it might have spread into the Park of its own accord. None were visible on the few scattered individuals observed in the vicinity of Skukuza in 1984 (Macdonald & Macdonald 1984). It is doubtful whether this biocontrol agent would be able to reach its host plants at the low densities currently present in the Park. These low densities might be the result of utilization by native herbivores: plants of the genus *Opuntia* are known to have been eliminated by elephants elsewhere in South Africa (Macdonald 1984) and, in July 1984, the only *O. vulgaris* seen in the Park were in sites protected from browsing (Macdonald & Macdonald 1984). In the Pafuri region in the north of the Park it is reported that a control programme using chemicals was launched in 1977/78 and that the entire infestation between the Limpopo and Luvuvhu rivers had been eradicated by 1981 (Anon. 1978 to 1981).

The only shrub species rated as having moderately severe impacts which have apparently been successfully eradicated are *Acacia dealbata* and *Nicotiana glauca*. *A. dealbata* was recorded in the 1950s as 'penetrating the natural river bank foliage' at the Sabie Hippopool (Van der Schijff 1969: 50) but had apparently been totally eliminated by the 1980s (Gertenbach 1984; Macdonald & Macdonald 1984). *N. glauca* was recorded in 1958 as infesting virtually the entire length of the Olifants River within the Park (Brynard & Pienaar 1960) and as also being present on the Luvuvhu River (Van der Schijff 1969). *N. glauca* was recorded as having been totally removed by 1984 (Gertenbach 1984) and was not detected during a survey of introduced plants in the Park carried out in July 1984 (Macdonald & Macdonald 1984). The successful elimination of this species, which has proven to be difficult to control elsewhere in the sub-continent, is possibly the result of the following two factors. Sprayed plants of this species were observed to be debarked by a beetle *Malabris ? aculata* (Brynard & Pienaar 1960). It is possible that this species acted as an effective biological control agent when the plants were subjected to other stress factors. In addition, the species has been observed to be heavily utilized by indigenous herbivores elsewhere in southern Africa (Macdonald, unpublished observations) and it is possible that the build-up in ungulate populations in the Park since 1958 (Pienaar 1982; De Vos *et al.* 1983) has resulted in the overutilization of this species. The elimination of *A. dealbata* from the Park might also have been facilitated by this browsing pressure, as unarmed Australian *Acacia* species have been shown to be susceptible to overbrowsing elsewhere in southern Africa (Macdonald 1984, 1985). The possibly alien *Ricinus communis* was observed in July 1984 to be almost entirely restricted to sites protected from heavy grazing by ungulates (Macdonald & Macdonald 1984). The pressure exerted by native ungulate populations is considered an important factor limiting the invasion of a wide range of introduced plant species elsewhere in southern Africa (Macdonald 1984, 1985; Macdonald & Macdonald 1984).

The only two introduced herbaceous plants that have been controlled on a large scale are *Catharanthus roseus* and *Xanthium strumarium*. *C. roseus* is a very conspicu-

ous species which is well known as a garden plant throughout southern Africa and it is possible that its control has been motivated for aesthetic reasons. Large numbers of individuals are recorded as having been removed in the Skukuza area between 1968 and 1974 (Anon. 1969 to 1974). It was still present in small numbers on the Sabie River bed in this area in 1984 (Macdonald & Macdonald 1984). It is recorded as having also been controlled on the Letaba River in 1974 and on the Luvuvhu and Limpopo rivers in 1981 (Anon. 1975, 1982).

Although *X. strumarium* was the plant species for which control operations were first mooted (in 1948), it is the one currently having the greatest infestation (Macdonald & Macdonald 1984). Since 1969 it has been stated that control, using available technology, is a hopeless task, particularly so if the infested portions of influent rivers outside the Park's boundaries were to remain uncontrolled (Anon. 1969). Accordingly, the only control that has been undertaken has been for aesthetic reasons and has mainly been confined to the mowing of road-verge infestations and the hand-removal of plants in areas visible to tourists (Anon. 1976, 1979). As road-verge infestations of alien plants that 'make a bad impression' (Anon. 1981: 5) have increased, so has the amount of control effort dedicated to their control. Thus *Tagetes minuta*, which was already established along the Sabie and Luvuvhu rivers by 1948 (National Parks Board files), was recorded as being controlled along the road verges for the first time in 1980-1981 (Anon. 1981).

The only herbaceous plant that is considered to have been eliminated from the Park is *Bidens formosa*, another well-known garden species that has become widespread as a roadside weed in southern Africa. Twelve individuals are recorded as having been removed from the recently constructed Olifants/Satara pipeline in 1973 (Anon. 1974). Although most of the Park is possibly too dry for this species, this control might have pre-empted yet another large-scale infestation.

The latest development in the control of introduced species in the Park has been the initiation of pre-emptive control of 'new' introduced species on influent rivers outside the Park's boundary. In 1980 the occurrence of the shrub *Sesbania punicea* in the region was noted and it was stated that it had not yet appeared in the Park (Anon. 1980). In 1984 it was reported that 61 plants of this species had been removed from the northern Sand River, a tributary of the Sabie (see Fig. 2) outside the Park's boundary (Anon. 1984). Throughout the 1960s, 1970s and 1980s the importance of controlling water-dispersed species in the headwaters of influent rivers outside the Park's boundaries has been repeatedly stressed.

The only control of a faunal invader within the Park has been that of *Rattus rattus*. The attempted eradication of the population in Skukuza village began prior to 1964 (Pienaar 1964). How successful this control has been is uncertain. What is known is that this rodent, which was initially thought to have been restricted to Skukuza (Pienaar 1964), has subsequently also been found in Pretoriuskop (Pienaar *et al.* 1980).

Impacts of control programmes

Almost all control operations for introduced plant species have been based on herbicide applications. From 1958 to at least 1979 the herbicide 2,4,5-T (in the formu-

lation KOP250 and dissolved in diesel or paraffin) was the chemical used on tree and shrub species (Brynard & Pienaar 1960; Van Wyk 1967; Anon. 1979; Gertenbach 1984). This is the herbicide which was later found to have dioxin contaminants and which, as a result, has been totally discontinued (Turner 1977). In the case of *M. azedarach* the toxin was mainly applied as a basal-stem frill treatment and as a result should not have resulted in too much pollution of non-target species. However, in the case of both *L. camara* and *O. vulgaris* the herbicide was applied as a whole-plant spray application. Mortality of adjacent non-target plant species is likely to have been considerable while the chances of dioxin contamination of indigenous fauna could have been appreciable. This chance is increased by the fact that it has been observed that wild ungulates often browse the regrowth from treated trees (Macdonald, unpublished observations). In one known incident inadequately supervised labourers poured a whole container of herbicide into the soil and this resulted in the death of a number of the indigenous trees at this locality (P. Van Wyk, pers. comm.). In recent years the herbicide Glyphosate, which has no herbicidal action following soil contact, has been used (Gertenbach 1984). This should markedly reduce the possibility of undesirable environmental side-effects.

The aerial applications of herbicides to infestations of the floating hydrophytes *S. molesta* and *P. stratiotes* will have resulted in the mortality of non-target species. There are no data on these effects and no indications that any surveys of these possible side-effects were conducted.

An important impact of these control programmes is the amount of the Park's management capability that they have begun to occupy. Although budgeted costs for these operations tend to underestimate the actual cost (for example, research and management officer's time devoted to these operations is not included) it is apparent that they have risen considerably since programmes were first initiated (Table 2). If, as is likely, new species are introduced in the future, which will require new control operations to be launched, then it is imperative that control strategies are implemented which will ensure that operations for the control of existing infestations become smaller, not greater, in each successive year.

CONCLUSIONS

The main reason for undertaking this study of introduced species in the Kruger National Park was to assess the susceptibility of South Africa's most extensive natural area to invasions by these organisms. However, the review of human usage in the pre-historic, historic and post-proclamation periods illustrates that its classification as 'pristine' or 'natural' is debatable. The invasions documented above should rather be viewed as those occurring in semi-natural ecosystems which are generally less modified than those in the agricultural areas of South Africa.

An important distinction between the management of the Park and that of the agricultural areas is that active efforts have been made to maintain the full complement of native species in the Park. Another difference is that attempts have been made to prevent or reduce the invasions of alien species into the Park. The latter dif-

ference did not manifest itself immediately the area was set aside for purposes of nature conservation: awareness of the problem posed by introduced species only arose approximately 40 to 50 years after the original proclamation of the reserve (approximately 20 years after it became a National Park). The first effective control programmes and policy statements came some ten years after this growth in awareness.

Most of the introduced species were first recorded in the Park after 1945. This might simply be an artefact due to increased study in later years. However, the upsurge in tourism in recent decades has markedly increased opportunities for the inadvertent introduction and subsequent establishment of introduced species.

Given the size of the Park and the wide variety of ecosystems it includes, it is perhaps remarkable that so few introduced species have become established. No definitely alien terrestrial vertebrates have managed to do so away from the immediate vicinity of human habitations. It is only in these transformed ecosystems that a few human commensals have been successful. Most of the introduced herbaceous plants, which comprise the majority of the alien flora, are similarly weeds mainly restricted to sites of intensive human disturbance. The carp found in some of the Park's rivers provides the only example of an alien vertebrate that has apparently been able to invade a 'natural' ecosystem. An alien mollusc in this habitat is one of the few introduced invertebrates known from the Park's natural ecosystems. Similarly, it is the rivers and their associated riparian habitats that show the most extensive invasions by introduced plants. However, substantial modifications in water quality and flow rates have almost certainly taken place in these rivers as a result of agricultural activities in the upper catchments and the construction of impoundments (Pienaar 1982, 1983). They might thus best be viewed as highly modified environments. If this is correct, then their observed susceptibility to invasion accords with the hypothesis that human disturbance favours these invasions (Macdonald 1984).

Herbivory by the Park's diverse native fauna has been indicated as possibly reducing the success of several alien plant invasions, e.g. those of *Acacia dealbata*, *Nicotiana glauca*, *Opuntia vulgaris* and *Ricinus communis*. Predation by large carnivores might have prevented the establishment of feral populations of any of the larger mammal species that have been introduced. Certainly the domestic livestock herds brought into the Park and adjacent areas in earlier years had to be continuously protected through carnivore destruction campaigns (Pienaar 1982). These biotic effects, possibly combined with the highly seasonal regime of water availability and the frequent occurrence of fire, have given rise to the current situation where very few introduced species are to be found in the savannas which cover most of the Park. Several pathogenic micro-organisms affecting indigenous mammals appear to be the only introduced organisms which have shown widespread and important invasions in these areas.

Since most of the mammals affected by these pathogens appear to have built up some resistance to their deleterious effects, at least at the population level, the most serious ecological impacts of introduced species are currently those of plants invading the Park's rivers. The control of these invasions has become increasingly demanding

of both funds and manpower. In certain cases the reinvasion of the river from upstream appears to make the control of the species within the Park impossible (e.g. *Eichhornea crassipes* and *Xanthium strumarium*) or very difficult (e.g. *Lantana camara* and *Melia azedarach*). Integrated management of these species throughout the entire catchment would appear to be essential. Alternatively, recurrent expenditure on controlling this reinvasion must be budgeted for indefinitely. The biological control of each of the above species should be investigated. The importance of continual vigilance for new invasions by the Park authorities is emphasized by the recent rate of invasion by 'new' species. Already this vigilance has paid dividends in the case of three introduced plants, *Bidens formosa*, *Salvinia molesta* and *Sesbania punicea*. These species appear to have been brought under control as a result of the initiation of control operations early in the invasion. In the case of *S. punicea*, the control was, for the first time in Park history, pre-emptive: the plants were removed from a riparian area upstream of the Park's boundary.

That the Park's authorities are learning from past experiences with introduced organisms is shown by the systematic surveying of staff gardens in the Park during 1986. All invasive plant species had to be removed immediately (W. P. D. Gertenbach, pers. comm.). Provision has even been made for the field inoculation of 'breeding nuclei' should rinderpest or some other introduced pathogen threaten the survival of the Park's large mammals (Pienaar 1983). The first full-time post has recently been created for a senior staff member whose sole duty it will be to plan and execute the alien plant control operations (W. P. D. Gertenbach, pers. comm.). With these and other recent developments, such as the adoption of biological control methods and sound strategies for the control of riverine and riparian invasions, it seems likely that the invasion of introduced species into the Kruger National Park can be contained indefinitely.

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The Invasion of Introduced Species into Nature Reserves in Tropical Savannas and Dry Woodlands

I. A. W. Macdonald

Percy FitzPatrick Institute of African Ornithology,
University of Cape Town, Rondebosch 7700,
Republic of South Africa

&

G. W. Frame*

International Union for Conservation of Nature and Natural Resources,
Avenue du Mont-Blanc, CH1196 Gland, Switzerland

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ABSTRACT

*The invasions of introduced species into five reserves in tropical savannas and dry woodlands are described. Vascular plants are the group having the most introduced species; invasions are least important in dry, regularly burned savannas, more important in moist, derived savannas (where scrambling shrubs are invading) and most important in wetlands (where trees, shrubs, herbs and aquatic macrophytes are invading). Control, which should be initiated early in an invasion, is being implemented for only a few species. Water-dispersed plants and herbaceous weeds are generally impossible to control using current technology. Biological control measures are urgently required for some invasive shrubs (e.g. *Chromolaena odorata*). Introduced vertebrates are generally less important, but exceptions are large mammalian herbivores in Australia and several near-native ungulates in southern Africa. Predation apparently limits the number of successful vertebrate invasions. Introduced mammalian pathogens have had severe ecological effects in Africa. Invertebrate invasions require more research.*

* Present address: P/a ADEFA, BP 5570, Ouagadougua, Burkina Faso.

INTRODUCTION

The savanna and dry woodland biomes cover large tracts in the tropics and subtropics of South America, Africa, Asia and Australia (Udvardy, 1975). This review of the occurrence, impacts and control of introduced species in nature reserves of these biomes concentrates on case studies of three areas in Africa, one in Indonesia and one in Australia (Table 1). The discussion of the trends emerging from these case studies incorporates published literature relating to reserves in other areas. The approach adopted, terminology and definitions are those described in Usher *et al.* (1988—this issue).

THE SERENGETI-NGORONGORO ECOSYSTEM

Most of the Serengeti-Ngorongoro Ecosystem lies within the 12 800 km² Serengeti National Park and the 8290 km² Ngorongoro Conservation Area in Tanzania and within the 1510 km² Masai-Mara Game Reserve in Kenya. The vegetation is a mosaic of *Acacia* woodlands except in the Serengeti National Park and the Ngorongoro Conservation Area where about 23% and 44% is grassland, respectively (Frame, 1986). The flora and fauna have been described in Sinclair & Norton-Griffiths (1979). Approximately 24 000 Maasai pastoralists live in the Ngorongoro Conservation Area and they graze more than 360 000 cattle *Bos indicus*, sheep *Ovis aries*, goats *Capra hircus* and donkeys *Equus asinus*.

Introduced species have not been considered to pose a major threat anywhere in the ecosystem. The only invasive introduced vertebrate species are the black rat *Rattus rattus*, which is known only from Seronera village within the Serengeti National Park (Senzota, 1982), and a bream *Tilapia* sp. (Table 2). The latter was introduced to the freshwater springs in the Ngorongoro Crater in the 1960s. The crater has no native fish species and the introduced *Tilapia* has thrived with no apparent deleterious ecological effects.

Of the twelve apparently introduced vascular plant species, only four are possibly having any significant ecological effects. *Tagetes minuta* is mainly restricted to disturbed road verge sites but has become important in a restricted portion of the ecosystem's high-altitude grasslands, where, in an 8 km² area of bushed short grassland, it thrives under a regime of heavy grazing (by cattle and wild herbivores) and intensive soil disturbance by mole rats *Tachyoryctes daemon*. Where these two biotic disturbance factors were most intense, *T. minuta* had effectively replaced the native grasses over an area of 10 to 15 ha in 1973.

The finger euphorbia *Euphorbia tirucalli* is thought to have been introduced to East Africa in the prehistoric period (Dale & Greenway, 1961). In the Serengeti ecosystem it is common in the driest locality, Oldupai

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TABLE 1
 Details of the Reserves Studied

<i>Reserve name</i>	<i>Country</i>	<i>Coordinates</i>	<i>Altitude (m, a.s.l.)</i>	<i>Rainfall (mm)</i>	<i>Size (km²)</i>	<i>Year of establishment</i>
Serengeti-Ngorongoro Ecosystem	Kenya and Tanzania— East Africa	1°15'S to 3°26'S and 33°52'E to 35°42'E	1200-1800	400-1000	35 500	Serengeti NP <i>de facto</i> 1929, proclaimed 1951 Ngorongoro CA 1959 Masai-Mara GR <i>de facto</i> 1948, proclaimed 1974 <i>de facto</i> 1898, proclaimed 1926
Kruger National Park	Transvaal— South Africa	22°20'S to 25°31'S and 30°50'E to 32°02'E	122-839	440-750	19 482	<i>de facto</i> 1898, proclaimed 1926
Hlululuwe-Umfolozi Game Reserve	Natal— South Africa	28°00'S to 28°26'S and 31°43'E to 32°09'E	60-750	650-985	900	1895
Baluran National Park	Java, Indonesia	7°50'S and 114°25'E	0-1247	900-1600	250	<i>de facto</i> 1930, proclaimed 1980
Kakadu National Park	Northern Territory— Australia	12°10'S to 13°30'S and 132° to 133°E		c. 1388	12 700	1979

TABLE 2
 Numbers of Native and Introduced Species, Recorded from the Serengeti-Ngorongoro Ecosystem, by Taxonomic Groups

Taxonomic group	Number of species						Sources of data	
	Native			Introduced				
	Endemic to:		Not endemic	Total	Total	Invasive		
	1000 km ²	East African Woodland/Savanna province						Africo-tropical realm
Pathogenic micro-organisms	?	?	?	?	18	2	2	Sinclair (1979) & Frame <i>et al.</i> (1979)
Vascular plants	?	?	?	?	456	12	12	Herlocker & Dirschl (1972)
Ferns and allies	?	?	?	?	11	0	0	P. J. Greenway (pers. comm.) &
Gymnosperms + angiosperms	?	?	?	?	445	12	12	A. R. Jonker (pers. comm.)
Molluscs	?	?	?	?	9	0	0	
Amphibians	?	?	?	?	24	0	0	Elzen & Kreulen (1979) & Kreulen (pers. comm.)
Fish (freshwater)	?	?	?	?	1*	1	1	
Reptiles	?	?	?	?	66	0	0	Kreulen (1979 and pers. comm.)
Birds	0	4	328	164	496	0	0	Schmidl (1982)
Mammals	?	?	?	?	118	1	1	Swynnerton <i>et al.</i> (1967) & Senzota (1982)

* This is almost certainly an underestimate. This group has not been adequately surveyed or reported on. The occurrence of numerous piscivorous birds in the ecosystem (Schmidl, 1982) indicates that fish are present in the west-flowing rivers. The total number of native species that might be present in the seasonal rivers flowing into Lake Victoria has been estimated at approximately 30 (M. N. Bruton, pers. comm.).

Gorge. It grows in loose tangled mats and is frequently eaten by black rhinoceros *Diceros bicornis* (Goddard, 1968).

Watercress *Rorippa nasturtium-aquaticum* was introduced to the Ngorongoro Crater, probably early in this century by European settlers wishing to use it for food. It has spread to form dense stands along about 1 km of one of the fast-flowing streams, and is heavily grazed by zebra *Equus burchelli* and eland *Taurotragus oryx* during the dry season. At Empakaai Crater, watercress was introduced into one of the streams on the outer eastern slope, probably in the 1950s or 1960s, but animal and human utilisation has prevented it from spreading. A few watercress plants were introduced to a stream inside Empakaai Crater in 1973 but were promptly eaten by wild herbivores or cattle. In Ngorongoro Crater and on the outer slope of Empakaai Crater, the watercress probably has displaced the indigenous aquatic plant, *Crassula granvikii*.

The only introduced plant that is common on the Serengeti plains is the Mediterranean annual legume, *Medicago laciniata*, whose seeds are thought to have been introduced attached to army coats sold to the Maasai after the Second World War. In general, introduced plants are unimportant in the grasslands and open woodlands of the Serengeti National Park. In the late 1960s it was determined that between 50% and 85% of the park's woodlands were burned each year (Owen, 1971). Most of the introduced plant species recorded from the park are not well suited to a regime of annual or biennial burning.

Introduced diseases have had profound effects on some ungulates and carnivores. Rinderpest (reviewed in Sinclair, 1979), which is believed to have been introduced into Africa in the 1880s, devastated Maasai cattle, blue wildebeest *Connochaetes taurinus*, African buffaloes *Syncerus caffer* and giraffes *Giraffa camelopardalis* in the Serengeti ecosystem from 1890 onward, but in 1963 the disease disappeared. Some Carnivora are subject to occasional epidemics of undiagnosed diseases, which sometimes appear to be distemper (e.g. Frame *et al.*, 1979). Cape hunting dogs *Lycaon pictus*, black-backed jackals *Canis mesomelas*, common jackals *Canis aureus*, and bat-eared foxes *Otocyon megalotis* are all susceptible. The Maasai who reside in the Ngorongoro Conservation Area, and who formerly occupied the entire ecosystem, possess dogs *Canis familiaris* and cats *Felis catus* in addition to their livestock. All of these species probably contribute to the transmission of diseases to wild mammals.

KRUGER NATIONAL PARK

The Kruger National Park is South Africa's oldest and biggest national park (Table 1). The park's major rivers all rise outside its western boundary,

running through farms and mining areas before entering the park. The landscapes, climate, vegetation and history of the park are described elsewhere (Gertenbach, 1980, 1983; Piennaar, 1983). This account of the invasions of introduced species into the park is a summary of a more detailed account (Macdonald, in press).

Most of the introduced species in the park are vascular plants (Table 3). Of the 113 species considered to have established self-seeding populations, only 26 were rated as having moderate or high ecological impacts (Macdonald & Gertenbach, in press). Of these, ten are trees and shrubs, *Lantana camara* and *Melia azedarach* currently being the most important. Both have extensively invaded riparian vegetation along the two major rivers in the south of the park, the Sabie and Crocodile Rivers. Smaller invasions have occurred on other of the park's affluent rivers and at scattered points within the park where these species had been injudiciously introduced to restcamp and staff gardens. In most of these latter cases it has been possible to eliminate the species using a combination of hand-weeding and spot-spraying with arboricides. However, where the plants occur along major rivers which have dense stands in their upper reaches outside the park boundary, their eradication within the park has not yet been achieved. In the case of the Crocodile River the situation is even worse as the southern bank is outside the boundary, in farmland where neither species is controlled. Both *L. camara* and *M. azedarach* are dispersed by water and frugivorous birds and their complete control along these rivers is made virtually impossible by the existence of reinvasion sources close to the boundaries and, more particularly, along the affluent rivers. The situation is similar for the majority of the park's 26 important introduced plant species; 13 are primarily water-dispersed and several of the 10 species which are mainly animal-dispersed are also water-dispersed.

Eighty-nine introduced vascular plant species are herbaceous weeds, many of which are associated with sites of human disturbance (Macdonald & Gertenbach, in press). The control of these is generally regarded as being impossible. The most important species, the large cocklebur *Xanthium strumarium*, was already well-established along the park's rivers by the 1940s, and it has been spread further in sand used for road-building activities. Like the majority of the park's introduced species, *X. strumarium* has been unable seriously to invade the regularly burned savannas of the park, which are largely free of introduced plants. By contrast, waterbodies within the park have been seriously invaded by the floating aquatic macrophytes, *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia molesta*. These are the vascular plant species considered most likely to give rise to serious ecological impacts within the park as they completely cover what were formerly open waterbodies. *Pistia stratiotes* and *S. molesta* have both

TABLE 3
 Numbers of Native and Introduced Species, Recorded from the Kruger National Park, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>						<i>Sources of data (mainly from Macdonald, in press)</i>
	<i>Native</i>			<i>Introduced</i>			
	<i>Endemic to:</i>		<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>	
	<i>South African Woodland/ Savanna province</i>	<i>Africo— tropical realm</i>					
Pathogenic micro-organisms	?	?	?	?	?	8	Neitz (1965, 1967) & De Vos & Lambrechts (1971)
Vascular plants	?	?	?	1771	156	113	Macdonald & Gertenbach (in press)
Ferns	?	?	?	26	1	1	
Angiosperms	?	?	?	1745	155	112	
Molluscs	?	?	?	73	4	2	Oberholzer & Van Eeden (1967), Van Bruggen (1966, 1968), & Sirgel (1979)
Ants	?	?	?	75	4	1	Prins (1964)
Fishes	?	?	?	50	1	1	Pienaar (1968, 1971, 1981)
Reptiles	30	71	3	104	0	0	Jacobson & Pienaar (1983) & Pienaar <i>et al.</i> (1983)
Birds	4	310	124	438	1	1	Kemp (1974)
Mammals	3	101	28	132	3 (+?1)	2 (+?1)	Pienaar (1963, 1964), Pienaar <i>et al.</i> (1980) & Rautenbach <i>et al.</i> (1979)

been controlled in campaigns which included the aerial application of herbicides. The former was largely eliminated from the Sabie River by 1985, four years after it first invaded the river. The latter was eradicated in 1983 from the small Mtshawu impoundment and the spring running into it, following nine years of intensive mechanical and chemical control (W. Gertenbach, pers. comm.). No control has been attempted on the extensive infestation of *E. crassipes* along the Crocodile River. This species first invaded the park in 1975 and from the outset it was park policy not to attempt control until the authorities responsible for the headwaters of the river were prepared to initiate control measures there.

The invasion of pathogens has seriously concerned the park's managers. The rinderpest virus, which entered the area in 1896, is the only introduced organism which is thought to have eliminated a native species from the area of the park. This is the tsetse fly *Glossina morsitans* which disappeared from the eastern Transvaal lowveld, apparently in response to the massive reduction in ungulate hosts that accompanied the rinderpest epidemic (Neitz, 1967). Eland were eliminated from the northern half of the park by rinderpest and only recolonised this area from the south more than 30 years later. There are several pathogens of the park's indigenous canids which are possibly introduced and which are thought to have been responsible for marked reductions in the abundance of the jackals, *Canis adustus* and *C. mesomelas*, and the Cape hunting dog. In addition, there is the suggestion that both cat flu and the mite *Notoedres cati*, causing cat mange, were introduced and have adversely affected the health of native felids.

The anthrax bacterium *Bacillus anthracis* is considered to have been introduced to southern Africa by man (Neitz, 1967). The first recorded outbreak occurred in 1959 and was attributed to infected cattle carcasses being washed down rivers into the park by flood waters (Pienaar, 1960). Massive mortalities in susceptible native mammal species have been recorded (Pienaar, 1960, 1961) and the disease has become 'endemic' (in the veterinary sense) in the northern portions of the park. Anthrax is considered to threaten the survival of the highly susceptible roan antelope *Hippotragus equinus* and accordingly a sophisticated and expensive aerial immunisation campaign is now carried out annually (Pienaar, 1983).

Very few introduced vertebrates have been able to establish populations within the park (Table 3) and most of these are restricted to transformed ecosystems, e.g. black rat, house mouse *Mus musculus* and house sparrow *Passer domesticus*. The domestic cat has been kept by staff within the park but, although recorded as interbreeding with the African wild cat *Felis lybica* (Pienaar, 1964), there are no indications that they have become feral. The southern African endemic antelope, *Pelea capreolus*, was introduced to the southern portions of the park in the 1970s and has established a small

breeding population. It is not known if it ever occurred naturally in the area and hence it is listed with a "?" in Table 3. The introduction of four other ungulates from central and southern Africa was proposed in the 1930s and 1940s but all of these attempts either failed or were aborted prior to the release of animals in the park. Bigalke (1947) stressed the undesirability of introducing non-native species to national parks and this seems to have heralded the beginning of a period in which unwise introductions were no longer undertaken. The only fish which has invaded the park, the common carp *Cyprinus carpio*, has done so unaided down the Olifants and Levuvhu rivers. Invertebrates are only poorly known. Of the four introduced molluscs, two are slugs restricted to staff gardens, one is an aquatic snail, *Lymnaea columella*, found at a few localities on influent rivers and the other is a terrestrial snail, *Acanthinula aculeata*, thought to have been introduced via the railway line that traverses the park. The four introduced ants are all human commensals of which only one, *Camponotus rufoglaucus*, is considered to occur away from human habitation. These introduced invertebrates are all considered to have only slight ecological impacts.

HLUHLUWE-UMFOLOZI GAME RESERVE

The reserve is situated in the first range of hills of the Natal escarpment where this abuts the eastern coastal plain of South Africa. Being an area of broken topography and varied geology and climate, the reserve holds an exceptionally diverse fauna and flora (Table 4). The environment, vegetation and recent history of the reserve have been described by Vincent (1970), Bourquin *et al.* (1971), Brooks & Macdonald (1983) and Whateley & Porter (1983).

The area of the present-day reserve was occupied by Iron Age communities, possibly from 1500 BP (Hall, 1979). This occupation had considerable impacts on vegetation and soils, the effects of which are still readily discernible (Feely, 1979). Even after proclamation there was bush-clearing, game-destruction and blanket aerial applications of organochlorine insecticides as part of a tsetse fly eradication campaign (Vincent, 1970). After the tsetse flies were eliminated, management in the form of bush clearance, carnivore and large herbivore population reduction and the fencing of boundaries has continued to reduce the 'naturalness' of the reserve (Brooks & Macdonald, 1983). Approximately one quarter of the reserve is burned annually to maintain the area's savannas (Macdonald, 1983). The tendency over the historical period has been for tree cover to increase throughout the reserve and it has been concluded that the open vegetation types are mostly of anthropogenic origin (Watson & Macdonald,

TABLE 4
 Numbers of Native and Introduced Species, Recorded from Hlululuwe-Umfolozzi Game Reserve, by Taxonomic Groups

Taxonomic group	Number of species					Sources of data		
	Native				Introduced			
	Endemic to:	Not endemic	Total	Total	Invasive			
	1000 km ² South African Savanna/ woodland province	Africo-tropical realm						
Pathogenic micro-organisms				?	1	1	Vincent (1970)	
Vascular plants	> 1	?	?	?	1 143	74	71	Porter (1974),
Ferns	?	?	?	?	17	0	0	Downing & Gibbs Russell
Gymnosperms	0	2	0	0	2	0	0	(1981), Macdonald (1983) &
Angiosperms	> 1	?	?	?	1 124	74	71	A. J. Wills (pers. comm.)
Ants	?	?	?	?	38	2	?	Prins & Cilie (1968)
Amphibians	?	?	?	?	26	0	0	Bourquin <i>et al.</i> (1971)
Fishes (freshwater)	?	?	?	?	21	0	0	Bourquin <i>et al.</i> (1971)
Reptiles	?	?	?	?	60	1	71	Bourquin <i>et al.</i> (1971),
								A. Knott (pers. comm.)
Birds	0	5	249	106	360	6	1	Macdonald & Birkenstock (1980),
								& Maclean (1985)
Mammals	0	3	63	17	83	9	4	Bourquin <i>et al.</i> (1971) &
								Smithers (1983)

1983). Currently, the reserve is a totally fenced enclave of highly managed natural ecosystems surrounded by densely populated and generally overgrazed subsistence farmland. All the reserve's major rivers arise outside its boundaries.

The important introduced plant species are all perennial woody plants, mainly trees (10 spp.), shrubs (12 spp.) and creepers (3 spp.). The American scrambling shrub, *Chromolaena odorata*, which is the most widespread introduced plant in the reserve, was first recorded in 1961 from a single locality, but by 1981 this wind-dispersed composite was already known from 154 of the 3700 500 m × 500 m grid squares within the reserve (Macdonald, 1983). Despite large-scale control programmes from 1978 to 1984, the area occupied by this species increased at an exponential rate (A. J. Wills, pers. comm.). *C. odorata* forms dense stands mainly in riparian vegetation and along the verges of forest patches. It is capable of growing through the canopy of native trees and shrubs and killing these through shading. An important ecological effect is that *C. odorata* is highly flammable and stands of the species carry fire from the regularly burned savannas and grassland into the canopies of forest and riparian trees. The ecotones between these communities are normally fire-excluding and most forest tree species are not fire-tolerant (Pammenter *et al.*, 1985). The net result is an attrition of forest patches and riparian fringe vegetation.

Several of the introduced woody plants produce fruits which are eaten and dispersed by native frugivores, e.g. *Melia azedarach* (the second most important species in the reserve), *Psidium guajava* and *Solanum mauritianum*. It has been suggested that the prolific production of these fruits could interfere with the dispersal of native fruiting species by these frugivores (Macdonald, 1983). Already it has been demonstrated elsewhere in Natal that an important native frugivore, the rameron pigeon *Columba arquatrix*, has switched its diet to one comprised almost entirely of the fruits of *S. mauritianum* (Oatley, 1984).

As in other reserves in Natal (Macdonald & Jarman, 1985), most of the introduced plants are invading along the banks of influent rivers. Between 1981 and 1985 two new woody plant invasions were recorded from the Umfolozi Rivers within the reserve: *Acacia mearnsii* (Macdonald, 1985) and *Sesbania punicea* (B. R. Culross, pers. comm.).

The least invaded habitat within the reserve was the regularly burned grassland. By 1981 only four introduced woody plants had been recorded in this habitat as compared to 11 on the forest edge and 12 in riparian habitats (Macdonald, 1983). In recent years *C. odorata* has invaded considerable areas of grassland in the higher rainfall northern portions of the reserve and it is likely that, currently, the least invaded habitat is the drier *Acacia* savannas in the south of the reserve. These are also regularly burned.

Browsing by native ungulates has been observed to limit the success of at least seven of the introduced woody plants (Macdonald, 1983, 1985). None of the herbaceous species is considered to pose a major threat to the reserve's ecosystems.

The only introduced reptile recorded from the reserve is a single individual of the American red-eared terrapin *Chrysemys scripta* (A. Knott, pers. comm.). This species has been introduced to several waterbodies in South Africa, presumably by aquarium enthusiasts (Newbery, 1984). The dumping of pet chelonians in nature reserves is recognised as a potentially serious conservation problem in the subcontinent (Greig, 1979) and it is predicted that *C. scripta* could become a major invader of wetlands (Newbery, 1984).

Of the birds, only the house sparrow has been able to maintain a breeding population within the reserve. The ring-necked pheasant *Phasianus colchicus*, intentionally introduced to the reserve in the 1930s, bred successfully for some years before disappearing. The Indian mynah *Acridotheres tristis*, which has successfully invaded much of Natal, has apparently been unable to breed in the reserve (Macdonald & Birkenstock, 1980). All colonising individuals of this species are actively discouraged, as with house sparrows at some of the outstations in the reserve in the 1950s. This policy kept some of these outstations free of house sparrows for several years (J. M. Feely, pers. comm.). The ostrich *Struthio camelus* was intentionally introduced in the 1940s but never bred. A subsequent introduction attempt was aborted in 1968 when the ethic of only re-establishing recently extinct native species in the reserve became the agreed policy of the Natal Parks Board (Macdonald & Birkenstock, 1980). The other unsuccessful bird species recorded were two domestic species, Muscovy duck *Cairina moschata* and pigeons *Columba livia*, which have escaped into the reserve but which have never bred there.

Amongst the mammals, attempts were made to establish several southern African species that were either non-native or questionably native to the reserve. Black wildebeest *Connochaetes gnou* and suni *Neotragus moschatus* both failed, even though the latter is native to areas within 40 km of the reserve. Both of these species live in habitats unlike those present in the reserve. Similarly, an early attempt to establish fallow deer *Cervus dama* failed. By contrast, introductions of giraffe (native to savannas c. 275 km north of the reserve—Goodman & Tomkinson, 1987) and impala *Aepyceros melampus* (native to similar savannas c. 100 km northeast of the reserve) have been highly successful. Both species have increased their numbers to the point where they were considered to be altering the habitat and population reduction operations have been initiated (Bourquin *et al.*, 1971; Brooks & Macdonald, 1983). The only other mammals that have established

feral populations have been black rats and domestic cats, which have remained around human habitations. Cats have been actively controlled as they were considered likely to be acting as reservoirs of cat flu (M. E. Keep, pers. comm.).

Rinderpest is an introduced pathogen that affected the reserve's native fauna. Although all the susceptible mammal species have apparently recovered to their original population levels (Bourquin *et al.*, 1971), the reduction it caused in the density of the yellow-billed oxpecker's *Buphagus africanus* mammalian hosts is thought to have resulted in this bird's local extinction (Stutterheim & Brooke, 1981). The mite causing sarcoptic mange is known to have been introduced when cheetah were re-established in the reserve from South West Africa in the late 1960s (M. E. Keep, pers. comm.). It is also likely to have been introduced on domestic dogs which hunt into the reserve from adjacent villages. Sarcoptic mange has been implicated in the decline of the black-backed jackal in the reserve over the last two decades (Keep, 1970); whether it was the primary cause is uncertain. The re-establishment of a lion *Panthera leo* population in the reserve over this period is an alternative explanation, c.f. Steele (1970). As in the Kruger National Park the possibly European 'canid' strain of the rabies virus (Neitz, 1967) has been recorded from dogs in the Hluhluwe-Umfolozi reserve. This disease also might have contributed to the decline in jackal numbers. Bovine tuberculosis has recently been found in African buffalo within the reserve (J. Flamand, pers. comm.).

BALURAN NATIONAL PARK

The Baluran National Park is located on the northeastern extremity of the island of Java. The topography is dominated by an extinct volcano, which rises from a coastal plain, and the park has 40 km of coastline. The area experiences a monsoon climate with a long dry season of 4–9 months duration (Anon., 1977). Although the whole island is classified as falling in Udvardy's (1975) 'Mixed island systems' biome, the detailed description of the park's vegetation indicates that it includes a savanna/woodland component (Anon., 1977). As is the case through most of South East Asia and Indonesia, the open vegetation types appear to be anthropogenic in origin with closed-canopy forest and woodland being present under pristine conditions (Wharton, 1968).

The park's alien flora (Table 5) is dominated by trees (7 spp.), shrubs (11 spp.) and climbers (3 spp.). Accounts of the vegetation of two other Javan parks—Ujung Kulong (Hommel, 1983) and Yang (Van der Zon & Supriadi, 1979)—indicate that two scrambling shrubs, *Lantana camara* and

TABLE 5
Numbers of Native and Introduced Species, Recorded from the Bahuran National Park, by Taxonomic Groups

Taxonomic group	Number of species						Sources of data		
	Native			Introduced			Total	Invasive	
	Reserve	Javan Province	Indomalayan Realm	Endemic to	Not endemic	Total			
Vascular plants	?	?	?	?	?	391	?	33	Anon. (1977) &
Ferns and allies	?	?	?	?	?	14	?	0	K. Kartawinata (pers. comm.)
Angiosperms	?	?	?	?	?	377	?	33	
Birds	0	6	75	60	60	141	0	0	Anon. (1977)
Mammals	0	0	22	3	3	>25	1 (+?)	1 (+?)	Anon. (1977)

Chromolaena odorata, which are both present in Baluran, are important in the more open savanna communities. However, other species present in Baluran which belong to genera with invasive introduced species in similar environments elsewhere are *Acacia arabica*, *Cissus quadrangula*, *Leucaena leucocephala*, *Opuntia eliator*, *Passiflora foetida*, *Ricinus communis* and *Sesbania grandiflora*.

No introduced bird species are recorded and the water buffalo *Bubalus bubalis* is the only listed introduced mammal (Anon., 1977). Both the water buffalo and the indigenous banteng *Bos javanicus* graze primarily in the small areas of savanna grassland (2.4 km²), seral monsoon forest (4.0 km²) and swamp/coastal forest (0.6 km²) in the southeast of the reserve (Anon., 1977). Concern has been expressed that competition from the water buffalo could be detrimentally affecting this last wild population of banteng in Java although a field investigation concluded that there was no evidence for competition. No control of water buffaloes was recommended until such time as they were shown to be adversely affecting the native biota. This *laissez faire* approach was further justified by the suggestion that anyway the park was no longer pristine (Ashby & Santiapillai, 1985).

The pig *Sus scrofa* is possibly an introduced species on Java. However, it has apparently been on the island a long time and is not known to be having any undesirable effects on native ecosystems. It was suspected that *S. scrofa* was outcompeting and possibly hybridising with the endemic Javan warty pig *Sus verrucosus*. However, research has indicated that the two species are segregated by different patterns of habitat utilisation and competition is not thought to be likely under current conditions (Blouch *et al.*, 1983).

KAKADU NATIONAL PARK

The Kakadu National Park is situated on the northern coast of Australia. The park is being proclaimed in stages with stage 1 having been proclaimed in 1979. The first stage of the park spans two of Udvardy's (1975) biogeographic provinces; the Northern Coastal and Northern Savanna Provinces. The former is classified as falling within the tropical dry or deciduous forest or woodland biome while the inland portion of the park falls within the tropical grassland and savanna biome. Much of the data on introduced species in the park (Table 6) comes from the Kapalga wetland system on the South Alligator River in the north of the park (Simbotwe & Friend, 1985).

The most important introduced plant in the park is the thorny shrub *Mimosa pigra* (Maddison & Salau, 1986; Skeat, 1986). This species was introduced approximately 80 years ago and is currently estimated to infest

TABLE 6
Numbers of Native and Introduced Species, Recorded from Kakadu National Park, by Taxonomic Groups

<i>Taxonomic group</i>	<i>Number of species</i>							<i>Sources of data</i>
	<i>Native</i>				<i>Introduced</i>			
	<i>Endemic to:</i>			<i>Not endemic</i>	<i>Total</i>	<i>Total</i>	<i>Invasive</i>	
	<i>1000 km²</i>	<i>Northern Coastal and Northern Savanna Provinces</i>	<i>Australian Realm</i>					
Vascular plants	?	?	?	?	1422	?	67	Skeat (1986)
Amphibians	?	?	?	?	> 17	0	0	Friend (1981) & Simbotwe & Friend (1985)
Reptiles	?	?	?	?	> 63	0	0	Braithwaite (1981), Simbotwe & Friend (1985) & Friend & Taylor (1984)
Birds	0	11	70	173	254	0	0	Blakers <i>et al.</i> (1984)
Mammals	?	?	?	?	> 30	?	> 5	Corbett (1981), Friend (1981) & Ridpath (1981)

300 km² in the Northern Territory. *M. pigra* forms impenetrable thickets in wetland areas and, if uncontrolled, could render the park's wetlands useless for the wide range of native animals that feed and breed there. First detected within the park in 1981, by 1986 there were 23 infestations known, ranging in size from a few plants to stands covering up to 4 ha. Elaborate control measures have been initiated (Maddison & Salau, 1986), including washing mud off vehicles entering the park, fencing all known infestations to prevent vehicles and feral mammals from spreading the seeds, and eliminating feral mammals from areas that are known to be infested. Small infestations are being controlled mechanically while large ones are subjected to herbicide applications (soil sterilants, spot spraying and aerial blanket spraying of foliar sprays have all been tried). An important component of the control programme has been the repeated monitoring of known infestations and systematic searching for new infestations. In 1986 four people were employed full time on the control programme and, due to the longevity of the seed, the programme will have to continue for at least ten years (Maddison & Salau, 1986).

The two floating macrophytes, *Eichhornia crassipes* and *Salvinia molesta*, were first discovered at a single locality in 1983 and both may have been intentionally and simultaneously introduced (Skeat, 1986). Manual control was effective in eliminating the small infestation of *E. crassipes* but *S. molesta* rapidly spread throughout the entire Magela Creek system. Herbicide control is considered impractical and currently the biological control agent, *Cyrtobagous salviniae*, is being introduced to the park (Skeat, 1986). Another plant species invading the wetlands is the tall African grass, *Brachiaria mutica*, which was intentionally introduced to the region as a pasture grass. Following the initiation of the feral water buffalo control programme in the mid 1970s, *B. mutica* increased rapidly. Even though its effects on the wetlands are thought to be considerable it is currently so widespread that control is considered impossible (Skeat, 1986).

Another grass, *Pennisetum polystachyon*, is invading dryland habitats within the park (it is thought to have spread from a thatched roof which was destroyed by a cyclone in 1974). It suppresses the native annual *Sorghum* grasses, which are currently the dominant component of the park's fuel load. Because *P. polystachyon* produces much greater fuel loads, the widespread replacement of *Sorghum* spp. by *P. polystachyon* could radically alter the park's fire regime. The control of this species is being accorded a high priority even though it is still rare within the park (Skeat, 1986).

Although no complete checklists of the park's reptiles and amphibians could be obtained, it appears that no introduced species occur in these groups (Table 6). However, it would seem that it is merely a matter of time before the introduced cane toad *Bufo marinus* reaches the park (Sabath *et al.*,

1981; Van Beurden, 1981). The species has already reached the eastern border of the Northern Territory and has been accidentally dispersed to Darwin, west of the park, on several occasions (Freeland & Martin, 1985). Wherever it has become established in Australia, it has reduced the populations of smaller native predators (Freeland, 1986). There appear to be no practical methods of preventing the cane toad from continuing its Australian range expansion.

Mammals are the only vertebrate group having introduced species within the park (Table 6). Ecological studies within the park (Corbett, 1981; Ridpath, 1981) and a detailed inventory of an area adjacent to the park (Kerle & Burgman, 1984) indicated that there are five introduced species—feral cat, horse *Equus caballus*, pig, cattle *Bos taurus* and water buffalo.

In the Kapalga wetland area of the park the water buffalo became the dominant herbivore, with densities of up to 50 km^{-2} and a mean biomass over all vegetation types of 4777 kg km^{-2} (Ridpath, 1981). Subsequently, more refined estimates in the same area gave an overall density of 13 km^{-2} and a biomass of 5200 kg km^{-2} (Ridpath *et al.*, 1983). In addition, maximum seasonal densities of other introduced species were 1 km^{-2} (feral cattle), 2 km^{-2} (horses) and 5 km^{-2} (pigs) (Ridpath, 1981).

The water buffaloes are thought to have markedly changed native habitats (Letts *et al.*, 1979). They concentrate during the dry season in moist habitats, such as the margins of permanent wetlands. At these times, particularly in years with a prolonged dry season, they can graze the herbaceous vegetation so heavily that various susceptible native plant species can be eliminated locally (Williams & Ridpath, 1982). Even more serious ecological impacts have been identified in the localised patches of monsoon forest which occur in the vicinity of these moist habitats (Braithwaite *et al.*, 1984). The buffalo move daily from feeding grounds on the river floodplains to rest in the shade of nearby forests. They use monsoon forest patches in preference to more open forest and some areas more intensively than others, the so called 'buffalo camps'. Quantitative study of 27 randomly selected sites in the park's forests indicated that a century of intensive buffalo use was correlated with radically altered patterns of foliage height diversity and with accelerated mortality of large trees. This is thought to be due to reduction in infiltration, correlated with soil compaction. The monsoon forest patches appear to be dependent on localised pockets of available ground water and the recharge of this water is apparently being seriously impeded. The secondary effects were extensive; the distributions of only 21% of 74 vertebrate species studied were apparently unaffected, herbaceous annual plants (including several important introduced species, e.g. *Cassia occidentalis* and *Hyptis suaveolens*) increased as a result of the disappearance of perennial ground vegetation, and the phenology of the surviving

perennial trees was substantially altered. It is uncertain whether severely affected monsoon forest patches will be able to recover, even if buffalo are removed, as the habitat is thought to be a relict from a more favourable climatic period (Braithwaite *et al.*, 1984).

It is planned to eliminate all feral ungulates, including buffalo, from northern Australia by 1992 as part of a national campaign to eradicate tuberculosis and brucellosis (Friend & Taylor, 1984). Control operations have necessitated the construction of buffalo-proof fences in the park (Friend, 1981). Although this has resulted in lower buffalo densities (Ridpath *et al.*, 1983) it remains uncertain whether eradication is feasible.

None of the other introduced mammals appears to have ecological effects as significant as those of the water buffalo. It has been suggested that removal of buffaloes might lead to increased problems with feral pigs (Ridpath, 1981). The control of these introduced animal and plant species is obviously the most expensive aspect of current biological management activities in the park.

DISCUSSION

Plant invasions are apparently being experienced less in the drier portions of these biomes; fire and herbivory by large native mammals appear to be limiting factors. Herbivory of an introduced mammal had this effect on *Brachiaria mutica*. Invasions tend to be most intense in both aquatic habitats (where a few South American floating macrophytes are universally a problem) and wetlands (including riparian zones) of these drier savanna reserves. In the moister areas, particularly where the savannas appear to be anthropogenic in origin, shrubs and scramblers such as *Lantana camara*, *Chromolaena odorata* (Ngampongsai, 1978), *Mikania scandens* (Ranjitsinh, 1984) and *Parthenium hysterophorus* (Ali, 1980), are seriously invasive, often on a biome-wide scale. These invasions, unless successfully combated, will have disastrous consequences for nature reserves. Biological control techniques will have to be perfected for the important species if there is to be any long-term hope for the survival of these ecosystems (Macdonald, 1983; Ranjitsinh, 1984).

The importance of initiating control measures early in an invasion is illustrated by the contrasting campaigns to eradicate the same aquatic weeds in Kruger and Kakadu National Parks. In the former, *Salvinia molesta* was eradicated chemically following its early detection in an isolated waterbody, whereas the control of *Eichhornia crassipes* is considered impossible as it was well-established in an entire river system by the time it entered the park. In Kakadu, the infestation of *S. molesta* was the more extensive of the two at

the time of their simultaneous detection and is now considered impossible to control using mechanical and chemical measures. The smaller infestation of *E. crassipes* was successfully eradicated manually. This principle also applies to different infestations of the same species in a reserve, as is illustrated by the variable success obtained in eradicating *Lantana camara* from different areas within Kruger National Park.

The ecological effects of introduced plants are diverse. Aquatic habitats (rivers, streams and marshes) are often radically transformed by a range of introduced species, all of which tend to form dense, monospecific stands. Where introduced plants markedly alter the distribution, amount and flammability of the fuel load, their effects can be considerable. More subtle effects, such as the postulated changes in native fruit-frugivore relationships, will manifest themselves slowly and will require detailed research for their detection.

The significance of the dispersal of introduced species down rivers flowing into nature reserves is shown in both the Kruger National Park and Hluhluwe-Umfolozzi Reserve case studies. The inclusion of whole catchments in any future nature reserves proclaimed in these biomes is justified on this ground alone.

Although, on present evidence, it appears that introduced invertebrates are not of major significance in the nature reserves of these savanna and woodland biomes, it should be borne in mind that these organisms have hardly been studied in these reserves. Pathogens have had major deleterious impacts on nature reserves in these biomes, at least in Africa. The presence of introduced pathogens in introduced mammals in northern Australia has prompted the agricultural sector to initiate control programmes. Given the *laissez faire* attitude towards introduced mammals in nature reserves that is generally found in this region (e.g. McIlroy *et al.*, 1986) it is unlikely that such an ambitious and expensive operation would have been launched for conservation reasons.

In trying to limit further deleterious introductions of pathogens and parasites there will be an increasing need for strict veterinary controls around nature reserves (e.g. De Vos & Lambrechts, 1971; Young, 1971). As these biomes characteristically hold populations of highly mobile large mammals, it will probably become necessary to fence them in their entirety, as has already been done in the two southern African case study reserves. It is important that the migratory behaviour of the dominant ungulates is understood and that boundary fences are located so that the ecosystem's major migration routes are not affected (Berry, 1981; Pienaar, 1983). The minimum requirements for these artificial barriers need also to be determined (e.g. Lewis & Wilson, 1977). Although veterinary fences have been called the 'fences of death' by southern African conservationists (e.g.

Owen & Owen, 1980), it may be that these fences are essential to the survival of these large mammal-dominated systems where introduced pathogens are involved (e.g. Berry, 1981).

In general, invasions by introduced vertebrates do not pose major problems in the nature reserves of these biomes. This is particularly true for small mammals, birds, reptiles and amphibians, in which groups introduced species are generally absent. The only global exceptions to this appear to be a few human commensal species which have established localised feral populations around sites of human habitation within these reserves, e.g. feral cats, black rats, house mice and house sparrows. Although data were not available from the two non-African reserves, very few introduced fish species are known. There appear to be two classes of large mammals which can establish populations in these nature reserves. In the southern African reserves it is only species from the same region (but not native to the reserve itself) and from habitats similar to those in the reserve which appear to be capable of invading, e.g. *Pelea capreolus* in the Kruger National Park and giraffe and impala in the Hluhluwe-Umfolozi Reserve. In the relatively species-poor mammal communities of Java and northern Australia (compare Tables 2-6) it is apparently much easier for a wide variety of large mammal species to invade. However, even in Australia, which is renowned for its unusually high susceptibility to mammal invasions (Myers, 1986), it is noteworthy that neither *Rattus rattus* nor *Mus musculus*, which are widespread elsewhere on the continent, have been able to invade natural communities in these relatively complex savanna ecosystems.

An hypothesis which can be advanced to explain the observed pattern of vertebrate invasions of these savanna reserves hinges on the importance of predation in limiting the initial establishment of introduced species in these groups. In the Serengeti ecosystem there are 27 species of native mammalian carnivores. The 1977 population estimates give mean densities per 1000 km² of 89 lions, 365 spotted hyaenas *Crocuta crocuta*, 28 cheetah *Acinonyx jubatus*, 25 leopard *Panthera pardus* and 6 Cape hunting dogs (Frame, 1986). These species are capable of killing the full range of domestic livestock that have been introduced to the area by man and no feral populations have become established. Kruger National Park has a similarly diverse and dense carnivore population. Once again, no ungulates which are not adapted to this predation pressure have become established. In the Hluhluwe-Umfolozi Reserve the large predator community lost several species and was subjected to a continuous population reduction campaign during the early years of the reserve's establishment (Brooks & Macdonald, 1983). It was during this period that impala and nyala *Tragelaphus angasi*, thought to be native but which had become locally extinct, were successfully introduced and re-established. Even fallow deer became temporarily

established in the reserve during this period, dying out in the early 1950s (C. J. Ward, pers. comm.) when predator populations, in particular that of spotted hyaenas, built up again. In the late 1960s and early 1970s, repeated attempts to re-establish eland in the reserve failed and predation from the newly re-established lion population was considered a causal factor in this failure (Bourquin *et al.*, 1971). In Baluran National Park, by contrast, only the leopard and possibly the red dog *Cuon alpinus* could be considered potential predators of feral stock. The tiger *Panthera tigris* was already locally extinct by this time (Anon., 1977). In Kakadu National Park there are no mammalian predators capable of taking large domestic stock, such as water buffalo or horses. The dingo *Canis familiaris dingo* is the only 'native' carnivore present and it generally feeds on medium-sized marsupials and smaller vertebrates (Robertshaw & Harden, 1985). It is, however, capable of killing introduced mammals the size of sheep or smaller (Thomson, 1984) and Kakadu National Park has no invasive herbivores smaller than sheep.

Support for the hypothesis that predation is important in preventing the establishment of vertebrates in these biomes comes from the biology of the only amphibian species that has successfully invaded. The cane toad, through its poisonous secretions, immediately reduces (and sometimes eliminates) the populations of native predators of amphibians as it expands into new areas (Freeland, 1986).

In the future, vertebrate invasions should become less of a problem in these nature reserves. This is because almost all of these invasions were the result of intentional introductions. With the growth in awareness of the potential problems posed by introduced species, such introductions should decrease. Alternatively, if the predation hypothesis is correct and if these nature reserves tend to lose their predatory species over time, as has been predicted for quasi-insular reserves based on island biogeographic theory (Diamond *et al.*, 1982), the problem could become more widespread.

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CHAPTER 3**THE INVASION OF SOUTHERN AFRICAN NATURE RESERVES
- SOME CASE STUDIES****Summary of main points arising from the chapter**

In the papers that make up this chapter the basic questions addressed are mainly the same as those in the previous chapter. In order to avoid unnecessary repetition, I will not invariably summarize those findings of the current chapter which simply repeat those of the broader studies carried out as part of Chapter 2. I will only do so where a finding adds insight into the processes underlying these invasions.

Which taxonomic groups have alien species invading the case study reserves?

Although all taxonomic groups addressed in these papers were shown to have invasive species in at least one of the reserves studied, vascular plants were consistently shown to have the most invasive species.

Of the 73 alien vascular plant species invading the Cape of Good Hope Nature Reserve, 68 were Angiosperms and 5 Gymnosperms. Dicotyledonous species were the major invaders of intact ecosystems within the reserve, with monocotyledonous species being mainly confined to sites heavily disturbed by human activities (Paper 5). Of the 113 invasive alien plant species recorded from the Kruger National Park, 112 were Angiosperms and one was a fern (Paper 8). All of the 71 plant species invading the Hluhluwe-Umfolozi Reserve were Angiosperms (Paper 10). This dominance of the invasive alien flora of nature reserves in both these biome-types by Angiosperms was true also of the reserves outside southern Africa (Papers 7 and 10). Such a dominance of invasive floras by Angiosperms is a global phenomenon (Heywood 1989). Few Gymnosperms and Pteridophytes have been successful as alien invaders anywhere in the world. This dominance of invasive floras by flowering plants is what could be expected given the relative numbers of extant species in these three major groupings of the vascular plants, i.e. 96% of the estimated 250 000 species of vascular plants are Angiosperms, with Gymnosperms making up only 0,3% and fern and fern-allies the remainder (Mabberley 1987). In fact, if anything, Gymnosperms make up a disproportionately high proportion of the invasive alien flora of the Cape of Good Hope Nature Reserve relative to their occurrence

in the world's flora. This is undoubtedly a consequence of the large number of introductions of Gymnosperms that have been made for silvicultural purposes in the region (e.g. Poynton 1979). Thus Gymnosperms now make up 12,7% of a list of 741 species of introduced trees successfully cultivated in South Africa (Von Breitenbach 1984).

The virtual absence of Pteridophytes as invaders in southern Africa is discussed elsewhere in this thesis (Chapter 4, Paper 12). However, it needs to be stressed that natural long-distance dispersal of ferns is much more effective than in most Spermatophytes: Adersen (1990), for example, has demonstrated that Pteridophytes have colonised the Galapagos Archipelago about ten times as efficiently as have Spermatophytes. It is thus not surprising that a fern, Pteridium aquilinum is thought to be the world's most widely dispersed vascular plant (Heywood 1989). The relative paucity of successful Pteridophyte aliens can simply be explained by suitable taxa having, in most cases, already having invaded an area naturally. The low total number of Pteridophyte species globally, relative to the Spermatophytes (Mabberly 1987), and their relatively low level of small-scale endemism (Paper 7, Brockie et al. 1988, Loope et al. 1988, Adersen 1990) are both in agreement with this interpretation.

Do these reserves show differential levels of invasion by alien species from any of these groups?

The only really interesting inter-reserve comparisons that can be made on the basis of the papers included in this chapter, are those relating to the intercontinental comparisons (Papers 7 and 10). The main points that emerged from these comparisons were that;

- i) of the Mediterranean-type reserves, the Cape of Good Hope Nature Reserve was the most severely invaded by alien tree species and, by contrast, probably the least invaded by alien herbaceous species (in particular, by grasses), and
- ii) of the savanna reserves, the African ones were the least invaded by alien vertebrates.

The collation of standardised data sets for these nature reserves presents an excellent opportunity for testing some of the predictions that exist regarding the relative susceptibility to invasion of different biomes and biogeographical regions. Some of these tests have already been made in the final paper in the SCOPE Working Group's report (Usher 1988). However, in terms of matters important to the present study, two of the key issues

were not addressed in this summary.

Is native species richness related to invasibility?

The first of these is the relationship between species richness and invasibility. It was one of Elton's basic conclusions arising from his thorough study of the subject that "natural habitats on small islands seem to be much more vulnerable to invading species than those of the continents. This is especially so on oceanic islands, which have rather few indigenous species." (1958, p. 147). This contention, although not thoroughly tested, has become entrenched in the scientific perception of invasions, to the extent that the "Impact of alien plants and animals on island ecosystems" was one of only three fields of study identified for intensive investigation by the "Expert Panel on Ecology and Rational Use of Island Ecosystems" of the Man and the Biosphere Programme (UNESCO 1973). The high priority given to this topic was justified in part "because their ecosystems are particularly vulnerable to disruption by alien species" (UNESCO 1973). The obvious, though generally unstated, corollary to this hypothesis is that species-rich continental ecosystems should be relatively resistant to alien invasions.

This relationship, if true, ought to make the ecosystems of southern African nature reserves particularly resistant to alien invasions as, at least for plants, the subcontinent has some of the highest levels of species richness recorded anywhere in the world. These extraordinarily high levels of plant species richness are present at all spatial scales (Cowling *et al.* 1989). This high species richness also manifests itself in the subcontinent's vertebrate fauna (Siegfried 1989). It is thus highly relevant to the present study to investigate whether Elton's hypothesis is born out by the results of this nature reserve study.

Taking the data from all the nature reserves for which species totals were available, it was possible to compute regressions for the number and proportion of invasive species in the vascular plant flora, avifauna and mammal fauna of most reserves included in the study (Papers 7 and 10, Brockie *et al.* 1988, Loope *et al.* 1988).

If the number of alien vascular plant species recorded in a reserve (I) is taken as an index of its susceptibility to invasion, and this number is then related to the number of native species (N) in the reserve, no obvious inverse relationship is apparent (Figure 3.1). The overall regression relationship between these two variables was not significant. However, within two of the biome-types there were significant positive relationships: For the five savanna reserves the regression,

$$I_{sav} = 0,06N_{sav} - 3,$$

accounted for 89% of the variance in I_{sav} . In the case of the four arid-land reserves the regression,

$$I_{des} = 0,08N_{des} - 2,$$

accounted for 93% of the variance in I_{des} . Thus it can be concluded, at least for these two biome-types, that the factors controlling the number of native species known from a reserve also play a role in determining the richness of its invasive alien flora. Obviously these factors will include the size of the reserve - larger reserves tending to hold more species than smaller reserves, the range of habitats within the reserve, and the completeness of the botanical inventory of the reserve. In order to obtain an index of invasion which would compensate, at least to some extent, for the uncontrolled variation between reserves in such factors, I used the index "V" (Paper 7) which is computed as,

$$V = 100 I/S \%$$

where S is the total of alien and native species ($I + N$) recorded for the reserve.

When this index was compared with the number of native species known from the reserve, the simple linear regression relationship was significant (Figure 3.2). This is not unexpected as the index has the number of native species as an important contributor to its divisor - which would result in an automatic inverse correlation even if the number of alien species was constant over all reserves (c.f. Brown 1989). However, if this number were constant this would not necessarily imply that all reserves were equally susceptible to invasion. It is logical to predict that, if all areas were equally susceptible, then smaller reserves and those with fewer habitats ought not only to hold fewer native species but also fewer alien species. Thus a significant decrease in V as S increases, cannot simply be disregarded as being an automatic mathematical relationship with no biological significance. The interpretation of the statistical significance obtained for this regression might be complex, but the practical significance of the observed relationship is obvious: First, the index clearly is successful in compensating for the positive correlation shown between I and N in the two continental biomes. Second, the reserves with low numbers of plant species tend to be those with the highest proportions of aliens, although there is wide variation in this proportion. Above a value of 600 native species the value of V

tends to be restricted in a narrow range of values between 5% and 8%. Further, it is apparent that the island reserves really do tend to show higher proportions of alien species in their floras (five of the seven island reserves show positive deviations from the regression, and all seven have absolute values of V greater than any of the savanna or arid land reserves). Not only do the Mediterranean-type reserves tend to have absolute (I_{Med}) and relative (V_{Med}) numbers of invasive vascular plants greater than those of the other continental biome-types, but these are the only continental reserves which show major overlaps in the value of V with the island reserves.

When the same relationship was investigated for birds, the regression relationship was again highly significant (Figure 3.3), once again with the same qualification of this "significance" being necessary. The pattern shown by the different biome-types was once again clear and resembled that shown in the vascular plant data. However, as the common logarithm of V was used in this case, those reserves with no invasive alien bird species [three of the five savanna reserves (Paper 10) and two of the three small temperate islands (Brockie *et al.* 1988)] were excluded from this analysis.

In the case of mammals, the regression of the number of invasive aliens in a reserve on the total number of native mammals was significant,

$$I = 5,45 - 0,038N \quad (F_{20} \text{ d.f.} = 7,41; P = 0,01).$$

The only reserve for which no estimate of the number of native mammals was available, was the small Kings Park reserve in the Mediterranean-type climate area of Western Australia. It is known to have five invasive alien mammal species and is likely to have less than 20 native mammals (Tingay and Tingay 1982). As such, this reserve would be likely to reinforce the pattern shown by the other reserves (Figure 3.4): Islands tend to have the lowest numbers of native species and the highest of invasive aliens, while the composition of the mammalian fauna of Mediterranean-type reserves tends to be more similar to that of islands than is that of any other continental biome-type. The savanna reserve from northern Australia appears to be an exception, but see the discussion in Paper 10 and Chapter 5, Paper 20 on the "insular" nature of the Australian mammal fauna.

Thus, in all three taxonomic groups, the reserve data tend to support the hypothesis that oceanic islands (particularly tropical islands in the case of birds) are proportionally more invaded than these three types of continental ecosystems. Of the three continental biome-types studied, Mediterranean-type reserves tend to show the highest proportion of invasive species in both their vascular floras and higher vertebrate faunas. This

is in keeping with the widely held hypothesis that this biome-type is actually more severely invaded than are other continental biome-types. The latter finding agrees with the results of the southern African reserve analysis for alien bird species (Chapter 2, Paper 1).

Is endemism related to invasibility

Another biogeographic/evolutionary postulate that has been advanced to explain the high vulnerability of island biotas to alien invasion, is their history of evolution in isolation from the mainstream of the earth's terrestrial biota located on the continents. This has generally not been explicitly formulated as a series of testable hypotheses, but instead has been expressed as the "loss of competitiveness" (Carlquist 1980) or "reduced aggressiveness" (Loope and Mueller-Dombois 1989) of their species or the "disharmony" apparent in the taxonomic composition of their biota (Loope and Mueller-Dombois 1989). The extent to which this "insularization" of the biota has occurred, is generally taken to be reflected in the level of endemism shown by the various taxonomic groups on an island or archipelago (Loope and Mueller-Dombois 1989).

What is pertinent to the present study is whether one can use the level of endemism shown by a taxonomic group within a particular area as a quantitative predictor of that area's susceptibility to invasion by alien species in this taxonomic group. The nature reserve data set assembled in this study provides a unique opportunity for testing this possibility over a range of continental and insular biome-types.

Endemism at the species level in each taxonomic group was rated in a standardized manner for each nature reserve according to the Udvardy (1975) biogeographic provinces (Usher *et al.* 1988). Some of the island case studies had to be excluded as endemism was only related to the island itself and not to the biogeographic province within which the island was located (Brockie *et al.* 1988). The distribution patterns were generally only well enough known for vascular plants, birds and mammals for endemism to be determined in large enough samples of reserves to allow for statistical testing.

Using birds as the study group, there were 16 reserves with adequate data and the regression of the common logarithm of V on the percentage of species endemic to the biogeographic province within which the reserve was located (E), was highly significant:

$$\text{Log } V_{\text{bird}} = 0,0742 + 0,18E_{\text{bird}} \quad (F_{14} \text{ d.f.} = 12,7; P = 0,003).$$

The pattern shown by the different biome-types was similar to

that shown in the relationships between invasions and native species richness: Islands were most invaded and showed the highest endemism. Savanna and arid-land reserves were generally least invaded and had the lowest levels of endemism. Reserves in Mediterranean-type biomes were generally intermediate in both characteristics. In order to achieve a more useful presentation of this relationship the regression was recomputed using the common logarithms of both V and E (Figure 3.5). This eliminated three of the reserves which had zero values for endemism at this scale (one on an island close to the North American coast, one arid-land reserve in the USA, and one Mediterranean-type reserve in Chile), but the regression was still highly significant;

$$\text{Log } V_{\text{bird}} = 0,711\text{Log } E_{\text{bird}} - 0,1275 \quad (F_{11} \text{ d.f.} = 21,1; P = 0,0008).$$

The data were fewer in the case of vascular plants; no savanna reserve in the sample, for instance, had sufficient information available on its flora to enable this endemism to be computed. If the number of alien plants in a reserve was compared with the percentage endemism of its flora, the regression was significant;

$$I_{\text{plant}} = 29,9 + 2,1E_{\text{plant}} \quad (F_9 \text{ d.f.} = 12,7; P = 0,003).$$

However, the number of alien species is not considered to be as good a measure of the relative extent of invasion in this group as is the index V. When the regression was recomputed using V_{plant} as the dependent variable, it was not significant at the $P < 0,05$ level used throughout this study:

$$V_{\text{plant}} = 10,76 + 0,216E_{\text{plant}} \quad (F_9 \text{ d.f.} = 1,99; P = 0,19).$$

One of the major reasons for the reduced significance of this regression relative to that of the simple number of alien plant species, was the very low percentage that aliens made up of the Cape of Good Hope Nature Reserve's flora. This reserve had the highest endemism (82,9%) of any in the sample but, because of its exceptional native species richness, when the number of its invasive species was expressed as a percentage of the total flora, this was the third lowest value in the sample (6,5%). An interbiome comparison within southern Africa had previously shown that, whereas there was no significant difference among the biomes in the absolute number of accidentally-introduced invasive vascular plant species per reserve, when these were expressed relative to the number of native species in the reserve, fynbos reserves had significantly lower values (Chapter 1, Paper 1). Thus the exceptional native species richness of the fynbos

biome's flora appears to introduce a 'bias' into this index of the extent of invasion. Notwithstanding the lack of significance of this regression, for reasons of comparability with the previous plots of this taxonomic group, this relationship is presented as Figure 3.6. The same pattern as described above for birds is again apparent.

For mammals the relationship was best shown when V_{mammal} was expressed as the common logarithm (Figures 3.7 and 3.8). When this statistic, from all the reserves for which it could be computed, was compared with E_{mammal} for these reserves, the regression was not significant at the $P < 0,05$ level;

$$\text{Log } V_{\text{mammal}} = 0,814 + 0,01E_{\text{mammal}} \quad (F_{12} \text{ d.f.} = 4,45; P = 0,056)$$

However, the largest deviations from this regression were those of two island reserves which, although having high values of V , had anomalously low values of E for their 'native' mammalian fauna (Figure 3.7). In both cases these mammals were mainland species that had colonised the island or archipelago relatively recently and could not be differentiated from their mainland conspecifics (Brockie *et al.* 1988). Under these circumstances it is only a question of definition which divides the 'native' mammals from the introduced aliens, i.e. the mammal fauna can not be considered to be a truly insular fauna. If only the continental reserves were considered (Figure 3.8) the regression was highly significant;

$$\text{Log } V_{\text{mammal}} = 0,34 + 0,04E_{\text{mammal}} \quad (F_8 \text{ d.f.} = 17,79; P = 0,003)$$

In this taxonomic group, once again, Mediterranean-type reserves tended to have values of both V and E intermediate to those of the oceanic island and the other continental biome-types.

Thus, for all three taxonomic groups the same patterns emerge: Reserves with low native species numbers and high levels of endemism tend to have higher numbers and/or proportions of invasive alien species in their biotas. In terms of the biome-types included in this study, this means that oceanic islands tend to be most invaded and the Mediterranean-type biomes, which occur as isolated patches on the larger continents, show higher levels of invasion than do the other continental biome types. The quasi-insular nature of the fynbos biome had previously been identified as being a possible biogeographical explanation for the apparently higher susceptibility of this biome to alien invasions than the other southern African terrestrial biomes (Chapter 1, Paper 2). Similarly, the apparent high susceptibility to invasion by alien rodents of mesic coastal isolates in the Namib Desert had been related to the quasi-insular nature of such areas (Chapter 1, Paper 1).

These results from the terrestrial biotas of nature reserves are mirrored by those from the freshwater ecosystems of southern Africa. Thus the southern Cape river systems have fish faunas which are characterized by low native species richness (Paper 7), high endemism, high numbers of invasive alien fish species and a correspondingly high level of endangerment of native taxa by these aliens (Bruton and van As 1986, Skelton 1987). These southern river systems fall within a distinct ichthyofaunal province which is much smaller in extent than the province which lies to the north of it and takes in much of the African tropics and subtropics. The southern African river systems which fall within this latter province tend to have fish faunas with high native species richness, low endemism and low numbers of invasive alien fish species which are not considered to be threatening the survival of native fish species (Papers 9 and 10, Bruton and van As 1986, Skelton 1987).

Within the reserves do the ecosystems show different levels of invasion?

In both the Cape of Good Hope Nature Reserve (Paper 5) and the Kruger National Park (Paper 8) many of the invasive plant species were herbaceous "weeds" which were most common in areas of intense human disturbance. However, other alien plant species, predominantly woody perennials, were shown to have invaded relatively undisturbed areas of natural vegetation in both these reserves and the other Southern African case study reserve, the Hluhluwe Umfolozi Game Reserve (Paper 10).

The general conclusion from the inter-continental savanna reserve comparison was that plant invasions were most intense in wetland habitats and least in xeric habitats with mesic habitats being intermediate (Paper 10).

Are the characteristics of the invading species related to those of the ecosystems they are invading?

In the analysis of the alien plants invading the Cape of Good Hope Nature Reserve it was observed that their life-form distribution was markedly dissimilar to that of the reserves native flora: Those life-forms such as geophytes and dwarf shrubs which were well represented in the native flora had few or no alien species. By contrast, trees and tall shrubs and annual herbs which were minor components of the native flora, were the dominant elements in the alien flora (Paper 5).

This finding has several important implications: First, any attempt to generalize as to what attributes of the species made

them successful invaders of this reserve would be bound to fail unless one recognized that there were at least two totally distinct groups involved. This need to recognize the general dichotomy between generalist "weedy species" and "ecosystem-specialist" invaders is one of the important observations that has been made in several of the papers in this thesis (e.g. Paper 14 in Chapter 4). Second, it tends to support the contention that the dominance of tree invaders in this biome is a consequence of the relative paucity of native tree species adapted to fynbos ecosystems (c.f. Campbell *et al.* 1979, Chapter 1, Paper 2 and Chapter 7, Paper 24). Although the "empty niche" hypothesis for explaining the success of alien invasions is difficult to elaborate in terms of current definitions of an ecological niche (Johnstone 1986), the concept is still useful in explaining many of the successful invasions observed in nature e.g. the invasion of predatory fish into the southern river systems of the Cape (Bruton and van As 1986). The differential impact that invasions have had on the survival of species in invaded native communities has similarly been explained in terms of the "extent of its [the community's] prior experience with functionally similar species" (Diamond and Case 1986, p.75). This really amounts to alien species which can be considered as filling "vacant niches", e.g. mammalian carnivores on formerly carnivore-free oceanic islands, having much more serious impacts than aliens which simply supplement native species in already "occupied niches". Mooney and Drake (1989) have expressed this same concept as; "Introductions that perform a system function considerably different from that of the resident species can have a large impact."

What are the causal mechanisms underlying these relationships?

The observation that diverse native faunas and floras in these nature reserves appear to be less invaded, and possibly less impacted, by alien species in these groups, reflects the finding that has been made for extensive surveys of oceanic islands (Case, unpublished as cited in Diamond and Case 1986) and for comparisons of the fauna of whole continents and island archipelagos (Brown 1989). Our finding (Paper 6) that, even within one taxonomic group, those life-forms that were more diverse tended to be those that had fewer successful alien invaders, is simply an extension of this phenomenon.

The obvious interpretation of these findings is that inter-specific interactions with the members of a diverse native community limit the successful establishment of alien species. This is the same conclusion reached by Diamond and Case (1986). One specific aspect of this interaction is predation. The above

authors consider that the "epidemic success of introduced mammals on many islands may reflect the escape from continental predators as well as from continental competitors" (Diamond and Case 1986). The intercontinental comparison of savanna reserves yielded several lines of argument that support the contention that this predation is in fact important in limiting vertebrate invasions (Paper 10). This, once again, accorded with the results of the preliminary broad analyses carried out in Paper 1 of the previous chapter.

There were also several examples from the case study reserves of herbivory by generalist herbivores serving as an equivalent "sieve" for determining the success of certain alien plant invasions (Papers 6, 9 and 10). Herbivory in such cases can best be considered as being equivalent to predation, particularly if it results in the mortality of the affected plant.

In all these cases, such effects seem to be most important where the alien invasion is just starting, e.g. the effects of ungulate herbivory on the first few established plants of Cortaderia selloana in the Cape of Good Hope Nature Reserve (Paper 6), the disappearance of Acacia dealbata from the Kruger National Park (Paper 9) or the observed early failure of several ungulate introductions to both this park and to the Hluhluwe Umfolozi Game Reserve (Papers 9 and 10). Such extinctions of introduced species when their populations are still low have been termed "bridgehead extinctions" by both Elton (1958) and Diamond and Case (1986). It is one of the useful findings of the present study that nature reserve invasions are similarly susceptible to such early extinctions and that the probability of such extinctions occurring is enhanced where there is a diverse native fauna and flora.

How extensive are these invasions?

Most of the papers in this chapter simply summarised presence/absence data on invasions at the species and nature reserve level. Very few of the case study reserves had quantitative data on the extent of invasions. The exception to this in the southern African reserves was the data on the extent of alien woody plant invasions in the Cape of Good Hope Nature Reserve (Paper 6). For this reserve, mapped extents of "dense" infestations indicated that these increased from 1,4% of the reserve's area in 1952, to 3,8% in 1961, to 6,8% in 1969 and, despite intensification of control efforts in the late 1970s, to 7,6% in 1984. Very intense control measures continued to be implemented in the 1980s and these dense infestations were reduced to 5,4% of the reserve's area by mid 1987. Surveys in 99 permanent 10,5ha circular plots showed alien woody plants to be

present in 92% of such plots in 1966 and again in 1976-1980. Repeat surveys in 1986 of 40 of these plots located in the area of most intensive control operations, showed that frequencies of occurrence of the main invaders, Acacia cyclops and A. saligna, had only declined slightly since the previous surveys. However the control operations had markedly reduced the frequency of occurrence of Pinus pinaster (from 17,5% in 1966 to 2,5% in 1986) and the density of all species. Density reductions were greatest in the larger height classes.

These quantitative data and analyses on the long-term invasion and control of a multi-species alien plant invasion of a nature reserve are apparently unique. Similar plot surveys have been conducted elsewhere on the Cape Peninsula but the infestation data are not backed-up by quantitative control data (McLachlan et al. 1980).

What ecological effects are these invasions having?

As these case-study surveys were mainly review and synthesis exercises, and as very little quantitative research had been done on the ecological effects of alien invasions in these reserves, most of the information on this topic presented in this chapter was of a qualitative, and often anecdotal nature. Most effects had to be inferred from published and unpublished reports on changes in the abundance or behaviour of native species in the reserves. Very little work has been done on ecological processes in these reserves, particularly insofar as these might have been affected by alien invasions. Thus, at a process level, the information on the effects of alien invasions was even sketchier.

The major ecological effects identified were;

- i) the reduction in the density of native plants in dense infestations of alien woody plants in the fynbos reserve (Papers 6 and 7),
- ii) altered geochemical cycling following the establishment of these dense thickets (Paper 6),
- iii) altered composition and feeding ecology of the vertebrate fauna in response to woody plant invasions of fynbos (Paper 6),
- iv) hybridization of the introduced amphibian Xenopus laevis with the native X. gilli in this reserve (Paper 7),
- v) altered patterns of herbivory on native plants arising from the introduction of non-native ungulates to the fynbos reserve

- (Paper 5) and the more mesic savanna reserve (Paper 10),
- vi) reduced diversity/density of submerged native aquatic plants following invasions by alien aquatic macrophytes in the one savanna reserve (Paper 8),
- vii) marked reductions in the populations of susceptible mammal species as a result of the introduction of alien pathogens to the savanna reserves (Papers 9 and 10),
- viii) consequent reductions in the density and range of native species heavily dependent on the affected mammal species (Papers 9 and 10),
- ix) the range expansion of bird species in response to the creation of a "new" habitat by alien floating aquatic macrophytes (Paper 9),
- x) the hybridization of the native cat Felis lybica with the introduced F. catus (Paper 9),
- xi) the destruction of native tree vegetation as a result of shading and fire regime alteration following an area's invasion by the scrambling shrub Chromolaena odorata (Paper 10), and
- xii) altered feeding behaviour of native frugivores following the invasion of an area by alien fruiting trees and shrubs, and the possible implications of this for the dispersal of native plants dispersed by these frugivores (Paper 10).

Which invasions are the most important from a nature conservation perspective?

Within these case-study reserves, the woody plant invasions occurring in the Cape of Good Hope Nature Reserve are considered to be the invasion with the greatest potential to bring about the extinction of several native species (Papers 6 and 7). Not only was it predicted that these invasions, if uncontrolled, could give rise to the extinction of several of the highly localised endemic plants found within the reserve, but there are indications that the ecological effects of dense stands of these trees could also reduce the survival prospects of other types of native species, e.g. the frog Xenopus gilli (Papers 6 and 7).

Alien aquatic macrophytes and a number of alien trees and shrubs are considered also to pose serious threats to the integrity of native communities in the savanna reserves studied. Possibly Melia azedarach should be considered the most

significant plant invader of the Kruger National Park's terrestrial ecosystems and Chromolaena odorata that of the Hluhluwe Umfolozi Reserve (Papers 9 and 10).

Within the savanna nature reserves, the effects of introduced diseases on the ecologically important large-mammal component of their biota were indicated as being extremely significant (Papers 9 and 10). The local extinction of tsetse flies Glossina spp. from the Kruger National Park (Papers 9 and 10) and the temporary local extinctions of the yellowbilled oxpecker Buphagus africanus from this reserve (Hall-Martin 1987) and from the Hluhluwe-Umfolozi Game Reserve (Paper 10), are all probable consequences of the reduction in populations of susceptible ungulates by the introduced Rinderpest virus. The latter is the only known example where the final cause of the extinction of a terrestrial vertebrate throughout South Africa (Kemp 1980) is thought to have been the the introduction of an alien organism. As it transpires, the extinction was only temporary, with the species reinvading the Kruger National Park from the north after an absence of some 80 years (Hall-Martin 1987). Other factors were probably more important in the initial decline which led to this species' elimination from South Africa (Paper 19 in Chapter 5).

Introduced diseases and parasites have probably also played a significant role in the declines of several native canid species in these reserves (Papers 9 and 10). The impact of the introduced bubonic plague Yersinia pestis on native rodent populations was not apparent from these case-study reserves, but, in the drier interior of the region, it has apparently been considerable, giving rise to periodic mass mortalities which apparently leave whole areas free, or virtually free, of rodents (Davis 1964, Nel 1967). Such periodic reductions in the biomass of this important component of the fauna must have had profound effects on ecosystems in the affected regions but these appear never to have been assessed. Fortunately, as in the case of most introduced diseases (Paper 9), there appears to have been strong selection for resistance in the originally susceptible species and the ecological impact of this alien pathogen is probably much less now than it was in the early part of the present century (Gill et al. 1987).

All the alien diseases mentioned in these case studies seem to have gone through a highly virulent phase initially when the affected mammal populations were decimated. These populations have all subsequently recovered, with the possible exception of the Cape hunting dog Lycaon pictus, but factors other than introduced disease are probably operating in this case (Paper 9, 10 and 19). The exceptions to this generalized pattern appear to be anthrax (the alien status of which is disputed by some authorities) and rinderpest. The latter is considered to pose a potentially serious threat to the region's wildlife if it is once

again introduced (Paper 9) and another widespread outbreak of the former disease occurred during 1990 within the Kruger National Park.

Novel alien diseases must be considered to pose a potentially serious threat to the wildlife of the subcontinent, as they are considered to do globally (c.f. Soule and Wilcox 1980b).

It is noteworthy that alien vertebrates do not appear to pose major conservation problems in these reserves. The only possible exceptions are the overutilization of native plants by non-native ungulates introduced from elsewhere in the region and the hybridization of native species and introduced congeners (Papers 6, 7, 9 and 10).

The invasion of these reserves by introduced invertebrates has been poorly studied; only in the case of the invasion of fynbos reserves by the Argentine ant Iridomyrmex humilis have the possible conservation effects been studied and in this case they are considered to be serious (Paper 7).

What can be learned from the history of control programmes?

These were reviewed in order to ascertain what determines the relative ease with which different invasions can be controlled.

The principles that emerged from the consideration of control operations carried out in the case-study reserves were as follows:

i) Invasions, however small, cannot be eradicated from a reserve unless one has an effective killing technique which is sufficiently selective to be compatible with the maintenance of biodiversity of the native community invaded.

Thus the relatively uncommon Eucalyptus lehmannii maintained its frequency in the Cape of Good Hope Nature Reserve's monitoring plots by coppicing following treatments (Paper 6). Similarly, Rattus rattus invasions persist in the Kruger National Park (Paper 9) and no control can be implemented for Xenopus laevis in waterbodies it shares with the rare endemic X. gilli (Paper 7). The ant Iridomyrmex humilis is considered to pose a serious threat to native communities in the fynbos biome, but no control is currently being implemented for this species in nature reserves (Paper 7), simply because no selective control technique is known (see also Papers 2 and 3 in Chapter 2).

ii) In terms of the relative ease with which alien plant species can be controlled within reserves, these case studies indicate that the crucial factor is the extent to which a species is capable of re-invading areas that have been cleared. In this context, regeneration of the cleared stand from soil-stored seed

is equivalent to the site having been re-invaded from elsewhere. In certain cases, such as the regeneration of alien plants in the riverbeds of Namib Desert rivers, following clearing operations (Tarr and Loutit 1985), it is by no means certain which mechanism is giving rise to this "re-invasion".

Thus, for example, in the Cape of Good Hope Nature Reserve, species of Hakea and Pinus which do not accumulate high densities of long-lived seed in the soil, have been easily controlled relative to all the species of Acacia which do (Papers 5 and 6). The same principle applies in the Kruger National Park where isolated infestations in the middle of the park of Lantana camara have been eradicated while those along the banks of rivers which flow into the park have persisted despite strenuous control efforts (Paper 9). In the latter cases the re-invasion is thought to be by waterborn seed from uncontrolled infestations in the upper catchment. The water-dispersed Xanthium strumarium in this reserve and the wind-dispersed Chromolaena odorata in the Hluhluwe-Umfolozi Game Reserve provide two further southern African examples where this re-invasion of cleared areas has prevented the successful containment of an alien plant invasion (Papers 9 and 10).

iii) All other factors being equal, the absolute size of an infestation when control is first initiated is critical for determining the likelihood of eradication. Thus the Hakea species within the Cape of Good Hope Nature Reserve have all been eradicated following their early detection and control within the reserve (Papers 5 and 6). These same species have proven to be difficult to control elsewhere on the Cape Peninsula where they were established in greater numbers prior to the initiation of control operations (McLachlan et al. 1980, Stirton 1978). The coppicing Acacia saligna has been more effectively controlled in this reserve than its non-coppicing congener, A. cyclops. This is ascribed to the fact that A. saligna was not as well-established in the reserve at the time control operations were begun (Paper 6). The Eichhornia crassipes/Salvinia molesta comparison in the Kruger and Kakadu National Parks provides another good example of this point (Paper 10).

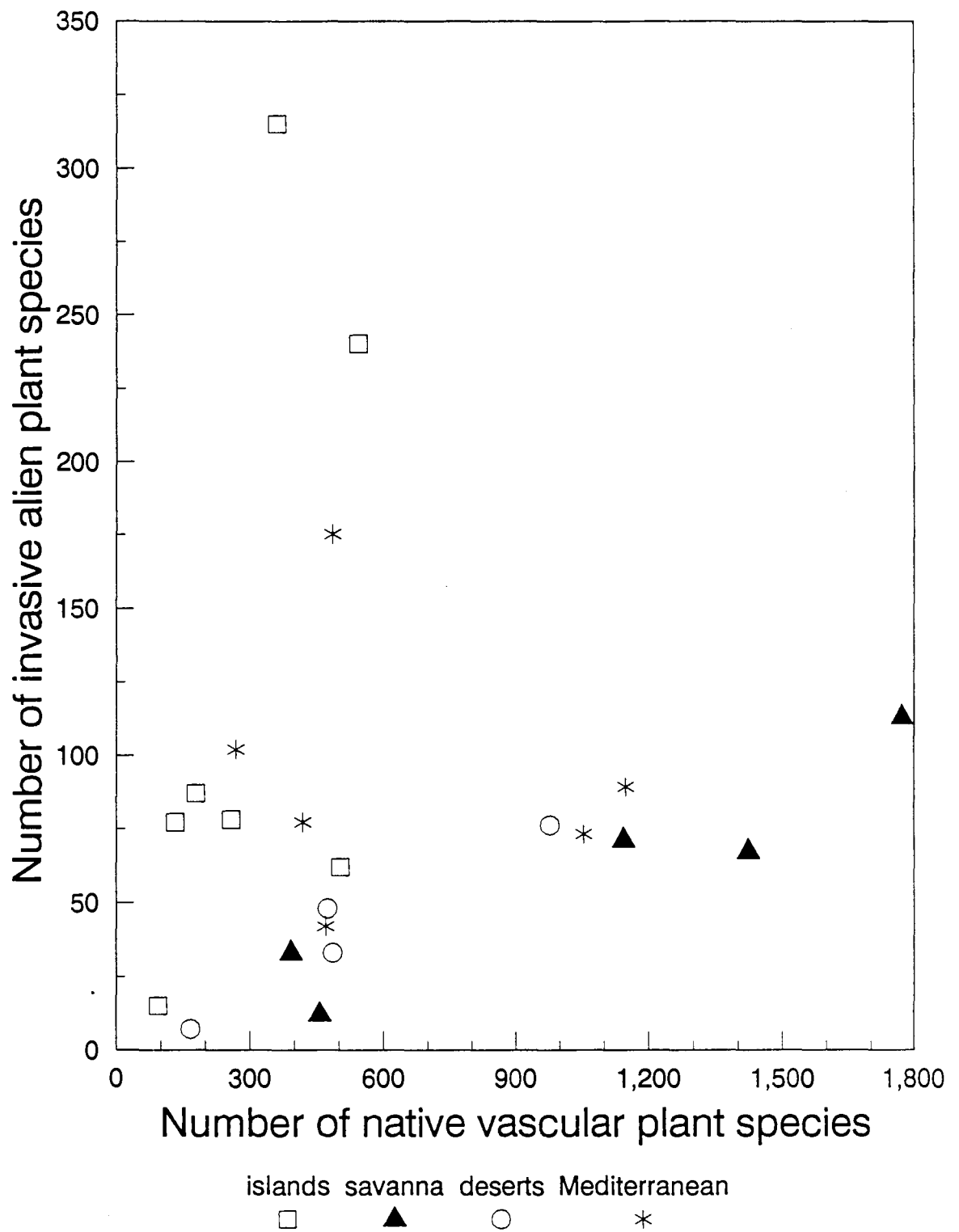


Figure 3.1. Scatter diagram of the number of invasive alien vascular plants against number of native species occurring in nature reserves classified by biome type (for sources see text).

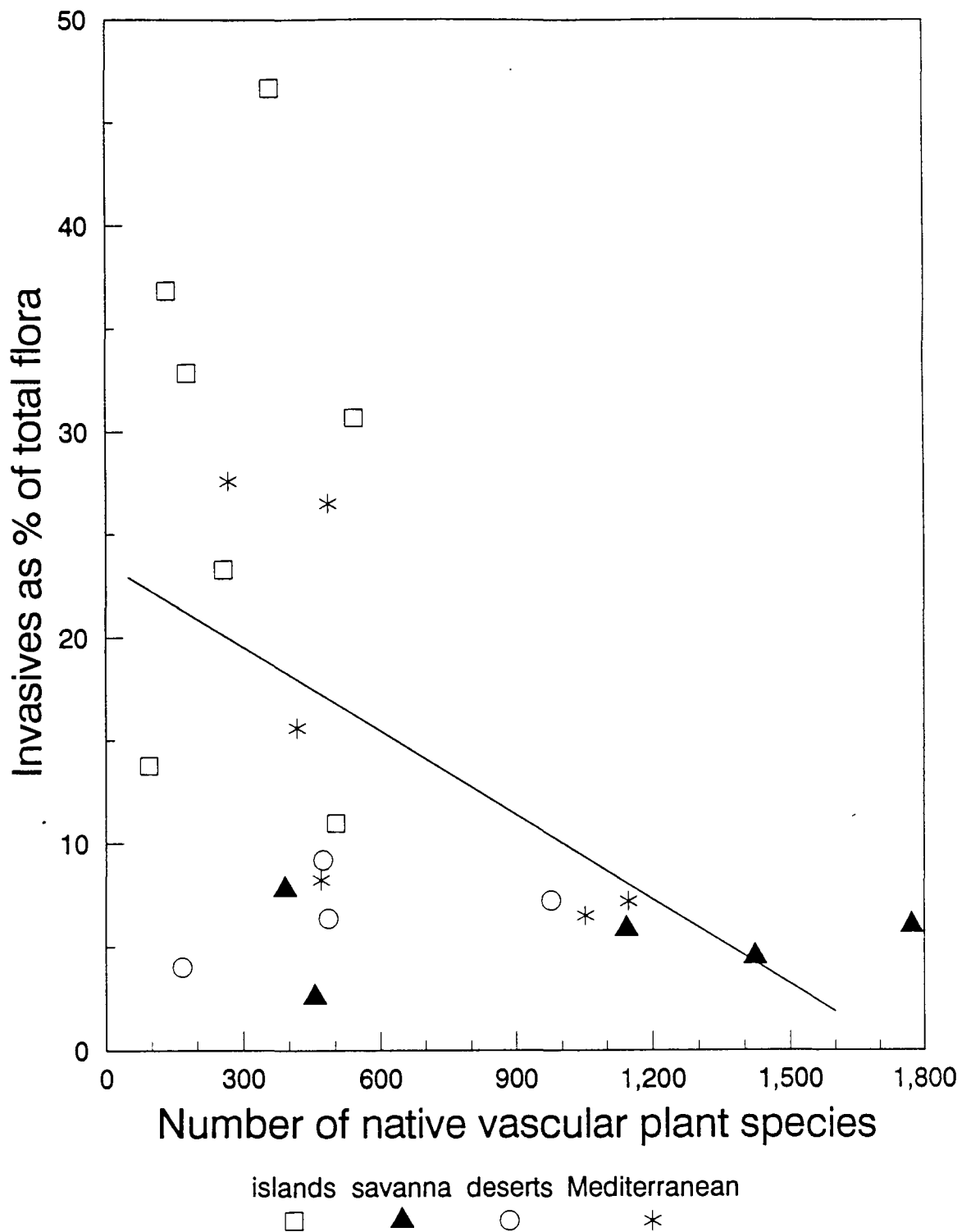


Figure 3.2. Scatter diagram of the percentage of invasive alien vascular plants in the reserve flora against the number of native species occurring in nature reserves classified by biome type (for sources see text). The linear regression over all reserves is shown.

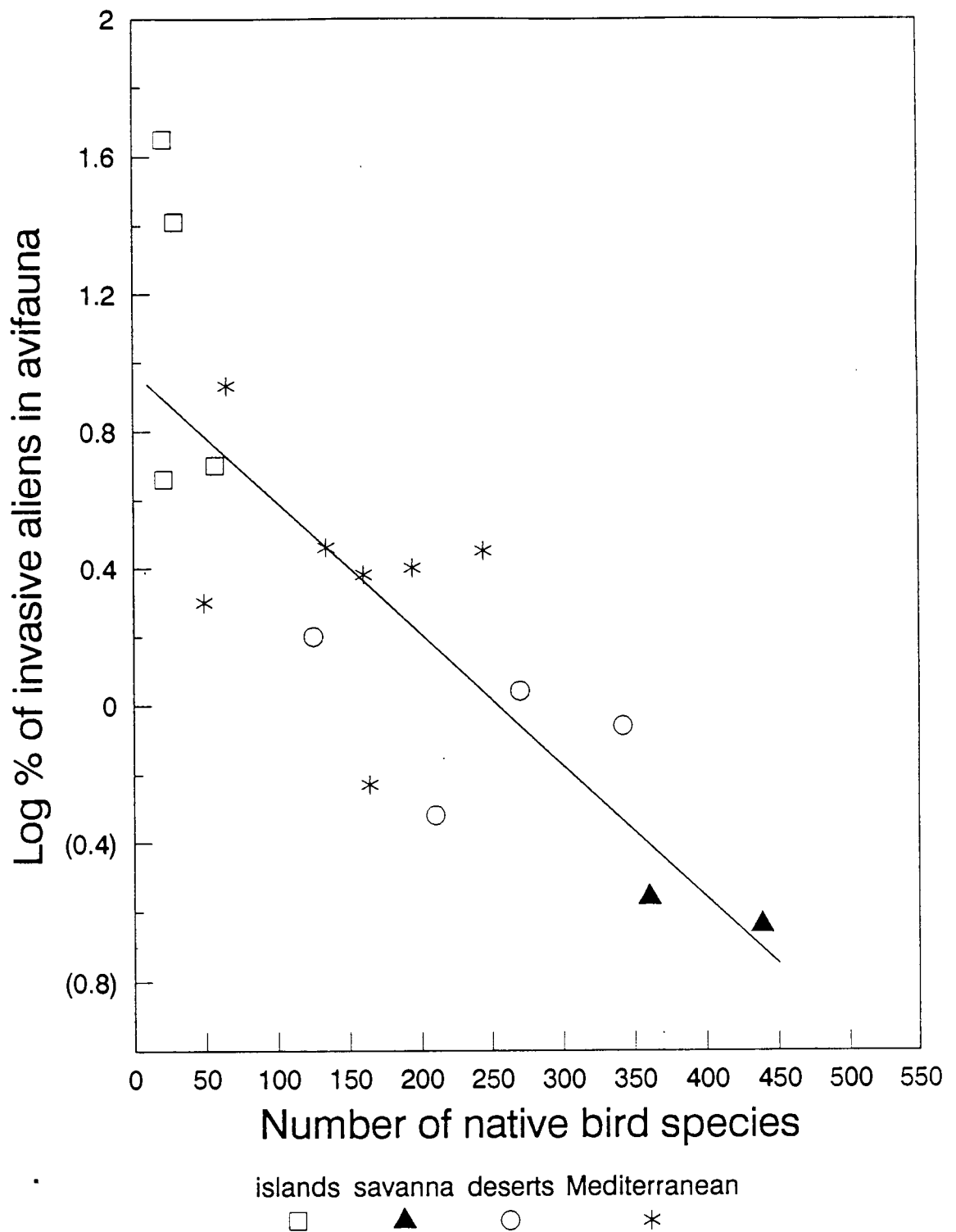


Figure 3.3. Scatter diagram of the percentage of invasive alien bird species in the reserve avifauna against the number of native species occurring in nature reserves classified by biome type (for sources see text). The linear regression over all reserves is shown.

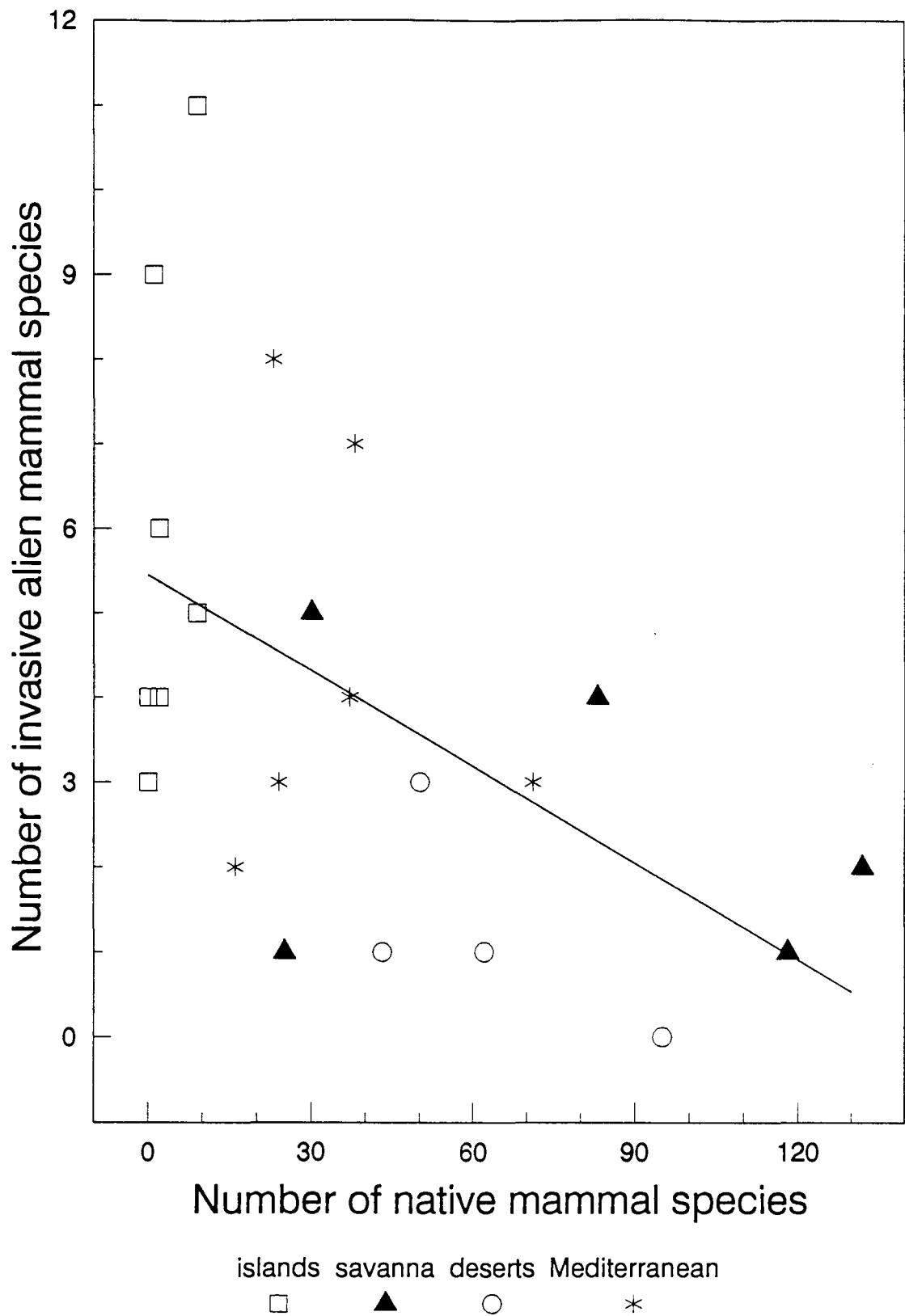


Figure 3.4. Scatter diagram of the number of invasive alien mammal species against number of native species occurring in nature reserves classified by biome type (for sources see text). The linear regression over all reserves is shown.

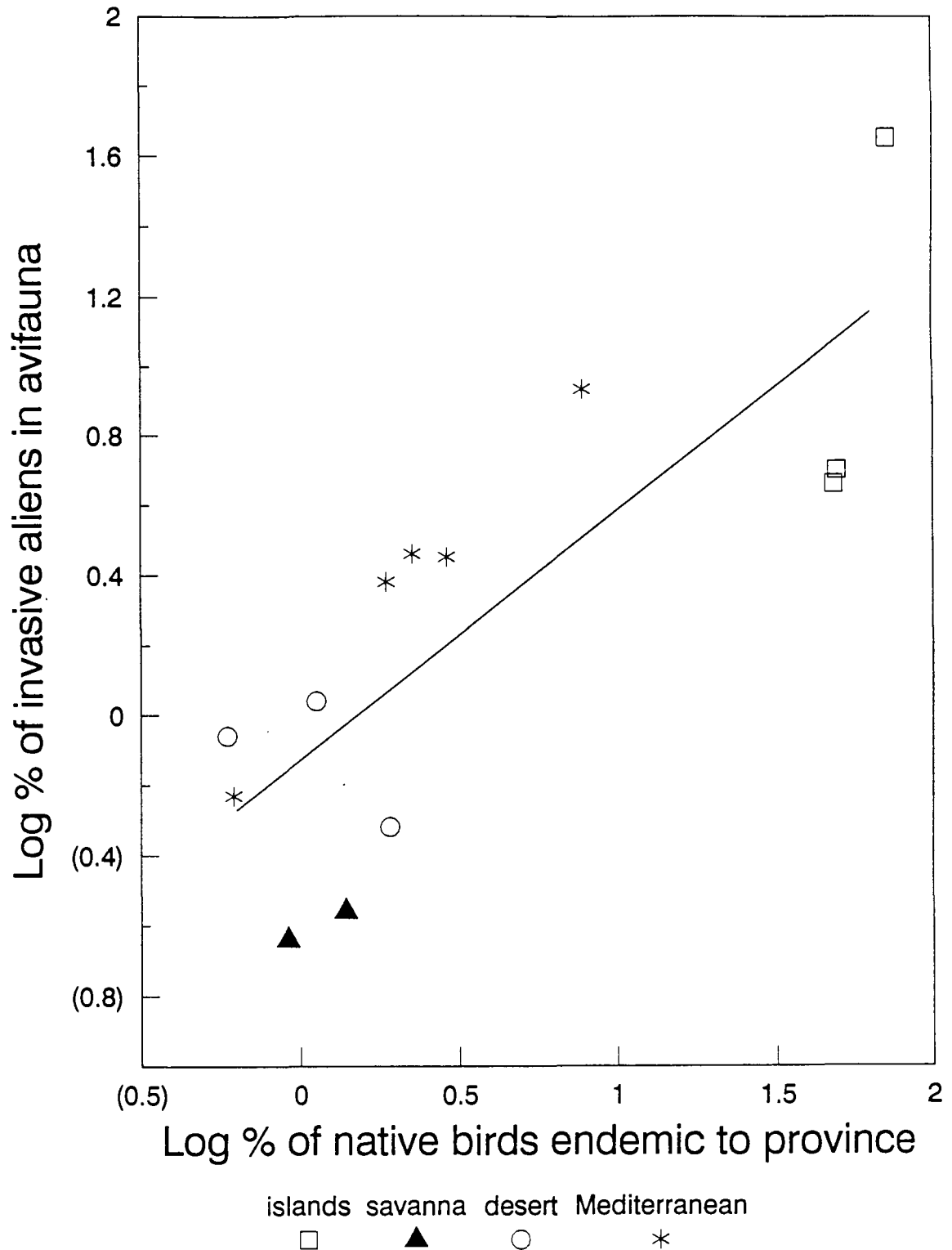


Figure 3.5. Scatter diagram of the common logarithm of the percentage of invasive alien bird species in the reserve avifauna against the common logarithm of the percentage of native species endemic to the biogeographic province, classified by biome type (for sources see text). The linear regression over all reserves is shown.

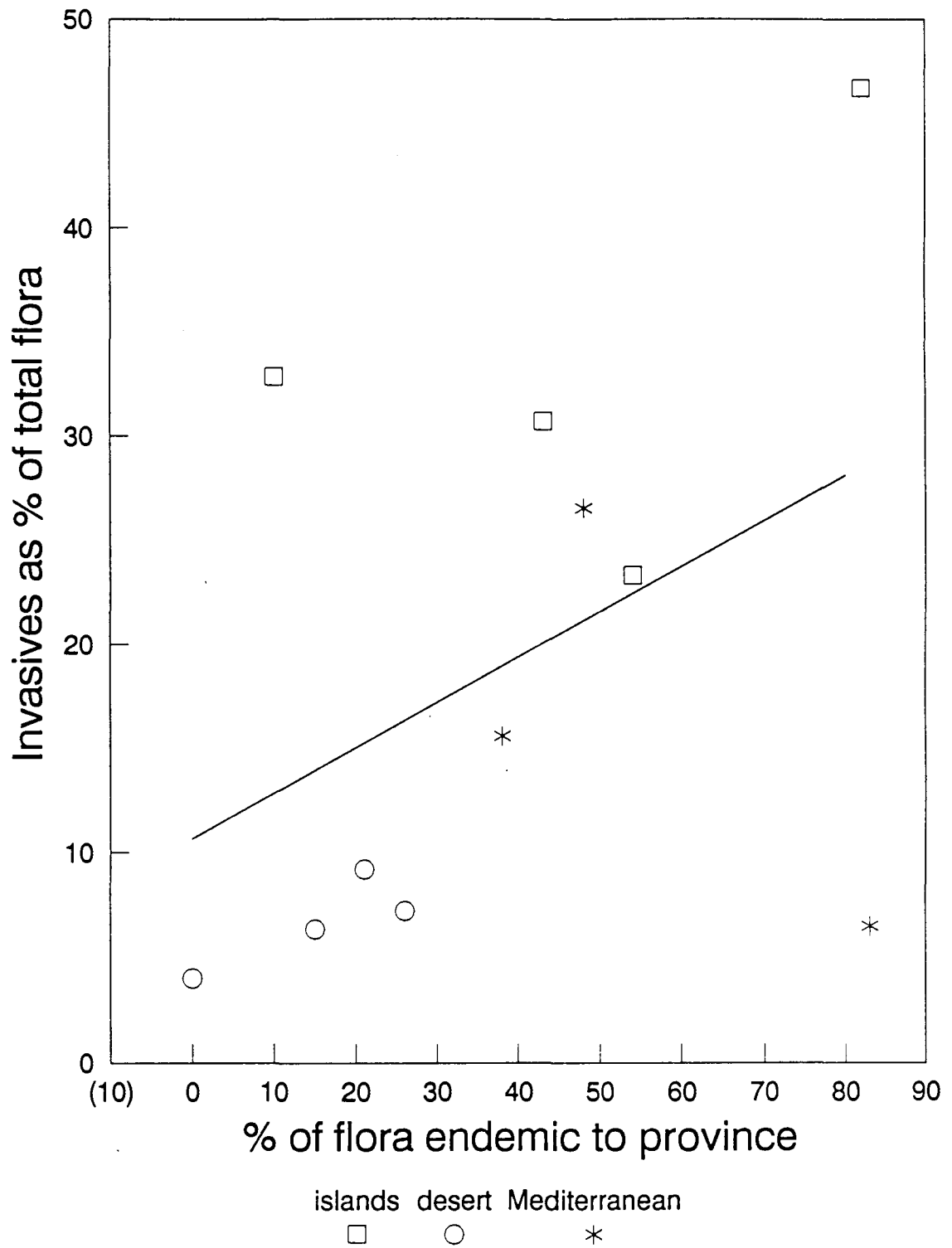


Figure 3.6. Scatter diagram of the percentage of invasive alien vascular plant species in the reserve flora against the percentage of native species endemic to the biogeographic province, classified by biome type (for sources see text). The linear regression over all reserves is shown.

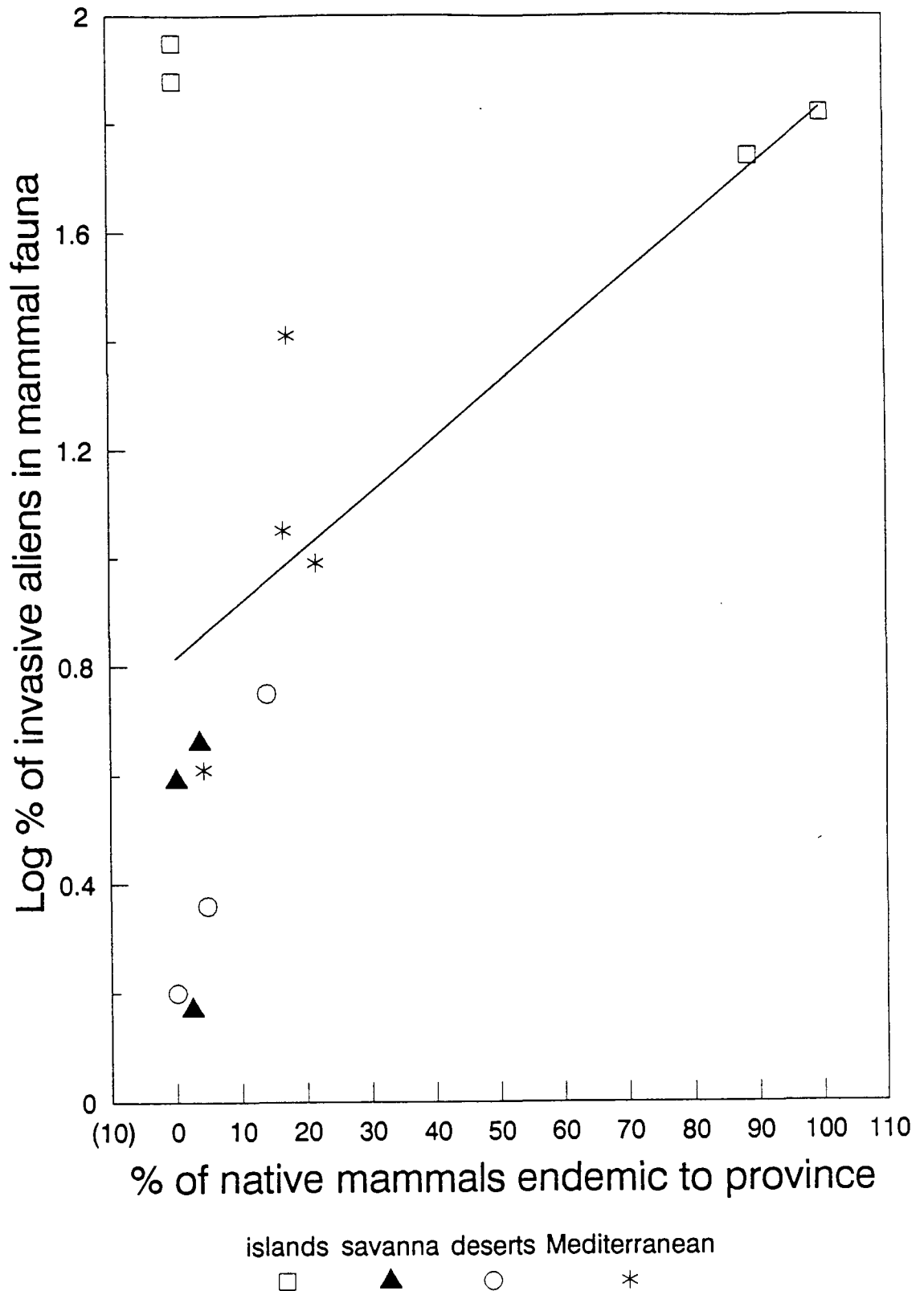


Figure 3.7. Scatter diagram of the common logarithm of the percentage of invasive alien mammal species in the reserve mammal fauna against the percentage of native species endemic to the biogeographic province, classified by biome type (for sources see text). The non-significant linear regression over all reserves is shown.

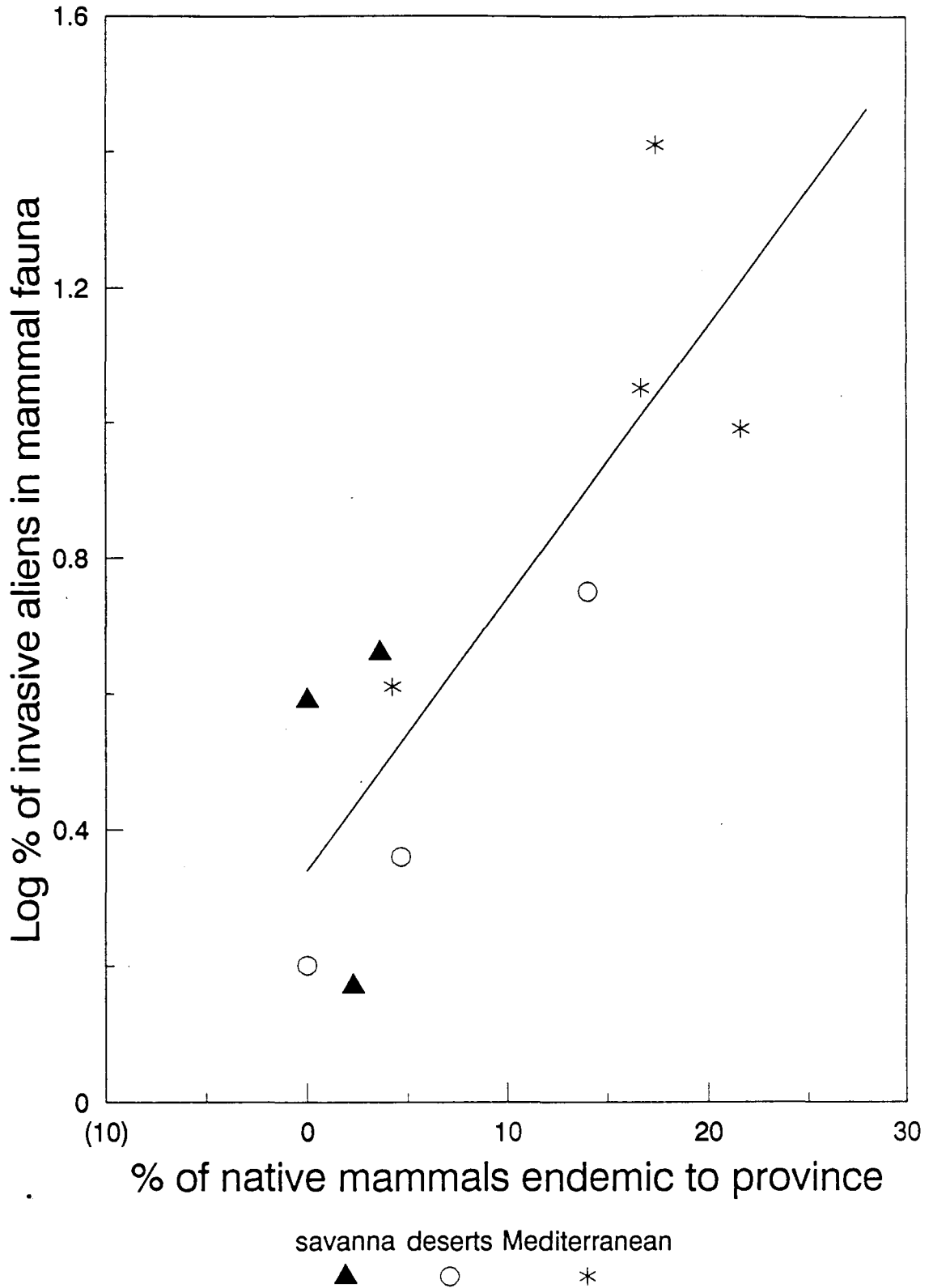


Figure 3.8. Scatter diagram of the common logarithm of the percentage of invasive alien mammal species in the reserve mammal fauna against the percentage of native species endemic to the biogeographic province, classified by biome type. Only continental biome types included (for sources see text). The significant linear regression over all reserves is shown.