Biogeography and ecology of African waterbirds

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To my Parents

......mobility and opportunistic behaviour enable them to exploit ephemerally superabundant water habitat resources typical of more xeric parts of Africa.......

Table of contents

ABSTRACT

Patterns of distribution and diversity for African waterbirds are investigated at the continental, sub-continental, ecosystem and species levels. The focal species is the Great White Pelican Pelecanus onocrotalus, one of South Africa's 'Red Data' bird species. The 'focal' ecosystem is Rondevlei Bird Sanctuary (34°04'S, 18°30'E), one of the few conserved areas in Africa set aside especially for waterbirds. Biogeographically, waterbirds partition Africa much more coarsely (into 8 vs 18 avifaunal zones) than do non-aquatic birds. Waterbird species diversity (number of species) and endemism are higher outside the tropics, and exhibit longitudinal gradients, with higher diversity in the east. Non-aquatic bird diversity is higher in the tropics and varies latitudinally. Spatio-temporal variation in habitat availability and quality are the primary factors which control waterbird distribution, and the dynamic nature of waterbird dispersion is an adaptation to dramatically fluctuating habitats. About 69% of the variance in African waterbird species diversity can be explained in terms of present-day environmental variation. Part of the unexplained variance is attributed to the effects of historical factors, with areas of unexpectedly high species diversity possibly acting as refugia during dry climatic phases.

At the sub-continental level there is a decline in species diversity and endemism as one moves from relatively mesic areas in the eastern half of southern Africa to xeric areas in the west. However, the decline in waterbird diversity is not as steep as that for non-aquatic birds. Moreover, it is also not as steep for mobile waterbirds as for essentially sedentary waterbirds. This apparent incongruence is explained by the ability of mobile waterbirds to exploit ephemerally superabundant resources typical

of the western xeric half of southern Africa.

At the ecosystem level, patterns of long-term temporal variation in waterbird abundance and diversity at Rondevlei Bird Sanctuary show strong seasonal variation which is correlated with variation in the abiotic environment, especially measures of water depth, rainfall and water and ambient temperature. Relationships between waterbird diversity/abundance and the environment are mediated through the availability of shallow water and mud habitats and food. High water level and rainfall lead to dramatic decreases in shallow water and mud habitat availability. During the warmer months (December-April), fish and invertebrate prey are much more numerous and are more readily available. Results of this relatively long-term study corroborate, and expand on, those from a more detailed 13-month study of Rondevlei's waterbirds.

At the species level, there is marked seasonal variation in dispersion and group size in a population of Great White Pelicans in the southwestern Cape Province of South Africa. Mean group size is highest, and dispersion lowest, during the warm, dry austral summer months (December-February). Conversely, during the relatively cool wet months (May-September), pelican dispersion is high and group size low. Negative correlations between pelican abundance and foraging activity at Rondevlei are explained in terms of variation in the availability of suitable foraging habitat and fish prey. Infrequently visited water bodies are as essential for the conservation of this pelican population as are frequently used ones, since more than half the population relies on them for nine months of the year. This pelican population breeds at only one site, Dassen Island ($33^0 25$'S, $18^0 12$'E), in a wave-like fashion with three peaks between September and March, coinciding with periods of high visitation and foraging activity at Rondevlei.

The Great White Pelican is a major predator of freshwater fish throughout much of Africa. Therefore, its detailed population time-activity budgets are analysed using an integrative bioenergetics model to estimate fish consumption by the southwestern Cape Province population. This pelican population consumes about 184 tonnes of fish annually. Of this, 69% is required for adult existence, 17% for rearing chicks and 14% for flight. Per capita consumption averaged 840g per day, or 8.8% of body mass.

INTRODUCTION

Rationale

Waterbirds, especially wildfowl, are among the most well-studied members of the class Aves (e.g. the journal Wildfowl; Delacour 1954-1964; Hale 1980; Hancock & Elliot 1978; Johnsgard 1981; Kahl 1972; Kear & Duplaix-Hall 1975; Ripley 1977; Crivelli & Schreiber 1984; Scott 1972; Todd 1979). However, relatively little research has been done on waterbird community ecology, and virtually nothing on their biogeography. Indeed, current ideas on avian community ecology (e.g. Cody & Diamond 1975; Wiens 1983) and biogeography (e.g. Brown & Gibson 1983; Fittkau 1969; Vuilleumier 1975) are based primarily on results from studies of terrestrial birds. This bias towards terrestrial birds is perhaps due to their generally more sedentary natures (Curry-Lindahl 1981). Waterbirds are much more mobile (Curry-Lindhal 1981), tend to be erratic in their utilisation of a given wetland ecosystem (Frith 1967) and, consequently, have relatively large dispersions (Curry-Lindhal 1981). Terrestrial birds are therefore much more susceptible to local selection pressures than are waterbirds, and thus, are more tractable study organisms for eco-evolutionary investigations (Crowe 1978).

The dearth of information on waterbird community ecology and biogeography would not be a serious matter if waterbird biology was controlled by processes thought to be important for terrestrial birds. However, the minimal information available on waterbird biogeography (e.g. Colahan 1984; Moreau 1966; Reichholf 1975; Siegfried 1981; Winterbottom 1967, 1972) suggests that they exhibit distribution and diversity patterns markedly different from birds with non-aquatic habitats. For example, Reichholf

(1975) showed that, unlike most other bird groups, the diversity of waterfowl in South America increases at higher latitudes. Moreover, Winterbottom (1967, 1968b) found a remarkable homogeneity in the aquatic avifauna throughout much of eastern and southern Africa; in sharp contrast to the marked zonation observed in terrestrial birds (Chapin 1932; Crowe & Crowe 1982). Thus, waterbird distribution/diversity patterns may be influenced by different ecological processes than those for terrestrial birds, and, on that basis alone, warrant separate investigation.

If patterns of waterbird mobility reflect the climatic and ecological processes which control them, i.e. short term intra- and longer term inter-seasonal variations in wetland ecosystems (Leitch & Kaminski 1985), an understanding of their community ecology and biogeography could be invaluable conservation and management tools. In fact, wetland biotopes, especially in relatively xeric continents such as Africa, are accorded a high conservation priority (Huntley 1978; Noble & Hemens 1978; Smart 1976), because they suffer more drastically from man's abuse of the environment than most of the world's other major biotopes (Fog & Lampio 1982). Waterbirds have also been shown to be good indicators of the impact of man's 'development' activities on wetlands (Saeijs & Baptist 1977). Moreover, owing to the well-known disregard foraging waterbirds have for political boundaries (e.g. Din 1979), quantitative studies of waterbird distribution, diversity and abundance may be instrumental in assessing and monitoring the dynamics of wetlands on an international scale (Atkinson-Willes 1976; Szijj 1972).

Last, but not least, waterbirds are generally large and conspicuous and have attractive plumages and, in many cases, spectacular behavioural displays. They therefore add appreciably to the attraction of conserved areas. However, their aesthetic value extends further than mere recreation. This is reflected in the massive accumulation of field cards and field sheets compiled by amateur ornithologists who are, like me, fascinated by the dynamic nature of waterbird biology. These field cards and sheets have proved to be the cornerstones of the data bases underlying this thesis.

Aims and approach

The aims of this thesis are to describe and explain patterns of distribution, diversity (measured as number of species) and abundance, for African waterbirds in terms of spatial and temporal variation in the quality and quantity of wetland habitats. A quantitative, statistical approach is employed throughout this thesis. However, I also rely on graphical representations to explain relationships between waterbirds and their environment which are not clearly elucidated by uni- or multivariate statistical analysis.

Scope

The research comprising my thesis was conducted at four levels: the continent, sub-continent, ecosystem and species. On the basis of the expectation that similar selection pressures act on morpho-eco-ethologically similar waterbird species, at the first three levels, waterbird species were analysed both separately and in guilds (Karr 1983). More specifically, the scope of this dissertation is as follows.

Chapter 1

Geographical patterns of distribution, species diversity (number of species) and endemism of waterbirds in mainland Africa south of the Sahara Desert are described and interpreted in the light of present-day and possible past environmental conditions, especially measures of the availability of lake, river and swamp biotope. When possible, patterns and underlying processes which influence waterbird species diversity in Africa are compared with those described by Reichholf (1975) for South America.

Chapter 2

In this chapter, I use the same approach as in the preceding one, but focus on southern Africa south of the Cunene and Zambezi rivers. The primary aim of this finer-grained study is to identify possible subtle patterns which may have eluded my Afrotropical scale study. Moreover, southern Africa encompasses a range of biomes from rain forest to desert, including large areas of semi-desert karoo, which are characterized by highly erratic rainfall. It is in the karoo that the dynamic nature of waterbird biogeography should be most evident. Finally, in addition to relating geographical variation in waterbird diversity to variation in measures of natural environmental conditions, I also analyse correlations between waterbird diversity and various measures of the availability of man-made and/or modified impoundments.

Chapter 3

I test and expand my ideas on broad scale waterbird distributional dynamics, by focusing on short and long-term temporal variation in waterbird utilisation of Rondevlei Bird Sanctuary (Cape Province, South Africa) in relation to fluctuations in the biotic and abiotic environment. The 'vlei' which dominates the Sanctuary is a relatively common South African biotope, and Rondevlei is an important nature reserve which provides food, shelter and/or breeding grounds for large populations of many waterbird species.

Chapter 4

This and the remaining two chapters focus on the Great White Pelican *Pelecanus onocrotalus*, a species whose abundance patterns typify the fluctuations observed in waterbirds at Rondevlei. The Great White Pelican was selected for the species level aspect of my thesis for several reasons: 1) it is widespread in Africa (Snow 1978); 2) has been assigned 'Red Data' status in South Africa (Brooke 1984); 3) is involved in nutrient cycling on a large scale in terms of biomass (Din 1979); and 4) has had its local distribution and abundance monitored over many years (Cooper 1976-1979). In Chapter 4, distributional dynamics of the Great White Pelican are analysed in the light of seasonal variation of group size and overall dispersion, timing of breeding, and fluctuation in the biotic and abiotic environment. Moreover, since distribution and abundance data available for this population span several decades, I am able to test the generality of ideas developed during my own intensive 13-month field study of Rondevlei's pelicans.

Chapter 5

This chapter examines detailed species/habitat relationships described in Chapter 3. On the basis of a 13-month study of time activity budgets of Great White Pelicans at Rondevlei Bird Sanctuary and at Dassen Island, the population's sole breeding site, variation in breeding activity and in visitation and foraging are studied in relation to variation in environmental factors (e.g. water depth and rainfall).

Chapter 6

In this final chapter, I analyse seasonal variation in energy demands of the Great White Pelican Cape population using an integrative bioenergetics approach (Kendeigh, Dol'nik & Gavrilov 1977) based on the model described by Furness and Cooper (1982). This model helps to assess seasonal variation in existence energy demands, as well as the energetic requirements for: flights within and between feeding sites, flights from the breeding colony to feeding sites, foraging, egg production and chick rearing. This information also allows estimation of the impact of pelicans on their prey, and evaluation of the assumption by previous authors (e.g. Din 1979) that daily food consumption in the Great White Pelican is about 10% of body mass. The findings of this research may be of use in both academic studies of bioenergetics and those aimed at the management of piscivorous species and their prey.

Caveat

In order to communicate the results of my thesis as rapidly as possible, each chapter of this dissertation (except Chapter 3) was submitted for publication to a suitable international scientific journal as soon as it was completed. The publication status of these papers is indicated on their respective chapter title page. Chapter 3 is, at present, structured to link the two initial chapters with the last three. It will be modified somewhat before submission for publication. Although I have attempted to standardize the format of this dissertation, my 'publish as finished' strategy has resulted in a certain amount of repetition of information, especially in the first three chapters. I apologise for this unavoidable flaw in the dissertation, and hope that the SUMMARY AND SYNTHESIS section compensates for this deficiency by linking these six discrete papers into a cohesive thesis.

CHAPTER 1. Patterns of distribution, species diversity, endemism and guild composition of waterbirds in Africa

African Journal of Ecology (1985) 23: 89-120.

Biogeography has become a predictive science only in the last 15 years (Vuilleumier 1975; Nelson & Platnick 1981). This relatively 'late blossoming' from its descriptive phase can be attributed to a dearth of adequate distributional data (i.e. detailed summaries for entire floras and faunas) and of objective, repeatable methods of synthesizing distributional data for more than a few species [see Udvardy (1969) for a review of pre-computer approaches]. The publication of the Atlases of Speciation of African Birds (Hall & Moreau 1970; Snow 1978) has done much to improve the quality of African bird distributional data. Moreover, the development of relatively easy to use computer programs which can handle large sets of multivariate data (reviewed by Sneath & Sokal 1973) has helped biogeographers to come to grips with complex patterns of distribution. Diamond & Hamilton (1980) and Crowe & Crowe (1982) have employed such programs in their investigations of patterns of distribution and species diversity (number of species) for the non-aquatic birds covered by the Atlases. The aims of the present study are to: A) describe geographical patterns of distribution, species diversity and endemism of waterbirds in mainland Africa south of the Sahara Desert (hereafter referred to simply as Africa); B) interpret these patterns (i) in the light of present-day and possible past environmental conditions, and (ii) on the basis of taxonomic, morphological, behavioural and ecological characteristics of the aquatic avifauna; and C) compare, when possible, patterns of waterbird species diversity in Africa with those described by Reichholf (1975) for South America.

Methods

For the purpose of this study a waterbird is taken to be any species covered by the Atlases (i.e. breeding in Africa) which is dependent on non-marine aquatic biotope for feeding and/or breeding. Clearly, this definition involves a subjective element, but the choice of species to analyse was guided by standard African ornithological literature (e.g. Bannerman 1953; Jackson & Sclater 1938; Mackworth-Praed & Grant 1952-73; McLachlan & Liversidge 1978), and the advice of ornithologists who have had extensive field experience in Africa. The 156 species studied (Appendix 1.1) were investigated using the approach of Crowe & Crowe (1982). A grid with 119 quadrats (Fig. 1.1) was superimposed over the distribution map of each species. The distributional information was quantified by scoring each quadrat for each species according to the number of localities at which the species was found, thereby weighting the presence of the species. At this stage, I discarded data for 18 quadrats which had both relatively few species and which had been poorly sampled, as indicated by Map A in Hall & Moreau (1970).

From this 101 x 156 matrix, waterbird zoogeographical zones were identified by means of cluster analysis (Anderberg 1973; Field & McFarlane 1968), using the Bray-Curtis (1957) similarity measure and the unweighted pair-group agglomeration algorithm (Lance and Williams 1967), and multidimensional scaling (Shepard 1980). Cluster analysis and multidimensional scaling are complementary analytical approaches (Field, Clarke & Warwick, 1982). The former is useful in identifying hierarchical patterns of similarity, usually expressed in biogeographical studies as zones (e.g. subregions, provinces and districts). The latter

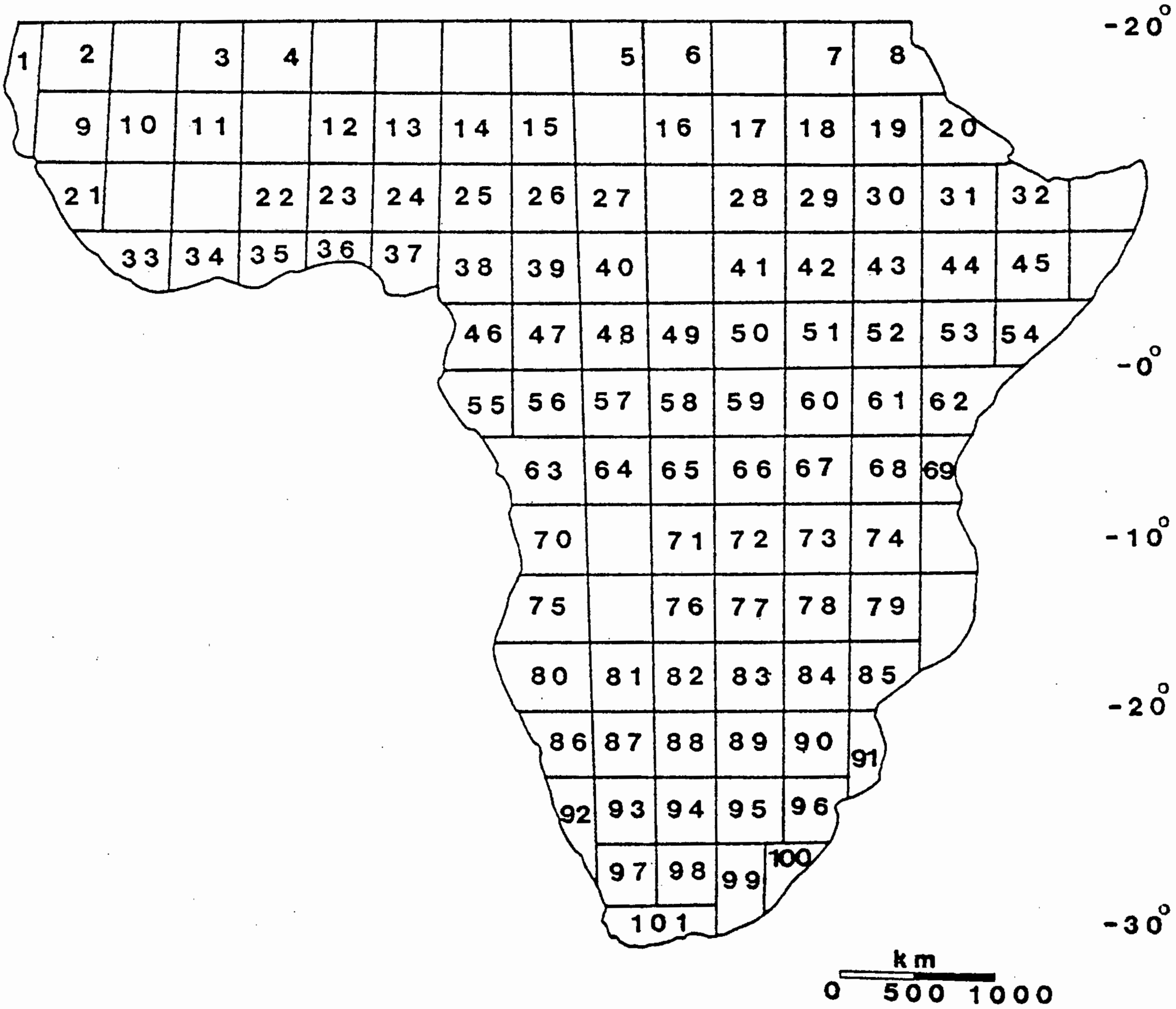

Fig. 1.1. The grid quadrat system used to extract data from Hall & Moreau (1970) and Snow (1978). Quadrats without numbers were excluded due to poor sampling (see text).

method helps to uncover gradients within and between clusters, thereby suggesting the possible effects of abiotic factors (e.g. temperature and rainfall) on distribution/diversity patterns.

Information statistic tests (Field 1969) were used to identify characteristic species for each zone. I define a characteristic species as one generally confined to (at least two thirds of its recorded occurrences), and widespread within, an avifaunal zone, and the limits of whose range help to delineate the boundaries of the zone.

Patterns of quadrat species diversity (number of species) were depicted as contour maps drawn with the aid of SACLANT (Diederiks, 1979), a computer program which fits an approximate contour surface to a set of data points using least squares polynomial analysis. Correlation and stepwise multiple regression analysis (Allen 1973) were used to identify environmental variables which may influence quadrat species diversity. The environmental variables investigated included measures of: rainfall, temperature, topographical relief, and the availability of riverine, swamp and lacustrine habitat (Table 1.1). Length of rivers, and perimeter and surface areas of swamps and lakes were digitized from equal-area projection maps (1 : 5.000.000 scale; Bartholomew 1973). The digitizer measured X and Y coordinates at intervals of approximately 0.3 mm along the course of rivers, and the distances between consecutive points were estimated in a Tektronix graphic computer system and added over the entire length of the rivers. The map scale factor was applied to obtain the true total length. Areas of lakes and swamps were determined by digitizing their perimeters in the same manner; the coordinates of

Table 1.1. Measures of quadrat environmental variation (and their abbreviations used in correlation and regression analyses of waterbird species and environmental variation

Permanent rivers number	PRN	digitized from Bartholomew (1973)
Permanent rivers length	PRL	" "
Non-permanent rivers/wadis number	WN	" "
Non-permanent rivers/wadis length	WL	" "
Lakes number	LN	" "
Lakes perimeter	LP	" "
Lakes area	LA	" "
Swamps/Marshes number	MN	" "
Swamps/marshes perimeter	MP	" "
Swamps/marshes area	MA	" "
Elevation diversity	NEL	number of elevation classes (Clark, 1967)
Elevation range	REL	the largest minus the the smallest elevation (Clark, 1967)
Mean elevation	ELXCL	the mean of 10 approximately uniformly spaced measurements (Clark, 1967)
Range monthly rainfall	RMRF	the largest minus the smallest value given in (Jackson, 1961)
Mean frequency rainfall	FRF	the mean of 10 approximately uniformly spaced measurements (Jackson, 1961)
Range annual rainfall	RRF	the largest minus the smallest value extracted for mean annual rainfall
Mean annual rainfall	ARF	the mean of 10 approximately uniformly spaced measurements (Thornthwaite, 1962)
Mean maximum temperature	TMAX	the mean of 10 approximately uniformly spaced measurements (Jackson, 1961)
Mean minimum temperature	TMIN	the mean of 10 approximately uniformly spaced measurements (Jackson, 1961)

Mean annual temperature	XAT	the mean of 10 approximately uniformly spaced measurements (Jackson, 1961)
Mean annual radiation	XRAD	the mean of 10 approximately uniformly spaced measurements (Jackson, 1961)
Range actual evapotranspiration	RAE	the largest minus the smallest value extracted for mean actual evapotranspiration
Mean actual evapotranspiration	XAE	the mean of 10 approximately uniformly spaced measurements (Thornthwaite, 1962)

the outline being introduced in the formula:

$$\text{Area} = \frac{\sum \left(X_i - X_{i-1}\right)\left(Y_i + Y_{i-1}\right)}{2}$$

The area thus obtained was adjusted to the given map scale.

In order to investigate the degree to which zonal species diversity of waterbirds with differing taxonomic, morphological, ecological and behavioural affinities reflects the pattern for Africa as a whole, I divided the 156 waterbird species among seven guild types (Table 1.2, Appendix 1.1). I employed a liberal definition of the term 'guild': an assemblage of species whose taxonomic, morphological, ecological or behavioural affinities require (or may have required) them to deal with similar selective pressures. Karr (1983) advocates a similar usage of the term guild. Since many of the African waterbird species have not been studied in detail, my categorization in some cases was a 'guestimate' based on the examination of the literature, advice from other ornithologists and from personal field experience. One way contingency tables were calculated for the component guilds of each guild type, using the frequency table program (P4F) of the BMDP series (Dixon 1981). If the various guilds are distributed randomly among the zones, one would expect the proportional representation of guilds in each zone to parallel that for all species of African waterbirds taken together. In these analyses I worked on a presence-absence basis, only considering species which were relatively widespread within zones, excluding those found only at three or fewer localities to minimize potential bias due to possible vagrants and very localized taxa.

Table 1.2. Species richness values, codes, abbreviations and definitions for African waterbird taxonomic, morphological, ethological and ecological guilds

Guild types	No. of species	Codes in Appendix 1.1	Guilds	Definitions
Taxonomic	17	1	ARDEIDAE	
	18	2	ANATIDAE	
	16	3	RALLIDAE	
	12	4	SYLVIINAE	
	22	5	PLOCEIDAE	
Body mass	60	1	SMALL	< 80 gm
	42	2	MEDIUM	> 80 < 400 gm
	54	3	LARGE	> 400 gm
Trophic	16	1	HERBVRS	At least 50% of time spent foraging on vegetable food
	92	2	INVERTVRS	prevalently invertebrates
	25	3	VERT/INV	mixed vertebrate/invertebrates
	23	4	VERTVRS	prevalently vertebrates
Mobility	66	1	SEDENT	purely local movements
	71	2	IRRMOB	irregular-opportunistic movements, sometimes over great distances
	19	3	REGMOB	regular migrants and/or moving geat distances
Foraging behaviour	70	1	WADING	probing, pecking in grass and/or moist soil wading, pecking with feet on/over water
	33	2	SWIM	surface swimming diving from surface or from height
Vegetation structure	53	1	GENVEG	no preferred vegetation type
	70	2	NONWOOD	associated with mainly non-woody vegetation
	33	3	WOOD	associated with mainly woody vegetation
Water habitat	18	1	STREAM	favours streams
	32	2	RIVER	favours rivers
	23	3	DISCRETE	favours ponds, lakes, etc.
	34	4	SWAMP	favours swamps and/or marshes
	49	5	HABGEN	relatively indiscriminate, utilizing at least three of the above habitats

Results

Distribution

The results of cluster, multidimensional scaling and information statistic analyses are summarized in Figs 1.2 and 1.3, and Table 1.3. I recognize only two subregions, FOREST and S-SAV in Fig. 1.3, and three provinces of the S-SAV Subregion. The boundaries of the remaining relatively arid zones are delineated by 'default' i.e. by the overlapping range limits of waterbird species of neighbouring relatively mesic zones, rather than by the ones of characteristic species. However, despite this drawback, I felt that it was of heuristic value to analyse the component waterbirds of these 'default' zones (hereafter D-zones). The main aim of these analyses was to determine whether the taxonomic, morphological, behavioural and/or ecological characteristics of species which persist in D-zones varied in some explicable fashion. Holm & Scholtz (1985) also employ default zones in their study of the biogeography of beetles of the Kalahari.

Species diversity and endemism

Geographical variation in African waterbird species diversity is illustrated in Fig. 1.4. Results of the waterbird species diversity vs environmental variation correlation and regression analyses are summarized in Appendix 1.2 and Tables 1.4 and 1.5. The availability of aquatic biotope as indicated by digitization is summarized by zone in Appendix 1.3. Results of various species diversity comparisons between the FOREST and S-SAV Subregions are summarized in Table 1.6. In this table, for all comparisons, the S-SAV Subregion has significantly ($P < 0.001$, ANOVA) higher values.

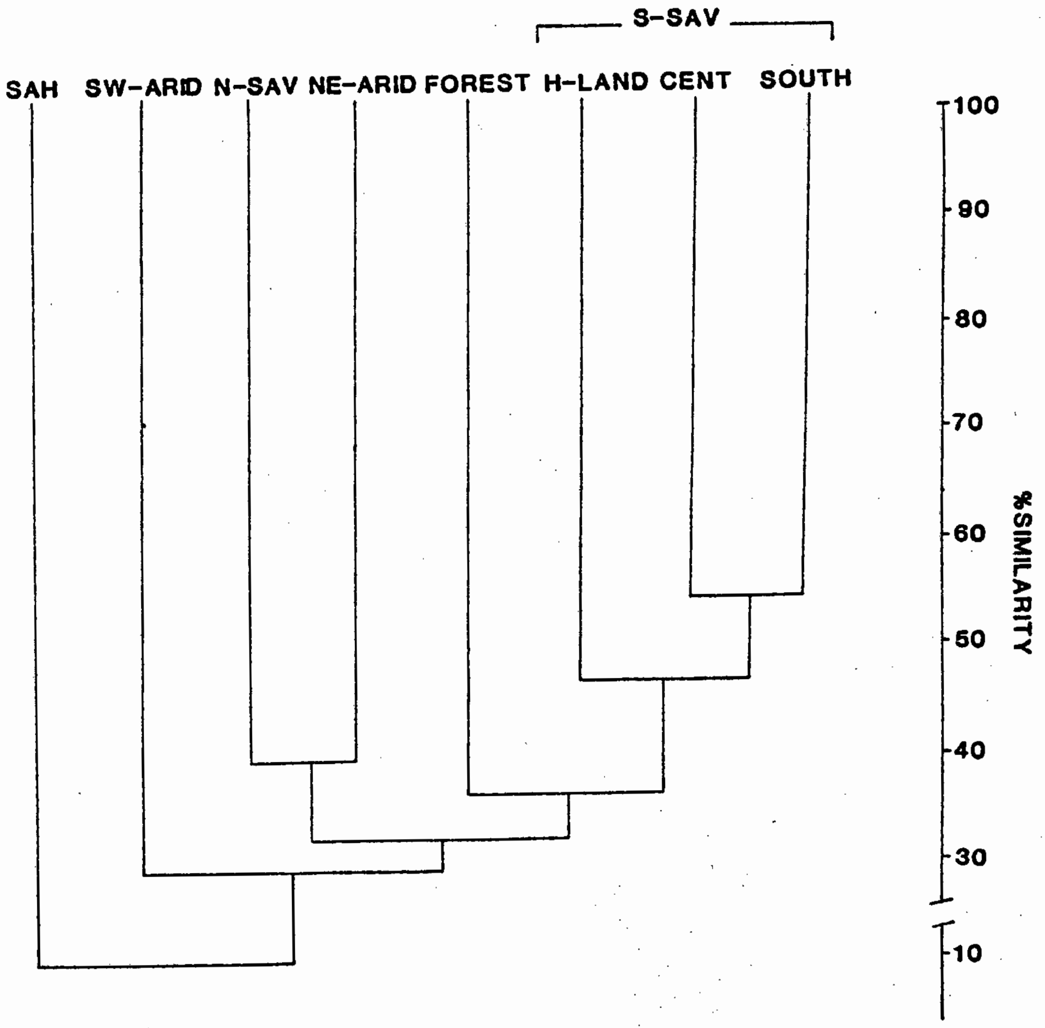

Fig. 1.2a. Avifaunal zones suggested by cluster analysis of 101 quadrats according to 156 species of African waterbirds.

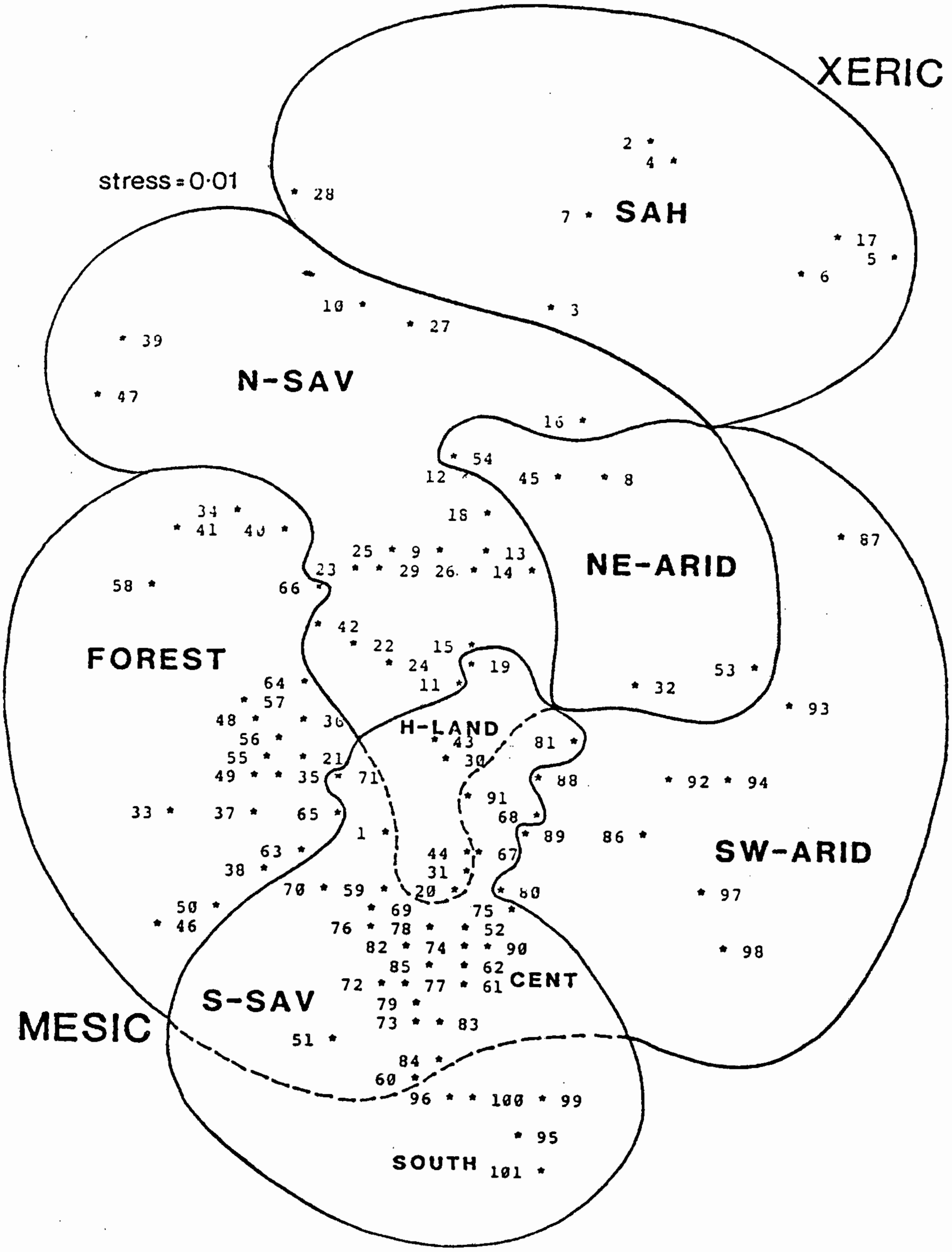

Fig. 1.2b. Avifaunal zones suggested by multidimensional scaling of 101 quadrats according to 156 species of African waterbirds.

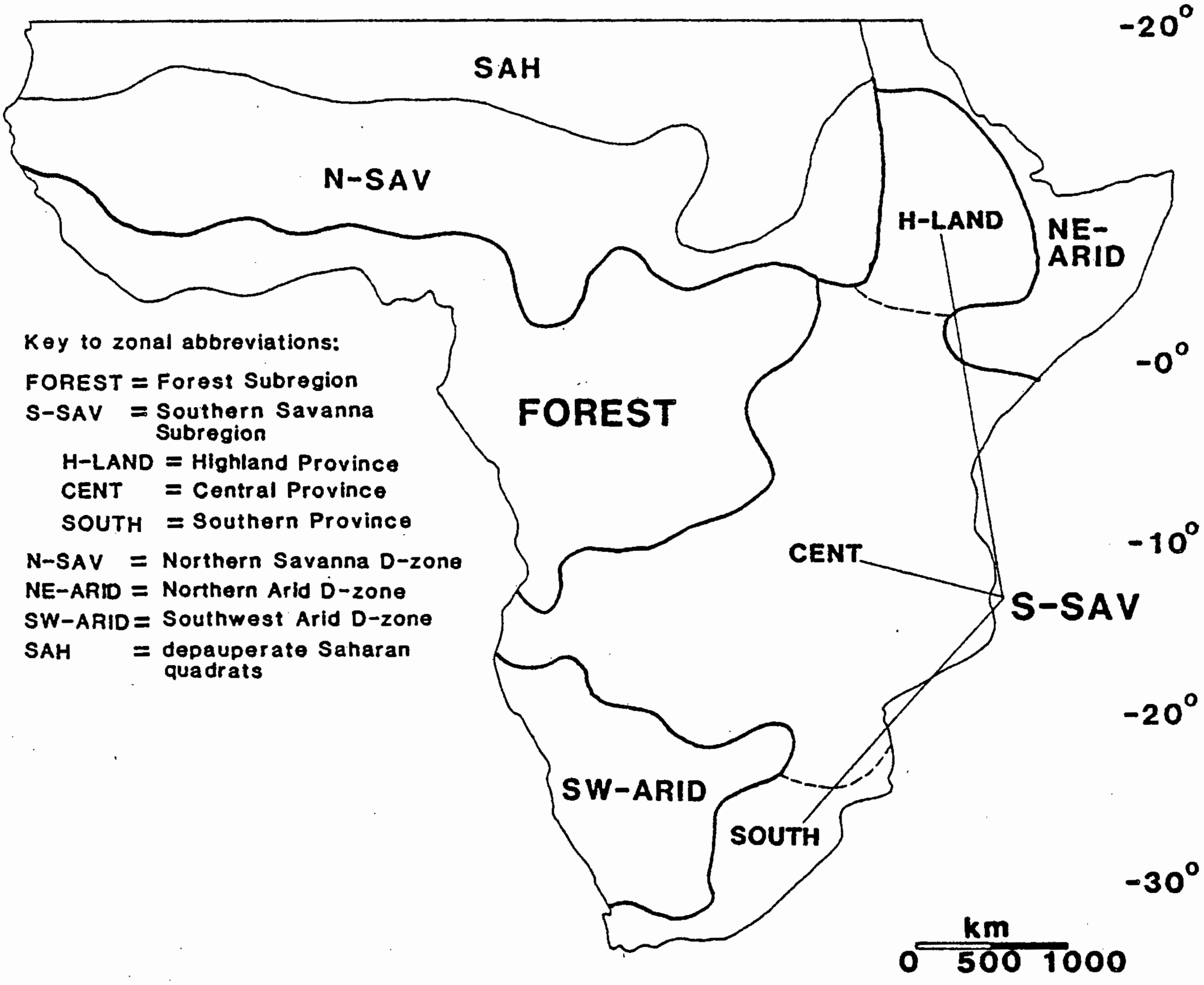

Fig. 1.3. African waterbird avifaunal zones and provinces suggested by the distribution of characteristic species listed in Table 1.3.

Table 1.3. Characteristic waterbirds (and attendant habitat information) of the zones depicted in Fig.1.3

Characteristic species	Zones	Typical habitat
	FOREST	
Pteronetta hartlaubi		- along forested watercourses
Hirundo nigrita		- forested rivers and mangroves
Malimbus nitens		- lower strata of heavy forest in swampy places
Alcedo quadribrachys		- reedy edges of lakes, non-turbulent backwaters of rivers and mangroves and swamps with open water
Tigriornis leucolophus		- small water courses under canopy in deep forest
Sarothrura pulchra		- usually near water in forests or dense thickets
Ploceus aurantius		- along river banks in bushes and trees or reed beds often in palms
Himantornis haematopus		- forest, along small watercourses and among leaf litter
Muscicapa cassini		- wooded banks of rivers
Alcedo leucogaster		- near streams in dense forest
Canirallus oculeus		- small watercourses and swamps under the forest canopy
Bostrichia rara		- forested swamps
	S-SAV	
Ploceus xanthops		- rank growth, reeds or bushes near streams
Anas undulata		- open waters of many kinds, fresh and salt, from the lowlands to high in the mountains
Euplectes orix		- edges of swamps and/or seasonally rank vegetation
Gallinago gallinago		- grassy marshes
Anas sparsa		- along well vegetated streams or lake edges
Anas erythrorhyncha		- fairly shallow freshwater
Euplectes axillaris		- swamps, wet grasses and river edges
Gallinula chloropus		- permanent waters and wet habitats
Acrocephalus gracilirostris		- reeds, papyrus and high grass in swamps
Netta erythrophthalma		- deep, permanent freshwater
Alcedo semitorquata		- reedy edges of lakes, non-turbulent open freshwater of mangroves, rivers and swamps.
Phalacrocorax carbo		- large stretches of water, impoundments

	H-LAND
Rougetius rougetii	- mountain swamps up to 4000m height
Cyanochen cyanoptera	- restricted to vicinity of ponds and streams in upland clearings above 2500m
	CENT
Ploceus xanthops	- rank growth, reeds or bushes near streams
Centropus cupreicaudus	- reed-beds and rank growth in swamps and along the banks of sluggish rivers
Cisticola pipiens	- marshes and swamps on ground that has been flooded
	SOUTH
Cisticola tinniens	- low sedge growth in marshes, swamps or ground that has been flooded
Tadorna cana	- partial to impoundements or ponds with shallow freshwater and wet mud, but also large deep lakes or brackish pans
Anas smithii	- temporary, shallow marshes and flood plains

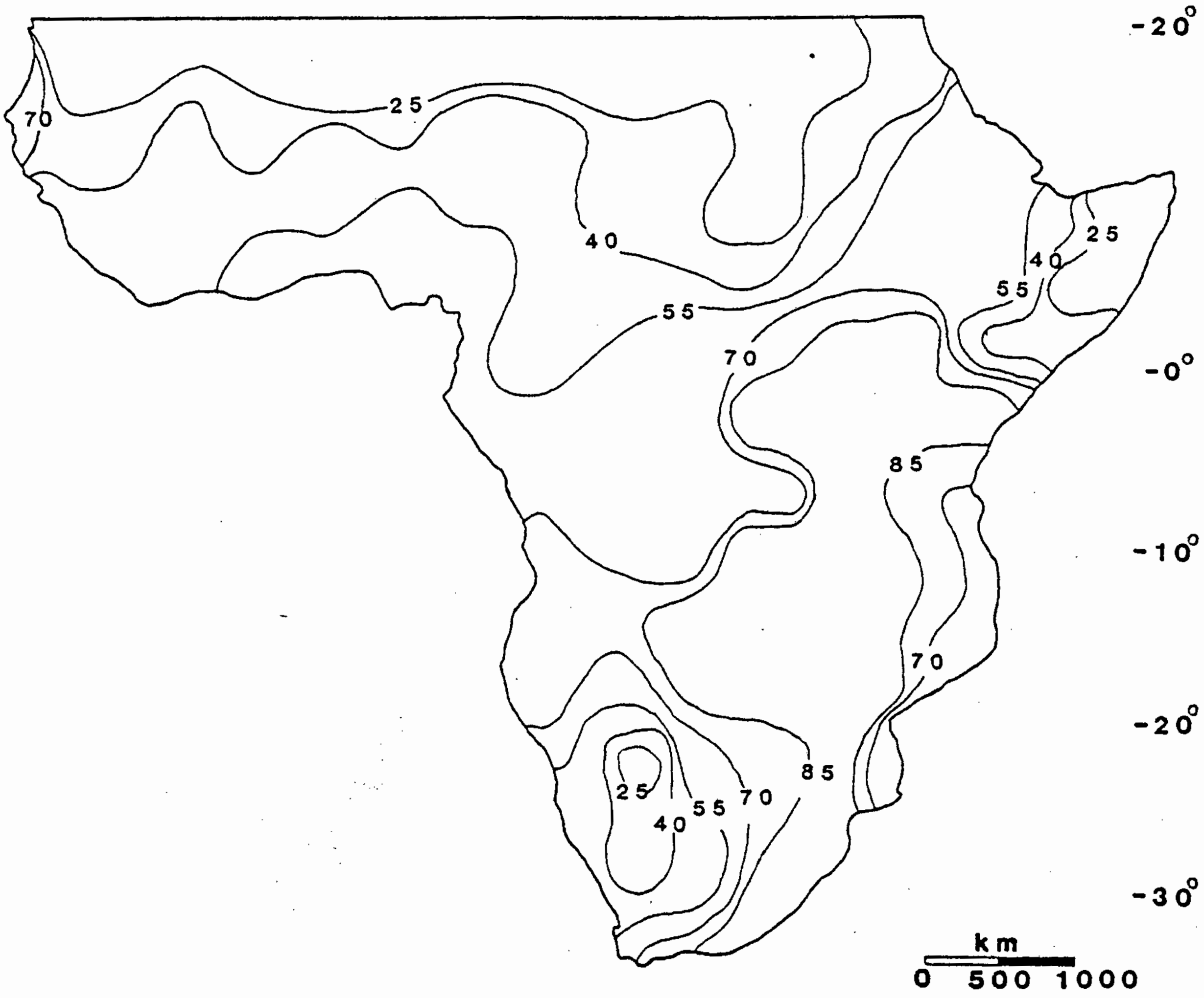

Fig. 1.4. Geographical variation in African waterbird species diversity.

Table 1.4. A matrix of correlation coefficients between African waterbird species richness and measures of present day environmental conditions. See Table 1.1 for a key to variable abbreviations

Variable name	SR*	PRL	PRN	WL	WN	LP	LA	LN	MP	MA	MN	NEL
PRL	0.533											
PRN	0.578	0.898										
WL	-0.421	-0.652	-0.560									
WN	-0.399	-0.598	-0.498	0.958								
LP	0.426	0.060	0.214	-0.213	-0.165							
LA	0.383	0.077	0.193	-0.149	-0.105	0.751						
LN	0.408	0.150	0.283	-0.276	-0.252	0.655	0.392					
MP	0.106	0.078	0.069	-0.051	-0.035	0.162	0.222	0.080				
MA	-0.014	-0.027	-0.032	-0.056	-0.052	0.101	0.139	0.150	0.867			
MN	0.159	0.213	0.208	-0.118	-0.098	0.197	0.213	0.196	0.882	0.681		
NEL	0.388	0.072	0.212	0.169	0.225	0.150	0.185	0.162	-0.120	-0.189	-0.093	
RMRF	0.201	0.305	0.420	-0.320	-0.276	0.296	0.082	0.271	0.011	-0.026	-0.002	0.150
TMAX	-0.383	-0.495	-0.391	0.641	0.618	-0.059	0.007	-0.143	0.056	0.149	-0.020	0.049
TMIN	-0.426	-0.080	-0.158	-0.097	-0.072	-0.008	-0.060	-0.130	0.071	0.086	0.078	-0.206
XAT	-0.455	-0.280	-0.304	0.279	0.282	0.043	0.070	-0.111	0.244	0.292	0.202	-0.186
ARF	0.256	0.553	0.490	-0.565	-0.525	0.125	0.059	0.108	0.087	-0.024	0.140	-0.015
RRF	0.164	0.095	0.216	-0.093	-0.059	0.194	0.090	0.164	-0.043	-0.085	-0.031	0.281
XRAD	-0.272	-0.514	-0.381	0.509	0.483	-0.003	0.003	-0.043	-0.069	0.041	-0.139	-0.053
FRF	0.347	0.557	0.493	-0.523	-0.479	0.237	0.218	0.142	0.140	-0.006	0.251	0.017
RAE	0.209	-0.085	-0.044	0.005	0.027	0.274	0.132	0.156	0.189	0.176	0.034	0.365
XAE	0.236	0.502	0.415	-0.552	-0.533	0.125	0.059	0.072	0.170	0.037	0.204	-0.161
REL	0.158	0.317	0.240	-0.378	-0.316	0.063	0.030	0.162	-0.090	-0.150	-0.006	0.079
ELXCL	0.372	0.229	0.226	0.112	0.106	0.128	0.375	0.064	0.080	-0.032	0.147	0.204

	RMRF	TMAX	TMIN	XAT	ARF	RRF	XRAD	FRF	RAE	XAE	REL
TMAX	-0.243										
TMIN	0.276	-0.205									
XAT	0.059	0.423	0.634								
ARF	0.641	-0.649	0.369	-0.047							
RRF	0.489	-0.042	0.142	0.091	0.271						
XRAD	-0.247	0.694	-0.296	0.180	-0.744	-0.098					
FRF	0.472	-0.617	0.302	-0.039	0.883	0.193	-0.748				
RAE	0.219	-0.075	0.091	0.019	-0.016	0.275	-0.008	0.007			
XAE	0.518	-0.629	0.368	-0.061	0.860	0.151	-0.690	0.769	0.033		
REL	0.381	-0.430	0.192	-0.155	0.646	0.139	-0.509	0.568	-0.006	0.550	
ELXCL	-0.245	0.155	-0.540	-0.143	-0.050	-0.095	-0.034	0.145	-0.282	-0.121	-0.018

* P = 0.05, r = 0.195; P = 0.01, r = 0.254; P = 0.001, r = 0.321.

Table 1.5. Summary of significant results of stepwise mulyiple regression analyses between quadrat species diversity and measures present day environmental conditions

Environmental variable	Sign of correlation	Change in coefficient of determination
No. of permanent rivers	+	.33
Minimum temperature	-	.11
Perimeter of lakes	+	.10
Maximum temperature	-	.08
No. of elevation classes	+	.04
Length of permanent rivers	+	.02
Total		.69

Table 1.6. Univariate statistics and results of analysis of variance tests between the FOREST and the S-SAV subregions

Zone		Total species richness	Ardeidae	Anatidae	Herb-eaters	Insectivorous	Vertebrate-eaters
FOREST							
	X	58.0	5.9	5.8	7.2	17.6	9.5
	Sd	11.6	1.9	1.9	2.0	3.7	2.3
	Max	78.0	11.0	11.0	11.0	25.0	13.0
	Min	37.0	3.0	3.0	3.0	11.0	5.0
	n	21.0	21.1	21.1	21.0	21.0	21.0
S-SAV							
	X	83.0	9.3	12.4	10.8	22.8	14.7
	Sd	14.4	4.1	2.3	1.4	4.9	2.9
	Max	114.0	16.0	16.0	15.0	34.0	20.0
	Min	49.0	2.0	7.0	8.0	14.0	7.0
	n	37.0	37.0	38.0	38.0	38.0	38.0
Tail	Probability	< 0.0001	0.0007	< 0.0001	< 0.0001	0.0002	< 0.0001

The percentage of endemism is 15% (16 endemic species out of a total 104) for the FOREST Subregion, and 26% (36 endemics out of a total of 139) for the S-SAV Subregion.

Taxo-morpho-eco-ethological guilds

Total and guild species diversity values for Africa and each zone are listed in Table 1.7. The statistically significant results of the analysis of the two subregions, three provinces and three D-zones are summarized in Table 1.8.

Discussion

Distribution

The distributional results of this study are consistent with those of Winterbottom (1967, 1968b) who found high coefficients of community between water bodies stretching from the Sudd to South Africa. The most obvious difference between my waterbird avifaunal map and those for non-aquatic birds is that there are far fewer zones in the map for waterbirds. Crowe & Crowe (1982) recognize 18 and 15 zones respectively for passerine and non-passerine birds. I recognize only four, the FOREST Subregion and the three provinces which comprise the S-SAV Subregion. In fact, the faunal zone map for African fish (Fig. 1.5) more closely parallels that for non-aquatic birds, and the 'boundaries' of my suggested waterbird zones are much less clear-cut. For example, the species rich (70 vs a mean of 21 for the surrounding quadrats) quadrat 1, which geographically is associated with quadrats comprising the N-SAV D-zone, grouped with quadrats of the S-SAV Subregion in the ordination (Figs 1.2a and 1.2b). Since, as I will show below, many waterbirds are opportunistic habitat-wise, highly

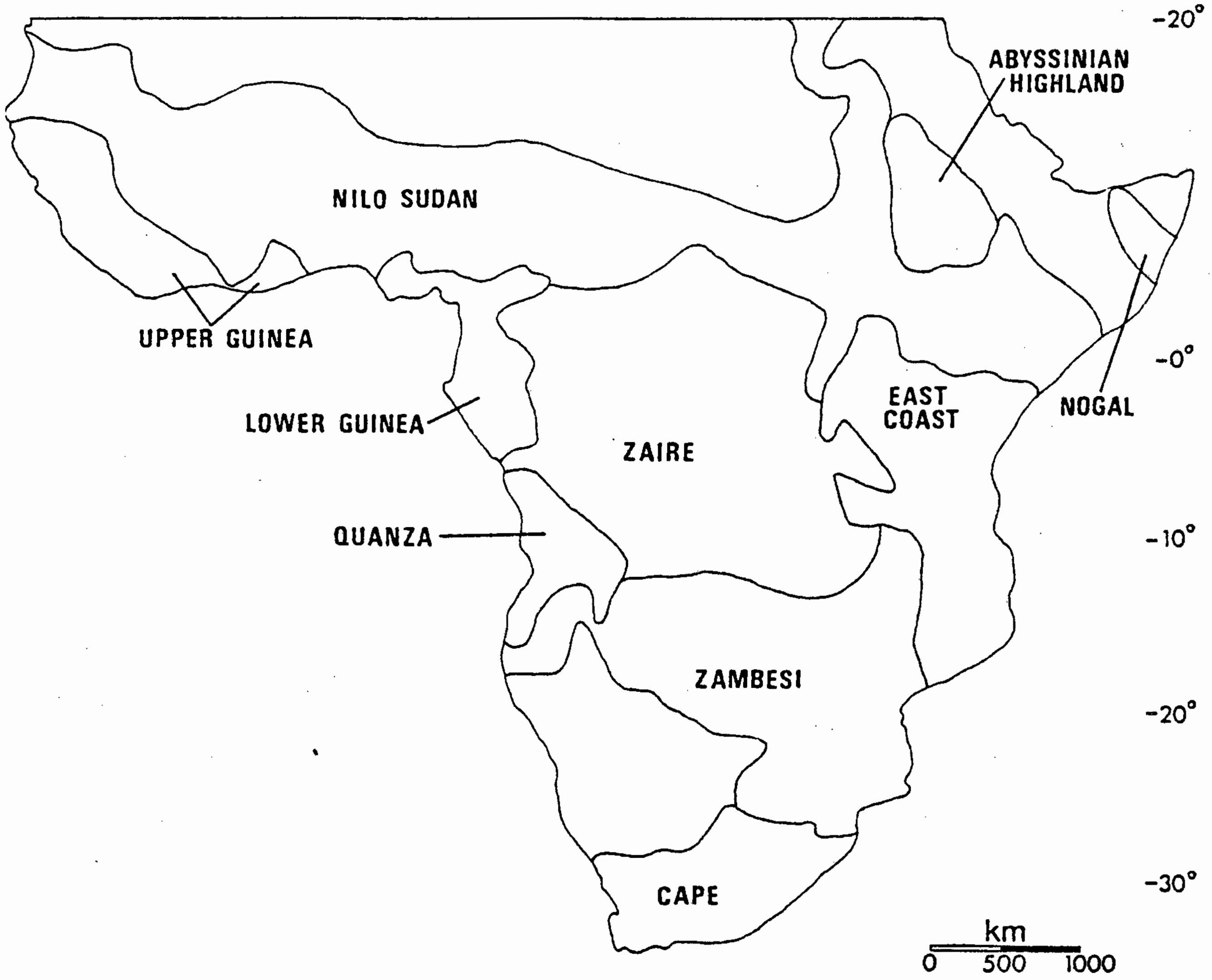

Fig. 1.5. A map of ichthyofaunal zones [adapted from Roberts (1975)].

Table 1.7. Guild species richness values for Africa and the various zones

	AFRICA	FOREST	S-SAV	N-SAV	NE-ARID	SW-ARID	H-LAND	CENT	SOUTH
No. of quadrats	101	21	36	19	5	10	6	25	5
Total species richness	156	104	139	88	59	76	92	137	105
Mean species richness*	59	58	83	38	36	51	68	88	84
Endemics		16	36	1	3	0	2	13	0
Taxonomic guilds									
ARDEIDAE	17	7	15	8	2	4	5	15	14
ANATIDAE	18	9	15	8	3	13	14	14	16
RALLIDAE	16	9	11	6	1	5	7	12	10
SYLVIINAE	12	3	6	2	0	2	3	9	4
PLOCEIDAE	22	9	13	5	2	1	5	16	5
Body-mass guilds									
SMALL	60	27	33	21	3	10	18	42	21
MEDIUM	42	26	35	25	9	13	22	36	29
LARGE	54	23	44	23	12	28	33	44	44
Trophic guilds									
HERBVRS	16	9	14	9	3	7	13	15	12
INVERTVRS	92	40	62	35	9	28	38	70	48
VERT/INV	25	15	16	12	4	6	10	17	16
VERTVRS	23	12	20	13	7	9	13	20	18
Mobility guilds									
SEDENT	66	30	32	14	2	7	17	43	21
IRRMOB	71	34	64	46	15	37	47	64	59
REGMOB	19	12	16	9	7	7	9	15	14
Foraging behaviour guilds									
WADING	70	36	58	38	14	25	35	59	51
SWIM	33	18	27	17	7	21	25	26	28
Vegetation structure guilds									
GENVEG	53	24	44	25	12	28	30	44	38
NON-WOOD	70	26	54	31	8	20	32	59	43
WOOD	33	26	14	13	4	3	11	19	13
Water habitat guilds									
STREAM	16	9	8	3	0	4	6	10	6
RIVER	31	18	19	14	1	5	9	20	13
DISCRETE	26	7	20	10	7	18	17	19	21
SWAMP	38	12	25	11	3	5	11	30	17
HABGEN	45	30	40	31	13	19	30	43	37

* obtained by dividing the sum of the species richness values of the quadrats comprising the zones by the number of quadrats.

Table 1.8. A summary of the statistically significant results of waterbird guild analysis

	Guilds significantly under and overrepresented*						
Zone name	Taxonomic	Body mass	Trophic	Mobility	Foraging behaviour	Vegetation structure	Water habitat
FOREST	(NS)	(NS)	(NS)	(NS)	(NS)	WOOD(+) NONWOOD(-) GENVEG(-)	HABGEN(+) RIVER(+) DISCRETE(-) SWAMP(-)
S-SAV	(NS)	SMALL(-) MEDIUM(+) LARGE(+)	(NS)	SED(-) IRRMOB(+) REGMOB(+)	(NS)	GENVEG(+) WOOD(-) NONWOOD(+)	HABGEN(+) STREAM(-) RIVER(-)
N-SAV	(NS)	MEDIUM(+) SMALL(-)	(NS)	SED(-) IRRMOB(+)	(NS)	(NS)	HABGEN(+) STREAM(-) SWAMP(-)
NE-ARID	(NS)	SMALL(-)	(NS)	REGMOB(+) SED(-)	(NS)	(NS)	HABGEN(+) DISCRETE(+) RIVER(-) STREAM (-)
SW-ARID	ANATIDAE(+) PLOCEIDAE(-) SYLVIINAE(-)	LARGE(+) SMALL(-)	(NS)	SED(-) IRRMOB(+)	SWIM(+)	GENVEG(+) WOOD(-) NONWOOD(-)	DISCRETE(+) HABEGEN(=) SWAMP(-) RIVER(-)
H-LAND	ANATIDAE(+) SYLVIINAE(-) PROCEIDAE(-) ARDEIDAE(-)	SMALL(-) LARGE(+)	HERBVRS(+)	SED(-) IRRMOB(+)	WATER(+)	(NS)	HABGEN(+) DISCRETE(+) SWAMP(-) RIVER(-)
CENT	(NS)	(NS)	(NS)	SED(-) IRRMOB(+)	(NS)	WOOD(-) GENVEG(+) NONWOOD(+)	HABGEN(+) RIVER(-) STREAM(-)
SOUTH	SYLVIINAE(-) ANATIDAE(+) PLOCEIDAE(-) ARDEIDAE(+)	SMALL(-) LARGE(+) MEDIUM(+)	(NS)	SED(-) IRRMOB(+) REGMOB(+)	(NS)	GENVEG(+) WOOD(-)	HABGEN(+) DISCRETE(+) STREAM(-) RIVER(-) SWAMP(-)

* in order of discrepancy, where (NS) = not significantly different, (+) = overrepresented, (-) = underrepresented.

mobile and/or widespread (Moreau 1966: 96), it is not unexpected that they partition Africa much less finely than do non-aquatic birds and fish.

The component species of D-zones are all found in one or both of the subregions. Two of the D-zones, the NE-ARID and SW-ARID, are much poorer in species than the other zones. Figure 1.2b shows that the N-SAV D-zone has affinities with both subregions, sharing with them species such as the Senegal Thicknee Burhinus senegalensis, Egyptian Plover Pluvianus aegyptius and White-collared Pratincole Glareola nuchalis. The NE-ARID D-zone has closest affinities with the N-SAV D-zone, but the majority of its species are ubiquitous, e.g. the Hamerkop Scopus umbretta, Yellowbilled Stork Mycteria ibis and Egyptian Goose Alophochen aegyptiacus. The SW-ARID D-zone has closest affinities with the S-SAV Subregion, sharing species such as the Black-necked Grebe Podiceps nigricollis, African Shelduck Tadorna cana, Cape Shoveller Anas smithii with it.

As Crowe & Crowe (1982) found for non-aquatic birds, the influence of rainfall on waterbird distribution patterns is reflected in the multidimensional scaling ordination (Fig. 1.2b). Quadrats with relativaly mesic conditions tend to cluster on the lower left corner of the ordination, grading to the upper right through semi-arid quadrats bordering on the Sahara.

Species diversity and endemism

Species diversity for non-aquatic birds both in Africa (Crowe & Crowe 1982) and South America (Fittkau 1969) decreases steeply with increasing latitude. This is not the case for waterbirds. Examination of Appendix 1 in Reichholf (1975) yields species diversity values of 42, 39 and 37 for the tropical, subtropical and temperate zones respectively. However, the lowland tropics of

South America encompass an area more than twice that of the combined subtropical and temperate zones. Therefore, Reichholf's results suggest that the South American waterbird species diversity per unit area is much higher outside the tropics. This result is consistent with those from a comparison of the FOREST and S-SAV Subregions of Africa according to total waterbird species diversity (Table 1.8). In fact, in Africa, there is a decidedly longitudinal species diversity gradient, with more species in the eastern than in the western and northern areas (Fig. 1.4).

The markedly higher percentage endemism outside the FOREST Subregion parallels the pattern found for waterbird species diversity, and contrasts with the results for non-aquatic birds, which exhibit a slightly higher level of endemism in the Forest Subregion (Crowe & Crowe 1982). This difference, together with the tendency for the few FOREST waterbird endemics to be highly stenotopic forest species [e.g. the White-crested Tiger Heron <u>Tigriornis leucolophus</u> (Amadon 1973: 270)], supports Moreau's (1966: 135) suggestion that there have been relatively fewer opportunities for speciation in the African tropical forest for waterbirds.

Moving to the results of correlation and stepwise multiple regression analyses (Tables 1.4 and 1.5), it is not unexpected that the availability of aquatic habitat and variation in temperature, topography and effective rainfall all apparently influence waterbird species diversity. However, the most important factors which promote waterbird species diversity include the number of permanent rivers and the perimeter of lakes (rather than their total length and surface area). Thus, the longitudinal, rather than latitudinal, diversity gradient in waterbird species diversity appears to be due to the dispersion of permanent rivers and the configuration of lakes (Appendix 1.3). I realize that my digitization results are not absolute assessments of the availability of aquatic biotopes, especially those too small to be depicted on the maps used in these analyses. Nevertheless, I feel that they do reflect relative differences in the biotope variables which I have assessed.

Apart from the environmental factors treated in the species diversity/environmental diversity regression analysis, an additional feature, unfortunately unquantifiable, appears to differentiate the mesic FOREST and S-SAV Subregions from the relatively xeric D-zones. This is the dispersion of surface sands, which abound in the D-zones and do not foster the formation of durable water bodies. Thus, availability and suitability of waterbird habitat appears to differ not only between areas of generally different climate, but also between areas of similar climate, which differ in soil permeability. This contention is supported by the significant negative correlation between species diversity with non-permanent rivers (WN and WL in Table 1.4), which usually traverse areas based on sandy soil.

Although African waterbird species diversity is significantly positively correlated with measures of present day environmental diversity (Table 1.4), only about 69% of the observed variance in this variable is explained (Table 1.5). Therefore, either sampling error or unmeasured biological phenomena also affect waterbird species diversity. If, as Diamond & Hamilton (1980) and Crowe & Crowe (1982) have suggested for African non-aquatic birds, some of the quadrats have encompassed potential dry climatic phase refugia which may have sustained high waterbird species diversity, they should be poorly and underpredicted by the regression analysis.

In other words, quadrats which could have contained dry-phase refugia for African waterbirds should have far more waterbird species than the regression predicts.

Possible refugia for waterbirds during dry climatic phases, as suggested by a plot of the residuals from the regression analysis (Appendix 1.2), may have existed in (1) the Bani/Macina flood plains in the upper Niger system; (2) the Hadejia-Camadougou water systems draining into the Chad basin; (3) the drainage system of Lakes Albert, Kyoga, Victoria etc., extending from the Ugandan highlands into the White Nile Sudd; (4) the water bodies included between the Uele and Lualaba-Congo systems in northeastern Zaire; (5) the lower Juba and the Tana and Galana river Systems; (6) the water bodies encompassed by the Great Ruaha/Njombe and upper Wembere systems including Bahi Swamps; (7) the upper reaches of Lufira-Lualaba, Zambezi, and Kafue River systems; (8) the Etosha depression which drains the area between the Cunene and the Cubango rivers; (9) the Cubango and Cuito rivers, the Okavango delta into which they drain, and Lakes Ngami and Dow; (10) the area encompassing the origins of river systems which feed the Makarikari Pans, Limpopo and Zambezi Rivers; (11) the area of Zambezi-Shire confluence. I am inclined to accept the idea of waterbird refugia, especially for the S-SAV Subregion, since the suggested refugia in Fig. 1.6 encompass large, relatively ancient drainage basins for major and reliable water systems (Fig. 1.7). Moreover, nearly a third of the S-SAV endemics have the core of their distribution centred on suggested S-SAV refugia. Therefore, the hypothesized waterbird refugia may have been the last to be affected by progressive and uniformly more arid conditions, and thereby acted as centres of evolution for S-SAV endemics which may have spread more widely as conditions became more favourable.

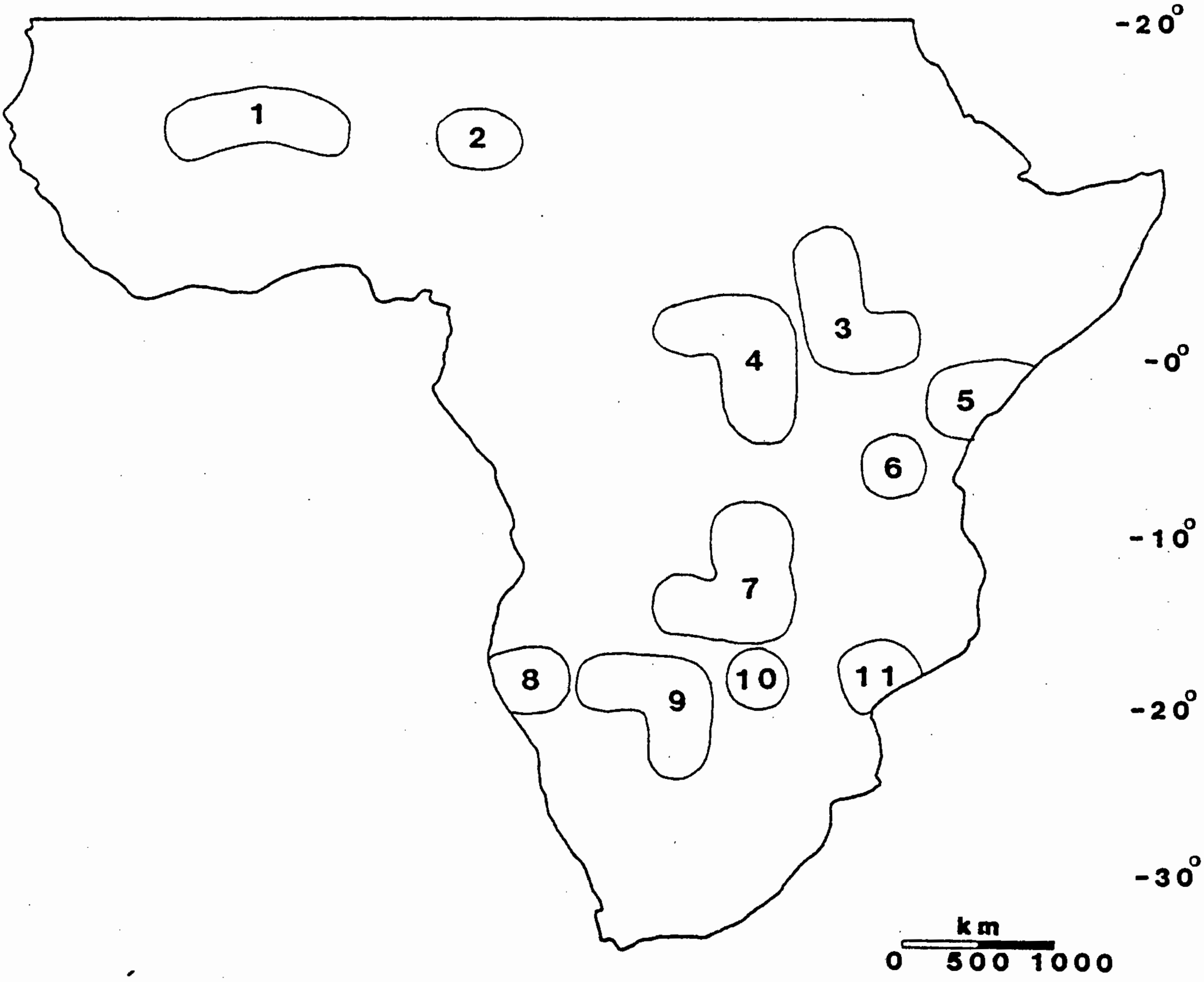

Fig. 1.6. Hypothetical waterbird refugia during climatic dry phases as suggested by Appendix 1.2.

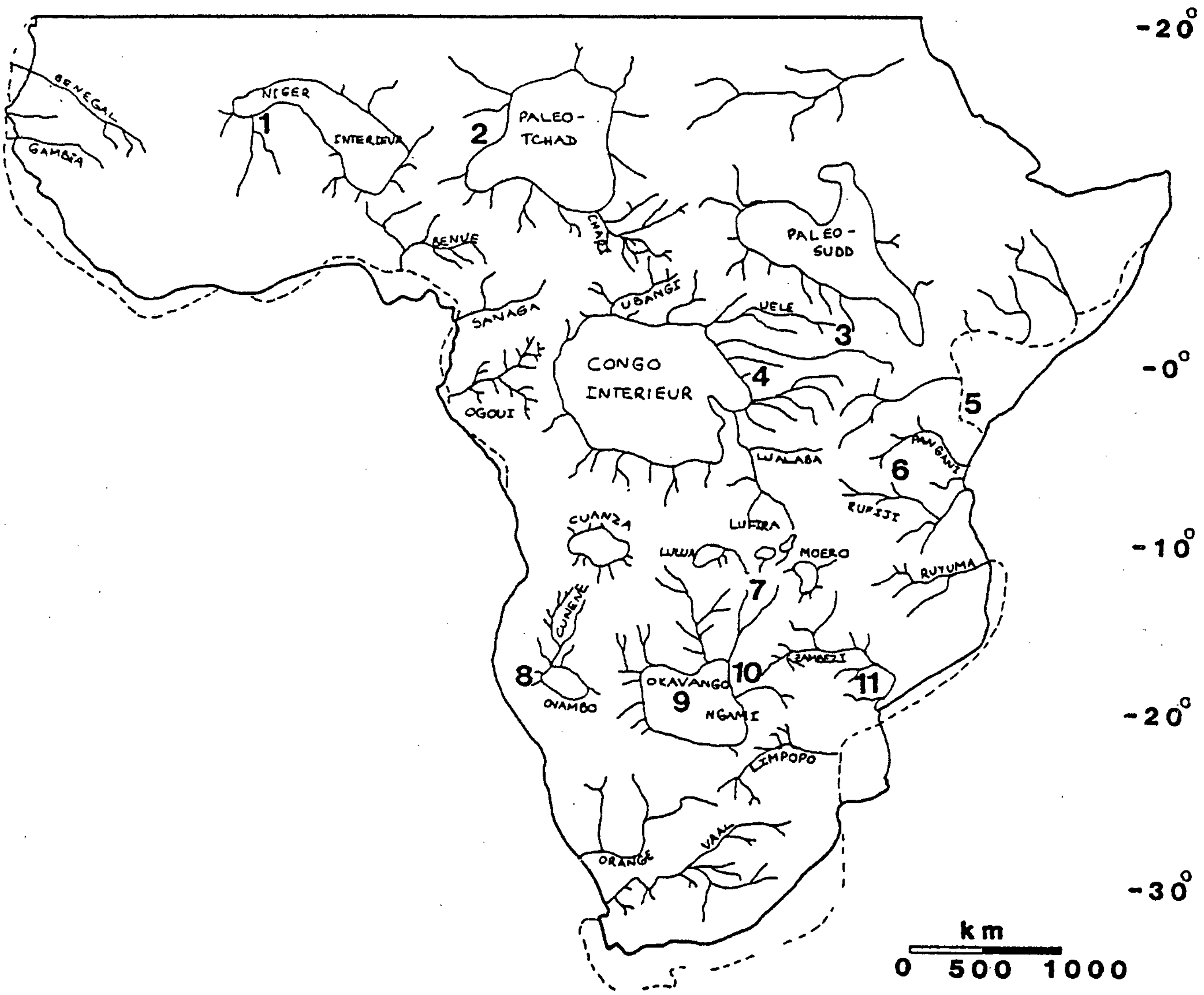

Fig. 1.7. Hydrography of Africa at the Miocene-Pliocene transition [after Howell & Bourlière (1963)].

Taxo-morpho-eco-ethological guilds

Taxonomic guilds

As in South America, the species diversity of Anatidae in Africa is lower in the tropics than in subtropical and temperate areas. Reichholf (1975) attributes the low anatid species diversity in the South American tropics primarily to diffuse competition from a rich fish fauna which is better adapted to local abiotic constraints and depletes commonly used food resources (mainly plants and invertebrates). Consistent with this view, the majority of South American tropical Anatidae are generalist feeders, while those with more specialized diets are more common in the higher latitudes, where their food resources are periodically superabundant. Additional corroborating evidence of the importance of patterns of fish diversity is the higher species diversity of predominantly fish eating herons in the South American tropics.

Reichholf's 'fish competition' hypothesis has little predictive value for African Anatidae and Ardeidae, despite the similarly high fish species diversity in tropical Africa (Lowe-McConnell, 1969). Rather than being dominated by generalist feeders, the tropical (i.e. FOREST Subregion) anatid fauna consists mainly (7 of 9 species) of predominantly plant or invertebrate feeders (Appendix 1.1). Moreover, African ardeid diversity is higher outside the tropics (Tables 1.6 and 1.7), and Ardeidae which feed on vertebrates are also more abundant in the S-SAV Subregion (7 of 15 species) than in the FOREST Subregion (1 of 7 species).

One possible explanation for the different patterns of ardeid diversity between Africa and South America is that the trophic structure of African Ardeidae is different from that in South America. However, a comparison of African and South American

Ardeidae, based on trophic information given in Hancock and Elliott (1978), suggests that this is not the case. The ratio of mixed to predominantly vertebrate feeders is 10 : 5 in South America and 10 : 7 in Africa. An alternative hypothesis which might explain patterns of ardeid diversity in both continents is that ardeid diversity is higher in areas which have relatively low topographic relief and are spatially and temporally variable with respect to shallow water habitat. This hypothesis is supported by the significant underrepresentation of the ARDEIDAE Guild in the H-LAND Province, which has mountainous topography. In fact, close examination of the distributions of species which comprise the ARDEIDAE Guild in Africa in general, and in the H-LAND Province in particular, shows that, unlike the Anatidae, the Ardeidae (with the noteworthy exception of the Green-backed Heron Butorides striatus) avoid mountainous areas. This guild is also overrepresented in the SOUTH Province, which has high values for the number of rivers and lakes (Appendix 1.3), markedly seasonal rainfall and is prone to local droughts (Jackson 1961).

An alternative hypothesis which accounts for the observed patterns of species diversity of Anatidae in both continents is: anatid species diversity is higher in areas with a greater diversity of discrete water biotopes such as lakes and ponds, which experience marked spatio-temporal variation in the availability of waterbird food resources. Rather than supporting a high diversity of waterbird habitat, the dense network of riverine biotope which dominates tropical forest water systems is relatively simple physiognomically (mainly deep channels with relatively steep and heavily vegetated banks), and is generally low in minerals, nutrient content and primary productivity (Beadle 1982: 68-70; Marlier 1973: 231-233; Roberts 1973: 250). Also it is low in the diversity and abundance of Crustacea and Mollusca (Roberts 1973: 246-250), important sources of food near the base of waterbird food chains. My digitization analysis (Appendix 1.3) indicates that other water biotopes favoured by waterbirds in general, and Anatidae in particular, (e.g. lakes, and swamps) are relatively few in number and localized in forests. This result is reflected by the underrepresentation of the DISCRETE and SWAMP Guilds in the FOREST Subregion (see water habitat guilds below) and the relatively limited distributions of Anatidae in that zone. Specifically, the mean species range (number of quadrats occupied) is 13.0 for FOREST Anatidae, significantly lower than the mean of 27.1 for S-SAV Anatidae ($P < 0.01$, Mann-Whitney U test). Moreover, most lakes in the tropical forested areas of the Amazon basin are relatively homogeneous physiognomically and in terms of water quality, and are closely related to the rivers from which they are derived (Marlier 1973: 232-236). Reichholf (1975: 13) discusses abiotic constraints to waterfowl utilization of neotropical water biotopes, but emphazises their role in intensifying competition with fish. I feel that it is not necessary to invoke competition, and that the opportunistic movements of many Anatidae allow them to exploit habitats which are spatially, temporally and nutritionally variable. In fact, this mobility enables Anatidae to exploit the periodic superabundance of food outside the tropics, thereby avoiding competition.

The generally 'as expected' diversity of African Rallidae is possibly a consequence of their relatively broad niches (Ripley 1977: 17) and 'as expected' mobilty statistics (see mobility guilds below). Habitatwise, 38% of the RALLIDAE Guild are classified as generalists (the HABGEN Guild among the water habitat guilds), vs 41% of the ARDEIDAE, 22% of ANATIDAE and less than 10% of the SYLVIINAE and PLOCEIDAE Guilds (Appendix 1.1). Trophically, 75% of the members of the RALLIDAE Guild are mixed feeders vs 59% of the ARDEIDAE, 22% of the ANATIDAE, 68% of the PLOCEIDAE, and 0% of the SYLVIINAE (marked with * in Appendix 1.1). Moving now to their mobility statistics, 38% of the RALLIDAE are sedentary and 62% mobile, not significantly different from the pattern for African waterbirds as a whole (42% sedentary and 58% mobile). Thus, a combination of broad niche and typical mobility has allowed Rallidae to exploit virtually all African aquatic biotopes, but relatively uniformly.

The general underrepresentation of warblers and weavers (SYLVIINAE and PLOCEIDAE in Table 1.8) in zones away from the Equator is possibly a consequence of a combination of their sedentary natures (11 out of 12 Sylviinae are classified as SED, and 19 of 22 Ploceidae in Appendix 1.1), and relatively specialized habitat requirements. Only one member of the SYLVIINAE and none of the PLOCEIDAE Guild falls into the HABGEN Guild among the water habitat guilds (Appendix 1.1).

Body mass guilds

The major feature which emerges from the analysis of these guilds is that the FOREST Subregion is not significantly different from the general African pattern of body mass distribution, while all of the remaining zones except the CENT Province, have an overrepresentation of the LARGE and/or MED Guilds and are underrepresented with regard to the SMALL Guild. I believe that this marked dichotomy between the tropical and subtropical zones is due to the combined effects of food availability and climatic fluctuation. Larger species generally have greater energy reserves (Calder 1974), and tend to be more mobile than smaller ones (only 25% of the SMALL Guild vs 78% of the LARGE Guild are classified as mobile in Appendix 1.1). Therefore, large birds may cope better in the less stable areas outside the tropical belt.

A possible alternative, but not mutually exclusive, hypothesis is that smaller species may be physiologically less well adapted to more dramatically fluctuating climate away from the tropical belt, e.g. the sharp diel temperature fluctuations in the Ethiopian highlands and in the desert steppe of northeastern and southwestern Africa. Underrepresentation of smaller body mass species accounts for the relative species poverty of zones such as NE-ARID and SW-ARID D-zones. In other zones where body mass guilds are also different from the expected African pattern, but which are relatively richer in species, paucity of smaller species is balanced by relative increase of the larger ones (MEDIUM and LARGE Guilds).

Trophic guilds

Unlike South America, in which about 70% of the waterbird species are predominantly vertebrate feeders (Reichholf 1975), only 21% of the 108 non-passerine waterbirds in Appendix 1.1 (Reichholf did not analyse passerines) are classified as predominantly vertebrate feeders and 47% as invertivorous or mixed feeders with a strong dependence on invertebrate food. In fact, 69% of the non-passerine African waterbirds in Appendix 1.1 feed at least partially on invertebrates, while only 45% and 30% feed on vertebrate and plant material.

In an attempt to investigate how the availability of the various food types fluctuates temporally, I have analysed relationships of each trophic guild to mobility guilds. If a certain food type is not equally available year round, this should be reflected in the ratio of its respective trophic guild vs different mobility guilds. Since (always excluding passerines) 40% of VERT/INVERTVRS are sedentary, vs 26%, 18% and 11% respectively for the VERTVRS, INVERTVRS and HERBVRS Guilds, it appears that, unlike a great number of African non-aquatic birds (e.g. Elgood et al. 1973), mixed feeders and not dominantly invertivorous waterbirds are less affected by seasonal extremes.

Moving now to the analysis of zones with respect to trophic guilds, the general 'as expected' pattern (Table 1.8), suggests that, within each zone, a broad range of foraging habitats is available and is exploited by a variety of waterbird species. The most discrepant result from the general African pattern concerns the overrepresentation of HERBVRS Guild in the H-LAND Province which may be due to the relatively high species diversity of herbivorous Anatidae in that zone.

Mobility guilds

African waterbirds are highly mobile (58% of species classed as IRRMOB and REGMOB in Appendix 1.1), especially when compared with non-aquatic birds (Curry-Lindahl 1981). The FOREST Subregion is the only zone which reflects the general African pattern, and in which the SED Guild is not significantly underrepresented (Table 1.8). A plausible hypothesis as to why there is a relatively 'high' representation of the SED Guild in the FOREST zone is that waterbird resources in the equatorial tropical forest are relatively more stable, and are distributed more predictably spatially and temporally.

Moving to the zones in which mobility guilds are significantly under and overrepresented, the IRRMOB Guild is overrepresented in all zones except the NE-ARID D-zone, which has an overrepresentation of the REGMOB Guild. When comparing the NE-ARID to other zones with a strongly fluctuating environment, we see that this D-zone experiences more seasonal, and thus relatively more predictable fluctuations of the climate and therefore in quality of bird habitat (Archer & Godman 1937, vol. I: lxviii-lxxi).

Foraging behaviour guilds

The overrepresentation of the SWIM Guild in the SW-ARID D-zone and H-LAND Province may be a consequence of a relatively large number of man-made impoundments in both zones and of natural ponds in the H-LAND Province (Appendix 1.3). Both of these biotopes provide sufficiently deep water and are therefore favoured by swimming species. This 'habitat' explanation is supported by the common overrepresentation in these zones of DISCRETE Guild species (Table 1.8).

Vegetation structure guilds

The majority of African waterbirds are either associated with non-woody vegetation (45% NONWOOD), or are not partial to a specific structural type (34% GENVEG); while only 21% are associated with woody vegetation (WOOD) (Appendix 1.1). In fact, with the exception of the FOREST zone (where the NONWOOD Guild is under, and the WOOD Guild overrepresented), non-woody vegetation is favoured, even in the relatively well-wooded CENT Province (Table 1.8).

The key to this dichotomy between forest and non-forest, and between the northern and southern part of Africa (the WOOD Guild less than predicted in CENT, SW-ARID and SOUTH), is the spatiotemporal availability of suitable habitat. When compared with other zones, the FOREST Subregion exhibits a general uniformity: spatially in terms of vegetation structure and temporally in terms of food availability. For example, the fringing vegetation of forested rivers lacks the structural and floristic heterogeneity of rivers in the S-SAV Subregion, where grassy dambos are interspersed with strips of open banks, clusters of reeds, isolated trees and/or stretches of closed canopy woody vegetation. Moreover, the bulk of the GENVEG Guild (which is overrepresented in southern zones and underrepresented in the FOREST Subregion), is dominated by mobile species (41 mobile vs 10 sedentary), while the majority of WOOD Guild species are sedentary (21 sedentary vs 12 mobile). This is consistent with the hypothesis of a major temporal uniformity of food availability in the FOREST Subregion.

On the other hand, the relative poverty of broad niched species (GENVEG Guild) in the FOREST Subregion, together with the small proportion (21%) of WOOD Guild species in Africa, supports the hypothesis that the vegetation structure of the western equatorial forest is not conducive to speciation for African waterbirds (Moreau 1966: 135). Amadon (1973) rightly points out that the bulk of waterbirds which occur in forest do so "in spite of it", since the vegetation structure of typical forest, which favours niche partitioning by non-aquatic birds, is not suitable waterbird habitat. The majority of the relatively low number of forest waterbirds persist in patches of non-forest habitat within the forest (e.g. clearings along water bodies).

Water habitat guilds

I suggest that the generally 'as expected' pattern for the STREAM Guild in the FOREST Subregion and its underrepresentation in the N-SAV and NE-ARID D-zones and the CENT and SOUTH Provinces is due to a dearth of suitable habitat in the latter zones. Rivers in the FOREST Subregion tend to be fed by many reliable streams, while the major rivers of the savannas of Africa are fed by relatively fewer permanent tributaries (Beadle 1982: 164).

The overrepresentation of the RIVER Guild in the FOREST Subregion and general underrepresentation elsewhere, is not due to the higher suitability of forest riverine biotope. Indeed, I maintain that forest rivers are less suitable for waterbirds (see above sections on taxonomic and vegetation structure guilds). A more plausible hypothesis for the overrepresentation of the RIVER Guild in the FOREST Subregion is simply that these species are the ones that are best able to persist in a zone poor in other waterbird habitats. This interpretation is supported by examination of the residual plot for the multiple regression analysis between species diversity and environmental diversity (Appendix 1.2). The ratio between quadrats in which species diversity is more (+ residual) to less (- residual) than predicted by environmental diversity is significantly lower (8 : 15 for FOREST Subregion; 43 : 24 for S-SAV Subregion; $P < 0,001$; χ^2test) for FOREST zone quadrats than for S-SAV zone quadrats. In other words, although there is a significant positive correlation between waterbird species diversity and measures of environmental diversity (Table 1.5), especially number of rivers, FOREST Subregion quadrats tend to have an underrepresentation of waterbirds more often than do S-SAV quadrats. The most likely cause of this striking difference is that rivers in the S-SAV Subregion tend to generate a considerable diversity of waterbird habitats (see vegetation structure guilds above), while FOREST Subregion rivers do not.

The underrepresentation of the DISCRETE and SWAMP Guilds in the FOREST Subregion, and the overrepresentation of the former in the H-LAND and SOUTH Provinces, appears to be a simple reflection of the availability of this habitat (LN in Appendix 1.3). The apparently anomalous overrepresentation of the DISCRETE Guild in the NE-ARID and SW-ARID D-zones reflects the limitations of the map scale employed in my digitization analysis which could not accurately quantify the availability of small discrete water bodies such as tugs in the NE-ARID and man made impoundments in the SW-ARID (see SWIM Guild above).

Finally, the overrepresentation of broader habitat niche species, HABGEN, in all zones, is possibly due to their more opportunistic and mobile nature (78% of HABGEN are mobile).

Appendix 1.1. African waterbirds analised in this study and their guild characteristics and presence/absence in zones for guild analyses

Species	Guild type								Guild zone presence/absence								
	TAX	MOB	BMS	FOR	HAB	VEG	TPH		FOR	SSV	NSV	NEA	SWA	HGD	CNT	STH	SAH
Tachybaptus ruficollis		2	2	2	3	1	3	*	1	1	1	1	1	1	1	1	1
Podiceps nigricollis		3	2	2	3	1	2		0	1	0	0	1	0	1	1	0
Podiceps cristatus		2	3	2	3	1	3	*	0	1	0	0	1	1	1	1	0
Anhinga rufa		2	3	2	5	1	4		1	1	1	0	1	1	1	1	0
Phalacrocorax carbo		2	3	2	5	1	4		0	1	1	1	1	1	1	1	0
Phalacrocorax africanus		3	3	2	5	1	4		1	1	1	1	1	1	1	1	0
Pelecanus onocrotalus		2	3	2	5	1	4		1	1	1	0	1	1	1	1	0
Pelecanus rufescens		2	3	2	5	3	4		1	1	1	1	0	1	1	1	0
Botaurus stellaris	1	1	3	1	4	2	4		0	1	0	0	0	0	1	1	0
Tigriornis leucolophus	1	1	3	1	1	3	3	*	1	0	0	0	0	0	0	0	0
Ixobrychus minutus	1	2	2	1	4	2	3	*	1	1	1	0	0	0	1	1	0
Ixobrychus sturmii	1	3	2	1	2	3	3	*	1	1	1	0	1	1	1	1	0
Gorsachius leuconotus	1	1	2	1	5	3	3	*	1	1	1	0	0	0	1	1	0
Nycticorax nycticorax	1	2	3	1	5	1	4		0	1	0	0	0	1	1	1	0
Ardeola ralloides	1	2	2	1	2	2	3	*	0	1	1	0	0	0	1	1	0
Ardeola rufiventris	1	2	2	1	2	2	3	*	0	1	0	0	0	0	1	1	0
Butorides striatus	1	2	2	1	5	2	3	*	1	1	1	1	0	1	1	1	0
Egretta garzetta	1	2	3	1	5	1	3	*	0	1	0	0	0	0	1	1	0
Egretta vinaceigula	1	2	2	1	4	2	3	*	0	0	0	0	0	0	0	0	0
Egretta ardesiaca	1	2	2	1	5	2	3	*	1	1	1	0	1	1	1	1	0
Egretta intermedia	1	2	3	1	2	1	4		0	1	0	0	0	0	1	1	0
Egretta alba	1	2	3	1	2	1	4		0	1	1	0	0	0	1	0	0
Ardea cinerea	1	2	3	1	5	1	4		0	1	0	0	1	0	1	1	0
Ardea purpurea	1	2	3	1	4	2	4		0	1	0	0	0	0	1	1	0
Ardea goliath	1	2	3	1	5	2	4		1	1	1	1	1	1	1	1	0
Balaeniceps rex		2	3	1	4	2	4		0	1	1	0	0	0	1	0	0
Scopus umbretta		2	2	1	5	3	3	*	1	1	1	1	1	1	1	1	0
Ciconia nigra		2	3	1	5	1	3	*	0	0	0	0	0	0	1	1	0
Ciconia episcopus		3	3	1	2	2	3	*	1	1	1	0	0	1	1	1	0
Ephippiorhynchus senegalensis		2	3	1	5	2	4		1	1	1	0	0	1	1	1	0
Anastomus lamelligerus		3	3	1	4	2	2		1	1	1	1	1	1	1	1	0
Mycteria ibis		2	3	1	5	1	4		1	1	1	1	1	1	1	1	0
Bostrichia rara		2	3	I	4	3	2		1	0	0	0	0	0	0	0	0
Platalea alba		2	3	1	3	2	3	*	0	1	1	0	1	0	1	1	0
Platalea leucorodia		3	3	1	3	2	3	*	0	0	0	1	0	0	0	0	0
Plegadis falcinellus		2	3	1	5	1	2		0	1	0	0	0	0	1	1	0
Phoenicopterus ruber		3	3	1	3	1	2		0	1	0	1	1	1	1	1	0
Phoeniconaias minor		3	3	1	3	1	1		0	1	0	0	1	1	1	1	0
Dendrocygna bicolor	2	2	3	2	3	1	1		1	1	1	0	0	1	1	1	0
Dendrocygna viduata	2	2	3	2	3	1	1		1	1	1	1	1	1	1	1	0
Cyanochen cyanoptera	2	1	3	1	3	2	1		0	0	0	0	0	1	0	0	0
Tadorna cana	2	2	3	2	3	1	2	*	0	0	0	0	1	0	0	1	0
Alophochen aegyptiacus	2	2	3	1	5	2	1		1	1	1	1	1	1	1	1	1
Plectropterus gambensis	2	2	3	1	5	2	1		1	1	1	0	1	1	1	1	0
Pteronetta hartlaubi	2	1	3	2	2	3	2		1	0	0	0	0	0	0	0	0
Sarkidiornis melanotos	2	2	3	1	3	3	2	*	1	1	1	0	0	1	1	1	0
Nettapus auritus	2	2	2	2	3	1	1		1	1	1	0	0	1	1	1	0

Anas sparsa	2	1	3	2	1	1	2	*	1	1	0	0	1	1	1	1	0
Anas capensis	2	2	3	2	3	1	2	*	0	1	0	0	1	1	1	1	0
Anas undulata	2	2	3	2	5	1	1		0	1	0	0	1	1	1	1	0
Anas erythrorhyncha	2	2	3	2	3	2	2	*	0	1	0	0	1	1	1	1	0
Anas hottentota	2	2	2	2	3	1	2	*	0	1	1	0	1	1	1	1	0
Anas smithii	2	2	3	2	3	1	2	*	0	1	0	0	1	0	0	1	0
Netta erythrophthalma	2	2	3	2	3	1	1		0	1	0	0	1	1	1	1	0
Oxyura punctata	2	2	3	2	3	1	2	*	0	1	0	0	1	1	1	1	0
Thalassornis leuconotus	2	2	3	2	5	2	1		1	1	1	0	1	1	1	1	0
Circus ranivorus		1	3		4	2	4		0	1	0	0	1	0	1	1	0
Haliaeetus vocifer		1	3	2	3	1	4		1	1	1	0	1	1	1	1	0
Pandion haliaetus		3	3	2	5	3	4		0	0	0	1	0	0	0	0	0
Himantornis haematopus	3	1	2	1	1	3	3	*	1	0	0	0	0	0	0	0	0
Canirallus oculeus	3	1	2	1	1	3	3	*	1	0	0	0	0	0	0	0	0
Sarothrura pulchra	3	1	2	1	5	3	2		1	0	1	0	0	0	1	0	0
Sarothrura rufa	3	1	2	1	5	2	2	*	1	1	0	0	0	0	1	1	0
Sarothrura lugens	3	2	2	1	4	2	2	*	0	0	0	0	0	0	1	0	0
Sarothrura ayresi	3	3	2	1	4	2	2		0	1	0	0	0	0	0	1	0
Rougetius rougetii	3	1	2	1	2	1	2		0	0	0	0	0	1	0	0	0
Rallus caerulescens	3	2	2	1	4	2	2		0	1	0	0	0	1	1	1	0
Amaurornis flavirostris	3	2	2	1	5	2	2	*	1	1	1	0	1	1	1	1	0
Porzana pusilla	3	1	1	1	4	2	2	*	0	1	0	0	1	0	1	1	0
Aenigmatolimnas marginalis	3	3	2	1	4	2	2	*	1	1	0	0	0	0	1	0	0
Fulica cristata	3	2	3	2	5	2	2	*	0	1	0	0	1	1	1	1	0
Porphyrio porphyrio	3	2	3	1	4	2	2	*	0	1	1	0	1	1	1	1	0
Porphyrio alleni	3	3	2	1	4	2	2	*	1	1	1	1	0	1	1	1	0
Gallinula angulata	3	3	2	1	5	3	2	*	1	1	1	0	0	0	1	1	0
Gallinula chloropus	3	2	2	1	5	2	2	*	1	1	1	0	1	1	1	1	0
Podica senegalensis		1	3	2	1	3	3	*	1	1	1	0	0	1	1	1	0
Grus carunculata		1	3	1	4	2	2	*	0	1	0	0	0	1	1	1	0
Balearica pavonina		2	3	1	4	2	2	*	0	1	1	0	0	1	1	1	1
Actophilornis africanus		2	2	1	5	2	2	*	1	1	1	0	1	1	1	1	0
Microparra capensis		2	1	1	5	2	2	*	0	1	1	0	0	0	1	1	0
Burhinus senegalensis		2	2	1	5	3	2		1	1	1	0	0	1	1	0	0
Burhinus vermiculatus		2	2	1	5	3	2		1	1	0	1	0	0	1	1	0
Vanellus crassirostris		1	2	1	4	2	2		0	1	0	0	0	0	1	0	0
Vanellus albiceps		2	2	1	2	1	2		1	1	1	0	0	0	1	0	0
Vanellus senegallus		1	2	1	5	2	2		1	1	1	0	0	1	1	1	0
Vanellus spinosus		2	2	1	5	1	2		0	1	1	1	0	1	1	0	0
Vanellus armatus		2	2	1	5	1	2		0	1	0	0	1	0	1	1	0
Charadrius marginatus		2	1	1	2	1	2		1	1	1	0	1	0	1	1	0
Charadrius pallidus		2	1	1	3	1	2		0	0	0	0	1	0	0	0	0
Charadrius tricollaris		2	1	1	1	1	2		0	1	1	0	1	1	1	1	0
Gallinago gallinago		3	2	1	3	2	2		0	1	0	0	0	1	1	1	0
Himantopus himantopus		2	2	1	3	1	2	*	1	1	1	1	1	1	1	1	0
Recurvirostra avosetta		2	2	1	3	1	2		0	1	1	1	1	1	1	1	0
Rostratula benghalensis		2	2	1	4	2	2		1	1	1	0	1	1	1	1	0
Pluvianus aegyptius		2	1	1	2	1	2		1	1	1	0	0	1	0	0	0
Glareola pratincola		3	1		5	1	2		1	1	1	1	0	1	1	1	0
Glareola nuchalis		3	1		2	1	2		1	1	1	0	0	0	1	0	0
Centropus cupreicaudus		1	2		5	2	3	*	0	1	0	0	0	0	1	0	0
Scotopelia peli		1	3		2	3	4		1	1	0	0	0	1	1	1	0
Scotopelia ussheri		1	3		2	3	4		0	0	0	0	0	0	0	0	0
Scotopelia bouvieri		1	3		2	3	4		1	0	0	0	0	0	0	0	0

Ceryle maxima		2	2	2	5	3	4		1	1	1	0	0	1	1	1	0
Ceryle rudis		2	2	2	5	1	4		1	1	1	1	0	1	1	1	0
Alcedo semitorquata		1	1	2	5	2	3	*	0	1	0	0	0	1	1	1	0
Alcedo quadribrachys		1	1	2	5	2	3	*	1	0	1	0	0	0	0	0	0
Alcedo cristata		1	1	2	5	3	3	*	1	1	1	0	1	1	1	1	0
Alcedo leucogaster		1	1	2	1	3	3	*	1	0	0	0	0	0	0	0	0
Halcyon senegaloides		2	2	2	1	3	3	*	0	0	0	0	0	0	0	0	0
Riparia riparia paludicola		2	1		1	2	2		0	1	1	0	1	1	1	1	0
Riparia riparia congica		1	1		1	1	2		1	0	0	0	0	0	0	0	0
Pseudochelidon eurystomina		3	1		2	1	2		1	0	0	0	0	0	0	0	0
Hirundo smithii		2	1		5	3	2		1	1	1	0	0	1	1	1	0
Hirundo nigrita		1	1		2	3	2		1	0	0	0	0	0	0	0	0
Motacilla alba aguimp		2	1	1	2	1	2		1	1	1	0	1	1	1	1	0
Motacilla clara		1	1	1	1	1	2		1	1	0	0	0	1	1	1	0
Laniarius mufumbiri		1	1		4	2	2		0	0	0	0	0	0	1	0	0
Laniarius bicolor		1	1		1	3	2		0	0	0	0	0	0	1	0	0
Bradypterus baboecala	4	1	1		4	2	2		0	1	0	0	0	1	1	1	0
Bradypterus graueri	4	1	1		4	2	2		0	0	0	0	0	0	0	0	0
Bradypterus carpalis	4	1	1		4	2	2		0	0	0	0	0	0	0	0	0
Acrocephalus gracilirostris	4	1	1		1	2	2		0	1	0	0	1	1	1	1	0
Acrocephalus rufescens	4	1	1		4	2	2		1	1	0	0	0	0	1	0	0
Chloropeta gracilirostris	4	1	1		3	2	2		0	0	0	0	0	0	0	0	0
Cisticola dambo	4	1	1		1	2	2		0	0	0	0	0	0	1	0	0
Cisticola galactotes	4	1	1		5	2	2		1	1	1	0	0	1	1	0	0
Cisticola carruthersi	4	1	1		4	2	2		0	0	0	0	0	0	1	0	0
Cisticola pipiens	4	1	1		4	2	2		0	0	0	0	0	0	1	0	0
Cisticola tinniens	4	1	1		4	2	2		0	1	0	0	0	0	1	1	0
Muscicapa cassini		1	1		2	3	2		1	0	0	0	0	0	0	0	0
Ploceus spekeoides	5	1	1		3	2	2		0	0	0	0	0	0	0	0	0
Ploceus aurantius	5	1	1		2	3	2	*	1	0	0	0	0	0	1	0	0
Ploceus castaneiceps	5	1	1		2	3	2	*	0	0	0	0	0	0	1	0	0
Ploceus xanthops	5	1	1		1	2	2	*	1	1	0	0	0	0	1	0	0
Ploceus subaureus	5	1	1		2	2	2	*	0	0	0	0	0	0	0	0	0
Ploceus castanops	5	1	1		5	2	2	*	0	0	0	0	0	0	1	0	0
Ploceus xanthopterus	5	1	1		1	2	2	*	0	1	0	0	0	0	1	0	0
Ploceus melanocephalus	5	1	1		2	1	2	*	1	1	1	0	0	0	1	0	0
Ploceus taeniopterus	5	1	1		2	1	2	*	0	0	0	0	0	0	0	0	0
Ploceus dicrocephalus	5	1	1		2	1	2	*	0	0	0	1	0	0	0	0	0
Malimbus nitens	5	1	1		4	3	2	*	1	0	0	0	0	0	0	0	0
Amblyospiza albifrons	5	1	1		4	3	1		1	1	0	0	0	1	1	1	0
Euplectes orix	5	1	1		2	2	1		0	1	0	0	1	0	1	1	0
Euplectes franciscanus	5	2	1		4	2	1		0	1	1	1	0	1	1	0	0
Euplectes nigroventris	5	1	1		4	2	2	*	0	1	0	0	0	0	0	0	0
Euplectes diadematus	5	1	1		4	2	2	*	0	0	0	0	0	0	1	0	0
Euplectes macrourus	5	1	1		4	2	1		1	1	1	0	0	1	1	0	0
Euplectes hartlaubi	5	1	1		4	1	2	*	1	1	0	0	0	0	1	0	0
Euplectes axillaris	5	1	1		2	2	1		0	1	1	0	0	1	1	1	0
Quelea erythrops	5	3	1		4	1	1		1	1	0	0	0	0	1	1	0
Nesocharis capistrata		1	1		4	3	2	*	0	0	1	0	0	0	0	0	0
Nesocharis ansorgei		1	1		4	3	1		0	0	0	0	0	0	1	0	0
Amandava subflava		1	1		2	2	2	*	1	1	1	0	0	1	1	1	0

@ Guild codes in Table 1.2.

* = 'mixed feeders' as referred in text.

Appendix 1.2. Actual and predicted waterbird species richness values for the 101 quadrats shown in Fig. 1.1 and standardized residuals from the multiple regression analysis

Quadrat	Observed richness	Predicted richness	Standardized	Standardized
				(-) (+)
1	70	78	-.58	******.
2	8	33	-1.77	******************.
3	26	29	-.24	**.
4	12	26	-1.05	***********.
5	8	26	-1.30	*************.
6	10	29	-1.38	**************.
7	19	30	-.82	********.
8	33	30	.16	.**
9	33	36	-.25	***.
12 R	40	25	.98	.**********
13	35	37	-.20	**.
14 R	50	37	.86	.*********
15	56	49	.43	.****
16	34	40	-.44	****.
17	6	25	-1.33	*************.
18	33	24	.57	.******
19	55	45	.65	.*******
21	56	72	-1.19	************.
22	41	56	-1.09	***********.
23	49	45	.27	.***
24	57	50	.44	.****
25	47	47	-.06	*.
26	46	45	.05	.*
28	17	24	-.50	*****.
29	42	33	.60	.******
30	64	61	.16	.**
32	47	44	.20	.**
33	53	49	.25	.***
34	39	38	.00	*
35	66	63	.20	.**
36	59	54	.33	.***
37	71	76	-.41	****.
38	72	66	.38	.****
40	44	50	-.48	*****.
41	37	37	-.00	*
42 R	63	41	1.53	.***************
44	75	67	.53	.*****
45	28	36	-.59	******.
46	58	65	-.51	*****.
47	19	52	-2.35	********************.
48	59	50	.59	.******
49 R	62	49	.90	.*********
50 R	78	61	1.16	.************
51 R	114	81	2.32	.***********************
52 R	100	81	1.30	.*************
53	40	46	-.44	****.
55	60	80	-1.41	**************.
57	55	63	-.58	******.
58	40	50	-.71	*******.
59 R	91	74	1.16	.************
60	102	100	.09	.*
61	103	99	.22	.**
62 R	96	59	2.59	.*************************
63	69	79	-.76	********.
64	55	66	-.79	********.
65	72	63	.57	.******
66	49	72	-1.68	*****************.
67	87	89	-.19	**.
68 R	80	66	.95	.**********
69	70	59	.70	.*******
71	66	70	-.32	***.
72 R	90	76	.93	.*********
73	93	89	.25	.***
74	86	93	-.53	*****.
75	73	76	-.24	**.
76 R	88	71	1.14	.***********
78	85	76	.57	.******
79	84	91	-.56	******.
80 R	75	52	1.58	.****************
81 R	63	35	1.91	.*******************
82 R	86	62	1.62	.****************
83 R	96	80	1.12	.***********
84	88	91	-.24	**.
85 R	89	67	1.49	.***************
86	56	45	.72	.*******
87	25	42	-1.25	*************.
88 R	66	52	.92	.*********
89	71	66	.30	.***
90	87	88	-.07	*.
91	68	64	.27	.***
92	48	45	.15	.**
93	33	40	-.56	******.
95	82	88	-.48	*****.
96	95	111	-1.16	************.
97	41	65	-1.72	*****************.
98	49	74	-1.76	******************.
99	87	95	-.62	******.
100	98	90	.49	.*****
101	76	92	-1.17	************.

Appendix 1.3. Univariate statistics for the availability of aquatic habitat based on the digitization analysis of Bartholomew (1973) maps of Africa

	FOREST	S-SAV	N-SAV	NE-ARID	SW-ARID	H-LAND	CENT	SOUTH	SAH
Sample size	21	34	19	5	10	6	25	5	8
PRN									
Mean	50.14	57.11	30.10	8.80	13.20	45.16	56.00	71.80	6.62
S.D.	20.48	29.75	18.09	6.53	14.14	47.72	24.65	22.15	6.80
Maximum	106.00	141.00	72.00	19.00	34.00	141.00	105.00	91.00	17.00
Minimum	26.00	8.00	6.00	2.00	0.00	20.00	8.00	38.00	0.00
PRL									
Mean	4832.69	4639.07	2952.93	960.54	1104.34	3585.62	4773.19	5432.86	444.96
S.D.	1505.40	2205.14	1712.40	230.04	1245.37	3197.24	1919.37	1715.13	445.31
Maximum	7619.02	9864.96	6126.52	1312.27	3611.59	9864.96	7485.79	7260.83	1178.74
Minimum	1823.92	1027.14	608.92	692.24	0.00	1079.15	1027.14	3086.46	0.00
WN									
Mean	6.85	16.14	27.36	44.00	36.30	51.33	8.64	5.40	37.50
S.D.	8.07	21.89	20.54	30.63	19.04	23.14	12.40	10.99	26.79
Maximum	26.00	82.00	79.00	92.00	73.00	82.00	46.00	25.00	82.00
Minimum	0.00	0.00	5.00	12.00	11.00	24.00	0.00	0.00	3.00
WL									
Mean	311.53	968.29	1558.59	2984.09	2581.17	3149.42	520.65	231.71	2297.04
S.D.	421.49	1389.75	1215.39	2210.33	997.67	1372.02	882.82	487.70	1337.96
Maximum	1419.98	5131.75	4449.42	6418.18	4063.90	5131.75	3289.17	1103.09	3907.45
Minimum	0.00	0.00	184.37	610.54	728.41	1566.57	0.00	0.00	154.60

LN

Mean	3.61	6.26	1.00	0.00	1.30	5.16	6.44	6.40	3.62
S.D.	4.18	5.83	1.10	0.00	1.82	4.79	6.22	5.32	6.92
Maximum	12.00	27.00	3.00	0.00	5.00	13.00	27.00	15.00	20.00
Minimum	0.00	0.00	0.00	0.00	0.00	1.00	0.00	2.00	0.00

LP

Mean	268.05	529.22	154.46	0.00	36.35	422.73	586.68	227.05	98.02
S.D.	299.38	605.59	310.19	0.00	57.52	234.10	684.49	240.34	180.62
Maximum	959.03	2536.14	1094.56	0.00	184.85	646.30	2536.14	646.65	522.80
Minimum	0.00	0.00	0.00	0.00	0.00	20.68	0.00	44.62	0.00

LA

Mean	778.88	5245.65	1535.37	0.00	76.18	2200.45	6566.02	323.05	155.48
S.D.	1011.85	9240.12	4957.64	0.00	131.11	2324.45	10445.18	340.58	306.86
Maximum	3349.87	35612.50	21362.25	0.00	366.87	6432.75	35612.50	905.50	888.87
Minimum	0.00	0.00	0.00	0.00	0.00	20.00	0.00	57.87	0.00

MN

Mean	2.71	4.35	4.36	0.60	0.10	7.16	4.16	0.60	1.00
S.D.	6.78	4.37	6.22	0.89	0.31	5.70	3.91	1.34	1.41
Maximum	27.00	16.00	19.00	2.00	1.00	16.00	14.00	3.00	4.00
Minimum	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00

MP

Mean	184.15	338.92	562.34	23.96	4.82	528.01	335.82	28.49	30.41
S.D.	484.21	380.92	862.98	32.92	15.25	543.70	337.68	63.71	52.17
Maximum	1900.28	1446.12	2553.65	63.79	48.24	1446.12	1151.63	142.46	114.76
Minimum	0.00	0.00	0.00	0.00	0.00	28.53	0.00	0.00	0.00

MA									
Mean	862.94	1656.12	3984.11	78.90	16.51	2339.33	1708.76	70.57	2045.96
S.D.	2168.27	2098.71	6776.58	115.34	52.21	2675.24	2015.60	157.81	5626.05
Maximum	7723.00	7519.50	20268.88	254.38	165.12	6878.13	7519.50	352.88	15965.62
Minimum	0.00	0.00	0.00	0.00	0.00	96.88	0.00	0.00	0.00
NEL									
Mean	2.66	3.61	2.26	3.60	2.50	5.33	3.12	4.20	2.12
S.D.	1.15	1.43	0.73	0.54	0.85	1.36	1.09	1.09	0.64
Maximum	4.00	7.00	4.00	4.00	4.00	7.00	5.00	5.00	3.00
Minimum	1.00	1.00	1.00	3.00	1.00	4.00	1.00	3.00	1.00
REL									
Mean	5.33	2.05	1.89	0.60	1.60	1.33	2.76	1.80	0.75
S.D.	1.39	2.46	2.28	0.89	1.77	1.21	3.09	2.04	0.88
Maximum	8.00	9.00	7.00	2.00	5.00	3.00	9.00	4.00	2.00
Minimum	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ELXCL									
Mean	2.80	3.67	2.75	2.76	3.67	4.13	3.58	3.56	2.73
S.D.	.68	0.99	0.48	0.60	0.24	0.53	1.10	0.54	0.47
Maximum	4.60	5.80	3.80	3.40	4.00	4.60	5.80	4.20	3.30
Minimum	1.60	1.00	1.60	1.90	3.30	3.40	1.00	2.90	2.00
KMRF									
Mean	39.45	26.17	27.09	10.80	8.82	25.16	27.94	18.20	10.53
S.D.	28.74	8.83	7.24	4.18	3.80	10.16	8.09	4.67	5.67
Maximum	132.50	50.50	40.50	15.00	15.00	38.00	50.50	24.00	21.00
Minimum	**19.50**	**10.00**	**12.00**	**5.00**	**3.98**	**10.00**	**17.00**	**12.50**	**4.00**

FRF

Mean	131.42	80.66	65.63	46.20	28.80	82.16	86.98	59.00	18.43
S.D.	26.51	30.04	32.25	23.26	11.10	27.48	33.39	25.59	17.42
Maximum	160.00	140.00	160.00	77.00	40.00	120.00	160.00	80.00	60.00
Minimum	60.00	15.00	30.00	12.00	15.00	50.00	42.50	15.00	7.50

RRF

Mean	1252.38	1176.47	1126.31	570.00	300.00	1566.66	1166.00	850.00	576.87
S.D.	973.45	578.82	1555.04	207.96	154.56	229.49	595.94	484.76	869.10
Maximum	2800.00	2700.00	7500.00	900.00	650.00	1950.00	2700.00	1550.00	2665.00
Minimum	0.00	200.00	400.00	400.00	150.00	1300.00	200.00	200.00	100.00

ARF

Mean	1722.57	882.77	850.38	253.60	324.93	856.05	982.15	673.06	265.37
S.D.	339.38	293.15	392.15	163.04	148.41	345.84	333.55	186.63	287.12
Maximum	2464.00	1518.50	1616.00	500.00	568.00	1302.00	1859.00	930.00	786.00
Minimum	1194.00	426.30	291.00	121.50	112.50	502.00	507.70	426.30	50.50

TMAX

Mean	28.43	31.44	33.53	32.80	33.24	35.05	30.70	30.80	35.67
S.D.	2.66	2.29	2.48	2.23	1.03	1.36	1.65	1.11	1.15
Maximum	33.80	36.30	36.30	36.30	33.80	36.30	33.80	31.30	36.30
Minimum	23.80	26.30	26.30	31.30	31.30	33.80	26.30	28.80	33.80

TMIN

Mean	21.02	11.61	19.07	20.90	7.80	14.16	12.96	2.40	17.75
S.D.	3.14	5.16	2.26	3.63	3.51	4.38	3.33	1.94	2.12
Maximum	25.50	21.50	23.00	26.00	11.50	21.50	19.50	5.50	22.00
Minimum	14.50	0.50	14.50	16.50	1.50	10.00	8.00	0.50	15.00

XAT									
Mean	19.98	19.21	21.91	21.84	17.26	21.90	19.51	14.70	22.67
S.D.	.56	2.40	0.94	0.78	1.68	0.99	1.12	1.54	0.53
Maximum	21.70	23.80	23.30	23.10	19.20	23.80	21.30	16.70	23.50
Minimum	19.20	12.50	19.80	21.00	14.80	20.80	16.90	12.50	22.10
XRAD									
Mean	429.38	485.52	507.31	501.20	532.10	492.50	486.84	465.80	532.87
S.D.	23.12	29.23	47.21	2.68	26.00	24.96	26.07	45.82	27.44
Maximum	475.00	548.00	555.00	506.00	565.00	525.00	548.00	502.00	550.00
Minimum	400.00	389.00	400.00	500.00	494.00	450.00	432.00	389.00	475.00
RAE									
Mean	365.71	415.20	435.15	477.80	239.60	489.66	392.36	447.00	173.37
S.D.	184.07	245.18	253.32	228.80	189.11	245.30	249.35	200.60	165.95
Maximum	798.00	1128.00	1056.00	732.00	695.00	762.00	1128.00	723.00	472.00
Minimum	141.00	64.00	92.00	161.00	59.00	127.00	64.00	268.00	34.00
XAE									
Mean	1219.52	743.08	823.57	298.60	389.90	582.50	813.28	660.60	266.25
S.D.	236.51	181.30	298.37	119.54	175.06	299.90	115.84	134.96	322.79
Maximum	1471.00	1033.00	1348.00	423.00	690.00	935.00	1033.00	861.00	1007.00
Minimum	359.00	159.00	169.00	140.00	66.00	159.00	591.00	482.00	37.00

CHAPTER 2. Patterns of distribution and diversity in southern African waterbirds

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With relatively few noteworthy exceptions (Moreau 1966; Winterbottom 1967, 1972; Reichholf 1975; Siegfried 1981), studies in Africa of continental and subcontinental patterns of avian distribution and/or diversity (e.g. Chapin 1923; Cook 1969; MacArthur 1972; Rabinovich & Rapoport 1975; Rapoport & Ezcurra 1979; Diamond & Hamilton 1980; and Crowe & Crowe 1982) have focused on birds from non-aquatic habitats. In Chapter 1 I have investigated broad distribution/diversity patterns for waterbirds on an Afrotropical scale. The primary differences between African aquatic and non-aquatic birds are that the aquatic bird fauna partitions Africa into fewer zoogeographic zones (Fig. 2.1), and waterbird diversity (measured as number of species) exhibits a longitudinal, not a latitudinal, gradient (Fig. 2.2).

In this chapter I examine patterns of waterbird distribution and diversity in southern Africa south of the Cunene-Zambezi rivers (Fig. 2.3) in more detail. In comparison with my afrotropical study I use a much denser grid (250 quadrats, Fig. 2.3), and include more varied and recent distributional information. Relative abundance of species is estimated more accurately and Palaearctic migrants, which form an important component of the southern African aquatic bird fauna (Winterbottom 1972) are included. As in Chapter 1, I analyse taxonomic, morphological, ecological and ethological 'guilds' to determine whether diversity patterns, exhibited by these subsets, parallel those found for the total waterbird fauna. I employ a liberal definition of the term guild: an assemblage of species whose taxonomic, morphological,

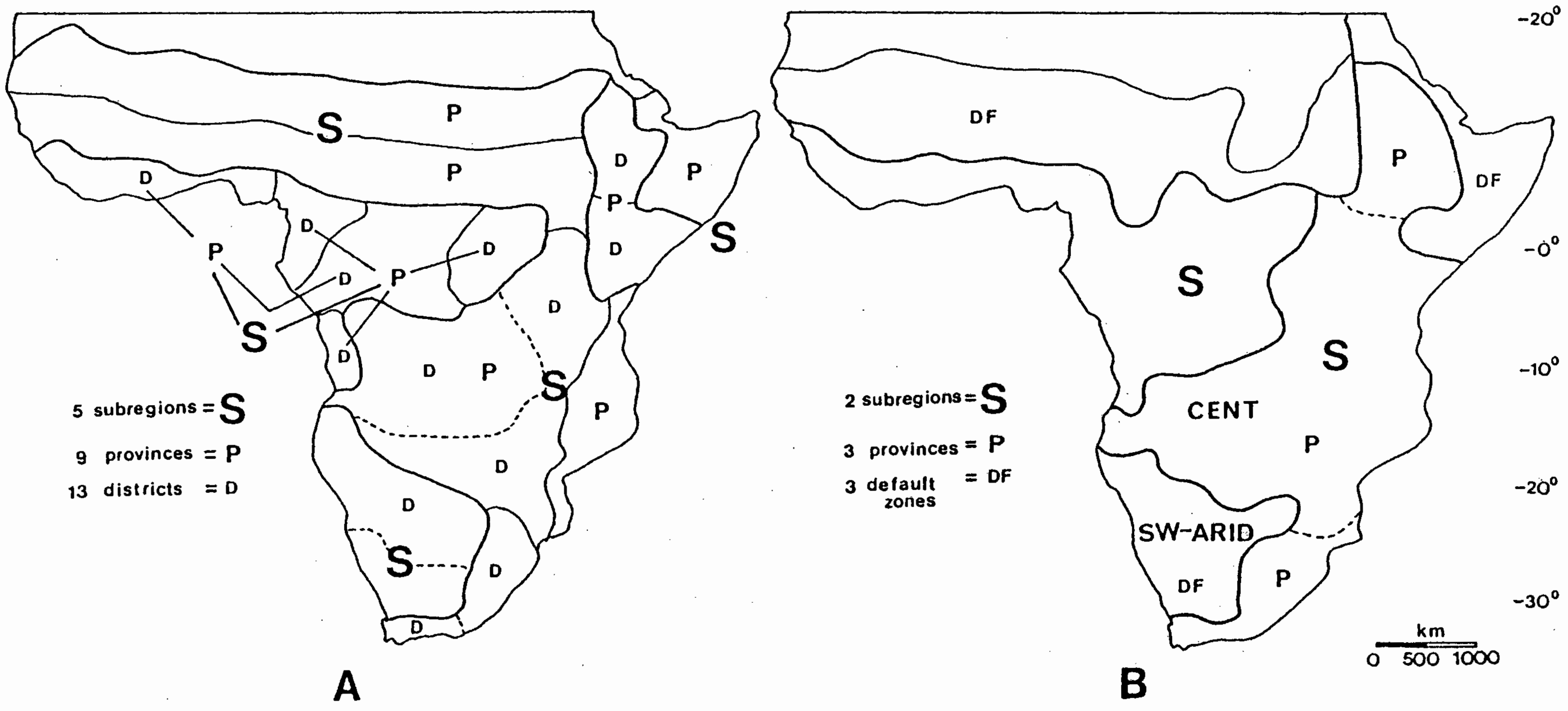

Fig. 2.1. African avifaunal zones recognized in A) Crowe & Crowe (1982) for terrestrial birds, and B) Chapter 1, for waterbirds.

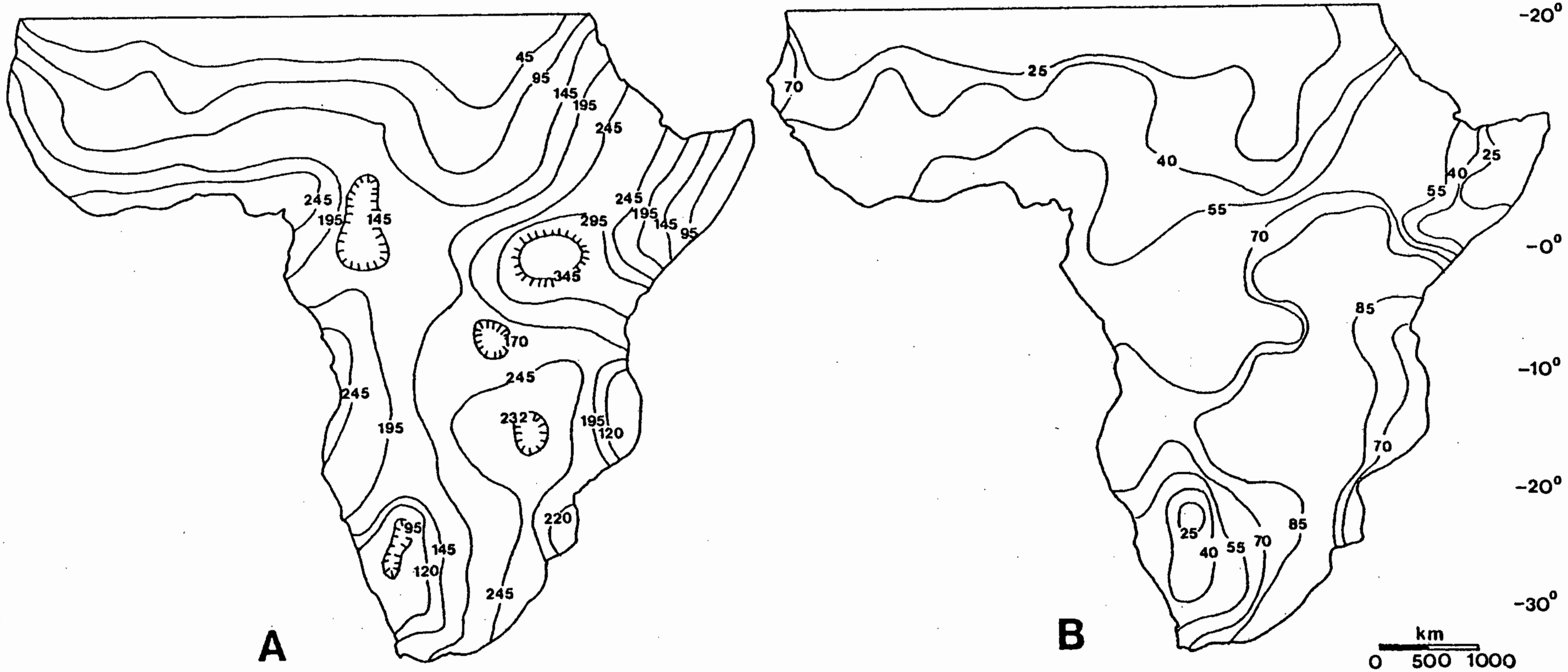

Fig. 2.2. Geographical variation in diversity of African A) terrestrial birds [after Crowe & Crowe (1982)], and B) waterbirds (as in Chapter 1).

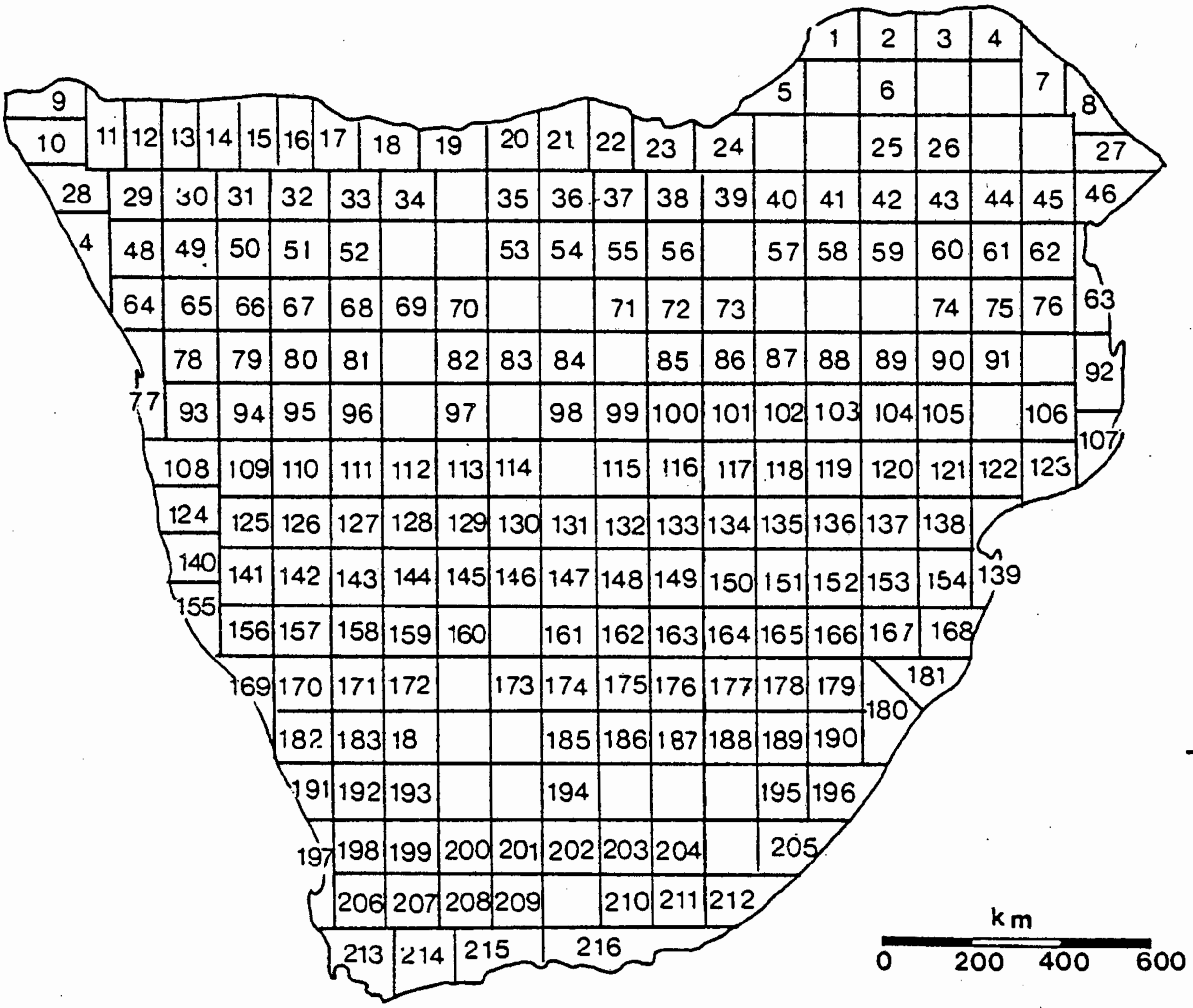

Fig. 2.3. The grid system used to extract distribution/diversity data for southern African waterbirds. Unnumbered quadrats were not analysed.

ecological or behavioural affinities require (or may have required) them to deal with similar selective pressures. I also relate geographical variation in total and guild diversity to variation in measures of natural environmental conditions. For quadrats which fall within South Africa, correlations between waterbird diversity and various measures of the availability of man-made and/or modified impoundments are analysed.

Data base and methods

Data base and extraction methods

For the purpose of this study, a waterbird is taken to be any species which is dependent on non-marine aquatic biotopes for feeding and/or breeding. Data were extracted from published and unpublished sources (see Acknowledgements and citations in the References marked with an asterisk) in order to estimate both the distribution and relative abundance of each species within each of the 250 quadrats (Fig. 2.3). This was done by scoring each species on a scale from 0 to 5: 0 = absent; 1 = rare or sparsely distributed; 2 = uncommon, but potentially widespread; 3 = common, but only in certain seasons or poorly represented habitats; 4 = common year round, but not widespread; 5 = common and widespread year-round. For some relatively poorly studied areas, e.g. in Namibia and Botswana, I relied chiefly on reports from local ornithologists and knowledge of waterbird ecological requirements. Therefore my scoring system can be criticized as being subjective. However, I feel that it is superior to a scheme based only on the presence or absence of species, since it takes into account the dynamic nature of waterbird dispersion (e.g. Gentilli & Bekle

1983). To minimize bias due to quadrats with inadequate information, I discarded data for 34 quadrats (those unnumbered in Fig. 2.3) which appeared to have been very poorly sampled (i.e. few sources of data and low diversity when compared with adjacent quadrats with similar aquatic biotopes). I analysed resident and migrant waterbird guilds separately. The remaining guilds were divided as in Chapter 1, although I tend to have more guilds per guild type in this chapter (Table 2.1). The 170 waterbird species considered, their migrant/resident status, and guild membership are listed in Appendix 2.1.

Numerical methods

Patterns of waterbird distribution were identified by means of cluster analysis (Anderberg 1973; Field & McFarlane 1968), using the Bray & Curtis (1957) similarity measure and a group-average sorting method (Lance & Williams 1967). Multidimensional scaling (Chapter 1) was not used here owing to the very large grid which exceded the program tolerance. Species which characterize the waterbird faunal zones indicated by cluster analysis were identified by means of information statistic tests (Field 1969). I define a characteristic species as one generally confined to (at least two-thirds of its recorded occurrences), and widespread within, an avifaunal zone, and the limits of whose range help to delineate the boundaries of the zone. The results of the cluster analysis and information statistic tests were then combined into a cartographic representation, using the distributional limits of characteristic species to delineate the boundaries of waterbird avifaunal zones.

Table 2.1. Species diversity values, codes, abbreviations, mobility percentages, and definitions for southern African waterbird taxonomic, morphological, ethological and ecological guilds. See Appendix 2.1 for more information on individual species

Guild types	No. of species	Codes in Appendix 2.1	Guild abbreviations	% in mobility classes 2-3	Guild names/ definitions
Taxonomic (TAX)	18	1	T-AR	78	Ardeidae
	7	2	T-CI	100	Ciconiidae
	18	3	T-AN	89	Anatidae
	4	4	T-AC	50	Accipitridae
	14	5	T-RA	57	Rallidae
	9	6	T-CH	55	Charadriidae
	16	7	T-SC	94	Scolopacidae
	7	8	T-LA	85	Laridae
	5	9	T-AL	60	Alcedinidae
	13	10	T-SY	23	Sylviidae
	6	11	T-MO	49	Motacillidae
	16	12	T-PL	44	Ploceidae
Body mass (BMS)	59	1	M-1	49	< 80 g
	53	2	M-2	70	> 80 < 400 g
	43	3	M-3	79	>400 < 2000 g
	15	4	M-4	86	> 2000 g
Trophic (TPH)	43	1	D-V	67	Predominantly vertebrates
	93	2	D-I	66	Prevalently invertebrates
	34	3	D-H	67	Mixed feeders with substantial vegetable component
Migratory status (MST)	137	1	S-R	59	Residents
	33	2	S-M	100	Migrants
Foraging mode (FOR)	17	1	F-S	94	Surface swimmers
	12	2	F-D	83	Divers
	78	3	F-TP	78	Peckers
	13	4	F-DH	54	Plunge divers
					Species using a water induced habitat without necessarily 'getting feet wet' :
	20	5	F-P	40	- Predominantly plant eaters
	30	6	F-A	37	- Predominantly animal eaters
All species	170			67	

Geographical variation in resident and migrant waterbird diversity (measured as number of species per quadrat) was depicted as contour maps drawn with the aid of SACLANT (Diederiks 1979), a computer program which fits an approximate contour surface to a grid of data points (in this case, quadrat diversity values), using least squares polynomial analysis. Correlation, regression and stepwise multiple regression programs in the BMDP Series (Dixon 1981) were used to identify environmental factors which may influence waterbird guild diversity. The environmental variables included in these analyses are listed in Table 2.2. Length of rivers, and the perimeter and surface areas of lakes, swamps and mud flats, within each quadrat were estimated from equal area projection maps (1:5 000 000 scale) employing the digitization methods described in detail in Chapter 1. If waterbird diversity is largely a function of the environment, paleo-ecological events (e.g. wet-dry climatic cycles and attendant shifts in the dispersion of biotopes) may not have influenced southern African waterbird diversity to the same degree that they appear to have influenced terrestrial and waterbird diversity on an Afrotropical scale (Diamond & Hamilton 1980; Crowe & Crowe 1982; Chapter 1). If, however, regression analysis fails to explain most of the variance in waterbird diversity, I feel that consequences of geographically localized ecological events of ancient, and/or recent origin (e.g. habitat modifications by modern man), may have influenced southern African waterbird diversity in addition to the effects of present-day 'natural' environment.

In my studies of the possible effects of impoundments (ranging in size from small farm dams to large man-made lakes) on waterbird

Table 2.2. Measures of quadrat environmental conditions (and their abbreviations) used in correlation and regression analyses of waterbird species diversity and environmental variation

Measurements	Abbreviations	Definitions and source
Mean annual rainfall	RF	the mean of 10 approximately uniformly spaced measurements (Thornthwaite 1962)
Mean maximum temperature	TMAX	the mean of 10 approximately uniformly spaced measurements (Jackson 1961)
Mean elevation	XALT	the mean of 10 approximately uniformly spaced measurements (Clark 1967)
Elevation range	RALT	the largest minus the smallest elevation (Clark 1967)
Permanent river number	PRN	digitized from Bartholomew (1973)
Permanent river length	PRL	" "
Non-permanent rivers/wadis number	NNPR	" "
Non-permanent rivers/wadis length	LNPR	" "
Lakes number	LN	" "
Lakes perimeter	LP	" "
Lakes area	LA	" "
Swamps/marshes number	MN	" "
Swamps/marshes perimeter	MP	" "
Swamps/marshes area	MA	" "
Mud flats number	NMF	" "
Mud flats perimeter	PMF	" "
Mud flats area	AMF	" "

diversity, a series of correlation and bivariate regression analyses were done for quadrats which fall within South Africa (ca 50% of the total study area). Impoundment information was extracted from a register of dams compiled by the South African Department of Water Affairs. Variables studied included impoundment density (number per quadrat), and quadrat mean, range and/or total values for: impoundment catchment area, depth, volume and surface area. Multiple regression analysis could not be employed in this aspect of my research, because some of the quadrats had missing data for at least one of the 'impoundment' variables. Since impoundment density in quadrats 206 and 213 in the southwestern Cape Province was much higher than that for the remaining quadrats, thereby potentially biassing regression results, I have excluded information from these quadrats from subsequent analyses. A preliminary regression analysis of total waterbird diversity against impoundment density indicated that the relatively xeric quadrats (with less than 400 mm of annual rainfall) which occur mainly in western South Africa have disproportionately lower waterbird diversity than those with relatively high rainfall for a given number of dams. Therefore, I analysed the relatively xeric (< 400 mm rainfall) and mesic (> 400 mm rainfall) quadrats separately in correlation and regression analyses.

Results

Distribution

As in my Afrotropical-scale study (Chapter 1), the cluster analysis and information statistic test results (Fig. 2.4 and

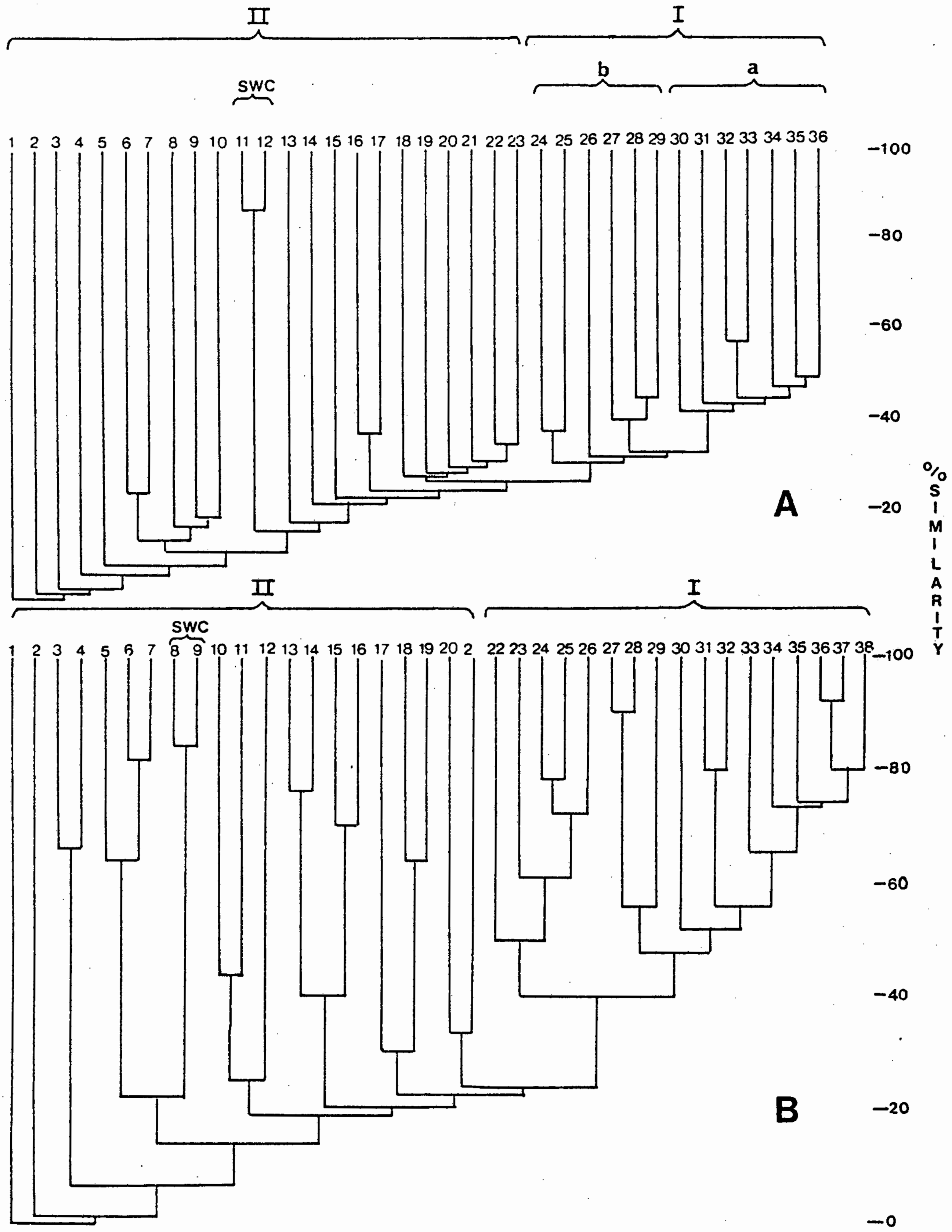

Fig. 2.4. Southern African avifaunal zones as suggested by cluster analyses of 216 quadrats according to A) 137 resident and B) 33 migrant waterbird species. See Appendix 2.2 for list of quadrats which comprise dendrogram terminal points.

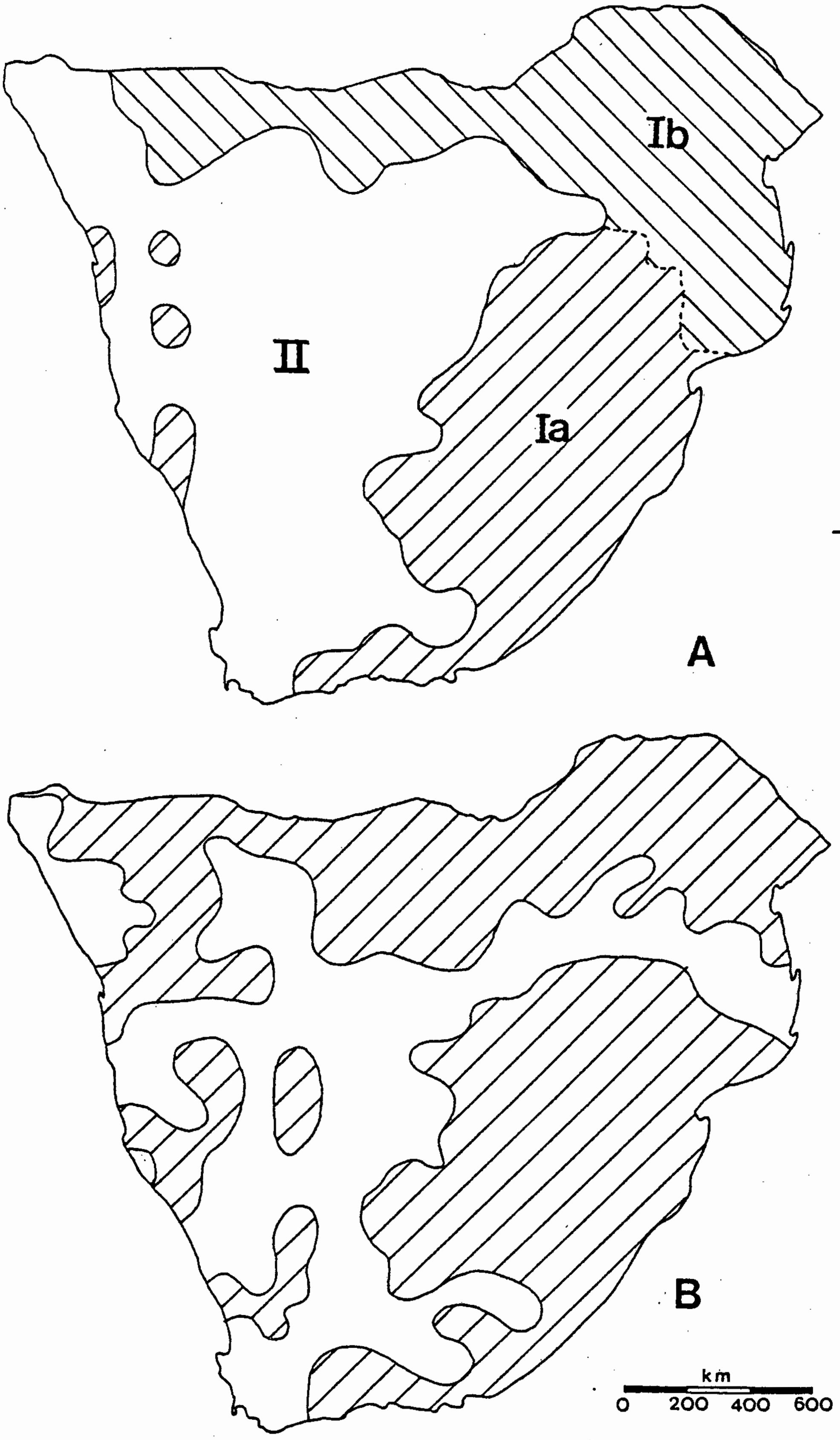

Fig. 2.5. Southern African avifaunal zones for A) resident and B) migrant waterbirds as suggested by results of the cluster analyses and the distributions of characteristic species as listed in Appendix 2.1.

Appendices 1 and 2) suggest that waterbirds partition southern Africa into two avifaunal zones, one in the east and north, the other in the west (Fig. 2.1b; Fig. 2.5). The western zone is a 'default' zone, delimited mainly by the range limits of species which do not occur within its boundaries. In fact, the southern African waterbird fauna, with only two endemic species (the South African Shelduck Tadorna cana and the Cape Shoveller Anas smithii), is essentially a depauperate version of that found to the north.

Despite their broad correspondence, there are several interesting differences between the distributional results of this study and those of Chapter 1. First, in the analysis of resident birds (the guild most comparable to the results of my Afrotropical waterbird study), certain quadrats which are geographically in the western zone, appear to be 'enclaves' of the east-north zone (Fig. 2.5a). Moreover, this east-north zone is partitioned, roughly along the Limpopo River valley, into two contiguous subzones. The boundary between these subzones corresponds to the southern boundary of the Central Province in my Afrotropical-scale analysis (CENT in Fig. 2.1b), although it falls somewhat farther south. In the analysis of migrants (Fig. 2.5b), the east/north zone is bisected by a 'corridor' of west zone quadrats which extends along the Limpopo valley. Despite its fragmentation, the east-north zone in the migrant analysis also appears to penetrate farther west than in the resident analysis. Lastly, in both resident and migrant cluster analyses (Fig. 2.4a and 2.4b), quadrats from the southwestern Cape Province (nos 197, 206, 207, 213, 214; labelled SWC in Fig. 2.4) form a well-defined cluster apparently imbedded in the west zone portion of the dendrograms.

Diversity

Patterns of resident and migrant waterbird diversity in southern Africa exhibit an essentially longitudinal north/east-west gradient, higher in the eastern and northern areas (Fig. 2.6). All waterbird guild diversity measures show significant positive correlations with longitude. Only anatid diversity and the diversity of some guilds dominated by Anatidae is significantly correlated with latitude (Table 2.3), a result consistent with my Afrotropical-scale study. Although migrant and resident diversity are strongly positively correlated ($r = 0.88$; $P < 0.001$), reciprocal regressions of migrant and resident diversity for all quadrats, and regressions of migrant and resident diversity vs longitude for a band of quadrats between 20 and 27°30'S, reveal several subtle patterns. In the first two analyses, quadrats in which migrant diversity is over-represented, i.e. large positive residuals at least one standard deviation above the regression line, are largely confined to western southern Africa (quadrats marked with an 'M' in Fig. 2.7), whereas those in which residents are overrepresented, are mainly in the east (quadrats marked with 'R' in Fig. 2.7). Results of regression analyses of residents and migrants vs longitude, are summarized in Figs 2.8a and 2.8b, and show that the resident diversity curve is much steeper than the migrant diversity curve. This suggests that the species 'subtraction' effect for resident birds, as one moves west, is more severe. Indeed, the negative slope of a similar regression of the resident/migrant ratio (Fig. 2.8c) supports this interpretation.

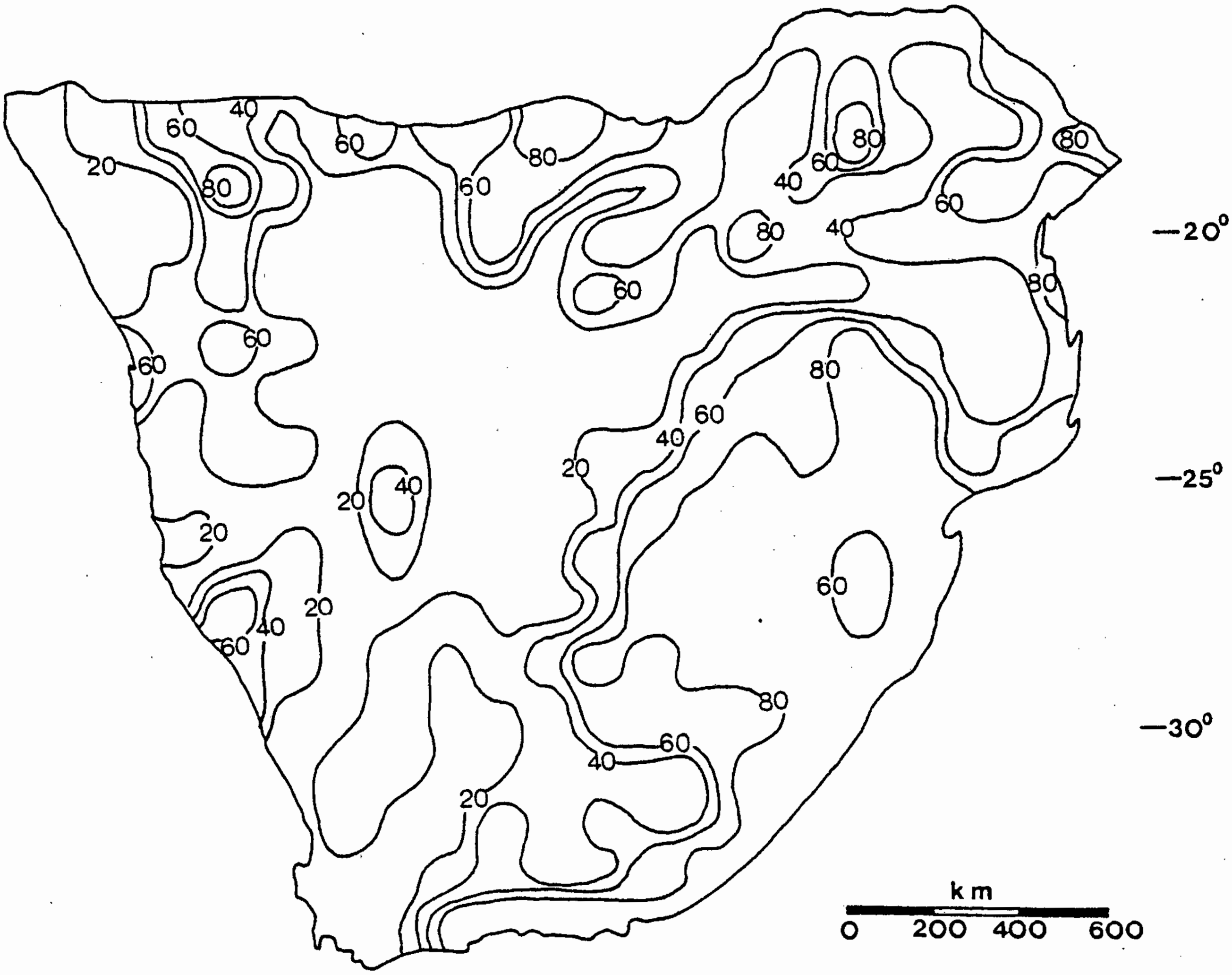

Fig. 2.6. Geographical variation in southern African waterbird species diversity.

Table 2.3. Correlation coefficients between measures of waterbird guild diversity, environmental variables, latitude and longitude

	S-R@	S-M	T-AR	T-CI	T-AN	T-RA	T-CH	T-SC	T-AL	T-SY
S-M	0.88*									
T-AR	0.93	0.83								
T-CI	0.74	0.68	0.75							
T-AN	0.85	0.79	0.77	0.60						
T-RA	0.83	0.81	0.75	0.59	0.74					
T-CH	0.79	0.81	0.72	0.63	0.63	0.65				
T-SC	0.79	0.95	0.73	0.61	0.68	0.73	0.77			
T-AL	0.85	0.69	0.78	0.62	0.61	0.66	0.65	0.63		
T-SY	0.88	0.72	0.77	0.55	0.67	0.70	0.64	0.62	0.80	
T-MO	0.68	0.51	0.56	0.41	0.48	0.51	0.45	0.48	0.65	0.77
T-PL	0.86	0.69	0.77	0.59	0.62	0.67	0.65	0.64	0.82	0.84
T-AC	0.88	0.79	0.83	0.64	0.69	0.73	0.69	0.73	0.77	0.79
T-LA	0.74	0.81	0.69	0.51	0.63	0.61	0.71	0.76	0.56	0.60
M-1	0.94	0.86	0.85	0.65	0.72	0.77	0.79	0.81	0.86	0.91
M-2	0.95	0.90	0.91	0.74	0.76	0.84	0.80	0.82	0.83	0.81
M-3	0.94	0.88	0.90	0.69	0.93	0.81	0.73	0.79	0.72	0.76
M-4	0.91	0.82	0.86	0.79	0.82	0.71	0.71	0.73	0.71	0.74
D-V	0.97	0.86	0.96	0.76	0.79	0.77	0.75	0.77	0.84	0.82
D-I	0.97	0.94	0.89	0.71	0.83	0.84	0.84	0.88	0.80	0.85
D-H	0.95	0.84	0.87	0.69	0.87	0.82	0.72	0.74	0.79	0.84
F-S	0.85	0.79	0.77	0.60	0.98	0.73	0.65	0.69	0.60	0.67
F-D	0.87	0.83	0.81	0.61	0.86	0.76	0.65	0.75	0.67	0.71
F-TP	0.96	0.94	0.93	0.77	0.82	0.83	0.84	0.88	0.79	0.79
F-DH	0.88	0.80	0.83	0.65	0.65	0.71	0.75	0.73	0.89	0.78
F-H	0.91	0.75	0.83	0.66	0.67	0.75	0.69	0.69	0.83	0.85
F-C	0.90	0.74	0.79	0.56	0.69	0.72	0.64	0.65	0.81	0.96
RF	0.60	0.47	0.54	0.35	0.41	0.51	0.37	0.44	0.55	0.58
TMX	-0.34	-0.22	-0.27	-0.25	-0.21	-0.22	-0.33	-0.22	-0.42	-0.35
XALT	0.03	0.09	0.01	-0.08	0.19	0.16	-0.10	0.05	-0.06	0.03
RALT	0.17	0.09	0.10	0.14	0.22	0.17	0.10	0.09	0.23	0.17
NPR	0.62	0.47	0.55	0.36	0.51	0.48	0.46	0.41	0.65	0.63
LPR	0.64	0.49	0.57	0.41	0.51	0.48	0.48	0.44	0.70	0.61
NNPR	-0.42	-0.33	-0.38	-0.27	-0.25	-0.32	-0.28	-0.30	-0.47	-0.42
LNPR	-0.47	-0.37	-0.43	-0.30	-0.33	-0.34	-0.33	-0.34	-0.51	-0.46
NL	0.25	0.20	0.25	0.12	0.13	0.13	0.20	0.16	0.16	0.27
PL	0.17	0.22	0.15	0.10	0.07	0.11	0.23	0.20	0.18	0.16
AL	0.07	0.14	0.05	0.06	-0.00	0.02	0.16	0.14	0.11	0.06
NS	0.10	0.03	0.12	0.06	-0.00	-0.02	0.03	-0.00	0.06	0.13
PS	0.09	-0.00	0.11	0.02	0.00	0.00	-0.04	-0.04	0.07	0.17
AS	0.09	0.01	0.11	0.04	0.04	0.05	-0.04	-0.03	0.06	0.17
NMF	-0.08	0.02	-0.05	0.00	-0.04	-0.07	-0.00	0.06	-0.19	-0.13
PMF	-0.01	0.06	-0.00	0.02	0.01	-0.05	0.06	0.07	-0.13	-0.05
AMF	0.00	0.05	0.00	0.02	0.01	-0.05	0.06	0.05	-0.08	-0.01
LAT	0.07	0.03	-0.01	-0.00	0.32	0.06	-0.02	0.01	0.01	0.10
LNG	0.57	0.40	0.53	0.39	0.30	0.36	0.43	0.35	0.61	0.61

	T-MO	T-PL	T-AC	T-LA	M-1	M-2	M-3	M-4	D-V	D-I
T-PL	0.72									
T-AC	0.59	0.76								
T-LA	0.42	0.54	0.69							
M-1	0.76	0.92	0.84	0.71						
M-2	0.61	0.80	0.84	0.77	0.90					
M-3	0.55	0.73	0.82	0.73	0.84	0.86				
M-4	0.56	0.70	0.82	0.67	0.80	0.84	0.89			
D-V	0.62	0.80	0.89	0.75	0.89	0.94	0.92	0.92		
D-I	0.65	0.81	0.85	0.78	0.94	0.95	0.92	0.88	0.92	
D-H	0.66	0.88	0.81	0.69	0.91	0.90	0.92	0.86	0.90	0.91
F-S	0.47	0.61	0.70	0.64	0.72	0.75	0.93	0.85	0.80	0.83
F-D	0.53	0.67	0.74	0.68	0.78	0.82	0.92	0.81	0.86	0.86
F-TP	0.59	0.78	0.85	0.78	0.91	0.96	0.93	0.90	0.95	0.97
F-DH	0.60	0.77	0.83	0.76	0.87	0.88	0.77	0.77	0.88	0.86
F-H	0.71	0.97	0.80	0.61	0.93	0.87	0.78	0.76	0.86	0.86
F-C	0.81	0.85	0.82	0.63	0.92	0.83	0.79	0.76	0.85	0.86
RF	0.57	0.65	0.55	0.40	0.61	0.59	0.49	0.47	0.56	0.55
TMX	-0.39	-0.42	-0.31	-0.26	-0.39	-0.30	-0.26	-0.25	-0.32	-0.31
XALT	0.03	-0.02	-0.01	-0.09	0.00	0.00	0.11	0.03	-0.00	0.05
RALT	0.24	0.23	0.07	0.00	0.18	0.08	0.19	0.14	0.12	0.16
NPR	0.54	0.69	0.50	0.34	0.65	0.55	0.55	0.49	0.57	0.57
LPR	0.56	0.69	0.50	0.37	0.66	0.58	0.56	0.51	0.60	0.59
NNPR	-0.41	-0.46	-0.40	-0.22	-0.43	-0.41	-0.33	-0.35	-0.40	-0.38
LNPR	-0.42	-0.49	-0.43	-0.27	-0.47	-0.45	-0.39	-0.40	-0.46	-0.43
NL	0.24	0.32	0.28	0.23	0.27	0.23	0.23	0.18	0.25	0.23
PL	0.17	0.20	0.25	0.26	0.22	0.19	0.13	0.13	0.18	0.19
AL	0.10	0.09	0.15	0.18	0.12	0.10	0.03	0.06	0.08	0.09
NS	0.11	0.13	0.10	0.20	0.10	0.10	0.06	0.06	0.13	0.05
PS	0.09	0.11	0.06	0.19	0.09	0.11	0.02	0.03	0.11	0.03
AS	0.07	0.09	0.08	0.17	0.09	0.10	0.03	0.05	0.10	0.05
NMF	-0.12	-0.17	-0.07	0.01	-0.11	-0.06	-0.04	0.04	-0.06	-0.04
PMF	-0.10	-0.13	0.02	0.06	-0.05	-0.00	0.01	0.14	0.01	0.01
AMF	-0.08	-0.09	0.05	0.06	-0.03	0.01	0.01	0.14	0.03	0.02
LAT	0.05	0.03	0.01	-0.02	0.03	-0.08	0.22	0.13	0.01	0.08
LNG	0.57	0.66	0.51	0.32	0.62	0.55	0.41	0.44	0.54	0.51

	D-H	F-S	F-D	F-TP	F-DH	F-H	F-C	RF	TMX	XALT
F-S	0.86									
F-D	0.84	0.84								
F-TP	0.90	0.82	0.85							
FD-H	0.80	0.65	0.70	0.85						
F-H	0.92	0.66	0.72	0.84	0.81					
F-C	0.85	0.68	0.73	0.81	0.79	0.86				
RF	0.61	0.39	0.45	0.54	0.52	0.65	0.62			
TMX	-0.32	-0.21	-0.24	-0.29	-0.39	-0.40	-0.35	-0.30		
XALT	0.07	0.15	0.13	0.03	-0.11	-0.02	0.05	0.09	0.58	
RALT	0.18	0.19	0.18	0.12	0.15	0.20	0.15	-0.00	-0.49	-0.04
NPR	0.64	0.51	0.49	0.54	0.56	0.66	0.61	0.61	-0.48	-0.01
LPR	0.64	0.50	0.51	0.57	0.60	0.66	0.61	0.63	-0.49	-0.04
NNPR	-0.41	-0.25	-0.30	-0.38	-0.40	-0.45	-0.43	-0.57	0.30	0.10
LNPR	-0.46	-0.33	-0.36	-0.43	-0.42	-0.48	-0.47	-0.57	0.38	0.14
NL	0.27	0.16	0.21	0.22	0.22	0.31	0.27	0.31	-0.26	-0.25
PL	0.16	0.08	0.13	0.18	0.23	0.18	0.15	0.21	-0.15	-0.09
AL	0.05	-0.00	0.04	0.09	0.15	0.07	0.06	0.12	-0.09	-0.04
NS	0.10	0.00	0.01	0.07	0.12	0.14	0.16	0.12	-0.22	-0.41
PS	0.09	-0.01	-0.01	0.04	0.12	0.13	0.17	0.06	-0.10	-0.26
AS	0.10	0.03	-0.02	0.05	0.12	0.12	0.17	0.04	-0.04	-0.13
NMF	-0.09	-0.03	-0.01	-0.01	-0.12	-0.14	-0.13	-0.16	0.21	0.01
PMF	-0.03	0.03	0.01	0.04	-0.07	-0.10	-0.05	-0.06	0.09	-0.01
AMF	-0.02	0.03	0.01	0.05	-0.03	-0.07	-0.02	-0.01	0.04	-0.01
LAT	0.10	0.33	0.20	0.01	-0.06	-0.00	0.06	-0.14	-0.06	0.06
LNG	0.54	0.31	0.34	0.51	0.54	0.64	0.61	0.69	-0.40	-0.20

	RALT	NPR	LPR	NNPR	LNPR	NL	PL	AL	NS	PS
NPR	0.31									
LPR	0.33	0.92								
NNPR	-0.04	-0.58	-0.56							
LNPR	-0.08	-0.65	-0.63	0.91						
NL	-0.10	0.26	0.15	-0.20	-0.22					
PL	-0.09	0.19	0.15	-0.17	-0.18	0.49				
AL	-0.06	0.08	0.09	-0.10	-0.11	0.20	0.93			
NS	-0.16	0.10	0.06	-0.06	-0.09	0.51	0.16	0.03		
PS	-0.16	0.06	0.05	0.05	0.02	0.12	0.02	-0.00	0.65	
AS	-0.13	0.02	0.02	0.11	0.10	0.00	-0.01	-0.01	0.37	0.86
NMF	-0.20	-0.22	-0.22	0.15	0.09	-0.02	-0.04	-0.03	-0.02	-0.04
PMF	-0.19	-0.16	-0.16	0.09	0.01	-0.02	-0.03	-0.02	-0.01	-0.03
AMF	-0.15	-0.11	-0.11	0.04	-0.02	-0.02	-0.03	-0.02	-0.01	-0.02
LAT	0.41	0.14	0.09	0.09	0.04	0.00	-0.07	-0.10	-0.08	-0.18
LNG	-0.03	0.67	0.66	-0.64	-0.66	0.34	0.22	0.12	0.27	0.15

	AS	NMF	PMF	AMF	LAT
NMF	-0.03				
PMF	-0.02	0.69			
AMF	-0.02	0.44	0.93		
LAT	-0.15	0.03	-0.07	-0.10	
LNG	0.05	-0.17	-0.09	-0.04	-0.06

[@] see Tables 2.1 and 2.2 for a key to abbreviations.

[*] $P = 0.05$, $r = 0.13$; $P = 0.01$, $r = 0.17$.

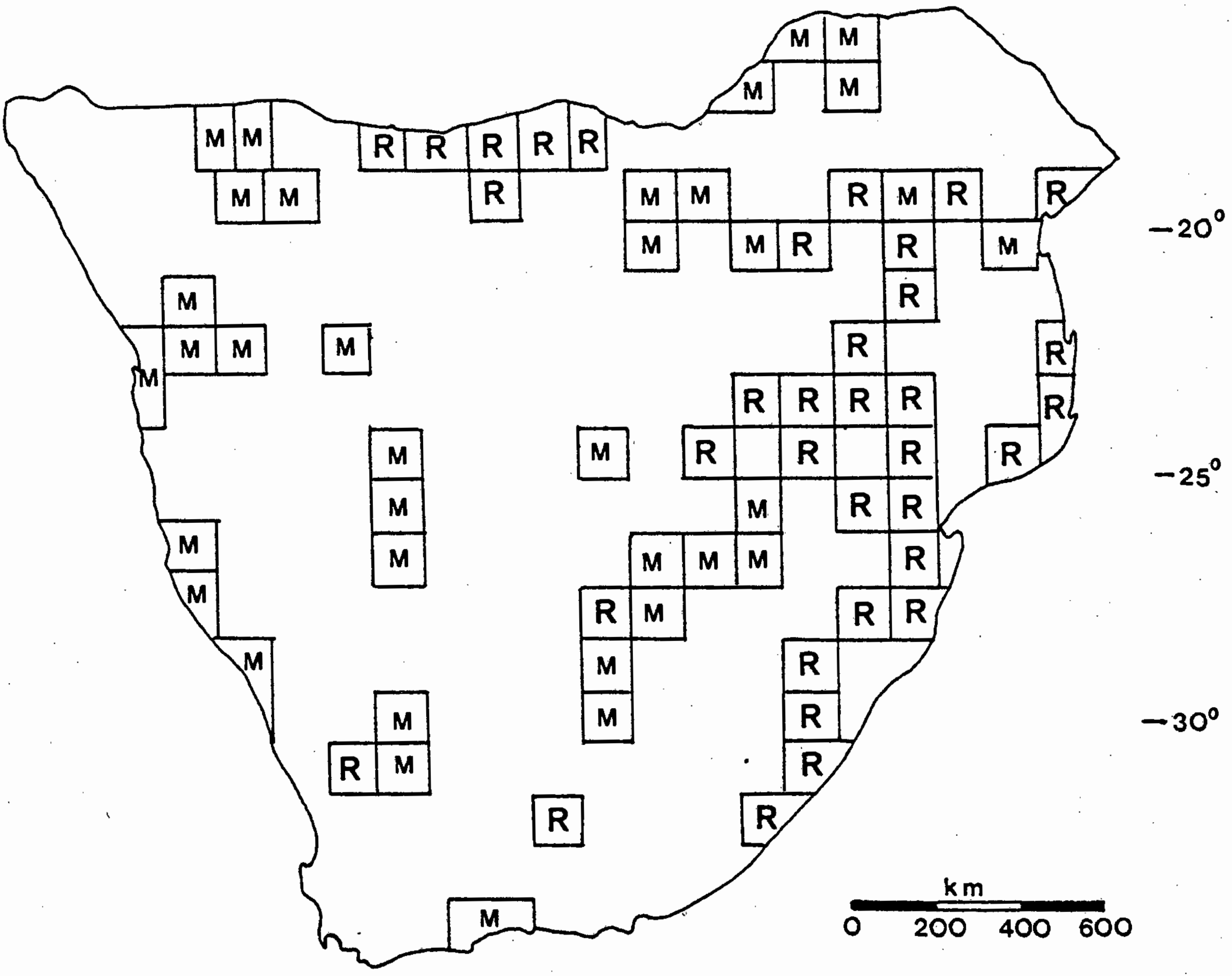

Fig. 2.7. Geographical distribution of quadrats 'overrepresented' (at least one standard deviation above the regression line) in resident (R) and migrant (M) waterbird diversity, as suggested by the residual plot of reciprocal resident-migrant regression analyses.

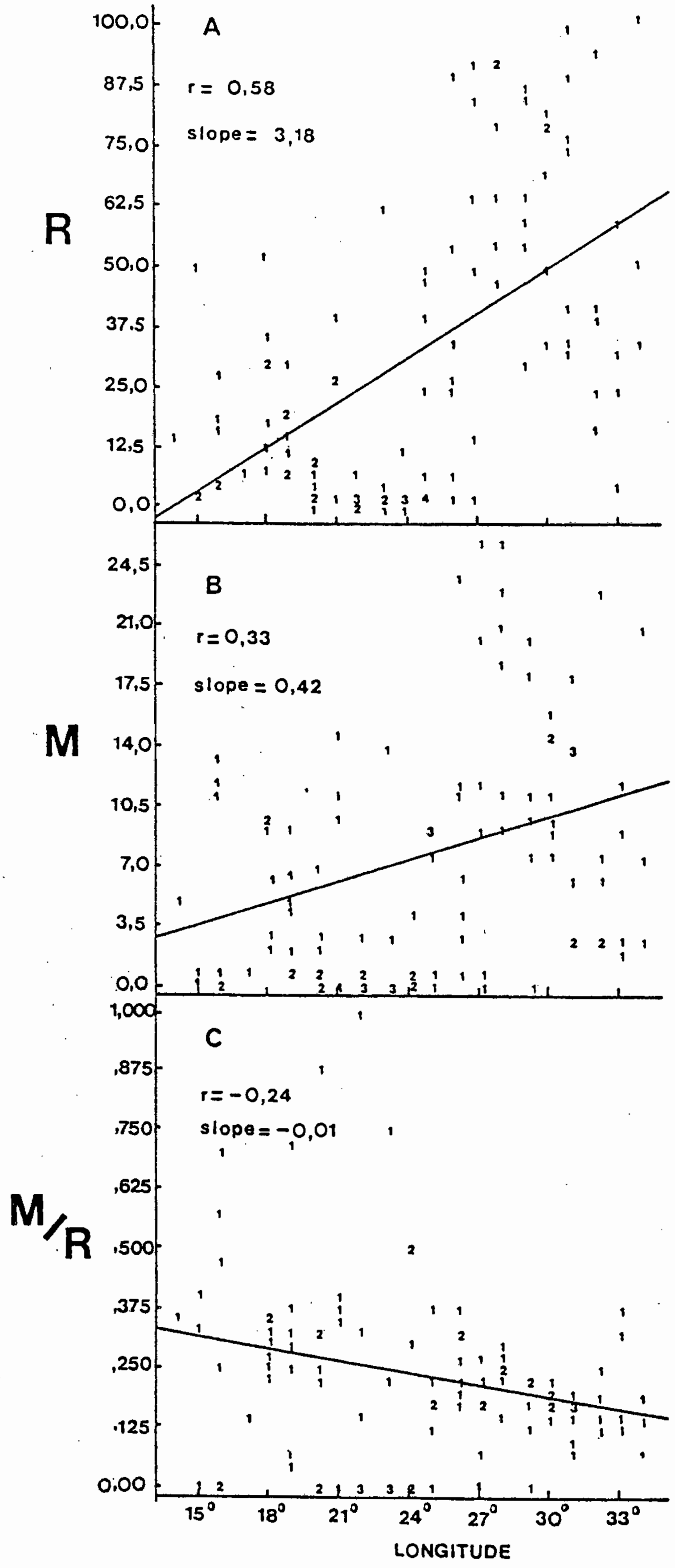

Fig. 2.8. Results of regression analyses of measures of southern African waterbird diversity versus longitude: A) residents (R), B) migrants (M), and C) migrant/resident ratio (M/R).

Results of the correlation and multiple regression analyses of resident, migrant and guild diversity for waterbirds against measures of environmental variation are summarized in Tables 2.3 and 2.4. The dominant environmental variables in these analyses are mean annual rainfall (RF) and the availability of aquatic habitat, especially the length (LPR) and number (NPR) of permanent rivers. Moreover, among the regression analyses, there are trends in total R^2 which seem to be related to mobility, size and foraging mode. Resident (S-R), smaller body mass (M-1, M-2), herbivore (D-H) and 'dry-feet' foraging (F-P, F-A) guild diversity tend to be better predicted by environmental variation than that for the migrant (S-M), larger body mass (M-3, M-4), invertebrate feeder (D-I) and 'wet-feet' foraging (F-D, F-S) guilds.

Impoundments

The correlation and bivariate regression analyses of impoundment variables against measures of waterbird diversity (Table 2.5) show several consistent patterns. First, within the relatively xeric, western quadrats , impoundment density (ID) is the only impoundment variable significantly correlated with diversity measures. Secondly, within the mesic quadrats, ID is not correlated with any diversity measure, and some guilds [e.g. Anatidae (T-AN), Scolopacidae (T-SC), Laridae (T-LA)], tend to be correlated with measures of impoundment area, and others [e.g. Accipitridae (T-AC), Charadriidae (T-CH)] with volume measures or volume plus area.

Table 2.4. Significant ($P < 0.05$) results of stepwise multiple regression analyses between waterbird guilds and environmental diversity measures. Guilds are ranked according to their total R^2, environmental variables in ascending step order followed by the contribution to total R^2 in parentheses

Total R^2	Guild*	Entering variables and their contribution to total R^2
0.59	T-PL:	LPR(0.49), RF(0.07), NL(0.02), RALT(0.01)
0.51	T-AL:	LPR(0.49), RF(0.02)
0.48	T-SY:	NPR(0.40), RF(0.06), AS(0.02)
0.42	T-MO:	RF(0.33), LPR(0.07), RALT(0.02)
0.39	T-AR:	LPR(0.33), RF(0.06)
0.37	T-AC:	RF(0.31), NPR(0.04), PL(0.02)
0.33	T-RA:	RF(0.27), NPR(0.04), XALT(0.02)
0.31	T-AN:	NPR(0.27), XALT(0.04)
0.29	T-CH:	LPR(0.24), PL(0.03), PMF(0.02)
0.27	T-SC:	LPR(0.20), RF(0.04), NMF(0.03)
0.26	T-LA:	RF(0.16), PL(0.04), PS(0.02), LPR(0.03)
0.19	T-CI:	LPR(0.17), RF(0.02)
0.52	M-1:	LPR(0.49), RF(0.06), NL(0.01)
0.43	M-2:	RF(0.36), LPR(0.07)
0.38	M-3:	LPR(0.31), RF(0.04), XALT(0.01), NL(0.02)
0.35	M-4:	LPR(0.27), PMF(0.05), RF(0.03)
0.52	D-H:	LPR(0.42), RF(0.07), NL(0.01), XALT(0.01), AS(0.01)
0.42	D-V:	LPR(0.36), RF(0.06)
0.41	D-I:	LPR(0.35), RF(0.06)
0.58	F-P:	LPR(0.45), RF(0.09), NL(0.02), AS(0.01), RALT(0.01)
0.50	F-A:	RF(0.39), NPR(0.38), AS(0.03)
0.41	F-DH:	LPR(0.36), RF(0.04), PL(0.01)
0.40	F-TP:	LPR(0.33), RF(0.06), PMF(0.01)
0.33	F-D:	LPR(0.26), RF(0.03), XALT(0.02), NL(0.02)
0.31	F-S:	NPR(0.27), XALT(0.03), PMF(0.01)
0.48	S-R:	LPR(0.41), RF(0.07)
0.33	S-M:	LPR(0.25), RF(0.04), NMF(0.02), PL(0.02)

* see Tables 2.1 and 2.2 for a key to abbreviations.

Table 2.5. Summary of significant results of correlation analyses between quadrat guild diversity and measures of impoundment availability

	Xeric quadrats			Mesic quadrats		
Guilds[1]	Impoundment variable(s)	r	df	Impoundment variable(s)	r	df
Residents	*[2] ID[3]	0.29	50	* ITVOL	0.38	32
				* IXVOL	0.40	32
				* IRVOL	0.38	32
Migrants				** ITAR	0.45	35
				* IXAR	0.38	32
				* IRAR	0.40	32
Anatidae	* ID	0.36	50	* ITAR	0.36	35
				* IRAR	0.34	32
Rallidae	* ID	0.32	50	* ITAR	0.35	35
				* IXAR	0.35	32
				* IRAR	0.35	32
Charadriidae				* ITVOL	0.41	32
				** IXVOL	0.48	32
				* IRVOL	0.46	32
				** ITAR	0.44	35
Scolopacidae				** IXAR	0.53	32
				** IRAR	0.51	32
Alcedinidae	* ID	0.29	50			
Accipitridae				* ITVOL	0.37	32
				* IXVOL	0.34	32
				* ITAR	0.34	35
Laridae				** ITAR	0.45	35
				** IXAR	0.46	32
				** IRAR	0.47	32
Diet-vertebrates				* ITVOL	0.37	32
				* IXVOL	0.38	32
				* IRVOL	0.37	32
				* ITAR	0.34	35
Diet-invertebrates				* IXVOL	0.35	32
				* IRVOL	0.34	32
Diet-mixed with veg. component				* ITVOL	0.35	32
				* IXVOL	0.39	32
				* IRVOL	0.36	32

Body-mass 1				* ITVOL	0.41	32
				* IXVOL	0.43	32
				* IRVOL	0.40	32
Body-mass 3	* ID	0.33	50	** ITAR	0.45	35
				* IXAR	0.40	32
				* IRAR	0.42	32
Body-mass 4				* ITVOL	0.42	32
				* IXVOL	0.41	32
				* IRVOL	0.39	32
Surface swimmers	* ID	0.34	50	* IXAR	0.40	32
				* IRAR	0.41	32
Peckers				* IRVOL	0.35	32
				* ITAR	0.34	35
				* IXAR	0.34	32
Plunge divers	* ID	0.28	50	* ITVOL	0.41	32
				* IXVOL	0.41	32
				* IRVOL	0.41	32
				* ITAR	0.37	35
				* IXAR	0.36	32
				* IRAR	0.35	32
'Dry feet' plant eaters				* IXVOL	0.35	32

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[1] See Table 2.1 for complete guild information.

[2] Significance level: * = P < 0.01; ** = P < 0.001.

[3] ITVOL = total impoundment volume, IXVOL = mean impoundment volume, IRVOL = range of impoundment volume, ITAR = impoundment total area, IXAR = mean impoundment area, IRAR = range of impoundment area, ID = impoundment density (number per quadrat).

Discussion

Distribution

Despite its overall much finer grained analysis, the present study uncovers only two biologically interesting distributional patterns markedly different from those found in Chapter 1. First, the smaller quadrat size allowed the detection of several east-north zone 'enclaves' in the western zone. I suggest that the 'enclave' quadrats encompass isolated areas of reliable and ecologically diverse aquatic habitat which is relatively common in the east-north zone. For example: quadrat 77 encompasses the estuaries of the Kuiseb and Swakop Rivers; quadrat 79 contains the highlands around the Auas Mountains which are the source areas of many Namibian rivers; and quadrats 156 and 169 encompass the interfluve of the Fish and Orange Rivers, including the Orange River estuary. These areas support populations of species whose distributions are largely confined to the east-north zone quadrats, e.g. the Great Crested Grebe *Podiceps cristatus*, Lesser Flamingo *Phoeniconaias minor* and Purple Gallinule *Porphyrio porphyrio*.

The second difference, the southward extension to the Limpopo valley of the boundary between the two subzones which comprise the east-north zone, is, in part, due to differences in species which statistically best characterize the northern subzone as opposed to the Central District of Chapter 1, which emphasized the importance of species essentially endemic to the Central District. However, in the present study, species which are more widespread in Africa, e.g. the Streakybreasted Flufftail *Sarothrura boehmi*, Blackshouldered Wattled Plover *Vanellus albiceps*, and Locust Finch

Ortygospiza locustella, characterize the northern subzone. Thus, this boundary shift could be an artifact of the geographical limits of my study area. However, the finer scale of this study draws attention to the importance of the Limpopo valley as a zoogeographical barrier. Benson et al. (1962) long ago emphasized the significance of the Limpopo valley as an avian zoogeographical barrier, identifying it as a corridor of xeric habitat dominated by *Colophospermum mopane* woodland. The transition of this vegetation type into the equally xeric *Acacia* and *Commiphora* wooded steppe on the plateau of eastern Botswana is equally 'desertic' for waterbirds, and might explain the greater northeastern penetration, of the western zone in both this and my Afrotropical-scale study (SW-ARID in Fig. 2.1b), relative to that identified by non-aquatic birds (Fig. 2.1a).

Comparison of the distribution for resident and migrant waterbirds, re-emphasizes the importance of the Limpopo valley. In the migrant analysis, the valley forms a west zone 'corridor' (Fig. 2.5b), possibly a combined effect of the dry nature of the Limpopo valley during summer months (Harrison 1984). The geomorphology of the valley, also is not conducive to the formation of large floodplains, favoured habitat of many migrant waterbirds. In fact, I suggest that the greater westward penetration of the east-north zone in the migrant analysis (compare Figs 2.5a and 2.5b) may be due to the seasonal availability of floodplains and extensive non-permanent water systems such as large mud flats (e.g. quadrats 38, 54, 55, 56, 72 encompassing the Makarikari Pans), and major wadis (e.g. quadrats 68 and 81 including the interfluve between the Black and the White Nossob Rivers).

The biogeography of the southwestern Cape quadrats, which unite to form 'long-tailed', discrete clusters in both resident and migrant cluster analyses (Figs 2.4a and 2.4b), is a matter of dispute. Moreau (1952) states that the southwestern Cape avifauna is essentially a subset of that of eastern South Africa. However, Chapin (1932) and Winterbottom (1959) include the southwestern Cape in a southwest arid zone. With particular regard to waterbirds, Winterbottom (1967, 1968b) reiterates his position, stressing that the avifaunas of the southwestern Cape, and probably Namibia, differ significantly from his "East African Tropical Aquatic Avifauna" which encompasses water systems from the Nile Sudd down to Lake St Lucia in Natal. In both my southern African resident and migrant cluster analyses, southwestern Cape quadrats do not associate with the bulk of eastern quadrats (Fig. 2.4). However, examination of the similarity matrices generated by the cluster analyses, reveals a different position. In the resident analysis, they are more similar to quadrats in the eastern zone, and, in the migrant analysis, to western zone quadrats. In my Afrotropical-scale study (Chapter 1), which specifically excluded migrants, the southwestern Cape also clustered with the east-north zone.

The reason why the southwestern Cape behaves differently biogeographically for resident and migrant waterbirds remains obscure. One possible explanation of its west-zone affinities in the migrant analysis is that, historically, the avifauna of the the area has karooid affinities (Winterbottom 1968c), and that its present migrant avifauna is relict in nature. Owing to the inherently mobile nature of many waterbirds (Appendix 2.1), I feel that this hypothesis is unlikely. Other ecological and geological explanations are that: 1) migrants visit the southwestern Cape only during the relatively dry austral summer and therefore cannot utilize the fluctuating water habitat made available by winter rainfall; 2) the bulk of the southwestern Cape which is potentially habitable by migrant waterbirds receives too little rain overall, with most of the areas with locally high rainfall being associated with mountain systems (Fuggle 1981); 3) the Palaearctic migrant component of the southwestern Cape is dominated by 'marine' waders (Siegfried 1981) which prefer the relatively mild ambient temperatures in that area; and 4) the geomorphology of the southwestern Cape does not favour the formation of highly productive, shallow water bodies. On the other hand, the high concentration of impoundments in the southwestern Cape provides relatively deep-water aquatic habitat which favours resident waterbirds, hence the east-north zone affinities in the resident analysis.

Diversity in general

The general longitudinal gradient of waterbird diversity in southern Africa is the result of a subtraction effect from the relatively species-rich eastern parts of Africa. I attribute this subtraction effect to the combined influences of rainfall and geomorphology. Annual rainfall in southern Africa shows a marked east-west gradient (Clark 1967). Moreover, it also shows a general east-west trend in reliability (Onesta & Verhoef 1976). Even when and where there is adequate rain in the west, the porous, sandy soil which dominates that part of southern Africa (Clark 1967) does not favor the formation of durable water bodies which could sustain a waterbird fauna. Anatid diversity (T-AN), the only real exception to this pattern, also has a significant positive correlation with latitude. This exception is possibly a consequence of the high mobility of many southern African Anatidae

(Winterbottom 1972, Oatley & Prŷs-Jones, in press). In fact, their opportunistic mobility, often over long distances, enables them to reach even small, remote water bodies. Thus, the latidudinal gradient in anatid diversity is possibly the result of exploitation of ephemeral water bodies, especially impoundments, which abound in the southern part of the subcontinent (Noble & Hemens 1978).

The explanation I offer for the general longitudinal pattern of waterbird diversity in southern Africa also has bearing on the differences found between resident and migrant waterbird diversity, and between waterbird diversity in general and that of terrestrial birds. The extremely seasonal and unpredictable rains which fall on the relatively porous soils of western southern Africa favour the creation of ephemeral aquatic biotopes usually fed by wadis and other non-permanent rivers. These biotopes generate a short-term flush of resources, especially food, e.g. invertebrates and tadpoles (Weir 1969), which is readily exploited by migrants; hence, their less dramatic longitudinal subtraction effect (Fig. 2.8). Thus, my results are consistent with the hypothesis that migrant birds use a periodical superabundance of food and/or habitat which cannot be utilized fully by resident birds (Morel & Bourlière 1962; Willis 1966). This ephemeral superabundance of aquatic resources in western southern Africa also explains the much sharper subtraction effect of terrestrial birds relative to waterbirds (Guillet & Crowe 1984).

In comparison with my Afrotropical-scale study, results of the waterbird vs environmental diversity correlation and stepwise multiple regression analyses show only one major difference. Mean annual rainfall (RF) is much better correlated (r = 0.57 vs 0.26) with resident diversity (S-R). This is probably due to the generally lower rainfall ($\bar{x}$ = 377 mm vs 926 mm for Africa as a whole) and the strong east-west rainfall gradient in southern Africa.

Guild diversity: comparisons

The diversity of resident waterbirds in southern Africa is much better predicted by variation in the environment than that of migrant waterbirds. The most obvious explanation of this difference is that the environmental data used in the regressions reflect year-round conditions in the quadrats, i.e. the conditions under which resident waterbirds must exist. Migrant waterbirds, as I have said above, appear to exploit ephemeral and seasonally superabundant resources, thereby avoiding unsuitable conditions which may predominate in many quadrats through much of the year.

In addition to the differences between resident and migrant diversity, Table 2.4 shows that the diversity of small waterbirds which feed mainly on plant food in the vicinity of, but not in water [i.e. members of the 'dry feet' (F-P) guild dominated by Ploceidae] tend to be better predicted by year-round environmental conditions within quadrats. This 'tracking' of local conditions by these species, together with their ability to shift their feeding niches opportunistically, allows them to exploit what is locally available. Skead (1964) and Elliott (1973) demonstrate this clearly for Ploceidae. However, the diversity of guilds whose members forage in water and/or mud (e.g. Scolopacidae and Anatidae), especially those which are large (e.g. Ciconiidae), have relatively narrower foraging niches, and are dependent on animal food, tend to be poorly predicted. I attribute this low predictability to a lack of foraging flexibility, compensated for by relatively high mobility. In other words, these species are dependent on a relatively limited variety of foraging habitat and/or food types whose availability varies considerably spatially and temporally, requiring the birds to move, sometimes over large distances.

In this regard, it is necessary to draw attention to the distinction between mobility sensu lato, and migration. Appendix 2.1 shows that several 'resident' waterbirds are often highly mobile within southern Africa, even if not in any regular fashion (e.g. the Yellowbilled Duck Anas undulata, the Redknobbed Coot Fulica cristata, and the Avocet Recurvirostra avosetta). In fact, relatively mobile, resident waterbirds are very well represented in highly aquatic guilds (F-S and F-D) and vertebrate-eaters (D-V), and are poorly represented in 'dry feet' (F-A) and invertebrate feeder (D-I) guilds (Table 2.1). The larger body-mass guilds, M-3 and M-4, which are characterized by vertebrate-eaters with more aquatic foraging modes, are the worst predicted by variation in the environment.

Finally, I focus on differences between ardeid and anatid diversity which figured importantly in my Afrotropical-scale study and in Reichholf's (1975) study of waterbird biogeography in South America. In South America, ardeid diversity is highest in the tropics and lowest in temperate areas, whereas the reverse pattern is found in the Anatidae. For the Afrotropics, both ardeid and anatid diversity tend to be higher away from the tropics, and I explained this in terms of geographical variation in habitat suitability.

Working on a much finer scale within southern Africa, I find somewhat more complex relationships between ardeid and anatid diversity. Ardeid diversity, and to a lesser extent, anatid diversity exhibit the same general geographical pattern as that found for the other waterbird taxonomic guilds. Each has an area of consistently high diversity centred on the upper reaches of the Vaal and Olifants Rivers' drainage systems in the Transvaal, and from the Komati down to the Mzimvubu Rivers' drainage systems (on the Indian Ocean coast). However, ardeid diversity tends to decrease from this centre of high diversity dramatically towards the west and south, and relatively gradually to the north and east, in much the same way as does overall waterbird diversity (Fig. 2.6). Anatid diversity, on the other hand, shows an additional minor centre of high diversity in the southwestern Cape Province, and decreases much more sharply to the north and east. This pattern is shown clearly in an examination of the residual plots of ardeid and anatid diversity vs resident diversity (Fig. 2.9).

I feel that these differences between ardeid and anatid diversity reflect the availability of aquatic habitat and certain abiotic conditions. Aquatic biotopes suitable for Anatidae (e.g. 'discrete' pond-like water bodies) abound in the southwestern Cape; whereas shallow, protected stretches of vegetated water preferred by Ardeidae, are much more readily available in the eastern and northeastern part of my study area. Supporting evidence for this 'habitat' suitability hypothesis is the positive correlation between anatid diversity and impoundment density in the quadrats of western South Africa and the lack of such correlation for ardeid diversity (Table 2.5). I would also suggest that Anatidae make good use of the very high density of impoundments in the southwestern Cape which, as I have said above, tends to be an order of magnitude higher than elsewhere. Rowan

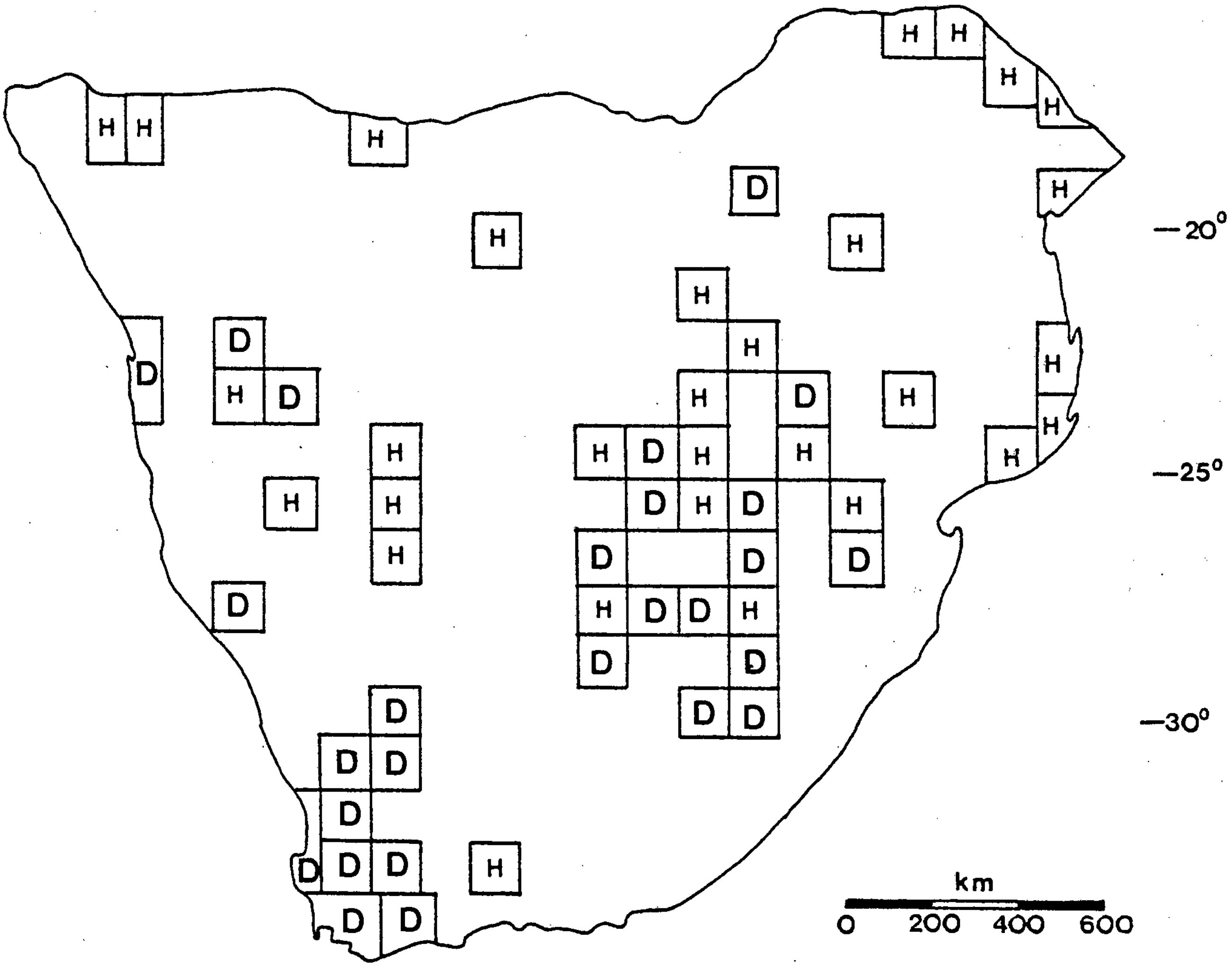

Fig. 2.9. Geographical distribution of quadrats 'overrepresented' in ardeid (H) and anatid (D) diversity, as suggested by the residual plots of reciprocal Ardeidae-Anatidae regression analyses.

(1963), Winterbottom (1969) and Siegfried (1970) have also drawn attention to the role of impoundments in extending the range of certain Anatidae (e.g. the South African Shelduck and the Spurwinged Goose *Plectropterus gambensis*). Other studies (Rowan 1963; Siegfried 1965, 1976; Geldenhuys 1979) have invoked temperature as a potentially limiting factor for certain Anatidae, but this hypothesis cannot be used to distinguish factors which differentiate Anatidae and Ardeidae, because both ardeid and anatid diversity are significantly negatively correlated with ambient temperature (Table 2.3). An additional, yet unexplored, reason for high anatid diversity in the southwestern Cape is a possible preadaptation to salt water which enables several Anatidae (e.g. the South African Shelduck, the Cape Shoveller *Anas smithii*, the Maccoa Duck *Oxyura maccoa*, the Cape Teal *A. capensis*) which are adapted to inland saline biotopes, to utilize brackish water biotopes along the western Atlantic coast (W.R. Siegfried, pers. comm.). These same species may be excluded from northeastern southern Africa by unfavourable regimes of ambient temperature (Rowan 1963; Siegfried 1965; Snow 1978; Geldenhuys 1979).

Centres of high waterbird diversity

In the present study, as in my Afrotropical-scale research (Chapter 1), the diversity vs environment multiple regression analyses failed to predict the waterbird diversity of certain quadrats. In fact, the total R^2 in my analysis of residents, is only 48% vs 69% for the Afrotropics as a whole. This low R^2 might reflect the relative shortage and clumped nature of major, reliable, aquatic ecosystems in southern Africa (Siegfried 1970). Moreover, since southern Africa is not a centre of endemism for waterbirds, I suggest that quadrats or groups of quadrats whose waterbird diversity is much higher than predicted in the regressions contain or comprise true refugia (sensu Crowe & Crowe 1982). In other words, although these quadrats may not have acted as centres of speciation for waterbirds, they encompass reliable and diverse aquatic ecosystems and catchment systems which would withstand dry climatic cycles longest. Suggested refugia occur within the following quadrats (Fig 2.10): (1) quadrat no 16 (52 spp.) the origin of the major southern tributaries of the Cubango River, and the Ovambo River drainage into the Etosha Pan; (2) quadrat 18 (72 spp.) Kavango and Cuito Rivers confluence; (3) quadrats 36 and 53 (76, 77 spp.) the Okavango system including Lake Ngami; (4) quadrats 21 and 22 (88, 91 spp.) the eastern Caprivi strip including the confluences of Cuando, Linyote and Zambezi Rivers; (5) quadrats 31 and 32 (82, 101 spp.) the peak of Otavi including the origin of the Ugab and Ovambo River systems; (6) quadrats 45 and 63 (83, 123 spp.) Save and Revue Rivers including their origins; (7) quadrat 71 (60 spp.) Lake Dow which drains Makarikari pan; (8) quadrats 77 and 79 (68, 71 spp.) Windhoek highlands drainage into the Atlantic Ocean in Walvis Bay area; (9) quadrat 89 (95 spp.) the central southern tributaries of Limpopo River which drain the eastern Soutpansberg Mountains; (10) quadrat 128 (54 spp.) Nossob and Auob interfluve including the Kalahari Gemsbok National Park; (11) quadrats 118, 134-136, 149-152 and 163 (88-199 spp.) the Vaal drainage giving rise to a system of major dams and lakes including Nyl Lake and Barberspan,

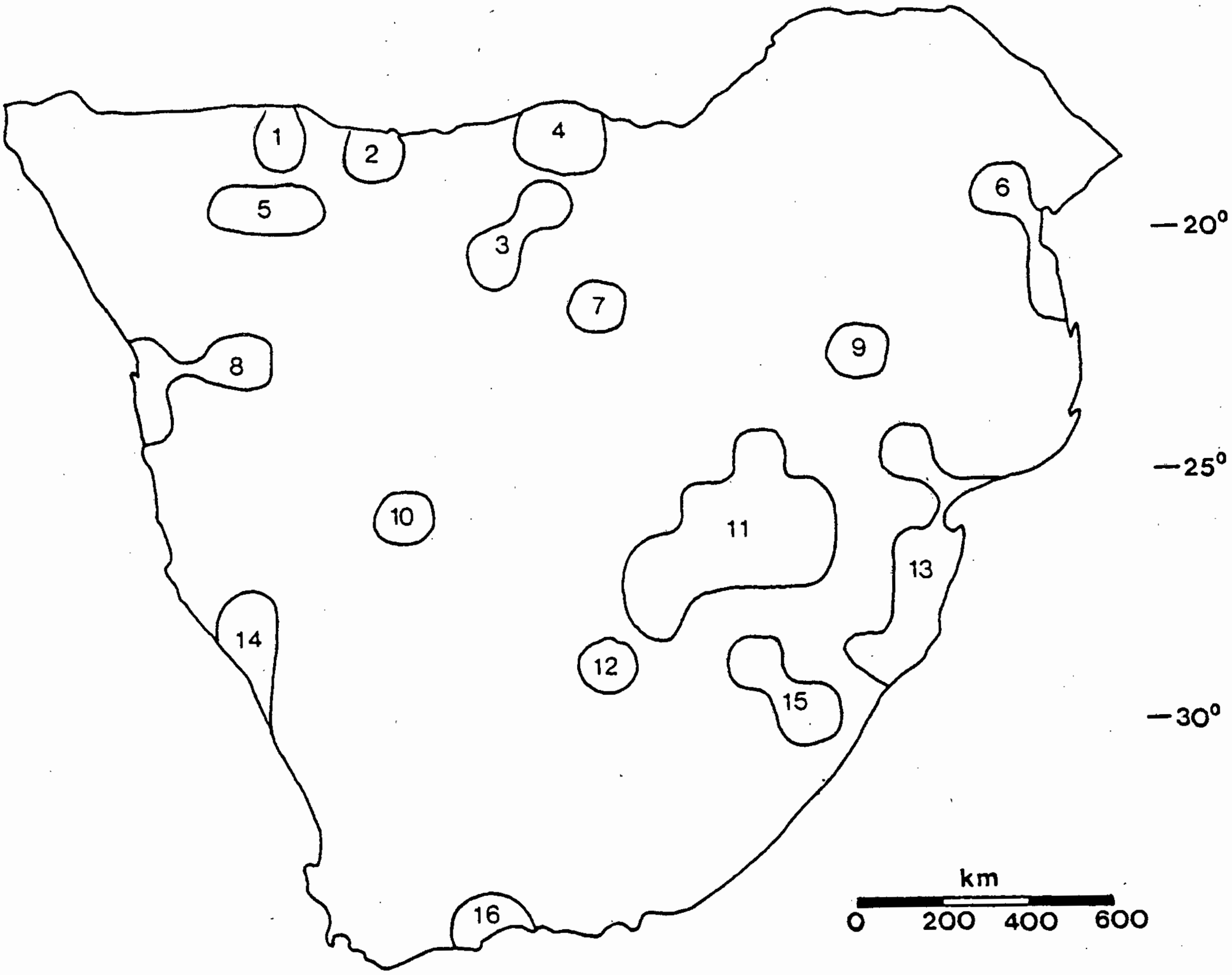

Fig. 2.10. Hypothetical waterbird refugia during dry climatic phases as suggested by a multiple regression analysis of resident diversity (S-R) against measures of environmental diversity. All refugia quadrats are at least one standard deviation above the regression line.

Hartebeespoort, Loskop, Potchefstroom, Vaal and Bloemhof Dams, in its upper part; and (12) quadrat 175 (84 spp) sustaining in its lower part numerous small endorheic systems known locally as pans; (13) quadrats 121, 139, 154, 168 and 181 (105-125 spp.) including the Kruger National Park and Usutu, Drakensberg and Lebombo Mountains, and their drainage into the Indian Ocean comprising major estuarine and lagoon systems such as Incomati, Maputo, St Lucia and Umfolozi; (14) quadrats 156 and 169 (65, 56 spp.) three major non-permanent tributaries of the Orange River and its estuary; (15) quadrats 178 and 190 (97, 112 spp.) Lesotho Mountains and their drainage into the Indian Ocean; (16) quadrat 215 (82 spp.) the drainage of Groot Swartberg Mountains with several major estuaries in the Indian Ocean.

Impoundments

The artificial creation of aquatic habitat may modify waterbird distribution and diversity considerably, sometimes fostering large aggregations of birds (Siegfried et al. 1975). Moreover, various waterbird guilds respond differently to impoundments in xeric and mesic rainfall regimes (Table 2.5). I interpret the positive correlations between the diversity of resident waterbirds (S-R), Anatidae (T-AN) and Alcedinidae (T-AL) and density of impoundments (ID) in xeric quadrats to be a consequence of the absence or relatively ephemeral nature of the preferred natural habitat(s). Two results of these analyses are consistent with this interpretation. First, the lack of any significant correlations between ID and guild diversity measures within the more mesic quadrats in the east, which presumably encompass adequate amounts of preferred habitat throughout the year. Second, migrant diversity (S-M) is not significantly correlated with ID in the xeric quadrats, since the natural habitats utilized by migrants are normally available while they are in southern Africa.

The dichotomy between guilds which appear to be dependent primarily on impoundment volume, e.g. Accipitridae (T-AC) and Charadriidae (T-CH), and those which may rely more on impoundment area, e.g. Scolopacidae (T-SC) and Laridae (T-LA), may be a consequence of two alternative but not mutually exclusive ecological strategies. The first strategy is adopted by relatively sedentary birds which appear to depend primarily on temporally reliable water habitat (as reflected by relatively high values for measures of impoundment volume). The second strategy, is employed by more mobile waterbirds which often occur in large flocks and utilize the littoral zone. These species can also exploit relatively ephemeral water bodies, especially when they occur in large expanses (as reflected by relatively high values of measures of impoundment area).

Deficiencies and remedies

Large-scale biogeographical syntheses such as this suffer from certain obvious deficiencies. First and foremost, the biotic data underpinning most such studies, e.g. checklists, 'birds of ...' type books, are descriptive, rather than explicitly quantitative. They have been collected without such syntheses in mind, using a variety of sampling methods and intensities. Moreover, they lack the temporal dimension necessary to give statistically robust predictions. This is essential if we hope to cope with seasonal and/or cyclic climatic variations, e.g. droughts vs wet cycles, which in southern Africa are the rule and not the exception. This limitation is most troublesome when inherently mobile taxa such as waterbirds are studied. Similar criticisms apply, but perhaps to a lesser extent, to the use of environmental data. The primary difficulty in this instance is the applicability of gross information which can be extracted from maps, dam registers, etc., and of 'normal' or mean climatic statistics from fixed weather stations, in some instances far from sites at which biotic data were collected.

Although regional bird atlases (e.g. Cyrus & Robson 1980; M. Kemp & A.C. Kemp in prep.; Hockey 1983) provide much better bird distributional information, the enforced static representation of their results limits their utility as data bases. However, the primary data upon which they are based do not suffer from this limitation, provided that precise information as to date, sampling method/intensity, locality, abundance and status (resident, vagrant, migrant) are noted. These broad-scale data can be 'calibrated' with long-term data for representative ecosystems which have been protected and monitored over long periods, e.g. Barberspan (Milstein 1975), Rondevlei (Middlemiss 1974; Banks 1980), and Lake St Lucia (Berruti 1980). Ornithological data should be curated by centres for bird study, e.g. along the lines of the British Trust for Ornithology or the proposed South African Bird Populations Data Bank within the South African Bird Ringing Unit (Prŷs-Jones 1984), which have suitably trained staff and adequate computer facilities for data capture, manipulation and archival. These centres should coordinate their activities with other organizations (e.g. agricultural and environmental affairs departments, nature conservancies, museums, meteorological stations) which collect ancillary biotic and abiotic data useful in identifying factors which determine patterns of biotic distribution. This would allow relatively easy analysis and exchange of information, and ensure a closer linkage between data used to identify patterns of biotic distribution and those used to explain them.

Even if high quality distributional data are available, it is difficult to compare communities and biotas. For example, although two quadrats or localities may have the same waterbird diversity, the species comprising their biotas may have markedly different biologies. In this study, I used the normal 'guild' approach to this problem, i.e. analysing species with commonn biological attributes, e.g. large size, preference for similar food, etc. However, I felt constrained by the lack of basic morphological and natural history data on waterbirds. Detailed single-species studies, e.g. Geldenhuys 1979 on the South African Shelduck, and syntheses along the lines of Rowan (1963), are needed to provide quantifiable, high quality data for species to be studied. This strategy will allow researchers to employ multivariate analysis of large suites of species [see Capen (1981); Gauch (1982) and Adams (1985) for recent reviews], rather than having to resort to many univariate analyses of potentially arbitrarily-defined, non-representative guilds. Moreover, a multivariate approach to community comparisons can help to identify species which form 'true' guilds, and which control or indicate important biological processes.

Lastly, the results of my studies of relationships between waterbirds and impoundments indicate an urgent need to repeat similar analyses when detailed bird and impoundment data are available for the whole study area. Given the economic importance of impoundments (Noble & Hemens 1978) and the critical conservation status of inland wetlands (Huntley 1978), a comparative study of the use of impoundments and natural aquatic biotopes, especially in relatively xeric parts of southern Africa could contribute considerably to our understanding of inter-relationships between waterbirds and their habitats.

Appendix 2.1. Southern African waterbirds analysed in this study and their guild and distributional characteristics. See Fig. 2.5 for a key to codes

	Guild types and codes						Characteristic species
	a					b	
Species	TAX	BMS	TPH	FOR	MST	MOB	
Great Crested Grebe		c					
Podiceps cristatus		3	1	2	1	2	
Blacknecked Grebe							
Podiceps nigricollis		2	1	2	2	3	
Dabchick							
Tachybaptus ruficollis		2	2	2	1	2	
Pinkbacked Pelican							
Pelecanus rufescens		4	1	1	1	2	
White Pelican							
Pelecanus onocrotalus		4	1	1	1	2	
Whitebreasted Cormorant							
Phalacrocorax carbo		4	1	2	1	2	
Reed Cormorant							
Phalacrocorax africanus		3	1	2	1	2	
Darter							
Anhinga melanogaster		3	1	2	1	2	
Grey Heron							
Ardea cinerea	1	3	1	3	1	2	
Blackheaded Heron							
Ardea melanocephala	1	3	1	3	1	2	
Goliath Heron							
Ardea goliath	1	4	1	3	1	2	ZONE-I
Purple Heron							
Ardea purpurea	1	3	1	3	1	2	ZONE-I
Great White Egret							
Egretta alba	1	3	1	3	1	2	ZONE-I
Little Egret							
Egretta garzetta	1	3	1	3	1	2	
Yellowbilled Egret							
Egretta intermedia	1	3	2	3	1	2	ZONE-I
Cattle Egret							
Bubulcus ibis	1	2	2	3	1	2	
Squacco Heron							
Ardeola ralloides	1	2	2	3	1	2	ZONE-I
Greenbacked Heron							
Butorides striatus	1	2	1	3	1	1	ZONE-I
Black Egret							
Egretta ardesiaca	1	2	1	3	1	2	ZONE-I
Slaty Egret							
Egretta vinaceigula	1	2	1	3	1	2?	
Rufousbellied Heron							
Butorides rufiventris	1	2	1	3	1	2	ZONE-I
Dwarf Bittern							
Ixobrychus sturmii	1	2	2	3	2	3	
Little Bittern							
Ixobrychus minutus	1	2	2	3	1	1	
Night Heron							
Nycticorax nycticorax	1	3	1	3	1	2	ZONE-I
Whitebacked Night Heron							

Gorsachius leuconotus	1	2	1	3	1	1	
Bittern							
Botaurus stellaris	1	3	1	3	1	1	
Hamerkop							
Scopus umbretta		2	1	3	1	2	
Marabou							
Leptoptilos crumeniferus	2	4	1	3	1	2	
Openbill							
Anastomus lamelligerus	2	3	2	3	2	3	ZONE-Ib
Saddlebill							
Ephippiorhynchus senegalensis	2	4	1	3	1	2	ZONE-Ib
Yellowbilled Stork							
Mycteria ibis	2	3	1	3	2	3	
Woollynecked Stork							
Ciconia episcopus	2	4	2	3	1	2	ZONE-Ib
Black Stork							
Ciconia nigra	2	4	1	3	1	3	
White Stork							
Ciconia ciconia	2	4	2	3	2	3	
Sacred Ibis							
Threskiornis aethiopicus		3	2	3	1	2	
Glossy Ibis							
Plegadis falcinellus		3	2	3	2	2	
African Spoonbill							
Platalea alba		3	2	3	1	2	ZONE-I
Greater Flamingo							
Phoenicopterus ruber		4	2	3	1	2	
Lesser Flamingo							
Phoeniconaias minor		3	3	3	1	2	
Spurwinged Goose							
Plectropterus gambensis	3	4	3	1	1	2	ZONE-I
Egyptian Goose							
Alophochen aegyptiacus	3	4	3	1	1	2	
African Shelduck							
Tadorna cana	3	3	2	1	1	2	ZONE-Ia
Knobbilled Duck							
Sarkidiornis melanotos	3	3	3	1	2	2	
Pygmy Goose							
Nettapus auritus	3	2	3	2	1	2	
European Shoveller							
Anas clypeata	3	3	2	1	2	2	
Cape Shoveller							
Anas smithii	3	3	2	1	1	2	
Black Duck							
Anas sparsa	3	3	2	1	1	1	
Yellowbilled Duck							
Anas undulata	3	3	3	1	1	2	
Redbilled Teal							
Anas erythrorhyncha	3	3	3	1	1	2	
Garganey							
Anas querquedula	3	2	3	1	2	2	ZONE-Ib
Cape Teal							
Anas capensis	3	3	2	1	1	2	
Hottentot Teal							
Anas hottentota	3	2	3	1	1	2	
Whitefaced Whistling Duck							
Dendrocygna viduata	3	3	3	1	1	2	
Fulvous Whistling Duck							
Dendrocygna bicolor	3	3	3	1	1	2	
Redeyed Pochard							
Netta erythrophthalma	3	3	3	2	1	2	
Maccoa Duck							
Oxyura maccoa	3	3	2	2	1	2	
Whitebacked Duck							
Thalassornis leuconotus	3	3	3	2	1	1	

Fish Eagle *Haliaeetus vocifer*	4	4	1	4	1	1	
European Marsh Harrier *Circus aeruginosus*	4	3	1	6	2	2	
African Marsh Harrier *Circus ranivorus*	4	3	1	6	1	1	
Osprey *Pandion haliaetus*	4	3	1	4	1	2	
Water Rail *Rallus caerulescens*	5	2	2	3	1	1	
African Crake *Crex egregia*	5	2	2	3	2	3	
Striped Crake *Aenigmatolimnas marginalis*	5	2	2	3	2	3	
Spotted Crake *Porzana porzana*	5	2	2	3	2	3	
Baillon's Crake *Porzana pusilla*	5	1	2	3	1	1	ZONE-I
Black Crake *Amaurornis flavirostris*	5	2	2	3	1	1	ZONE-I
Whitewinged Flufftail *Sarothrura ayresi*	5	2	2	3	2	3?	ZONE-Ia
Redchested Flufftail *Sarothrura rufa*	5	2	2	3	1	1	ZONE-I
Streakybreasted Flufftail *Sarothrura boehmi*	5	2	3	3	2	3?	ZONE-Ib
Purple Gallinule *Porphyrio porphyrio*	5	3	3	5	1	1	
Lesser Gallinule *Porphyrula alleni*	5	3	3	5	1	3	ZONE-I
Moorhen *Gallinula chloropus*	5	2	2	3	1	1	
Lesser Moorhen *Gallinula angulata*	5	2	3	3	2	3	ZONE-I
Redknobbed Coot *Fulica cristata*	5	3	3	1	1	2	
Finfoot *Podica senegalensis*		3	2	2	1	1	ZONE-I
Crowned Crane *Balearica regulorum*		4	1	3	1	2	ZONE-I
Wattled Crane *Grus carunculata*		4	1	3	1	1	ZONE-I
African Jacana *Actophilornis africanus*		2	2	5	1	1	ZONE-I
Lesser Jacana *Microparra capensis*		1	2	5	1	1	ZONE-I
Painted Snipe *Rostratula benghalensis*		2	2	3	1	2	
Ringed Plover *Charadrius hiaticula*	6	1	2	3	2	3	
Whitefronted Sandplover *Charadrius marginatus*	6	1	2	3	1	1	
Chestnutbanded Sandplover *Charadrius pallidus*	6	1	2	3	1	2	
Threebanded Sandplover *Charadrius tricollaris*	6	1	2	3	1	1	
Grey Plover *Pluvialis squatarola*	6	2	2	3	2	3	
Blacksmith Plover *Vanellus armatus*	6	2	2	3	1	2	
Whitecrowned Plover *Vanellus albiceps*	6	2	2	3	1	3	ZONE-Ib
Wattled Plover *Vanellus senegallus*	6	2	2	3	1	1	
Longtoed Plover *Vanellus crassirostris*	6	2	2	3	1	1	

Great Snipe Gallinago media	7	2	2	3	2	3	ZONE-I
Ethiopian Snipe Gallinago nigripennis	7	2	2	3	1	1	
Curlew Sandpiper Calidris ferruginea	7	1	2	3	2	3	
Pectoral Sandpiper Calidris melanotos	7	1	2	3	2	2	
Little Stint Calidris minuta	7	1	2	3	2	3	
Broadbilled Sandpiper Limicola falcinellus	7	1	2	3	2	3	
Ruff Philomacnus pugnax	7	2	2	3	2	3	
Terek Sandpiper Xenus cinereus	7	1	2	3	2	3	
Common Sandpiper Tringa hypoleucos	7	1	2	3	2	3	
Green Sandpiper Tringa ochropus	7	2	2	3	2	3	
Marsh Sandpiper Tringa stagnatilis	7	1	2	3	2	3	
Greenshank Tringa nebularia	7	2	2	3	2	3	
Wood Sandpiper Tringa glareola	7	1	2	3	2	3	
Bartailed Godwit Limosa lapponica	7	2	2	3	2	3	
Curlew Numenius arquata	7	3	2	3	2	3	
Whimbrel Numenius phaeopus	7	3	2	3	2	3	
Avocet Recurvirostra avosetta		2	2	3	1	2	
Stilt Himantopus himantopus		2	2	3	1	2	
Water Dikkop Burhinus vermiculatus		2	2	3	1	1	
Redwinged Pratincole Glareola pratincola		1	2	3	1	3	
Whitecollared Pratincole Glareola nuchalis		1	2	3	1	3	ZONE-Ib
Southern Blackbacked Gull Larus dominicanus	8	3	2	3	1	2	
Lesser Blackbacked Gull Larus fuscus	8	2	2	2	1	2	ZONE-Ib
Greyheaded Gull Larus cirrocephalus	8	2	2	3	1	2	
Caspian Tern Hydroprogne caspia	8	3	1	4	1	1	
Gullbilled Tern Gelochelidon nilotica	8	2	2	4	1	2	ZONE-Ib
Whitewinged Black Tern Chlidonias leucopterus	8	1	2	4	2	3	
Whiskered Tern Chlidonias hybridus	8	2	1	4	1	2	
Skimmer Rynchops flavirostris		2	1	4	1	1	
Black Coucal Centropus bengalensis		2	2	6	1	3	
Copperytailed Coucal Centropus cupreicaudus		2	1	6	1	1	ZONE-Ib
Whitebrowed Coucal Centropus superciliosus		2	1	3	1	1	ZONE-I

Grass Owl Tyto capensis		3	1	6	1	1	ZONE-I
Marsh Owl Asio capensis		2	1	6	1	1	ZONE-I
Fishing Owl Scotopelia peli		3	1	4	1	1	ZONE-I
Natal Nightjar Caprimulgus natalensis		1	2	6	1	1	
Pied Kingfisher Ceryle rudis	9	2	1	4	1	2	
Giant Kingfisher Ceryle maxima	9	2	1	4	1	2	
Halfcollared Kingfisher Alcedo semitorquata	9	1	1	4	1	1	ZONE-I
Malachite Kingfisher Alcedo cristata	9	1	2	4	1	1	
Mangrove Kingfisher Halcyon senegaloides	9	2	1	4	2	3	
European Sandmartin Riparia riparia		1	2	6	2	3	
African Sandmartin Riparia paludicola		1	2	6	1	2	
Cape Reed Warbler Acrocephalus gracilirostris	10	1	2	6	1	1	
Rufous Reed Warbler Acrocephalus rufescens	10	1	2	6	1	1	ZONE-Ib
African Marsh Warbler Acrocephalus baeticatus	10	1	2	6	2	3	
European Sedge Warbler Acrocephalus schoenobaenus	10	1	2	6	2	3	
African Sedge Warbler Bradypterus baboecala	10	1	2	6	1	1	ZONE-I
Fantailed Warbler Schoenicola brevirostris	10	1	2	6	1	3	
Moustached Warbler Melocichla mentalis	10	1	2	6	1	1	ZONE-Ib
Palecrowned Cloud Cisticola Cisticola brunnescens	10	1	2	6	1	1	
Shortwinged Cisticola Cisticola brachyptera	10	1	2	6	1	1	ZONE-Ib
Blackbacked Cisticola Cisticola galactotes	10	1	2	6	1	1	
Chirping Cisticola Cisticola pipiens	10	1	2	6	1	1	ZONE-Ib
Le Vaillant's Cisticola Cisticola tinniens	10	1	2	6	1	1	
Yellow Warbler Chloropeta natalensis	10	1	2	6	1	1	
African Pied Wagtail Motacilla aguimp	11	1	2	6	1	2	
Cape Wagtail Motacilla capensis	11	1	2	6	1	2	
Longtailed Wagtail Motacilla clara	11	1	2	6	1	1	
Yellowbreasted Pipit Anthus chloris	11	1	2	6	1	3	ZONE-Ia
Yellowthroated Longclaw Macronyx croceus	11	1	2	6	1	1	
Pinkthroated Longclaw Macronyx ameliae	11	1	2	6	1	1	
West African Boubou Laniarius bicolor		1	2	6	1	1	ZONE-Ib
Coppery Sunbird Nectarinia cuprea		1	2	6	1	2	ZONE-Ib

Yellow Weaver *Ploceus subaureus*	12 1 3 5 1 1	
Golden Weaver *Ploceus xanthops*	12 1 3 5 1 1	
Brownthroated Golden Weaver *Ploceus xanthopterus*	12 1 3 5 1 1	ZONE-Ib
Masked Weaver *Ploceus velatus*	12 1 3 5 1 1	
Thickbilled Weaver *Amblyospiza albifrons*	12 1 3 5 1 2	
Redheaded Quelea *Quelea erythrops*	12 1 3 5 1 2?	
Red Bishop *Euplectes orix*	12 1 3 5 1 1	
Cape Widow *Euplectes capensis*	12 1 3 5 1 1	
Golden Bishop *Euplectes afer*	12 1 3 5 1 2	ZONE-I
Yellowbacked Widow *Euplectes macrourus*	12 1 3 5 1 1	ZONE-Ib
Redshouldered Widow *Euplectes axillaris*	12 1 3 5 1 1	
Orangebreasted Waxbill *Sporaegintnus subflavus*	12 1 3 5 1 1	
Common Waxbill *Estrilda astrild*	12 1 3 5 1 2	
Quail Finch *Ortygospiza atricollis*	12 1 3 5 1 2	
Locust Finch *Ortygospiza locustella*	12 1 3 5 1 2	ZONE-Ib
Pintailed Whydah *Vidua macroura*	12 1 3 5 1 2	

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[a] Guild types, and [c] guild codes as in Table 2.1.

[b] 1 = purely local movements; 2 = irregular-opportunistic movements, sometimes over great distances; 3 = regular and/or great distance movements.

? = uncertain wether their mobility score is 2 or 3.

Appendix 2.2. Results of the southern African waterbird cluster analyses showing numbers of dendrograms terminal points and quadrats which they comprise, as synthesized in Fig. 2.4

Resident cluster		Migrant cluster	
Terminal points	Quadrat numbers	Terminal points	Quadrat numbers
1:	16,33,48,114	1:	9,16,29,33,34,37,48,52,58,69,82-84,86,93,97-99,114,124,143,145,146,158,159,162,182,183,192,200
2:	106	2:	85
3:	124,140,155	3:	20
4:	34,85,86,98-100,158	4:	96
5:	37,38	5:	40,60,74
6:	84,130-132	6:	130
7:	29,68,81,95,125,145-147 159,161	7:	129,131,132
8:	52	8:	42,95,125
9:	47,129	9:	197,206,207,213,214
10:	10,28,49,51,64,67,69,70,82,83,93,96,97,108,111,113,127,143,183,199,200	10:	67,111
11:	207	11:	73,141
12:	197,206,213,214	12:	28,64,106,108,157,170,171,199
13:	43	13:	46,75,76,92
14:	54,116	14:	107
15:	75,76,90,91	15:	91
16:	55,56,72	16:	202,210
17:	15,30,184,193	17:	10,49
18:	73,115	18:	47,94
19:	9,11,12,17	19:	113,127
20:	39,40	20:	155
21:	141,182,191	21:	147,160
22:	160,162		

23: 65,66,78,80,94,110,112,126,128,142,144,157,170-172,192,194,198,201-204,208-210

24: 26,41,42,58,59

25: 44,61

26: 46,92,107,122,123

27: 19,20

28: 3,4,7,8,62

29: 1,2,5,23,24,60,74

30: 13,14,31,32,50,79,109

31: 77,156,169

32: 18

33: 21,22,35,36,53,71

34: 133,148,153,216

35: 6,25,57

36: 27,45,63,87-89,101-105,117-121,134-139,149,150-152,154,163-168,173-181,185-190,195,196,205,211,212,215

22: 191

23: 17,19,44

24: 110

25: 30,54,70,100,115

26: 68,116,161,198

27: 51

28: 126

29: 109,208

30: 203,204

31: 148,173,174,185

32: 172,194,209

33: 90,122,123

34: 21,22,35,36,53,55,56,71,72

35: 13,18

36: 11,12,59,61,66,80,87-89,101-105,117,119,120,133,137,138,167,189

37: 1,2,5,6,14,15,23-27,31,32,38,39,41,45,50,57,63,65,77-79,112,118,121,128,134-136,139,144,149,150-154,163-166,168,169,175-181,186-188,190,195,196,205,211,212,215

38: 3,4,7,8,43,62,81,140,142,153,156,184,193,201,216

CHAPTER 3. Monthly and seasonal changes in the aquatic avifauna of Rondevlei Bird Sanctuary (Cape Province, South Africa)

Since many African waterbird species depend on dramatically fluctuating, often ephemerally superabundant, resources, they are characteristically highly mobile and opportunistic in their utilisation of aquatic ecosystems (Chapters 1 and 2). Moreover, dynamic local natural (e.g. heavy and unpredictable rainfall in sub-desertic catchment areas) and man-induced (e.g. artificially regulated impoundment regimes) changes in the availability of surface water affect the availability of these resources. Therefore, it is necessary to put broad scale studies of distribution and diversity of waterbirds (e.g. Reichholf 1975, Chapters 1 and 2) into a biologically meaningful context by estimating seasonal and between-year variation in waterbird community structure at representative aquatic ecosystems.

In this chapter, I analyse 12 years of monthly count data for waterbirds at Rondevlei Bird Sanctuary, an important waterbird reserve in the southwestern Cape Province, South Africa. Short-term studies, e.g. Banks (1980) and Chapters 4 and 5, suggest that the fluctuating environment at Rondevlei causes periodic variation in waterbird utilisation patterns. The aims of this study are to determine if there is long-term regular, monthly and/or year-to-year variation in waterbird diversity (number of species) and abundance at Rondevlei, and to relate any patterns found to variation in abiotic factors (e.g. precipitation, temperature, water depth) at the Sanctuary.

Study area and methods

Study area

Rondevlei Bird Sanctuary ($34^0 04'S$ $18^0 30'E$) is a 'coastal vlei' (flattish expanded stretch of river with marshy vegetation and seasonal standing water), a relatively common South African aquatic biotope (Noble & Hemens 1978). See Middlemiss (1974), Banks (1980) and Chapter 5 for a more detailed discussion of Rondevlei and its environs. The Sanctuary is an important nature reserve which provides food, shelter and/or breeding grounds for large populations of many waterbird species (Middlemiss 1974). The conservation importance of Rondevlei is enhanced by its location, since it is the only protected, large aquatic biotope amidst the highly developed suburbs of Cape Town.

The results of Banks' (1980) unpublished 13-month study of Rondevlei's waterbird community suggest that the seasonally fluctuating water levels at the Sanctuary have profound effects on its waterbird diversity (number of species) and abundance. More particularly, she found that, under high water depth conditions (> 4.45 m a.s.l. as measured at the Sanctuary's water depth gauge), the availability of very shallow water (< 15 cm) and mud habitats is greatly diminished (Fig. 3.1), leading to a decrease in the diversity and abundance of waterbirds dependent on these habitats, primarily waders. Under relatively low vlei depth conditions (< 4.45 m a.s.l.), the availability of these habitats increases dramatically (Fig. 3.1) at the expense of deep water (> 30 cm deep) habitat, which is used primarily by waterbirds which obtain their food by diving (e.g. Dabchick Tachybaptus ruficollis and Redeyed Pochard Netta erythrophthalma).

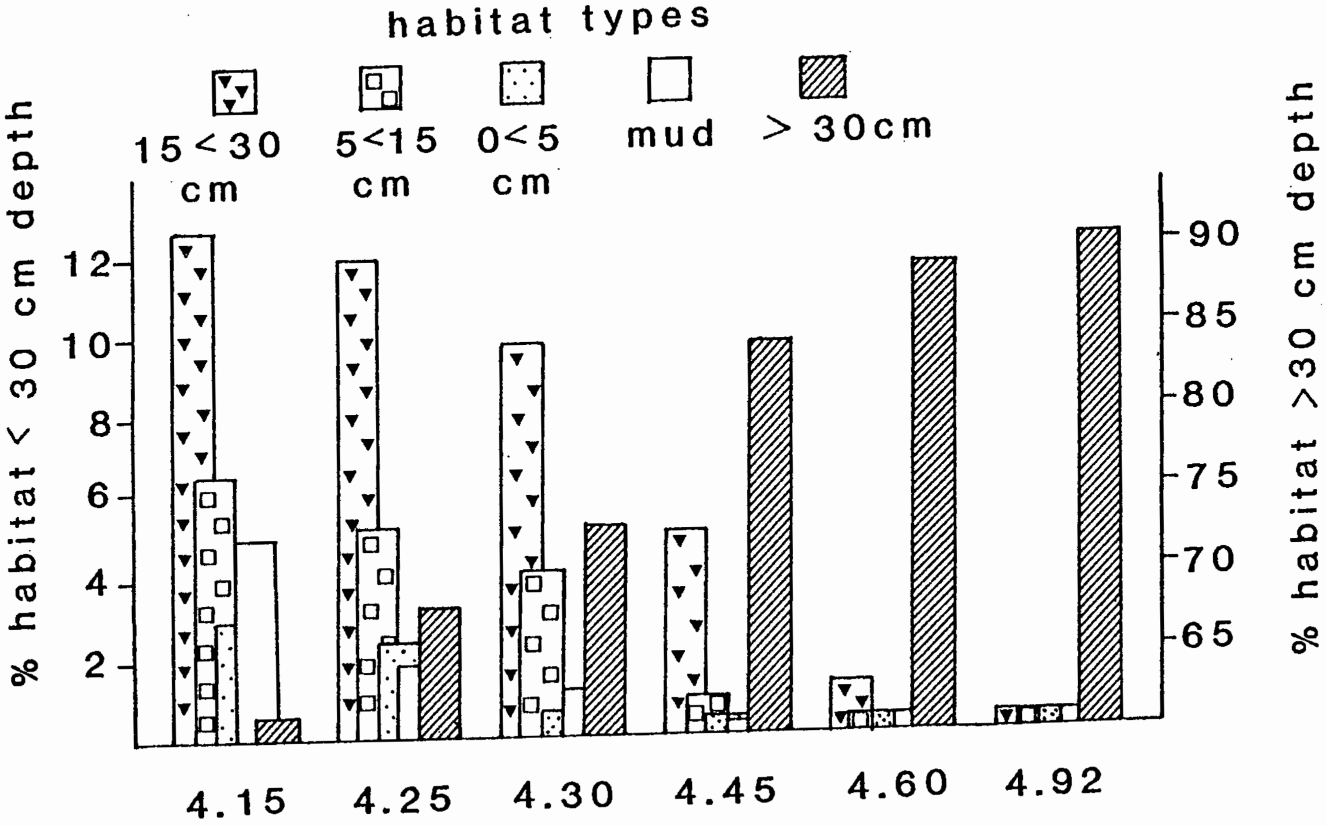

Fig. 3.1. Availability of a selected number of water depth and mud habitats, at different water levels at Rondevlei [after Banks (1980)].

Data base

The data base for this study is 130 monthly counts for 27 waterbird species (Table 3.1, Appendix 3.1) and abiotic environmental data (Table 3.2, Appendix 3.2) collected by Rondevlei's wardens between 1965 and 1976. In order to identify possible lag effects of environmental variables, abiotic data for the month immediately preceding each bird count were also analysed. The waterbird species studied include resident and both Palaearctic and intra-African migrant species which feed at the Sanctuary, and encompass a broad range of body mass, trophic and foraging behaviour guilds (Table 3.1). The study period includes the maximum climatic variation experienced at Rondevlei (Middlemiss 1974), encompassing months of relatively low, high and normal temperature, rainfall and water depth (Appendix 3.2).

Numerical methods

Cluster analysis (Field & McFarlane 1968) and multidimensional scaling (Shepard 1980) were used to identify patterns of similarity between the study months in terms of waterbird community structure. The Bray & Curtis (1957) measure of similarity and a group average sorting method (Lance & Williams 1967) were used in the cluster analysis. Cluster analysis allows the detection of hierarchical patterns of similarity (i.e. grouping patterns), whereas multidimensional scaling is more suitable for detecting possible gradients within and between clusters (Field, Clarke & Warwick 1982). Multidimensional scaling is thus a heuristic aid in determining possible gradient effects of abiotic factors on waterbird utilisation patterns. Waterbird and environmental variables which characterize groups of months

Table 3.1. Waterbird species, abbreviations, body mass and guild information, as analysed in this study

Waterbird species	Abbreviation	Mass	Guilds@			
		(in g)	Body mass	Diet	Foraging behaviour	Status
Dabchick *Tachybaptus ruficollis*	DABCIK	187	1	2	2	1
White Pelican *Pelecanus onocrotalus*	WPEL	10500	3	1	1	1
Reed Cormorant *Phalacrocorax africanus*	RECORM	692	2	1	2	1
Grey Heron *Ardea cinerea*	GRHERN	1440	3	1	3	1
Little Egret *Egretta garzetta*	LITEGR	500	2	1	3	1
Yellowbilled Egret *Egretta intermedia*	YBLEGR	500	2	2	3	1
Sacred Ibis *Threskiornis aethiopicus*	SIBIS	1586	3	2	3	1
Spoonbill *Platalea alba*	SPOONB	1790	3	2	3	1
Greater Flamingo *Phoenicopterus ruber*	GRFLAM	3400	3	2	3	1
Lesser Flamingo *Phoeniconaias minor*	LEFLAM	1900	3	3	3	1
Spurwing Goose *Plectropterus gambensis*	SPWGOS	2725	3	3	3	1
Egyptian Goose *Alophochen aegyptiacus*	EGYGOS	2130	3	3	3	1
Cape Shoveller *Anas smithii*	CPSHOV	661	2	2	1	1
Yellowbilled Duck *Anas undulata*	YBDUCK	992	2	3	1	1
Redbill Teal *Anas erythrorhyncha*	RBTEAL	473	2	3	1	1
Cape Teal *Anas capensis*	CPTEAL	447	2	2	1	1
Fulvous Whistling Duck *Dendrocygna bicolor*	FWISDK	800	2	3	1	1

Redeyed Pochard *Netta erythrophtalma*	REPOCH	772	2	3	2	2
Maccoa Duck *Oxyura maccoa*	MACCDK	544	2	2	2	1
Moorhen *Gallinula chloropus*	MOORHN	295	1	2	1	1
Redknobbed Coot *Fulica cristata*	RKCOOT	844	2	3	1	1
Curlew Sandpiper *Calidris ferruginea*	CSPPR	56	1	2	4	2
Little Stint *Calidris minuta*	LSTINT	24	1	2	4	2
Ruff *Philomachus pugnax*	RUFF	87	1	2	4	2
Avocet *Recurvirostra avosetta*	AVOCT	324	1	2	4	2
Stilt *Himantopus himantopus*	STILT	167	1	2	4	1
Whitewinged Black Tern *Chlidonias leucopterus*	WWBTRN	65	1	2		2

@ Body mass 1, 2, 3 = < 400g, > 400g <=1200g, > 1200g. Diet 1, 2, 3 = prevalently vertebrate, invertebrate, plant food. Foraging behaviour 1, 2, 3, 4 = swimming, diving, large pecker, small pecker. Status 1, 2 = resident, migrant.

Table 3.2. Measures of waterbird total and guild diversity (DIV) and abundance (AB), and of environmental variation analysed in this study; their abbreviations for current and preceding (PR) months (see text and Table 3.1 for explanation)

Abbreviations	Description
Waterbirds	
TOT-DIV	total number of waterbird species
RES-DIV	number of resident waterbird species
MIG-DIV	number of migrant waterbird species
TOT-AB	total number of waterbirds
RES-AB	number of resident waterbirds
MIG-AB	number of migrant waterbirds
BM1-AB	number of body mass class 1 waterbirds
BM2-AB	number of body mass class 2 waterbirds
BM3-AB	number of body mass class 3 waterbirds
DV-AB	number of prevalently vertebrate eating waterbirds
DI-AB	number of prevalently invertebrate eating waterbirds
DH-AB	number of prevalently plant eating waterbirds
FS-AB	number of waterbirds which obtain food by swimming
FD-AB	number of waterbirds which obtain food by diving
FBP-AB	number of big pecker waterbirds
FSP-AB	number of small pecker waterbirds
Environment	
RF / PR	Sanctuary total monthly rainfall (in mm)
WL / PR	mean monthly water level (in m a.s.l.) as measured at the Sanctuary's water depth gauge
WT / PR	mean monthly water temperature (in ^{o}C)
TMAX / PR	mean monthly maximum ambient temperature (in ^{o}C)
TMIN / PR	mean monthly minimum ambient temperature (in ^{o}C)

resulting from cluster analysis were identified by comparing each cluster with the remaining months using one-way analysis of variance (BMDP-P7D; Dixon 1983). The correlation analysis inbuilt in BMDP-P7D was used to identify one-to-one relationships between environmental and waterbird variables.

Results

Patterns of waterbird utilisation

The cluster and multidimensional scaling analyses (Fig. 3.2a and b) divide the study months into two major clusters, A and D. Cluster A consists primarily of austral winter-spring months (July-November) and cluster D of summer-autumn months (January-April). Cluster D is characterized by relatively high waterbird species diversity and abundance, particularly of species which forage in shallow water, and by relativaly low (though increasing) rainfall, normal (but decreasing) water level, and high temperature conditions. Cluster A is characterized by low waterbird diversity and abundance (particularly in species which forage in shallow water, e.g. waders), high water levels, normal (but decreasing) rainfall and low (but increasing) ambient/water temperature.

Cluster C (May-June/July) is transitional between clusters D and A. Clusters B, E, F and G comprise groups of months with generally low waterbird diversity. The results of the analyses of variance (Table 3.3) and the month-cluster's relative positions in Fig. 3.2b suggest that environmental factors which influence waterbird community structure at Rondevlei include: ambient and water temperature, rainfall and water level. Month-clusters in the upper right side of Fig. 3.2b (e.g. B and F) tended to have

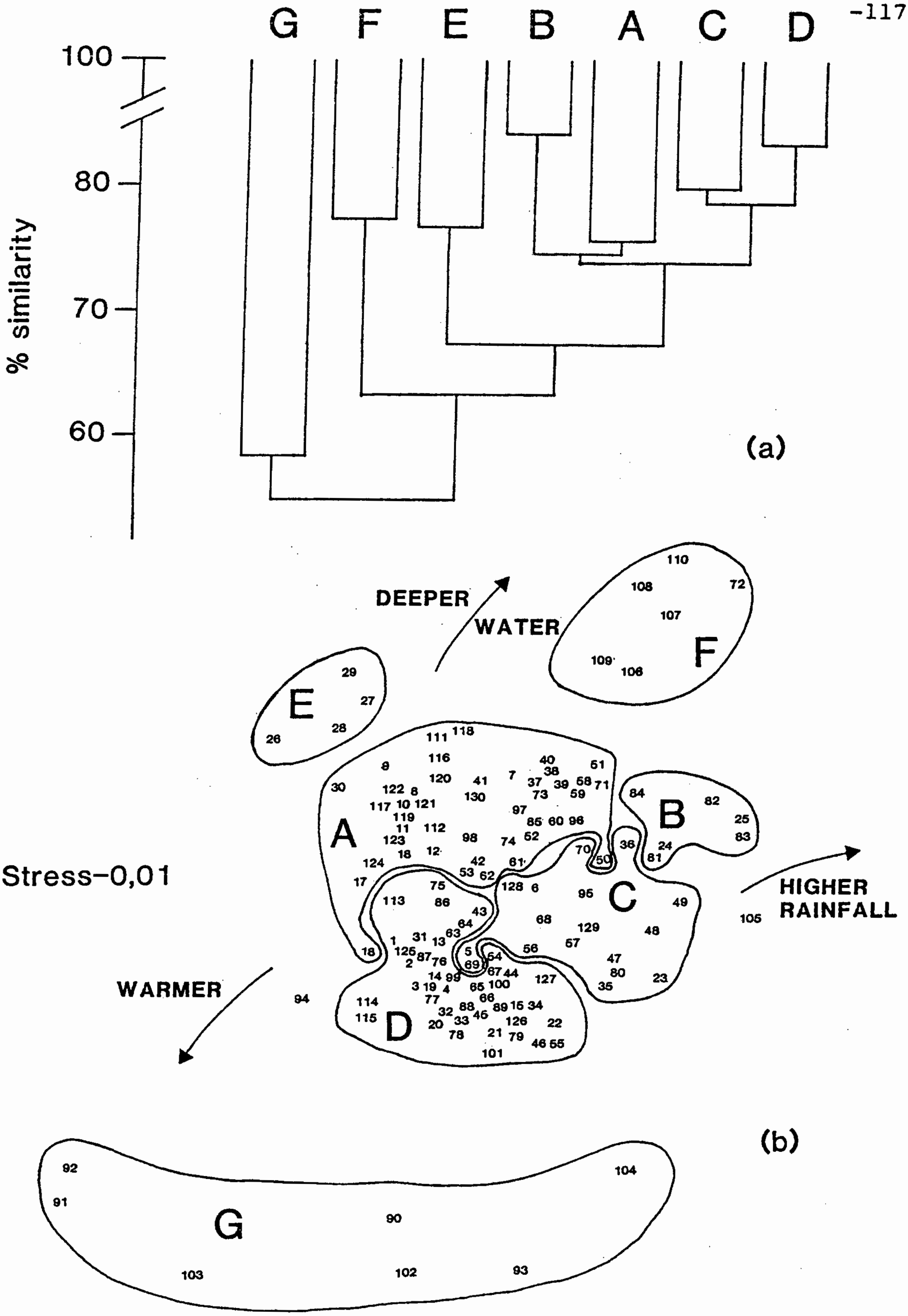

Fig. 3.2. Patterns of waterbird Sanctuary utilisation during 130 months reflected by: a) cluster analysis, and b) multidimensional scaling. See Appendix 3.1 for information concerning month codes (1-130), and the text for information on month-cluster codes (A-G).

Table 3.3. Waterbird total abundance and diversity statistics for month-clusters in Figs 3.3a & b. Significant results of the analysis of variance between month-clusters in terms of diversity/abundance measures of waterbird species and guilds, and of environmental diversity

	Month clusters						
	A	B	C	D	E	F	G
Waterbird mean total abundance @	1325	1191	1090	2209	1381	494	1781
S.D.	544	412	610	836	786	346	2874
C.V.	0.41	0.35	0.56	0.38	0.57	0.70	1.61
Waterbird mean diversity	19	17	20	24	16	13	17
S.D.	2.43	2.23	2.44	1.14	1.00	1.94	3.01
C.V.	0.13	0.13	0.12	0.05	0.06	0.15	0.18
Waterbird species							
DABCIK				(+) *	(-) NA		(-) **
WPEL				(+) ***		(-) *	(-) *
RECORM		(-) *		(+) ***		(-) **	(-) *
GRHERN	(-) ***			(+) ***	(-) NA	(-) **	
LITEGR							
YBEGR							
SIBIS						(-) NA	
SPOONB				(+) *			
GRFLAM		(+) *		(+) **		(-) *	
LEFLAM	(-) **	(+) ***			(-) NA		
SPWGOS	(-) ***		(+) *	(+) ***		(-) *	
EGYGOS	(-) *		(-) *	(+) ***			
CPSHOV		(-) *	(-) *	(+) **			(-) *
YBDUCK				(+) ***			
RBTEAL	(+) **				(-) NA		
FWISDK					(-) NA	(-) NA	(-) NA
REPOCH			(-) *		(+) ***		(-) NA
MACCDK					(+) ***	(-) NA	(-) NA
MOORHN			(+) **	(+) *	(-) NA		(-) **
RKCOOT			(-) *	(+) **			(-) *
CSNPPR	(-) ***			(+) ***			(+) **
LSTINT	(-) ***	(-) NA		(+) ***	(-) NA	(-) NA	(+) ***
RUFF	(-) ***	(-) NA		(+) ***	(-) NA	(-) NA	
AVOCT	(-) ***		(+) **	(+) ***	(-) NA	(-) NA	
STILT	(-) ***		(+) **	(+) ***		(-) *	
WWBTRN		(-) NA				(-) NA	(+) ***

Waterbird guilds							
TOT-AB	(-) *		(-) *	(+) ***		(-) **	
RES-AB			(-) **	(+) ***		(-) **	(-) ***
MIG-AB	(-) **			(+) *			(+) ***
BM1-AB	(-) **			(+) *			(+) ***
BM2-AB		(-) **	(-) **	(+) ***			(-) **
BM3-AB	(-) *	(-) ***		(+) **		(-) *	
DV-AB				(+) ***		(-) *	
DI-AB	(-) *			(+) ***		(-) *	(+) *
FS-AB		(-) **	(-) *	(+) ***			(-) ***
FD-AB		(-) *	(-)		(+) ***		(-) *
FBP-AB		(-) ***		(+) **		(-) *	
FSP-AB	(-) ***			(+) ***			(+) *
TOT-DIV	(-) *	(-) *		(+) ***	(-) **	(-) ***	(-) **
RES-DIV				(+) ***	(-) **	(-) ***	(-) ***
MIG-DIV	(-) ***	(-) ***		(+) ***	(-) *	(-) ***	
Environment							
RF			(+) **	(-) ***		(+) *	
RF-PR	(+) *			(-) ***		(+) ***	
WL	(+) ***		(-) **	(-) ***	(+) **	(+) ***	(-) ***
WL-PR	(+) ***	(-) *	(-) ***		(+) *	(+) **	(-) ***
WT	(-) *	(-) ***	(-) ***	(+) ***			
WT-PR	(-) ***	(-) **		(+) ***	(-) *	(-) **	(+) **
TMAX		(-) **	(-) ***	(+) ***		(-) *	
TMAX-PR	(-) ***	(-) *		(+) ***		(-) **	(+) **
TMIN		(-) **	(-) ***	(+) ***		(-) *	
TMIN-PR	(-) ***	(-) **		(+) ***	(-) *	(-) **	(+) *

@ S.D. = standard deviation, C.V. = coefficient of variation; other abbreviations as in Tables 3.1 & 3.2; significantly over- (+) and under- (-) represented at the P <= 0.05 (*), P <= 0.01 (**), and P <= 0.001 (***) levels; NA = zero counts within the cluster under study.

higher rainfall and lower temperatures than those on the lower left side (e.g. D and G). Month-clusters at or near the top of this figure (e.g. A, B, E and F) had deeper water than those at the bottom (e.g. D and G). This pattern is particularly highlighted by the positions of atypical months in Fig. 3.2b in terms of one or more environmental conditions. For example, December 1966 (month no. 18 in Fig. 3.2b and Appendix 3.2), although typical in water level and rainfall, had abnormally high ambient temperature. Thus, although it falls within cluster A, it is positioned closer to the normally warmer months which comprise cluster D. May 1975 (month no. 116), which had an abnormally high water level, is within cluster A rather than D. Conversely, November 1972 (month no. 86), which had a low water level, is in cluster D rather than A. April 1973 (month no. 91), which had relatively high water and ambient temperature, is in cluster G rather than D. Conversely, August 1974 (month no. 107) which falls within cluster F rather than A, had relatively high rainfall.

Waterbird diversity/abundance and environmental correlations

In general, waterbird diversity and abundance are positively correlated with ambient and water temperature and negatively correlated with rainfall (especially values for the previous month) and water level (Table 3.4). The few species whose abundance is positively correlated with water level (e.g. Cape Shoveller <u>Anas</u> <u>smithii</u> and Redeyed Pochard) belong to the swimmer and diver guilds, and are more strongly correlated with water level conditions in the previous month. However, examination of Fig. 3.3 shows that the correlation pattern between waterbird and environmental variables is complex. The greatest increase in

Table 3.4. Correlations between waterbird and environmental variables

	RF	RF-PR	WL	WL-PR	WT	WT-PR	TMAX	TMAX-PR	TMIN	TMIN-PR
[@]	[*]									
RF-PR	0.37									
WL	0.15	0.47								
WL-PR	-0.18	0.16	0.83							
WT	-0.67	-0.65	-0.32	0.11						
WT-PR	-0.43	-0.68	-0.66	-0.30	0.82					
MAX	-0.64	-0.63	-0.28	0.10	0.89	0.73				
MAX-PR	-0.43	-0.66	-0.63	-0.27	0.76	0.90	0.73			
MIN	-0.59	-0.67	-0.26	0.13	0.92	0.79	0.91	0.76		
MIN-PR	-0.46	-0.61	-0.61	-0.25	0.79	0.93	0.75	0.91	0.80	
DABCIK	-0.10	-0.05	0.16	0.22	0.11	0.07	0.11	0.08	0.14	0.10
WPEL	-0.22	-0.22	-0.09	0.01	0.27	0.33	0.31	0.33	0.31	0.37
RECORM	-0.14	-0.27	-0.10	0.02	0.22	0.24	0.32	0.33	0.24	0.22
GRHERN	-0.12	-0.34	-0.37	-0.28	0.31	0.48	0.32	0.46	0.32	0.49
LITEGR	-0.10	-0.08	0.05	0.11	0.09	0.03	0.13	0.08	0.10	0.05
YBLEGR	-0.12	-0.12	0.07	0.16	0.17	0.13	0.20	0.15	0.19	0.12
SIBIS	-0.09	-0.07	0.12	0.15	-0.01	-0.08	0.23	-0.01	0.05	-0.05
SPOONB	-0.15	-0.26	-0.22	-0.09	0.23	0.30	0.38	0.34	0.31	0.32
GRFLAM	-0.12	-0.14	-0.15	-0.12	0.10	0.09	0.18	0.18	0.09	0.11
LEFLAM	0.07	-0.04	-0.27	-0.32	-0.09	0.05	-0.06	0.06	-0.10	0.04
SPWGOS	-0.04	-0.25	-0.34	-0.27	0.17	0.41	0.14	0.36	0.20	0.40
EGYGOS	-0.20	-0.26	-0.22	-0.07	0.31	0.29	0.32	0.26	0.32	0.27
CPSHOV	-0.25	-0.19	0.16	0.31	0.38	0.24	0.32	0.16	0.39	0.23
YBDUCK	-0.04	-0.18	-0.10	0.00	0.32	0.30	0.21	0.25	0.27	0.27
RBTEAL	-0.16	-0.12	0.18	0.28	0.22	0.09	0.14	0.02	0.20	0.17
CPTEAL	0.14	0.09	0.15	-0.04	-0.27	-0.23	-0.24	-0.32	-0.27	-0.28
FWISDK	-0.06	-0.03	0.09	0.04	0.12	0.08	0.08	0.02	0.09	0.06
REPOCH	-0.18	-0.07	0.30	0.40	0.16	-0.05	0.14	-0.05	0.15	-0.07
MACCDK	0.03	0.06	0.23	0.23	-0.12	-0.20	-0.07	-0.15	-0.11	-0.20
MOORHN	-0.03	-0.08	-0.10	-0.10	-0.06	0.06	-0.03	0.06	-0.08	0.01
RKCOOT	-0.25	-0.21	0.15	0.31	0.35	0.21	0.30	0.28	0.34	0.24
CSNPPR	-0.12	-0.33	-0.52	-0.32	0.31	0.47	0.28	0.49	0.27	0.49
LSTINT	-0.09	-0.29	-0.65	-0.50	0.24	0.47	0.20	0.47	0.20	0.45
RUFF	-0.19	-0.30	-0.38	-0.20	0.38	0.46	0.34	0.42	0.36	0.45
AVOCT	-0.15	-0.30	-0.43	-0.23	0.30	0.47	0.27	0.43	0.28	0.47
STILT	-0.06	-0.27	-0.44	-0.36	0.14	0.34	0.11	0.37	0.09	0.34
WWBTRN	-0.15	-0.17	-0.19	-0.11	0.19	0.22	0.22	0.26	0.21	0.26
TOT-DIV	-0.32	-0.48	-0.35	-0.12	0.53	0.55	0.51	0.55	0.54	0.56
RES-DIV	-0.16	-0.30	-0.15	-0.04	0.26	0.27	0.26	0.28	0.29	0.28
MIG-DIV	-0.43	-0.56	-0.50	-0.18	0.70	0.73	0.66	0.72	0.67	0.74
TOT-AB	-0.35	-0.41	-0.21	0.01	0.51	0.48	0.51	0.53	0.50	0.51
RES-AB	-0.32	-0.33	0.02	0.20	0.45	0.34	0.44	0.38	0.44	0.35
MIG-AB	-0.17	-0.23	-0.32	-0.20	0.25	0.33	0.27	0.36	0.26	0.37
BM1-AB	-0.18	-0.24	-0.32	-0.20	0.26	0.34	0.27	0.37	0.26	0.38
BM2-AB	-0.31	-0.28	0.20	0.40	0.49	0.30	0.41	0.30	0.48	0.31
BM3-AB	-0.11	-0.18	-0.24	-0.21	0.10	0.16	0.20	0.23	0.10	0.17
DV-AB	-0.25	-0.31	-0.13	0.01	0.33	0.38	0.41	0.43	0.37	0.41
DI-AB	-0.28	-0.33	-0.29	-0.12	0.38	0.40	0.42	0.45	0.39	0.44
DH-AB	-0.24	-0.27	0.07	0.24	0.41	0.29	0.34	0.33	0.38	0.30
FS-AB	-0.31	-0.29	0.15	0.35	0.49	0.34	0.41	0.33	0.48	0.35
FD-AB	-0.22	-0.15	0.29	0.42	0.23	0.03	0.24	0.06	0.23	0.02
FBP-AB	-0.09	-0.16	-0.23	-0.21	0.08	0.12	0.17	0.20	0.07	0.13
FSP-AB	-0.16	-0.39	-0.66	-0.43	0.36	0.60	0.32	0.58	0.32	0.59

[@] Abbreviations as in Tables 3.1 & 3.2.

[*] P = 0.05, r = 0.18; P = 0.01, r = 0.23; P = 0.001, r = 0.29.

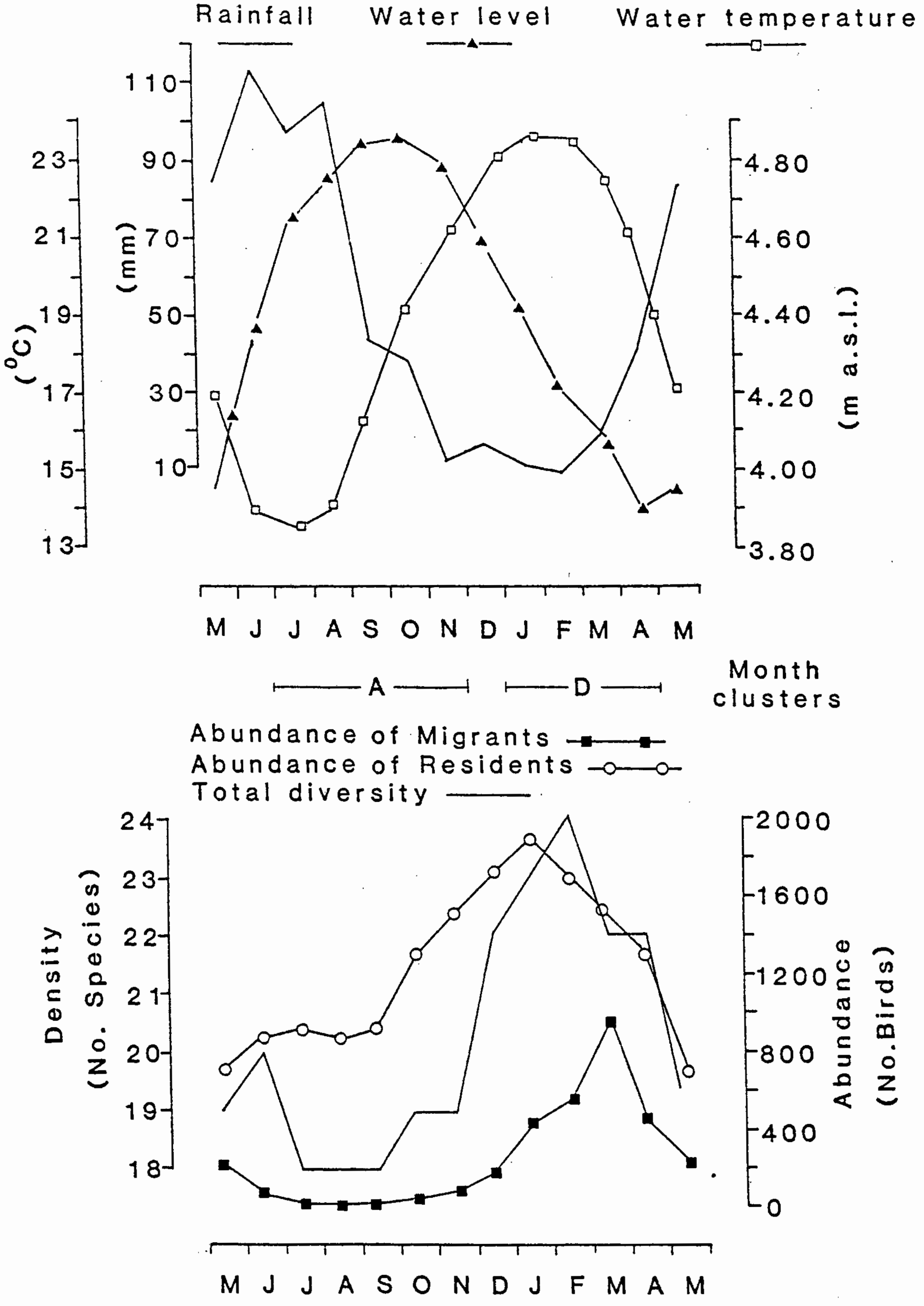

Fig. 3.3. Temporal relationship between monthly means for waterbird total diversity, resident and migrant abundance, and rainfall, water level and temperature. A and D = month clusters A and D in Fig. 3.2.

waterbird abundance occurs during November-March as water level is decreasing from relatively high values, and the abundance of resident waterbirds peaks in January (at the 4.45 m a.s.l. level), whereas migrant waterbird abundance peaks in March (at the 4.15 m a.s.l. level).

Discussion

Patterns of waterbird utilisation

Waterbird utilisation at Rondevlei shows a clear seasonal pattern (Figs 3.2 and 3.3). However, the Sanctuary's waterbird 'seasons' do not coincide precisely with traditional austral seasons (summer = November-February; winter = June-September). The January-April 'season' (D in Fig. 3.2 and Table 3.3) is characterized by high waterbird diversity and abundance for both residents and migrants. Banks (1980), in her short term study, also found high values for waterbird diversity/abundance at the Sanctuary during January-April and attributed these to increased availability of shallow water (< 30 cm) and mud habitat, due primarily to the effects of low water level. Strong positive correlations between Banks' (1980) and long-term monthly mean values for rainfall, water level, maximum and minimum ambient temperature, total waterbird abundance, and diversity ($r = 0.91, 0.93, 0.88, 0.89, 0.88, 0.73$; $P < 0.01$) indicate that a similar habitat availability hypothesis could explain waterbird diversity/abundance pattern in Rondevlei over the longer term.

Indirect supporting evidence of this habitat availability hypothesis is the fact that Palaearctic migrant waterbirds, although present in the southwestern Cape in October (Blaker & Winterbottom 1968; Pringle & Cooper 1977) do not come to Rondevlei in numbers until January-February (Appendix 3.1), when the water level at the vlei is low enough to allow a significant amount of shallow water habitat (Fig. 3.1, Appendix 3.2). Moreover, during the relatively warm January-April 'season', the 'quality' of the various habitats is improved by a proliferation of plant, invertebrate and vertebrate prey for waterbirds (Harrison 1958, 1962; Middlemiss 1974; Chapters 4-6).

Cluster A, the July-November waterbird 'season' is characterized by cool, deep water, conditions with a low availability of shallow water and mud habitats. Not unexpectedly, the primary reason for its low waterbird diversity/abundance values is the absence of migrants (Table 3.3).

The low waterbird diversity clusters (B, E, F and G in Figs 3.2a and 3.2b) represent extreme environmental conditions and usually low waterbird abundance (Table 3.3, Appendices 3.1 and 3.2). For example, in cluster E, the Red-eyed Pochard, Maccoa Duck _Oxyura maccoa_ and Yellowbilled Duck _Anas undulata_ are 'overrepresented', presumably exploiting the relatively deep water conditions at the vlei (high values for WL and WL-PR). Conversely, cluster B is characterized by months in two different years (June-July 1967 and June-September 1972) with low water level conditions, and high abundance values for Greater and Lesser Flamingos _Phoenicopterus ruber_ and _Phoeniconaias minor_. In months comprising cluster G (April-May 1973 and March-April 1974) there were persistent, extreme shallow water conditions. In fact, the vlei virtually dried out completely, and species which utilise shallow water/mud habitat, such as the Little Stint _Calidris minuta_, Curlew Sandpiper _C. ferruginea_ and Whitewinged Black Tern _Chlidonias leucopterus_ were among the few present in numbers. Cluster F comprises months with extremely low temperatures and high rainfall and water level conditions (July-November 1974, the highest rainfall season of the study period). Its low diversity/abundance and lack of characteristic species might therefore reflect the overall unsuitable conditions for the waterbird species investigated in this study.

Waterbird diversity/abundance and environmental correlations

The results of this study support Banks' (1980) primary conclusion, that the fluctuating water level at Rondevlei affects the waterbird community at the Sanctuary via its effects on habitat availability. However, they also indicate that there is a threshold-like relationship between waterbird diversity/abundance and water level. For example, only once water level drops below 4.45 m a.s.l. does the availability of shallow water and mud habitats increase dramatically (Fig. 3.1). The increased availability of these habitats is soon followed by an increase in the diversity/abundance of waders. Moreover, this study also suggests that relatively strong positive correlations found between water and ambient temperature and waterbird diversity/abundance, are presumably mediated through the effects of warmer conditions on the availability of a broad array of plant and animal food types (see below). The differential impact of water level and temperature on waterbird utilisation at Rondevlei, is perhaps best reflected by differences in the correlation pattern between members of the foraging and body mass guilds and environmental variables. The abundance of members of the medium mass (BM2-AB) and swimmer (FS-AB) guilds is more strongly correlated with temperature variables, whereas the abundance of small mass, wading waterbirds (BM1-AB and FSP-AB) is more strongly correlated with water level. This correlation pattern is consistent with the idea that the availability of habitat might be a primary limiting factor to the utilisation of 'shallow water' smaller waterbirds, and that of food to the 'warm, deeper water' waterbirds.

Rainfall

Rainfall affects waterbird diversity/abundance at Rondevlei primarily through the lag effect it has on water level. This lag relationship is illustrated by the significant positive correlation ($r = 0.47$; $P < 0.001$) between water level (WL) and rainfall for the preceding month (RF-PR) and the non-significant correlation ($r = 0.15$, $P > 0.05$) between WL and rainfall for the current month (RF) (Table 3.4). Moreover, the effects of rainfall on water level are cumulative and are typically associated with crossing the 90 mm 'threshold' (Fig. 3.3, Appendix 3.2).

Rainfall might also have another indirect effect on waterbird abundance at Rondevlei through its influence on waterbird prey. For example, rainfall is thought to trigger spawning of the Clawed Frog <u>Xenopus</u> <u>laevis</u> (Picker 1982), the commonest amphibian at Rondevlei (Middlemiss 1974). Clawed frog tadpoles might form an important component of the diet of the chicks of both the Reed Cormorant <u>Phalacrocorax</u> <u>africanus</u> (Middlemiss 1974) and Great White Pelican <u>Pelecanus</u> <u>onocrotalus</u> (J. Cooper pers. comm.; A. Guillet unpub. data).

Water level

As shown above, and by Banks (1980), the effect of water level on the aquatic avifauna at Rondevlei, appears to be mediated through its effects on the availability of shallow water (< 30 cm deep) and mud habitats. Kushlan (1978) also found a strong negative relationship between water level and waterbird habitat availability. Water level variation plays a major role in critical aspects of waterbird ecological fluctuations, such as variation in the availability of prey (Kushlan et al. 1975, Kushlan 1976); or foraging and/or nesting habitat (Whitfield & Blaber 1978, 1979a, 1979b).

The generally stronger positive correlations between the abundance of members of the swimmer guild (FS) (e.g. Redknobbed Coot *Fulica cristata*) and diver guild (FD) (e.g. Redeyed Pochard) with water level of previous months (WL-PR) probably reflect a lag effect in the variation of suitable foraging conditions in relatively deep water habitat. This could, for example, be the development/decay of flooded vegetation and its associated invertebrate fauna. The positive correlation between the abundance of members of the plant eater guild (DH-AB) with WL-PR and not with WL (current month water level) may also be due to such a lag effect. Shallow water habitat, on the other hand, is apparently suitable immediately as it becomes available, hence the relatively strong negative correlations between shallow water species and water level of the current month.

Temperature

Independent of its negative correlation with water level, the relevance of temperature to waterbird ecology in Rondevlei is probably mediated through its effects on both the crude and ecological density (sensu Kahl 1964) of a broad array of food types from small crustaceans to fish (Harrison 1958, 1962; Middlemiss 1974; Chapters 4-6). This is reflected in the relatively strong positive correlation of waterbird variables in general, and resident abundance in particular, with temperature variables (Fig. 3.3, Table 3.4).

Future research

Several other biotic and abiotic factors may also have a major impact on waterbird utilisation at Rondevlei. First, the high density of the exotic Common Carp _Cyprinus carpio_ at the vlei (Hamman et al. 1977) may affect the invertebrate prey community. One possible outcome of predation by carp is reduction of waterbird food resources both in the form of overall invertebrate biomass and submerged vegetation (Britton 1982). Indeed, Reichholf (1975) invokes competition between fish and waterbirds as being an important determinant of waterbird species diversity in South America. Since the Great White Pelican is the only predator at Rondevlei capable of taking large carp, both species at Rondevlei need to be studied to identify the roles each plays in that ecosystem. Additional attention should also be directed to interactive processes between turbidity and flooded vegetation which is an important component of Rondevlei's ecological fluctuations (Tschortner 1969; Banks 1980).

Appendix 3.1. Monthly counts statistics for waterbirds at Rondevlei between 1965-1976

Waterbird species	N	Mean	S.D.	S.E.	C.V.	Min.	Max.	Range
Tachybaptus ruficollis								
January	12	37.0	35.2	10.1	0.95	10	123	113
February	12	28.3	25.3	7.3	0.89	8	80	72
March	12	25.6	29.9	8.6	1.16	0	80	80
April	10	17.0	21.6	6.8	1.26	0	70	70
May	10	11.0	10.0	3.1	0.91	0	32	32
June	10	13.8	9.5	3.0	0.69	1	32	30
July	11	20.8	12.8	3.8	0.61	2	50	47
August	10	19.6	15.1	4.8	0.77	6	60	54
September	10	20.9	21.1	6.6	1.01	6	80	73
October	11	21.1	16.1	4.8	0.76	7	60	53
November	11	22.1	15.5	4.6	0.70	4	49	44
December	11	32.8	32.2	9.7	0.98	8	123	115
Pelecanus onocrotalus								
January	12	86.4	31.2	9.0	0.36	42	139	96
February	12	113.2	51.2	14.8	0.45	42	196	154
March	12	113.0	56.9	16.4	0.50	45	215	170
April	10	62.5	30.8	9.7	0.49	16	112	95
May	10	38.7	24.8	7.8	0.64	2	80	77
June	10	54.7	39.9	12.6	0.72	1	140	139
July	11	60.0	53.0	15.9	0.88	18	181	163
August	10	49.0	35.0	11.0	0.71	13	100	86
September	10	42.7	24.1	7.6	0.56	10	85	75
October	11	65.1	46.6	14.0	0.71	15	180	164
November	11	56.1	44.2	13.3	0.78	19	180	161
December	11	71.0	41.7	12.6	0.58	38	177	139
Phalacrocorax africanus								
January	12	43.1	28.3	8.1	0.65	9	113	104
February	12	37.2	24.5	7.0	0.65	3	85	81
March	12	32.2	26.2	7.5	0.81	5	85	79
April	10	31.3	23.6	7.4	0.75	5	85	79
May	10	23.7	25.2	7.9	1.06	1	85	83
June	10	22.2	24.4	7.7	1.09	6	85	78
July	11	21.4	26.7	8.0	1.24	1	85	84
August	10	17.1	19.8	6.2	1.15	2	66	64
September	10	13.8	18.2	5.7	1.32	0	60	60
October	11	23.5	29.6	8.9	1.25	0	100	100
November	11	35.5	32.2	9.7	0.90	0	100	100
December	11	48.1	36.2	10.9	0.75	8	115	107
Ardea cinerea								
January	12	8.4	3.2	0.9	0.38	3	12	9
February	12	11.0	6.0	1.7	0.54	2	24	21
March	12	13.3	7.4	2.1	0.55	3	30	27
April	10	11.7	4.7	1.4	0.40	4	18	14
May	10	7.6	4.0	1.2	0.53	2	15	13
June	10	7.2	3.9	1.2	0.54	2	15	13
July	11	5.4	3.6	1.0	0.65	2	15	13
August	10	3.3	2.5	0.8	0.75	0	8	8
September	10	3.3	2.7	0.8	0.82	1	8	7
October	11	4.5	2.9	0.8	0.64	1	10	9
November	11	4.8	3.3	1.0	0.70	0	10	10
December	11	4.3	2.8	0.8	0.66	1	10	9
Egretta garzetta								
January	12	6.2	8.7	2.5	1.41	1	30	29
February	12	10.7	12.9	3.7	1.20	1	40	39
March	12	7.8	8.4	2.4	1.07	1	29	28
April	10	4.3	3.3	1.0	0.75	1	11	10
May	10	2.9	2.6	0.8	0.90	0	8	8
June	10	2.0	1.6	0.5	0.79	0	6	6
July	11	0.8	1.1	0.3	1.35	0	3	3
August	10	5.5	14.9	4.7	2.72	0	48	48
September	10	9.1	25.0	7.9	2.75	0	80	80
October	11	8.6	16.6	5.0	1.93	0	55	55
November	11	7.2	12.9	3.9	1.79	0	43	43
December	11	5.9	8.6	2.6	1.45	0	30	30

Egretta intermedia								
January	12	11.9	27.9	8.0	2.33	1	100	99
February	12	8.1	13.7	3.9	1.68	0	50	50
March	12	5.6	5.1	1.4	0.91	0	15	15
April	10	3.1	2.4	0.7	0.78	0	7	7
May	10	2.7	2.6	0.8	0.96	0	8	8
June	10	3.0	3.4	1.0	1.12	0	8	8
July	11	0.8	1.6	0.5	1.98	0	5	5
August	10	2.7	5.4	1.7	1.97	0	14	14
September	10	4.5	9.5	3.0	2.10	0	30	30
October	11	5.0	8.7	2.6	1.71	0	30	30
November	11	6.5	8.5	2.5	1.31	0	30	30
December	11	6.9	8.0	2.4	1.16	1	30	28
Threskiornis aethiopicus								
January	12	1.2	1.4	0.4	1.13	0	4	4
February	12	1.5	1.2	0.3	0.79	0	3	3
March	12	2.1	1.6	0.4	0.77	0	5	5
April	10	1.2	1.0	0.3	0.86	0	3	3
May	10	1.6	2.9	0.9	1.82	0	9	9
June	10	1.4	2.5	0.8	1.79	0	7	7
July	11	2.1	3.3	1.0	1.59	0	10	10
August	10	2.0	2.8	0.8	1.38	0	8	8
September	10	4.1	5.8	1.8	1.42	0	16	16
October	11	7.2	13.4	4.0	1.86	0	40	40
November	11	6.2	17.8	5.3	2.86	0	60	60
December	11	8.3	22.2	6.7	2.65	0	75	75
Platalea alba								
January	12	6.5	6.0	1.7	0.92	0	16	16
February	12	9.7	9.0	2.6	0.93	1	30	29
March	12	9.1	7.0	2.0	0.77	1	24	23
April	10	5.4	3.5	1.1	0.64	1	13	12
May	10	5.7	7.7	2.4	1.36	0	27	27
June	10	2.9	2.2	0.7	0.75	0	6	6
July	11	1.5	1.8	0.5	1.21	0	5	5
August	10	2.4	3.9	1.2	1.61	0	11	11
September	10	1.8	5.1	1.6	2.79	0	16	16
October	11	2.3	4.3	1.3	1.84	0	11	11
November	11	5.7	15.5	4.6	2.72	0	52	52
December	11	6.2	11.1	3.3	1.78	0	38	38
Phoenicopterus ruber								
January	12	371.0	304.8	87.9	0.82	0	1040	1040
February	12	348.2	428.1	123.5	1.22	0	1200	1200
March	12	332.8	327.5	94.5	0.98	0	990	990
April	10	289.6	374.7	118.5	1.29	0	1099	1099
May	10	145.1	254.4	80.4	1.75	0	779	779
June	10	233.0	255.6	80.8	1.09	0	750	750
July	11	166.6	310.6	93.6	1.86	0	1041	1041
August	10	212.7	281.5	89.0	1.32	0	741	741
September	10	223.6	338.8	107.1	1.51	0	931	931
October	11	435.8	601.6	181.4	1.38	0	2000	2000
November	11	209.4	305.2	92.0	1.45	0	994	994
December	11	339.3	517.1	155.9	1.52	0	1520	1520
Phoeniconaias minor								
January	12	4.6	11.8	3.4	2.53	0	40	40
February	12	40.0	114.1	32.9	2.84	0	400	400
March	12	62.3	164.8	47.5	2.64	0	575	575
April	10	140.5	229.2	72.4	1.63	0	608	608
May	10	55.0	125.7	39.7	2.28	0	400	400
June	10	87.5	137.9	43.6	1.57	0	350	350
July	11	103.5	178.4	53.8	1.72	0	500	500
August	10	83.4	251.9	79.6	3.02	0	800	800
September	10	15.2	31.2	9.8	2.05	0	100	100
October	11	10.0	23.2	7.0	2.32	0	70	70
November	11	2.2	5.1	1.5	2.27	0	15	15
December	11	7.1	21.0	6.3	2.92	0	70	70

Plectropterus gambensis							
January	12	9.8	6.7	1.9	0.68	3	23	20
February	12	10.4	10.8	3.1	1.03	2	41	39
March	12	17.6	20.5	5.9	1.16	5	80	74
April	10	15.7	10.1	3.2	0.64	0	31	31
May	10	13.2	8.9	2.8	0.67	0	30	30
June	10	8.1	4.8	1.5	0.59	3	16	13
July	11	5.9	6.5	1.9	1.11	0	23	23
August	10	6.0	7.7	2.4	1.28	0	25	25
September	10	1.6	1.9	0.6	1.17	0	5	5
October	11	1.6	2.2	0.6	1.34	0	6	6
November	11	2.3	2.3	0.7	1.04	0	6	6
December	11	4.6	2.8	0.8	0.61	1	9	8
Alophochen aegyptiacus								
January	12	7.0	4.8	1.3	0.69	1	14	13
February	12	7.9	8.1	2.3	1.03	0	28	28
March	12	5.9	5.5	1.6	0.94	0	19	19
April	10	8.3	6.6	2.1	0.80	2	23	20
May	10	4.4	3.1	1.0	0.71	2	11	9
June	10	4.9	3.5	1.1	0.72	2	14	12
July	11	4.9	6.1	1.8	1.24	2	23	21
August	10	3.8	1.5	0.4	0.40	2	6	4
September	10	4.1	1.3	0.4	0.31	2	6	4
October	11	6.8	4.6	1.3	0.67	2	16	13
November	11	5.7	4.0	1.2	0.69	2	17	15
December	11	8.1	9.2	2.7	1.12	0	31	31
Anas smithii								
January	12	463.0	392.9	113.4	0.84	40	1250	1210
February	12	324.9	188.1	54.3	0.57	30	700	670
March	12	211.6	155.3	44.8	0.73	0	550	550
April	10	239.3	301.9	95.4	1.26	0	1000	1000
May	10	85.1	52.0	16.4	0.61	0	175	175
June	10	133.6	163.3	51.6	1.22	12	576	564
July	11	180.1	250.2	75.4	1.38	11	900	889
August	10	138.7	109.3	34.5	0.78	19	350	330
September	10	145.3	118.8	37.5	0.81	20	350	329
October	11	256.1	174.1	52.5	0.68	30	550	520
November	11	375.9	313.9	94.6	0.83	45	975	930
December	11	438.6	383.3	115.5	0.87	100	1500	1400
Anas undulata								
January	12	127.3	82.6	23.8	0.64	36	250	213
February	12	146.8	163.9	47.3	1.11	13	500	486
March	12	188.2	319.7	92.3	1.69	2	1000	998
April	10	72.0	93.2	29.4	1.29	0	300	300
May	10	83.6	85.7	27.1	1.02	0	250	250
June	10	51.5	41.8	13.2	0.81	2	135	133
July	11	55.8	53.5	16.1	0.95	20	202	182
August	10	47.6	47.6	15.0	0.99	9	150	141
September	10	41.5	37.1	11.7	0.89	10	140	130
October	11	62.9	77.5	23.3	1.23	10	250	240
November	11	76.2	73.4	22.1	0.96	20	250	230
December	11	74.3	52.4	15.8	0.70	8	175	167
Anas erythrorhyncha								
January	12	43.6	36.7	10.5	0.84	14	133	119
February	12	26.6	19.5	5.6	0.73	4	62	58
March	12	12.3	14.8	4.2	1.19	0	45	45
April	10	10.0	13.4	4.2	1.34	0	40	40
May	10	7.8	12.0	3.8	1.53	0	40	40
June	10	9.6	9.6	3.0	1.00	0	24	24
July	11	24.2	27.5	8.3	1.13	0	86	86
August	10	29.6	35.2	11.1	1.19	0	115	115
September	10	18.6	20.8	6.5	1.11	0	60	60
October	11	12.5	8.2	2.4	0.65	0	26	26
November	11	32.4	50.0	15.0	1.54	0	175	175
December	11	36.4	56.6	17.0	1.55	0	200	200

Anas capensis								
January	12	7.1	6.1	1.7	0.85	2	25	23
February	12	7.9	8.5	2.4	1.07	0	25	25
March	12	8.6	10.2	2.9	1.18	0	30	30
April	10	9.8	10.1	3.2	1.02	0	30	30
May	10	11.4	10.8	3.4	0.94	0	30	30
June	10	32.2	41.3	13.0	1.28	3	140	137
July	11	20.4	27.2	8.2	1.33	2	90	88
August	10	31.7	44.4	14.0	1.40	0	129	129
September	10	15.0	31.8	10.0	2.11	0	105	105
October	11	13.0	29.0	8.7	2.23	0	100	100
November	11	12.9	29.1	8.7	2.25	0	100	100
December	11	6.4	6.1	1.8	0.95	0	19	19
Dendrocygna bicolor								
January	12	1.6	2.8	0.8	1.77	0	8	8
February	12	1.0	3.0	0.8	2.91	0	10	10
March	12	1.1	4.0	1.1	3.46	0	14	14
April	10	0.0	0.0	0.0	0.00	0	0	0
May	10	0.0	0.0	0.0	0.00	0	0	0
June	10	1.5	4.4	1.3	2.93	0	14	14
July	10	0.1	0.3	0.1	3.16	0	1	1
August	10	0.3	1.1	0.3	3.16	0	3	3
September	10	0.9	1.6	0.5	1.84	0	5	5
October	11	0.5	1.0	0.3	1.72	0	2	2
November	11	0.3	0.9	0.2	2.54	0	3	3
December	11	1.4	2.5	0.7	1.70	0	7	7
Netta erythrophthalma								
January	12	84.2	108.4	31.3	1.28	10	388	378
February	12	47.7	66.3	19.1	1.39	4	233	229
March	12	6.0	6.1	1.7	1.01	0	17	17
April	10	6.9	6.9	2.1	1.00	0	20	20
May	10	5.2	5.8	1.8	1.11	0	15	15
June	10	8.0	8.4	2.6	1.04	0	20	20
July	10	21.2	22.5	7.1	1.06	0	65	65
August	10	31.7	27.3	8.6	0.86	0	80	80
September	10	72.4	86.7	27.4	1.19	4	270	266
October	11	107.8	159.3	48.0	1.47	2	450	448
November	11	116.0	134.7	40.6	1.16	6	450	444
December	11	67.1	61.6	18.5	0.91	0	225	225
Oxyura maccoa								
January	12	1.5	2.6	0.7	1.78	0	8	8
February	12	2.1	3.2	0.9	1.52	0	8	8
March	12	1.0	2.4	0.7	2.48	0	8	8
April	10	1.2	2.7	0.8	2.24	0	8	8
May	10	0.4	1.2	0.4	3.16	0	4	4
June	10	0.6	1.4	0.4	2.17	0	4	4
July	10	1.6	2.0	0.6	1.19	0	5	5
August	10	3.8	8.8	2.7	2.28	0	28	28
September	10	3.5	8.7	2.7	2.49	0	28	28
October	11	2.7	4.3	1.3	1.59	0	15	15
November	11	2.0	4.5	1.3	2.17	0	15	15
December	11	0.3	0.6	0.2	1.85	0	2	2
Gallinula chloropus								
January	12	49.1	27.5	7.9	0.56	10	80	70
February	12	51.5	27.8	8.0	0.54	6	96	90
March	12	64.4	51.1	14.7	0.79	1	200	199
April	10	60.5	56.9	18.0	0.94	1	200	199
May	10	54.1	59.7	18.8	1.10	1	200	199
June	10	55.7	58.4	18.4	1.04	3	200	196
July	10	51.4	59.4	18.7	1.15	2	200	197
August	10	34.8	27.4	8.6	0.78	6	80	74
September	10	34.8	27.4	8.6	0.78	6	80	74
October	11	40.1	33.2	10.0	0.82	4	100	96
November	11	31.4	28.0	8.4	0.89	5	80	75
December	11	47.1	30.8	9.2	0.65	7	80	73

Fulica cristata								
January	12	465.6	468.7	135.3	1.00	75	1700	1625
February	12	453.4	383.1	110.6	0.84	17	1250	1232
March	12	375.2	339.7	98.0	0.90	0	1000	1000
April	10	282.8	348.2	110.1	1.23	0	1000	1000
May	10	127.0	132.2	41.8	1.04	0	390	390
June	10	139.2	173.8	54.9	1.24	0	550	550
July	10	125.0	72.1	22.8	0.57	45	250	205
August	10	146.8	94.9	30.0	0.64	46	300	253
September	10	237.5	140.1	44.3	0.58	65	500	434
October	11	379.3	221.6	66.8	0.58	116	833	716
November	11	479.6	366.6	110.5	0.76	100	1350	1250
December	11	513.2	549.3	165.6	1.07	73	2000	1926
Calidris ferruginea								
January	12	10.3	8.4	2.4	0.81	0	24	24
February	12	39.0	28.1	8.1	0.72	11	110	99
March	12	61.2	34.0	9.8	0.55	0	106	106
April	10	76.8	70.1	22.1	0.91	0	200	200
May	10	27.2	46.4	14.6	1.70	0	150	150
June	10	10.0	14.5	4.6	1.44	0	42	42
July	10	1.3	2.4	0.7	1.92	0	6	6
August	10	0.7	2.2	0.7	3.16	0	7	7
September	10	1.5	1.8	0.5	1.18	0	4	4
October	11	1.0	1.8	0.5	1.74	0	5	5
November	11	2.4	2.7	0.8	1.11	0	6	6
December	11	10.3	10.1	3.0	0.98	0	27	27
Calidris minuta								
January	12	32.6	41.3	11.9	1.26	0	152	152
February	12	34.9	25.3	7.3	0.72	0	90	90
March	12	111.0	79.3	22.9	0.71	12	226	214
April	10	120.5	106.4	33.6	0.88	14	300	285
May	10	98.5	79.9	25.2	0.81	0	200	200
June	10	17.9	47.5	15.0	2.64	0	152	152
July	10	2.5	5.4	1.7	2.16	0	15	15
August	10	2.3	7.2	2.3	3.16	0	23	23
September	10	0.5	1.4	0.4	2.58	0	4	4
October	11	2.6	3.2	0.9	1.19	0	8	8
November	11	2.7	3.9	1.1	1.43	0	12	12
December	11	8.4	14.4	4.3	1.70	0	50	50
Philomachus pugnax								
January	12	9.3	8.2	2.3	0.89	0	30	30
February	12	16.8	17.6	5.0	1.04	0	62	62
March	12	20.2	18.4	5.3	0.91	0	53	53
April	10	14.9	17.4	5.5	1.16	0	60	60
May	10	7.0	18.8	5.9	2.69	0	60	60
June	10	0.0	0.0	0.0	0.00	0	0	0
July	10	0.0	0.0	0.0	0.00	0	0	0
August	10	0.0	0.0	0.0	0.00	0	0	0
Semptember	10	0.0	0.0	0.0	0.00	0	0	0
October	11	1.1	2.1	0.6	1.80	0	6	6
November	11	0.9	1.6	0.4	1.80	0	4	4
December	11	5.0	8.6	2.6	1.70	0	27	27
Recurvirostra avosetta								
January	12	53.5	68.2	19.6	1.27	0	210	210
February	12	118.4	143.0	41.3	1.20	2	543	540
March	12	112.9	76.4	22.0	0.67	15	273	258
April	10	90.9	118.2	37.3	1.30	0	400	400
May	10	41.5	56.4	17.8	1.35	0	160	160
June	10	36.2	40.3	12.7	1.11	0	100	100
July	10	6.1	12.3	3.8	2.01	0	38	38
August	10	4.0	7.3	2.3	1.82	0	22	22
September	10	5.8	13.6	4.3	2.35	0	42	42
October	11	4.0	5.7	1.7	1.42	0	14	14
November	11	4.3	6.0	1.8	1.40	0	14	14
December	11	11.7	18.5	5.5	1.57	0	62	62

Himantopus himantopus								
January	12	9.7	4.9	1.4	0.50	4	20	15
February	12	12.2	5.3	1.5	0.43	5	20	15
March	12	13.4	10.3	2.9	0.77	2	40	38
April	10	19.9	16.3	5.1	0.81	0	49	49
May	10	14.6	13.1	4.1	0.89	0	44	44
June	10	10.7	6.3	2.0	0.59	3	24	21
July	10	8.3	10.4	3.2	1.24	0	28	28
August	10	3.1	2.7	0.8	0.87	0	9	9
September	10	3.1	2.1	0.6	0.67	0	6	6
October	11	5.7	4.5	1.3	0.79	0	16	16
November	11	5.0	5.4	1.6	1.06	0	19	19
December	11	8.3	9.4	2.8	1.13	0	33	33
Chlidonias leucopterus								
January	12	294.1	330.6	95.4	1.12	35	1280	1244
February	12	352.8	585.5	169.0	1.65	1	2000	1999
March	12	660.4	1952.6	563.6	2.95	0	6850	6850
April	10	124.1	136.0	43.0	1.09	2	403	400
May	10	50.2	158.0	49.9	3.14	0	500	500
June	10	0.0	0.0	0.0	0.00	0	0	0
July	10	0.4	1.4	0.4	3.16	0	4	4
August	10	0.1	0.3	0.1	3.16	0	1	1
September	10	3.1	8.9	2.8	2.89	0	28	28
October	11	18.5	26.0	7.8	1.40	0	70	70
November	11	72.5	71.8	21.6	0.99	0	227	227
December	11	161.5	132.1	39.8	0.81	0	416	416

Appendix 3.2. Environmental data analysed in this study, months and codes used in Fig. 3.3

Month codes	@ RF	WL	WT	MAX	MIN	Month codes	RF	WL	WT	MAX	MIN
1 JAN	21	445	24	27	14	66 MAR	9	408	21	25	13
2 FEB	27	426	23	25	14	67 APR	9	396	18	21	11
3 MAR	66	412	23	24	13	68 MAY	66	391	15	20	7
4 APR	47	408	21	23	11	69 JUN	93	403	14	17	7
5 MAY	73	409	18	19	9	70 JUL	116	457	14	16	6
6 JUN	49	426	13	18	4	71 AUG	113	495	14	16	7
7 JUL	82	454	13	17	7	72 SEP	31	492	15	17	6
8 AUG	95	482	13	17	7	73 OCT	14	490	20	21	10
9 SEP	36	495	16	20	9	74 NOV	3	480	21	23	12
10 OCT	31	492	19	22	10	75 DEC	7	457	23	25	14
11 NOV	7	476	19	23	11	76 JAN	18	436	23	26	15
12 DEC	47	455	19	23	16	77 FEB	20	416	23	26	16
13 JAN	7	436	23	25	15	78 MAR	18	398	22	26	14
14 FEB	6	417	23	24	13	79 APR	51	391	18	22	10
15 MAR	53	406	24	24	13	80 MAY	93	393	16	20	9
16 OCT	19	483	18	22	10	81 JUN	64	403	14	18	8
17 NOV	9	473	19	24	12	82 JUL	42	424	14	18	7
18 DEC	10	458	20	34	14	83 AUG	72	447	14	17	7
19 JAN	13	454	22	24	15	84 SEP	40	464	17	19	9
20 FEB	0	421	24	27	15	85 OCT	109	462	20	22	11
21 MAR	7	402	25	25	13	86 NOV	0	449	21	26	13
22 APR	83	391	19	21	11	87 DEC	23	429	23	24	14
23 MAY	58	391	16	19	9	88 JAN	0	403	25	26	15
24 JUN	165	435	13	16	7	89 FEB	1	388	23	28	16
25 JUL	82	485	12	17	5	90 MAR	13	372	24	25	14
26 AUG	58	496	13	17	5	91 APR	8	360	25	26	12
27 SEP	29	495	16	20	8	92 MAY	36	360	18	20	9
28 OCT	42	494	18	21	10	93 JUN	44	378	16	19	8
29 NOV	38	476	20	24	13	94 JUL	162	386	15	17	8
30 DEC	6	464	22	25	16	95 AUG	48	415	15	17	6
31 JAN	19	445	22	24	14	96 SEP	79	446	16	18	8
32 FEB	12	425	20	24	13	97 OCT	18	460	19	23	11
33 MAR	0	407	23	26	14	98 NOV	5	455	21	25	14
34 APR	56	391	23	22	12	99 DEC	20	430	21	25	15
35 MAY	107	393	18	19	10	100 JAN	7	412	23	26	16
36 JUN	107	438	14	17	6	101 FEB	5	390	23	28	16
37 JUL	131	483	12	16	6	102 MAR	11	375	21	26	13
38 AUG	83	495	13	16	6	103 APR	3	365	21	24	12
39 SEP	8	494	15	19	7	104 MAR	138	375	16	20	9
40 OCT	60	494	18	20	9	105 JUN	244	442	14	18	9
41 NOV	8	494	21	24	12	106 JUL	65	500	14	17	6
42 DEC	22	464	23	24	13	107 AUG	324	505	14	17	7
43 JAN	22	445	22	25	14	108 SEP	53	502	15	18	7
44 FEB	7	435	24	26	15	109 OCT	40	492	19	20	10
45 MAR	19	454	24	26	15	110 NOV	22	488	22	23	13
46 APR	38	368	20	21	11	111 DEC	4	481	23	25	15
47 MAY	10	365	16	10	6	112 JAN	21	459	23	25	16
48 JUN	84	449	13	17	7	113 FEB	5	445	23	28	16
49 JUL	45	483	12	17	7	114 MAR	8	432	20	26	14
50 AUG	80	495	13	18	10	115 APR	70	422	19	22	11
51 SEP	73	494	16	18	7	116 MAY	170	463	17	20	10
52 OCT	75	494	19	20	11	117 JUN	56	492	15	19	8
53 NOV	6	494	22	22	11	118 JUL	147	494	14	16	7
54 DEC	5	464	22	25	15	119 AUG	91	492	14	17	7
55 JAN	4	476	24	26	16	120 SEP	22	492	19	21	10
56 FEB	17	434	22	26	14	121 OCT	50	492	19	20	16
57 MAR	2	429	22	26	14	122 NOV	18	489	20	22	12
58 JUL	144	407	12	15	5	123 DEC	0	480	24	26	14
59 AUG	87	436	13	16	7	124 JAN	0	451	24	27	16
60 SEP	71	464	15	17	7	125 FEB	7	431	25	25	15
61 OCT	37	489	19	22	11	126 MAR	25	419	22	24	14
62 NOV	12	496	20	21	11	127 APR	39	403	21	22	13
63 DEC	33	461	22	22	12	128 MAY	91	408	19	21	11
64 JAN	3	438	22	25	14	129 JUN	227	458	14	17	10
65 FEB	0	420	23	27	16	130 JUL	75	494	14	16	8

@ RF = rainfall (mm), WL = water level (m a.s.l.), WT = water temperature (°C), MAX & MIN = maximum & minimum ambient temperature (°C).

CHAPTER 4. Seasonal variation in group size and dispersion in a population of Great White Pelicans

Le Gerfaut (1981) 71: 185-194.

The Great White Pelican (Pelecanus onocrotalus) is assigned 'Red Data' status in South Africa (Brooke 1984), where, besides the Walvis Bay enclave breeding colony (over 400 breeding pairs, Berry et al. 1973), two apparently distinct populations occur, one in Natal, and the other in the southwestern Cape. Both populations breed at only one site, the Natal birds (1000-2000 breeding pairs, Berruti 1980) at Lake St. Lucia (28°00'S 32°30'E), and the Cape birds (c. 200 breeding pairs, Cooper 1980), at Dassen Island (33°25'S 18°12'E). The foraging range of the southwestern Cape population extends from the Olifants River estuary on the Atlantic coast, southwards to the Cape Flats and at De Hoop vlei (Fig. 4.1) in the east on the Indian Ocean. For this population, there is no single large water body which can provide a dependable and abundant supply of fish. Thus, apparently unlike other Great White Pelican populations studied to date (Feely 1962; Brown & Urban 1969; Din & Eltringham 1974; Whitfield & Blaber 1979b), the southwestern Cape population is small, and depends for its food supply on many relatively minor water systems of different types, which may have different seasonal regimes and patterns of fish prey density (Noble & Hemens 1978). My aims in this study are to describe and explain seasonal variation in group size and dispersion for the southwestern Cape Great White Pelican population, and to determine the relative conservation importance of water bodies which are regularly and irregularly used by Cape pelicans.

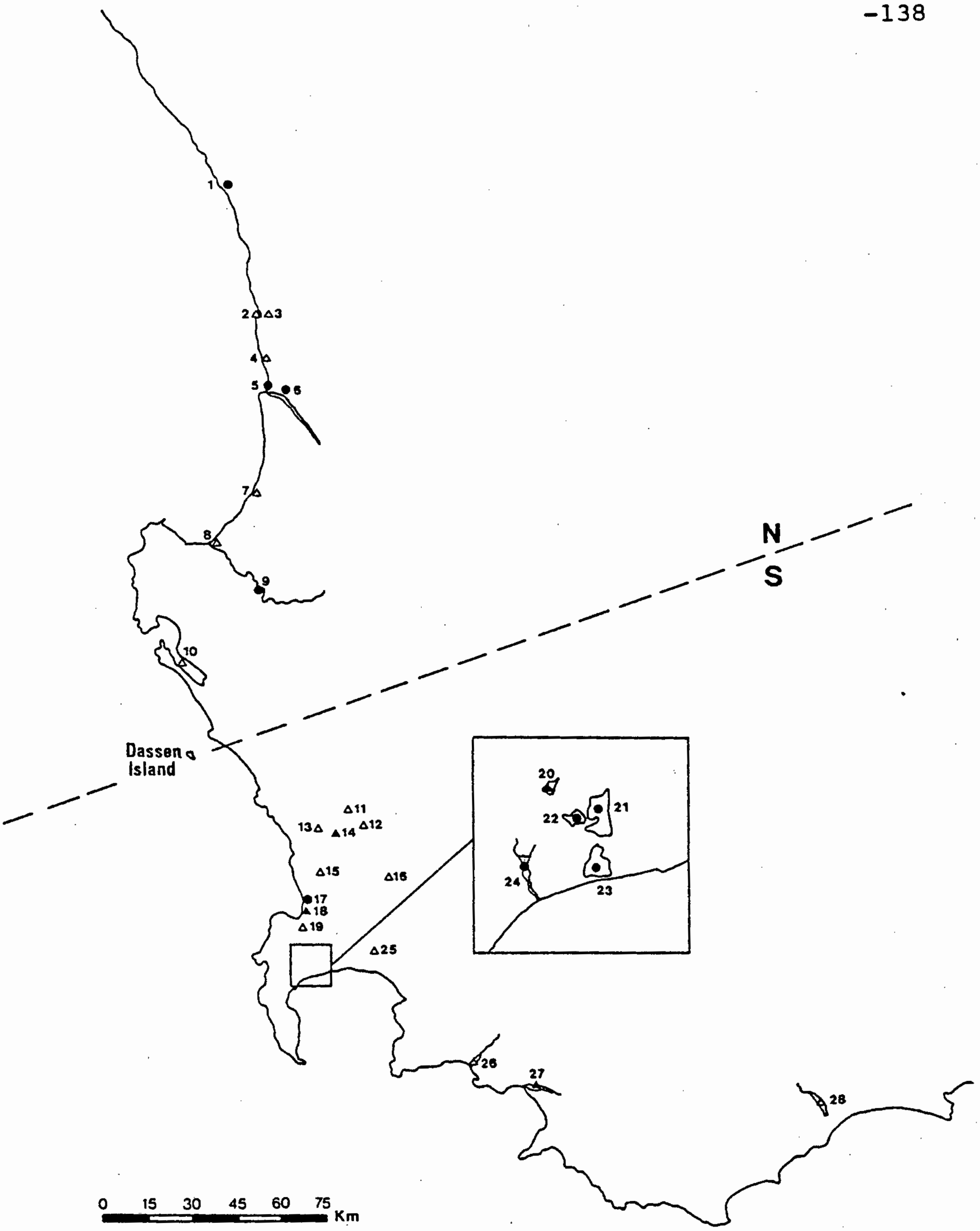

Fig. 4.1. Primary (•) and secondary (▵ , ▴) water bodies for southwestern Cape White Pelicans. All primary, and some secondary water bodies (▴), in both the northern (N) and southern (S) portions of the pelican foraging range, were surveyed at least monthly during 1977-78. The inset shows water bodies at which I collected my etho-ecological data. See Table 4.1 for names of water bodies and their map coordinates.

Study area and methods

Study area

My study area includes all water bodies known to be part of the southwestern Cape Great White Pelican distribution (Fig. 4.1; Table 4.1). Independent of their size and ecological regime, these water bodies may sustain small or large groups of pelicans, on a permanent or temporary basis. Herein, a water body is referred to as primary if groups of at least 10 pelicans have been known to visit it at least part of every month of the year, or secondary, if it is visited by fewer birds and/or is less persistantly visited. Water bodies visited by southwestern Cape Great White Pelicans, encompass the range of non-pelagic aquatic ecosystem types found in principal South African drainage systems, e.g. shallow sea water, long rivers typical for their erratic flow, vleis (flattish stretches of rivers with marshy vegetation and seasonal standing water), saline and freshwater pans (seasonal ponds with no outflow), coastal lakes, estuaries, and man made impoundments (Noble & Hemens 1978). Apart from the sparse vegetation cover of pans (mostly hygrophilous grasses and salt tolerant terrestrial vegetation), either emergent (e.g. Phragmites australis, Typha capensis, Scirpus spp., Cyperus spp.) or submerged (e.g. Potamogeton pectinatus) hydrophytes and/or algal growth may dominate other water system types. Several of these water systems harbor exotic fish species, e.g. Carp (Cyprinus carpio) and Largemouth Bass (Micropterus spp.), which form an important part of the diet of the Cape pelicans (Guillet pers. obs., Middlemiss 1974). These water bodies support very different standing crops of fish which, for example, in impoundments vary (for fish over 12 cm length) from 46 Kg ha^{-1} to 774 Kg ha^{-1} (Noble & Hemens 1978).

Table 4.1. Names and map coordinates for water bodies shown in Fig. 4.1

Water body no.	Water body name	Coordinates
1	Olifants River (Papendorp)	31° 42'S 18° 12'E
2	Lamberts Bay	32° 05'S 18° 19'E
3	Jakkalsriviervlei	32° 05'S 18° 20'E
4	Wadrifsoutpan	32° 12'S 18° 20'E
5	Elandsbaii	32° 19'S 18° 20'E
6	Verlorevlei	32° 19'S 18° 23'E
7	Rocher Pan (Die Vlei)	32° 36'S 18° 18'E
8	Velddrif (Groot-Bergrivier)	32° 47'S 18° 09'E
9	Kersfontein	32° 55'S 18° 20'E
10	Langebaan Lagoon	33° 08'S 18° 04'E
11	Kalbaskraal Nooitgedacht Plaas	33° 34'S 18° 42'E
12	Droëvlei Dieprivier	33° 38'S 18° 43'E
13	Driedfontein (Soutrivier)	33° 39'S 18° 31'E
14	Swellengift	33° 39'S 18° 37'E
15	Visserhok	33° 47'S 18° 33'E
16	Joostenbergvlaktedam	33° 48'S 18° 47'E
17	Rietvlei	33° 50'S 18° 29'E
18	Milnerton Lagoon	33° 53'S 18° 29'E
19	Blackrivier	33° 56'S 18° 29'E
20	Princessvlei	34° 03'S 18° 29'E
21	Zeekoevlei	34° 04'S 18° 31'E
22	Rondevlei	34° 04'S 18° 30'E
23	Strandfontein Sewage Work	34° 05'S 18° 31'E
24	Sandvlei	34° 06'S 18° 28'E
25	Merlustdam	34° 01'S 18° 45'E
26	Botrivier	34° 21'S 19° 05'E
27	Kleinrivier	34° 25'S 19° 21'E
28	De Hoop	34° 27'S 20° 25'E

Data set

The major sources of data for this study are: 2073 field card records from the collection of the Cape Bird Club which span the period 1938-1978; 5096 counts made at Rondevlei Bird Sanctuary by conservation officers during 1965-1978; published literature (Baron 1977; Cooper 1976, 1977, 1978, 1979), and 1180 counts made by myself, or observers under my direction, for monthly surveys from April 1977 to April 1978. Personal counts include records for all primary water bodies shown in Fig. 4.1. Finally, detailed surveys, which consisted of frequent counts and eco-ethological studies (e.g. of activities such as reproduction, flying, roosting, foraging, etc.), were made at Dassen Island and in a cluster of water bodies in the southern portion of the distribution (Fig. 4.1 inset), especially at Rondevlei Bird Sanctuary (no. 22 in Fig. 4.1), which at times harbored more than one third of the population (Chapter 5).

Since much of the pelican count data, except those under my direction were not collected systematically, I have combined all data for each water body according to the month of survey regardless of the year in which the surveys were made. The resulting patterns are taken to be generalised monthly patterns of dispersion and group size for the southwestern Cape pelicans. However, in order to test whether or not this combination of data distorts the 'true' patterns of pelican dispersion/group size for a given year, I have analysed separately data from the detailed counts made by myself and my observers from April 1977 to April 1978; and have compared the resulting patterns with generalised ones derived from combined data.

Results

Combined survey distortion

The dispersion/group size results for the combined counts, and for detailed 1977-78 counts, are displayed in Fig. 4.2. A comparison of the patterns shown in Figs. 4.2a and 4.2c, and in 4.2b and 4.2d, suggests that the dispersion/group size patterns indicated by the combined data set are representative ($r = 0.769$ and 0.791 respectively; $P < 0.01$) of those observed in a single year.

Pelican dispersion

There are two peaks of high pelican dispersion in the southwestern Cape, one between January and March/April, the other, between July and October (Fig. 4.2a). Correspondingly, there are two periods of low dispersion, one between March/April and June/July, and the other between November and December.

Pelican group size

There is a single period of high mean pelican group size between February/March and June, followed by one with lower values between July and February/March (Fig. 4.2b).

Relationships between pelican dispersion and group size

Not unexpectedly, a comparison of Fig. 4.2a and Fig. 4.2b shows that, in general, when pelican group size is on the increase, dispersion is decreasing, and vice versa. However, during February-March, both dispersion and group size increase.

Environmental factors and events in the pelican annual cycle

Figure 4.3 shows: (a) monthly variation in average rainfall and temperature at D.F. Malan Airport (33°58'S, 18°36'E; a centrally located weather station in the southern sector of the Cape pelican

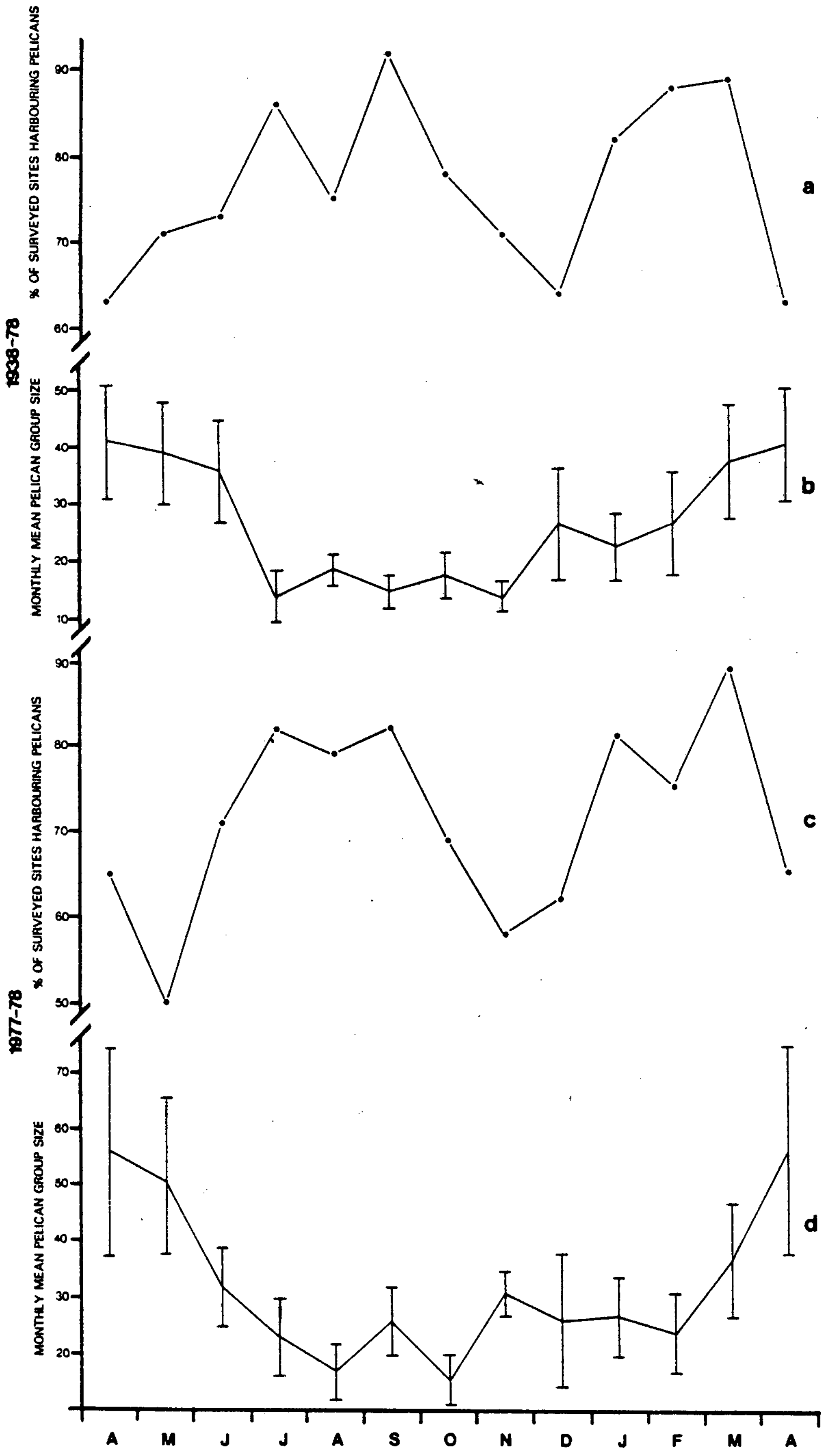

Fig. 4.2. Long-term (1938-78) and 1977-78 data on dispersion (a and c) and mean monthly group size (b and d) for southwestern Cape White Pelicans. Bars are ± 1 S.E.

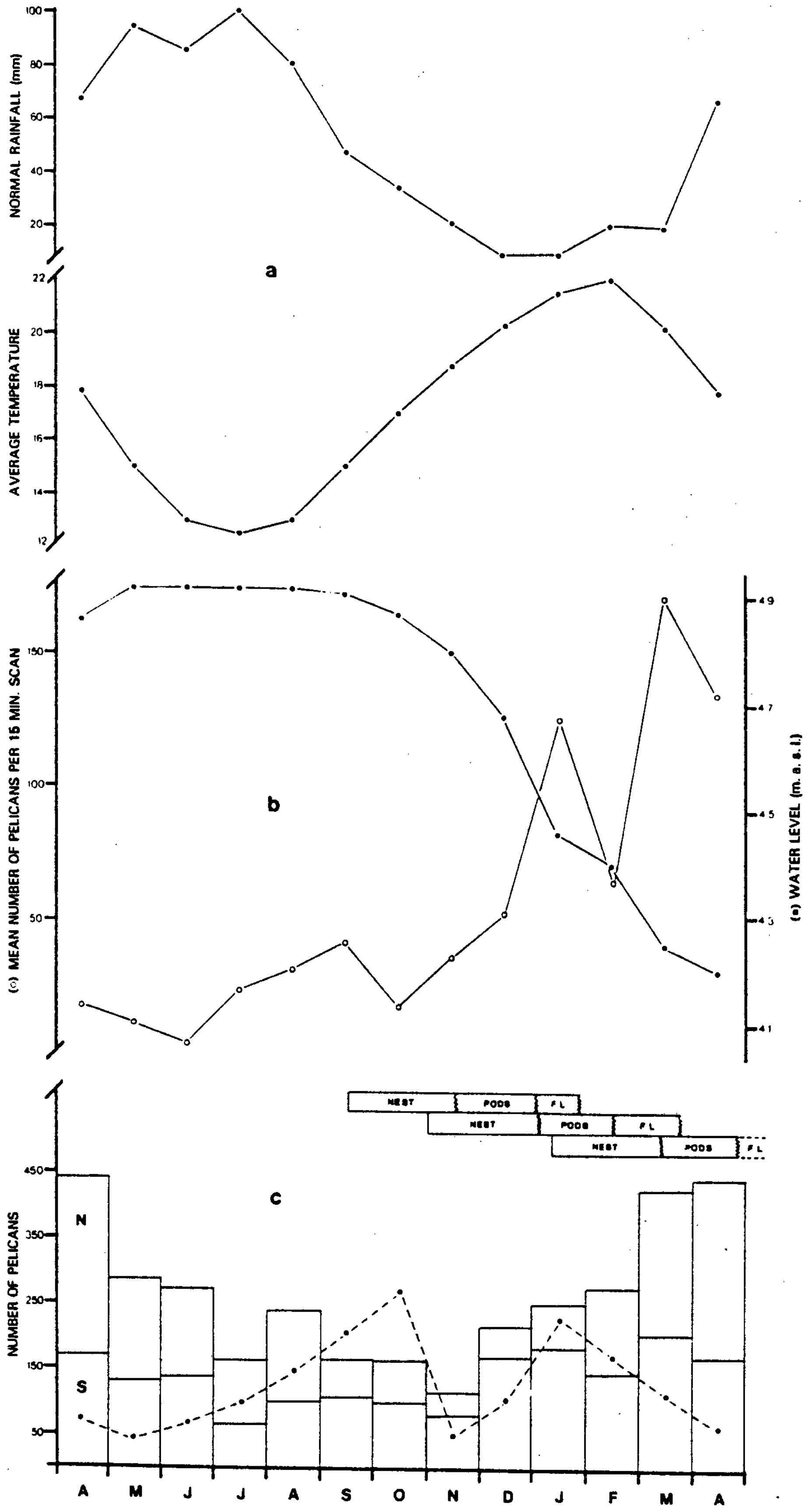

Fig. 4.3. Monthly variation in: rainfall and temperature at D.F. Malan airport (a); pelican group size and water level at Rondevlei Bird Sanctuary (b); and (c) in pelican flying activity (-O-) and breeding (NEST = pelicans on nest, PODS = chicks in groups, FL = juveniles commence fledging) during 1977-78, and long-term usage of northern and southern primary water bodies (N and S, see Fig. 4.1).

foraging range); (b) mean number of pelicans counted per 15 minute scan and vlei depth at Rondevlei during 1977-78; and (c), information on the three waves of 1977-78 pelican reproduction, flying activity (number of birds seen flying between water bodies per day during a dawn to dusk watch) in the southern portion of the pelican foraging range during the same period, and statistics for long-term dispersion/group size in northern and southern, and in primary and secondary waterbodies. Long term pelican dispersion (Fig 4.2a) is positively related ($r = 0.61$; $P < 0.05$), and long term mean group size (Fig. 4.2b) negatively related ($r = -0.63$; $P < 0.05$), to flying activity. Mean monthly pelican group size at Rondevlei during 1977-78 (Fig. 4.3b) is positively related to temperature (Fig. 4.3a; $r = 0.60$; $P < 0.05$), and negatively related to vlei depth (Fig. 4.3b; r 0.92; $P < 0.05$). From September to February, southern primary water bodies are favored by Cape pelicans over northern ones (Fig. 4.3c).

Discussion and Conclusions

The normal relationship between pelican dispersion and group size

To understand the normal inverse relationship between pelican dispersion and mean group size in the southwestern Cape one needs to consider the effects of changing rainfall and temperature on pelican habitat and prey density. During the cool wet months of winter and spring (June-October/November), pelican dispersion tends to be high and group size low (Figs. 4.2a, 4.2b and 4.3a). Heavy rainfall improves the habitat quality of many of the secondary water bodies, which, during the drier-warmer months, may contain little or no water. Conversely, the combination of heavy rainfall and low temperature adversely affects (although with somewhat of a lag effect) the pelican habitat quality and ecological prey density (Odum 1971) of the primary water bodies. The additional water input due to the rain leads to an overall increase in water depth and a decrease in water temperature, and the low surface water temperature forces the fish to seek out, and linger in, the warmer deeper water (Middlemiss 1974; Cambray et al. 1978; Hamman pers. comm.). In this deeper water the fish are out of the reach of foraging pelicans which normally feed in shallow water less than 1 m deep (Guillet unpub. data). This situation is clearly illustrated at Rondevlei Bird Sanctuary where there is a highly significant negative relation (Fig. 4.3b; $r = -0.92$, $P < 0.001$) between vlei depth and number of pelicans counted. For example, rarely more than 40 pelicans are seen when vlei depth exceeds 4.8 m.a.s.l., while as many as 205 birds may be seen during periods of lower vlei depth. By the end of summer (March/April to May), evaporation and drainage have caused a lowering of water depth in the primary water bodies, and the complete drainage of many of the secondary water bodies. At the same time, water temperature has risen and the fish prey have returned to shallow water (Middlemiss 1974; Cambray et al. 1978; Hamman et al. 1980), and thus, once again become available to foraging pelicans in primary water bodies.

Anomalous relationship between pelican dispersion and group size

There are two factors which I feel bring about the simultaneous increases in pelican dispersion and group size between February and March. These are an increase in the population, and an increase in the mobility of pelican foraging groups. The increase in the population is due to the influx of fledged juvenile and post-breeding adult pelicans from Dassen Island (Fig. 4.3c). The increase in mobility is shown by the high values of flying activity during February-March 1978 (Fig. 4.3c). The most obvious hypothesis as to why the Cape pelicans should need to visit more water bodies during this period is that the larger groups of pelicans, especially those birds feeding chicks on Dassen Island, require more food than a few water bodies can supply on a continuous basis.

Conservation importance of primary and secondary water bodies

Since the hatching and pre-fledging development of Cape pelican chicks appears to be correlated with the increased use of primary water bodies (Fig. 4.3c), I assume that these sites provide the bulk of food which is necessary for successful breeding. Moreover, during the breeding season, Cape pelicans rely more on southern than on northern primary water bodies, possibly because these offer better feeding opportunites, or merely because they are closer to Dassen Island. During the non-breeding season and the early phases of the breeding season, Cape pelicans rely heavily on secondary water bodies (Fig. 4.3c), presumably because environmental conditions do not favor the use of primary ones (see above). In fact, more than 50 percent of the population (assuming a total population size of c. 600 birds) frequent secondary water bodies for nine months of the year (Fig. 4.3c). Thus, the effective conservation of this small pelican population depends on the continued availability of secondary as well as primary water bodies.

CHAPTER 5. Temporal variation in breeding, foraging and bird sanctuary visitation by a southern African population of Great White Pelicans

Biological Conservation (1983) 26: 15-31.

The Great White Pelican Pelecanus onocrotalus is assigned 'Red Data' status in South Africa, breeding at only three sites: Lake St Lucia (28°00'S, 32°05'E) in Zululand, the enclave of Walvis Bay (22°40'S, 14°30'E), and Dassen Island (33°25'S, 18°12'E) in the southwestern Cape Province (Berry et al. 1973; Brooke 1984). The Zululand population consists of c. 1000-2000 breeding pairs (Berruti 1980), and aspects of its foraging and breeding have been studied (Feely 1962; Whitfield & Blaber 1979b). The population which breeds at Walvis Bay consists of c. 1000 adult birds, and its status and conservation have been studied by Berry et al. (1973). The southwestern Cape population is a very small one (c. 174-200 breeding pairs; Cooper 1980; Guillet, unpub. data), and its foraging range is restricted, in the main, to wetlands along the Atlantic coast (Chapter 4).

In this chapter I describe the breeding periodicity of the southwestern Cape Great White Pelicans, and their use of Rondevlei Bird Sanctuary (34°04'S, 18°30'E) from April 1977 to April 1978. My primary aim is to suggest how temporal variation in Sanctuary visitation, breeding and foraging by this Great White Pelican population may be influenced by variation in the environment.

Study area and methods

Study areas

Historically, Dassen Island is not the only breeding site for Great White Pelicans in the southwestern Cape. Great White Pelicans bred on Seal Island (34°08'S, 18°35'E) until at least 1956, when interference from the growing Cape Fur Seal Arctocephalus pusillus population, and the intensification of commercial sealing may have forced them to abandon this site (Rand 1963). The Great White Pelicans which nest on Dassen Island are protected and relatively easily observed. Protection is provided by personnel of the South African Sea Fisheries Institute who limit access of potential predators (mainly man and dogs) to the island. Rondevlei Bird Sanctuary (Fig. 5.1) was chosen as an intensive study area for several reasons. Firstly, and most importantly, it is used throughout the year by up to 50% of the southwestern Cape pelican population for roosting and foraging (Chapter 4). It also has a full-time staff of conservation officers who, since 1952, have monitored the numbers and species composition of Rondevlei's waterbirds, and environmental variables which may potentially influence their use of the Sanctuary (e.g. water depth, turbidity, rainfall, wind, ambient temperature). Ornithological study at Rondevlei is greatly facilitated by several natural vantage points and two 18m towers (Fig. 5.1), which allow observation of virtually all pelicans within the Sanctuary.

Sampling methods and data

Dassen Island was visited at approximately 35-day intervals during the Great White Pelican breeding season (mid-September to the end of March), and Sea Fisheries personnel provided additional information on pelican breeding biology. Nesting areas were observed from rocky outcrops about 60m from the nesting area or from the top of the island's lighthouse. Since breeding Great White Pelicans are extremely sensitive to disturbance (Brown & Urban 1969), I measured pelican breeding success as the percentage

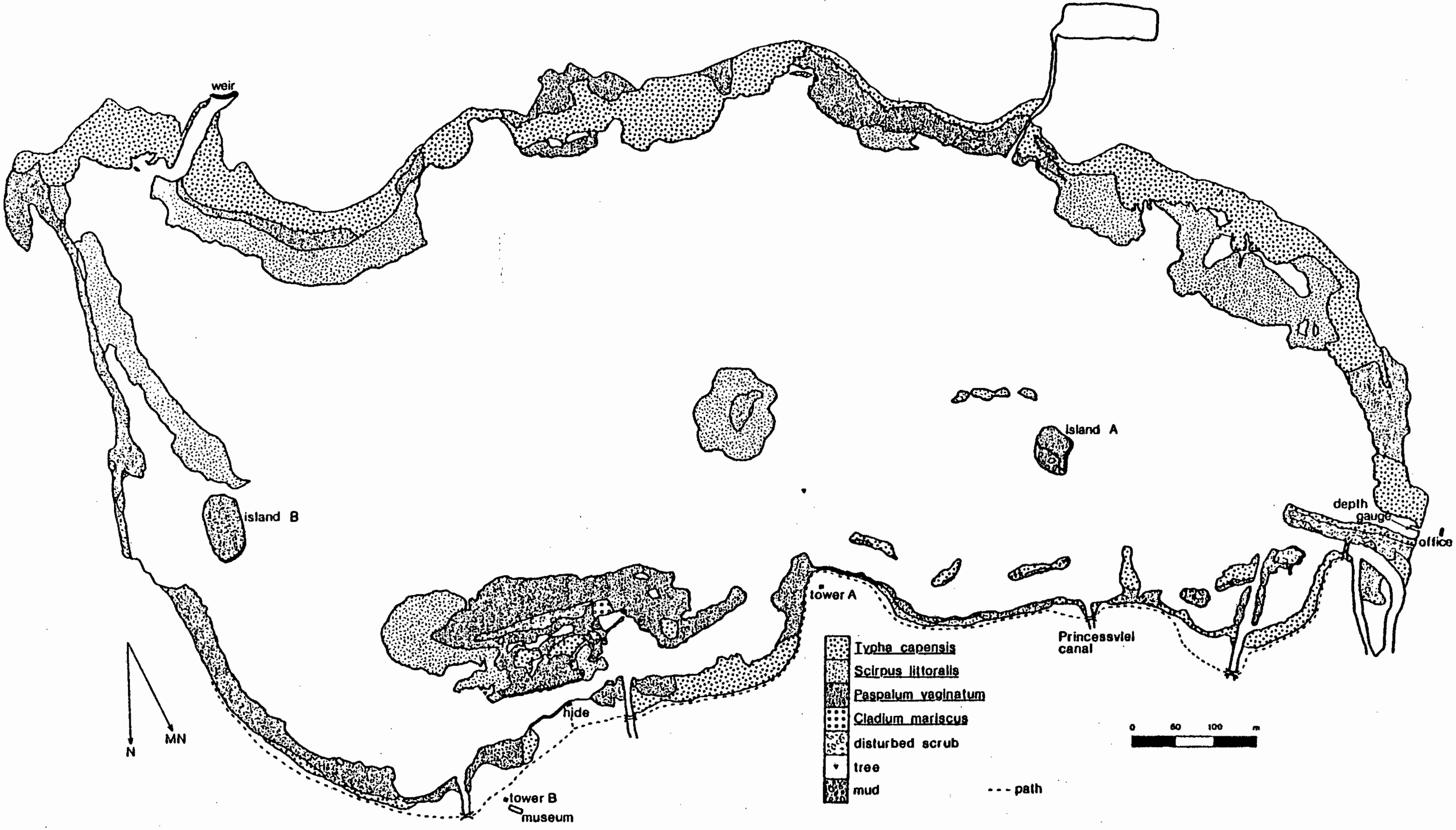

Fig. 5.1. Rondevlei Bird Sanctuary and its environs.

of prefledged chicks in an advanced stage of development, relative to the number of nests.

Rondevlei was visited on one day each month, from about 15 minutes before the time of local sunrise, until at least 45 minutes after time of local sunset. A total of 186 hours was spent observing pelicans at Rondevlei. Sanctuary visitation and foraging activity were monitored using the instantaneous scan sampling method (Altmann 1974). A 15 minute scan interval was considered to be adequate, since preliminary study using the focal animal method (Altmann 1974), indicated that the mean length of a Sanctuary visit and of a foraging bout were more than an hour. The environmental variables which I felt may influence the behaviour and ecology of Great White Pelicans are listed in Table 5.1.

My primary measure of Sanctuary visitation was mean number of pelicans seen per scan ($\bar{X}$P/S). In order to determine if this measure was correlated with broad trends of Sanctuary visitation during the study period and over the long term, I have selected three additional measures of Sanctuary visitation, conservator mean (C$\bar{X}$), maximum (CMAX) and minimum (CMIN) counts. These measures are respectively the mean, maximum and minimum number of Great White Pelicans counted by Rondevlei staff during each month. For the study period, Rondevlei's warden counted pelicans at least once a week during periods of low abundance (April-December), and nearly every day during periods of high pelican abundance (January March). If $\bar{X}$P/S was statistically significantly positively correlated with C$\bar{X}$, CMAX and CMIN for the study period, I assumed that my observation days were representative of Sanctuary visitation throughout the month. Also, if the environmental

Table 5.1. Environmental variables to which measures of foraging and Sanctuary visitation were related

Environmental variable	Abbreviations
day length = no. of scans per survey day	(DL)
long-term (since 1952) mean monthly rainfall in mm	(LRF)
current monthly rainfall in mm	(CRF)
mean wind force (of values taken hourly on a Beaufort scale) on the day of survey	(W)
long-term (since 1952) mean monthly ambient temperature in ^{0}C	(LT)
current mean monthly ambient temperature in ^{0}C	(CT)
mean ambient temperature in ^{0}C (of values taken hourly) on the day of survey	(SDT)
mean cloud cover (of values taken hourly on a scale of 0-8) on the day of survey	(CC)
water depth in m above sea level(as measured by a gauge situated near the warden's office, Fig. 5.1)	(DEP)
turbidity (one value taken per month on a clear, windless day) = the inverse of the depth in cm to which a Secchi disc may be seen	(TUR)

variable(s) which appear to influence $\bar{X}P/S$ during the survey period were also significantly and similarly related to $C\bar{X}$, CMAX and CMIN during a much longer period (1956-78), I assume that these environmental variables have influenced Sanctuary visitation over the long term.

I chose four measures of pelican foraging activity:

1. mean number of pelicans seen foraging per scan ($\bar{X}F/S$),
2. percentage of daily scans in which foraging birds were observed (%SCAN),
3. percentage of all pelicans observed during the survey day which were seen foraging (%F/D),
4. intensity of group foraging (IGF), according to Jarman's (1974) formula for Typical Group Size.

In an attempt to reduce several of the above-mentioned measures to a single assessment of overall foraging suitability of Rondevlei (SUIT), I have devised the following formula:

$$\text{SUIT} = \frac{C\bar{X} \cdot \bar{X}F/S}{\text{CMAX-CMIN} \cdot \%F/D}$$

In other words, SUIT is at its highest when there are large numbers of pelicans foraging at Rondevlei throughout the month, which spend relatively little time foraging to obtain their food requirements.

Statistical methods

Correlation and stepwise multiple linear regression analysis (Allen 1973) were used to relate dependent (i.e. 'pelican') variables to independent (i.e. environmental) variables. See Crowe (1979a, 1979b) for a discussion of the relative advantages and disadvantages of regression and correlation analysis, and Sokal & Rohlf (1969) and Sepkoski & Rex (1974) for a discussion of the statistical limitations of regression and correlation analysis in the investigation of ecological phenomena.

Results

During 1977-78 Great White Pelicans bred at Dassen Island in three major waves (Fig. 5.2). The first laying occurred in mid-September, the last in the second half of January. The reproductive success of the first wave was 25% (22 prefledging chicks from 89 nests), of the second wave 136% (202 prefledging chicks from 149 nests), and of the third wave 82% (23 prefledging chicks from 28 nests). All chicks from each breeding wave appeared to be of a similar age. Therefore, hatching appeared to be relatively synchronous within each wave. In Figure 5.2, temporal variation in the food requirements of this breeding colony, is plotted as the hypothetical cumulative body-mass of three chicks (one from each of the breeding waves) against time, since heavier chicks require more food, and adult parents should need to make more foraging trips to satisfy their young.

There is marked temporal variation at Rondevlei in pelican visitation, foraging, and foraging suitability (Tab. 5.2; Fig. 5.3). The results of a correlation and regression analysis

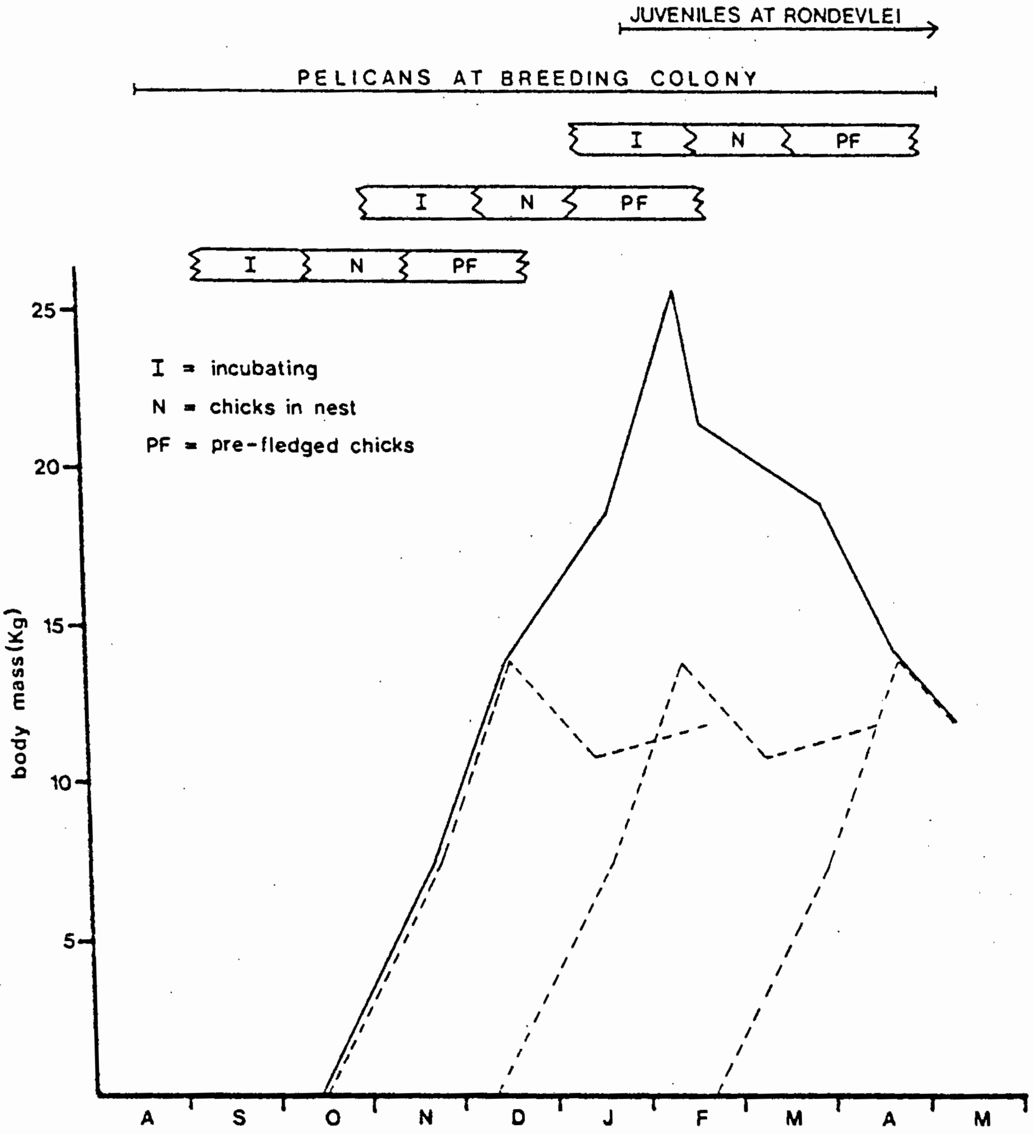

Fig. 5.2. The hypothetical growth curves (- - -), and the cumulative growth curve (——), of three pelican chicks from the breeding waves observed at Dassen Island during 1977-78, and major events in that pelican breeding season: I, adults incubating eggs; N, chicks in nest; PF, pre-fledged chicks well developed but unable to fly. Pelican body mass data are taken from Brown & Urban (1969).

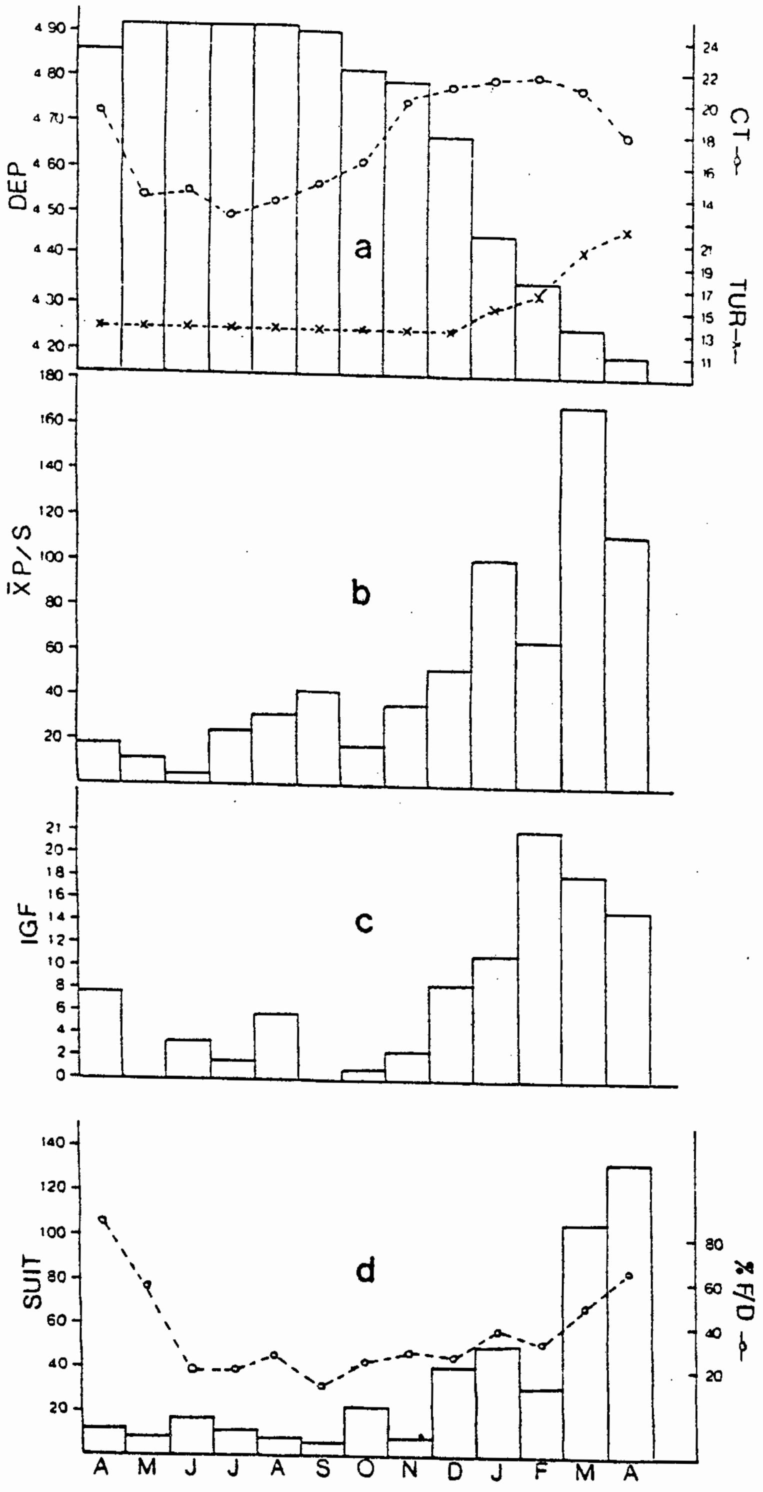

Fig. 5.3. Temporal variation in 'pelican' and environmental variables at Rondevlei during 1977-78. See Table 5.1 and the 'Sampling methods and data' section for explanations of the abbreviations.

Table 5.2. Data for Sanctuary visitation and foraging activity for Great White Pelicans at Rondevlei and for environmental variables to which these 'pelican' variables were related

	'Pelican' variables									Environmental variables									
Month	$\bar{X}$P/S*	C$\bar{X}$	CMAX	CMIN	$\bar{X}$F/S	%SCAN	%F/D	IGF	SUIT	DL	LRF	CRF	W	LT	CT	SDT	CC	DEP	TUR
April	18.31	27.00	43	2	13.92	68.75	76.02	60	0.23	48	66.9	74.6	6.11	17.1	18.8	18.75	4.17	4.86	0.011
May	11.19	10.55	18	3	5.55	78.72	46.60	20	0.17	47	93.6	110.5	4.72	14.6	13.8	17.83	0.75	4.92	0.011
June	3.71	9.00	10	8	0.38	26.67	10.24	10	0.74	45	85.3	25.3	1.80	14.0	13.9	16.42	0.25	4.92	0.011
July	24.28	10.33	25	2	2.21	61.70	9.10	0	0.32	47	100.3	279.9	0.91	12.1	11.9	14.36	4.45	4.92	0.011
August	31.48	12.81	53	1	5.04	56.25	16.01	0	0.19	48	79.9	210.8	6.39	12.9	13.3	15.88	0.68	4.92	0.011
September	42.18	23.00	161	3	0.36	30.00	0.85	10	0.15	50	47.4	32.3	1.03	13.9	14.6	18.33	5.64	4.91	0.011
October	17.62	22.80	85	3	2.26	51.22	2.83	50	0.24	61	33.9	15.1	0.96	16.1	16.1	17.10	1.75	4.87	0.011
November	35.97	19.33	93	2	6.34	36.07	17.63	80	0.18	61	21.4	5.6	7.02	18.0	19.8	18.39	7.12	4.80	0.011
December	52.27	27.29	40	5	8.06	49.20	15.42	95	0.54	63	8.8	18.3	6.81	19.5	20.9	21.59	1.34	4.68	0.011
January	125.02	55.88	154	17	35.38	45.31	28.30	95	0.34	64	8.6	7.1	1.15	20.6	21.5	23.53	1.17	4.46	0.013
February	64.37	66.33	140	7	13.99	57.35	21.73	95	0.43	68	15.2	0	1.39	20.9	21.5	23.90	5.42	4.40	0.014
March	170.19	122.48	211	16	65.66	85.94	38.58	85	0.52	64	13.8	21.8	9.38	19.6	20.7	19.09	0.82	4.26	0.020
April	133.84	68.50	101	32	70.32	74.03	52.54	70	0.56	76	66.9	26.0	0.38	17.1	17.9	16.98	7.53	4.20	0.022

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* see Table 5.1 and text for explanation of abbreviations.

between 'pelican' and environmental variables (Tables 5.3 & 5.4) show that water depth (DEP) and turbidity (TUR) are consistently and strongly related to measures of Sanctuary visitation. Depth is significantly negatively correlated, and turbidity positively correlated with virtually all 'pelican' variables. Sanctuary visitation patterns and environmental variation during my survey period seem to have been fairly typical of long term variation at Rondevlei. Long term monthly rainfall and temperature, $C\bar{X}$, CMAX, were strongly correlated ($r = 0.89, 0.72, 0.82, 0.98$; $P < 0.01$) with their survey period counterparts. CMIN and DEP were marginally non-significantly correlated ($r = 0.47$ and 0.49; $0.05 < P < 0.10$) with their survey period counterparts. Results of correlation analyses between Sanctuary visitation data and water depth and rainfall during 1956-78 (Table 5.5), show that depth and rainfall are significantly negatively correlated with $C\bar{X}$ and CMIN.

Discussion and Conclusions

Breeding

The marked wave-like breeding in Great White Pelicans which nest at Dassen Island is similar to that found in other populations of ground nesting Pelecanus spp. in Africa (Brown & Urban 1969; Crivelli, in litt.) and the United States (Knopf 1979). Unlike these other populations, the wave like breeding at Dassen Island was virtually discrete, i.e. the interval between the initiation of each wave was of the order of two months rather than a few days. In some Pelecanus populations, e.g. at lake Shala, Ethiopia (Brown & Urban 1969), and Darling River, Australia (Macgillivray, 1953), breeding pelicans succeed one another at the

Table 5.3. Correlations between 'pelican' and environmental variables at Rondevlei during 1977-1978

	Variables									
	$\bar{X}$PS@	C$\bar{X}$	CMAX	CMIN	$\bar{X}$FS	%SCAN	%F/D	IGF	SUIT	DL
C$\bar{X}$	0.92*									
CMAX	0.77	0.80								
CMIN	0.81	0.67	0.42							
$\bar{X}$FS	0.93	0.86	0.57	0.90						
%SCAN	0.42	0.51	0.10	0.33	0.58					
%F/D	0.28	0.33	-0.03	0.36	0.51	0.68				
IGF	0.76	0.85	0.56	0.62	0.73	0.44	0.38			
SUIT	0.88	0.82	0.50	0.93	0.96	0.51	0.37	0.71		
DL	0.73	0.69	0.57	0.71	0.69	0.22	0.13	0.70	0.76	
LRF	-0.52	-0.56	-0.68	-0.18	-0.28	0.14	0.13	-0.50	-0.29	-0.68
CRF	-0.49	-0.52	-0.65	-0.31	-0.39	-0.08	-0.19	-0.41	-0.38	-0.73
W	0.12	0.21	0.04	-0.23	0.11	0.32	0.30	0.11	0.02	-0.08
LT	0.60	0.67	0.56	0.39	0.48	0.14	0.27	0.73	0.46	0.75
CT	0.59	0.64	0.56	0.36	0.47	0.10	0.29	0.70	0.45	0.73
SDT	0.39	0.44	0.48	0.17	0.18	-0.06	0.11	0.58	0.16	0.52
CC	0.08	0.05	0.20	0.20	0.14	-0.07	0.11	0.12	0.14	0.37
DEP	-0.91	-0.90	-0.66	-0.84	-0.89	-0.43	-0.34	-0.89	-0.90	-0.87
TUR	0.86	0.84	0.54	0.89	0.95	0.56	0.40	0.73	0.96	0.70

	LRF	CRF	W	LT	CT	SDT	CC	DEP	TUR
CRF	0.82								
W	0.22	-0.12							
LT	-0.86	-0.79	0.21						
CT	-0.87	-0.80	0.29	0.98					
SDT	-0.79	-0.69	0.04	0.87	0.84				
CC	-0.05	-0.31	-0.28	0.07	0.15	-0.01			
DEP	0.53	0.56	-0.01	-0.73	-0.70	-0.50	-0.22		
TUR	-0.20	-0.34	0.01	0.39	0.37	0.09	0.25	-0.89	

@ see Table 5.1 and text for explanation of abbreviations.

* critical significance levels are: $r = 0.51$, $P < 0.05$; and $r = 0.64$, $P < 0.01$.

Table 5.4. Summary of significant results of 'pelican' vs environmental variables

	Pelican variables							
	$\overline{X}$PS*	C$\overline{X}$	CMAX	CMIN	$\overline{X}$FS	%SCAN	IGF	SUIT
Environmental variables	DEP	DEP	LRF	TUR	TUR	TUR	DEP	TUR
Relation	-	-	-	+	+	+	-	+
R^2	0.84	0.82	0.47	0.79	0.92	0.32	0.81	0.93

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* see Table 5.1 and text for explanation of abbreviations.

Table 5.5. Correlations between 'pelican' and environmental variables at Rondevlei between 1956 and 1978

Variables	$C\overline{X}$@	CMAX	CMIN	DEP
CMAX	0.885*			
CMIN	0.873	0.601		
DEP	-0.176	-0.120	-0.179	
RF	-0.219	-0.119	-0.270	0.074

@ see Table 5.1 and text for explanation of abbreviations.

* critical levels of signicance are: r = 0.16, P = 0.05; r = 0.21, P = 0.01.

same nesting sites. Brown & Urban (1969) and Macgillivray (1953) suggest that the limited availability of suitable nesting sites may directly influence the timing of breeding for individual pelicans, and hence for the whole population. There seems to be no such limitation of suitable nesting habitat at Dassen Island, since the pelicans which comprised the three breeding waves, nested in different areas within the colony. If nesting habitat is not limiting, what then is influencing the wave-like breeding at Dassen Island?

Blus and Keahey (1978), Knopf (1979) and Crivelli (in litt.), suggest that age of breeding Pelecanus spp. affects the timing of breeding, with younger and possibly inexperienced birds, nesting later and less successfully than older ones. I feel that this hypothesis also is not a likely explanation for the wave like breeding at Dassen Island, since the breeding productivity of late nesting birds (i.e. the last two waves) was higher than that for those which nested in the first wave. Indeed, I suspect that some of the birds which failed to nest successfully in the first breeding wave renested, and were successful in one of the following waves.

A possible alternative hypothesis as to why the southwestern Cape pelicans breed in waves is that subsets of the population experience different ecological regimes, which provide the necessary quality/quantity of some critical resource (e.g. food) at different times. When a sufficient number of pelicans have satisfied their basic physiological requirements for breeding, and can gather in sufficient numbers for the necessary social stimulation (Nelson 1978), they can initiate a breeding wave. Waterbodies such as Rondevlei appear to be important feeding and 'socialisation' centres at the advent of the pelican breeding season (Chapter 4). Since food in the form of fish is of critical importance to developing pelican chicks (Brown & Urban 1969), I suggest that the fluctuating availability of fish prey and suitable foraging habitat are important, if not prime, factors which influence the timing of breeding in this population. The availability of prey and foraging habitat at Rondevlei is, in turn, influenced by variation in water depth and temperature, and this is reflected in the patterns of pelican Sanctuary visitation and foraging activity.

Sanctuary visitation and foraging

All measures of Sanctuary visitation, foraging and foraging suitability are negatively correlated with the water depth at Rondevlei, or appropriately related to environmental variables which are significantly correlated with water depth, e.g. turbidity (Tables 5.3 and 5.4). I suggest that the causal nature of this strong statistical relationship could be the effect of decreasing water depth on the amount of suitable foraging habitat (i.e. relatively open water less than 1m deep, Chapter 4). When water depth at Rondevlei is greatest, the availability of shallow open water foraging habitat is at its minimum (Banks 1980).

Day length and temperature, which are positively correlated with Sanctuary visitation and/or suitability, have an indirect effect on Great White Pelicans. This effect is mediated through their influence on the availability of carp Cyprinus carpio, the major (in terms of numbers and biomass) prey species of Rondevlei Great White Pelicans (Middlemiss 1974). During periods of longer and warmer days, carp are more active (Hamman 1980; Hamman et al., 1980) and respond to the resulting increased water temperature by congregating and foraging in shallow water (Cambray et al. 1978; K.C.D. Hamman pers. comm.), thus increasing their availability to foraging pelicans. Seasonal variation in rainfall also has an indirect influence on Sanctuary visitation. During periods of heavy rainfall, water depth increases, although with somewhat of a lag effect, and the water temperature decreases. Both of these consequences of rainfall adversely affect the availability of carp to pelicans, since the fish become less active and seek out warmer deeper water (Hamman 1980; Hamman et al. 1980).

One possible direct effect that increased day length could have on my pelican study population would be to allow the birds to spend more time foraging, i.e. to satisfy their own physiological requirements for reproduction, and the food quality/quantity needs of their growing chicks. If this were the case in this study, one would expect to find significant, high positive correlations between day length (DL) and the percentage of daily scans in which pelicans were observed foraging (%SCAN) and the percentage of pelicans seen foraging during the day (%F/D). Since I found no such correlations (Table 5.3), my study animals appear not to have taken advantage of the potentially extra foraging time. Therefore, I feel that day length is probably little more than a cue to the pelicans of the state of more important environmental variables, i.e. food and foraging habitat.

If one superimposes diagrams of Sanctuary visitation, suitability and group foraging (Figs. 5.3b-d) over the diagrams of breeding and food requirement at Dassen Island (Fig. 5.2), it can be seen that Sanctuary visitation, social foraging and foraging suitability start rising in November-December, when the chicks of the first breeding wave have become independent of the nest. All three of these variables reach their highest values in February-April, i.e. during the second half of the breeding season, when the food requirement of the colony is at its peak due to the overlap of breeding waves.

The one environmental variable which was anomalously related to the 'pelican' variables was water turbidity. Unexpectedly, high turbidity had apparently no adverse effect on pelican foraging efficiency since the foraging suitability at Rondevlei is at its highest during periods of high turbidity (Figs. 5.3a and 5.3b). This conclusion is supported by S. K. Eltringham (pers. comm.), who has observed large numbers of pelicans foraging at Rwenzorie National Park, Uganda, despite continuously high turbidity. The strong positive statistical correlation between turbidity and 'pelican' variables is therefore probably spurious due to the strong correlation between turbidity and depth. Nightingale (1975) and Whitfield & Blaber (1979b) suggest that turbidity does influence foraging pelicans by causing them to change their foraging technique. They observed a high incidence of social foraging in relatively clear water. However, no correlation has yet been demostrated quantitatively between turbidity and foraging efficiency. One possible hypothesis which could be tested experimentally, is that high turbidity is in fact beneficial to foraging pelicans. In other words, increased turbidity may hinder the predator detection ability of the fish prey, and pelicans can thus get closer to the fish, and catch them more easily. This hypothesis is consistent with M. Bruton's (pers. comm.) suggestion, that in turbid water fish rely more on the lateral line system than on vision and therefore cannot precisely detect the direction of the approaching predators. Moreover, in turbid water fish easily panic and do not perform coordinated escape responses to the approach of a predator.

Long term patterns

Finally, water depth and rainfall, important environmental predictors of survey period Sanctuary visitation, were significantly and similarly related to measures of Sanctuary utilisation during 1956-78 (Table 5.5). This suggests that factors which seem to have influenced the use of Rondevlei by Great White Pelicans during 1977-78 may also have influenced Sanctuary visitation over the long term. However, a low correlation (albeit statistically significant) between two variables, as I have between 'pelican' and environmental variables in Table 5.5, is, at best, weak evidence of cause-effect relation. What is needed to evaluate such a relation is independent evidence. Banks (1980) provides this supportive evidence, since she found a highly significant negative correlation between utilisation of Rondevlei and water depth for many waterbird species, including _P. onocrotalus_.

Conservation

It is essential that Dassen Island, the only breeding site for this Great White Pelican population, be mantained disturbance free. Also, it might be productive to attempt to re-establish the Seal Island breeding site, e.g. by fencing off the former nesting areas. Since even important waterbodies such as Rondevlei appear to vary temporally in their use as foraging and roosting sites for pelicans it is desirable that alternative sites be provided and maintained. The need for additional foraging and roosting sites is especially acute during holiday periods, when many otherwise suitable sites are disturbed by recreational activities.

CHAPTER 6. Energy requirements of a Great White Pelican population and its impact on fish stocks

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The pelican family (Pelecanidae) comprises large fish-eating birds with a wide distribution both in the old and new world. The Great White Pelican Pelecanus onocrotalus occurs throughout the African continent where it commonly congregates into large colonies of several thousand breeding pairs, with the largest known colony, at Lake Rukwa, estimated to contain up to 40 000 pairs. The species may therefore be a major consumer of freshwater fish stocks of such lakes, and may compete with other fish consumers, including man. For this reason there have been several detailed studies of its biology (e.g. Brown & Urban 1969; Din & Eltringham 1974; Din 1979; Whitfield & Blaber 1979b) and attempts have been made to assess the food consumption by Great White Pelican populations (Din & Eltringham 1974; Din 1979; Berruti 1983), often assuming that pelicans consume daily a mass of fish equal to 10% of their body mass.

Previous analyses of the impact of Great White Pelicans on fish stocks have been further hindered by the fact that populations under study have consisted of several groups from discrete breeding colonies which have overlapping foraging and nonbreeding ranges. As a consequence, it has been difficult to obtain data on the seasonal variations in numbers, activity budgets, and breeding biologies of all the groups using particular foraging areas.

In this paper I present an analysis of the seasonal variations in energy demands of a small and discrete Great White Pelican population. I use an integrative bioenergetics approach (Kendeigh, Dol'nik & Gavrilov 1977) based on the model described by Furness & Cooper (1982). From an intensive study of this discrete population I have been able to assess energy demands over the period of one year for existence, flights at and between feeding sites, flights from the breeding colony to feeding sites, foraging, egg production and chick rearing. This paper therefore allows me to assess the impact of pelicans on their prey, to examine the seasonal variations in energy expenditures, to examine the relative amounts of energy allocated to different activities, and to assess how appropriate it may be to assume a food consumption of 10% of body mass per day. These considerations may be of value both for academic studies of bioenergetics, and for those interested in management assessment of the impact of fish predators.

Methods

Study area

The population of Great White Pelicans in the southwestern Cape Province of South Africa comprises a compact group of about 600 birds. These breed at a single locality and feed at a number of waterbodies which are all accessible and have been subject to simultaneous observations and censuses (Cooper 1976, 1977, 1978, 1979; Chapters 4 and 5). Foraging sites include both natural and man-made lakes, open and closed estuaries and rivers (listed in Chapter 4). Since pelicans feed by driving fish into shallow water, the length of shoreline m y be as important a parameter as the surface area of feeding sites. Total shore length and surface area of utilised sections of water bodies were obtained from 1:50 000 maps (Director of Surveys & Mapping 1966-80). Distances and areas were calculated using a digitizer analysed by a Tektronix graphic computer system. In order to compare results for the Cape population with another population, the same measurements were made for the waterbodies used by Great White Pelicans in the Rwenzorie National Park (Din 1979). In this case measurements were digitized from a 1:625 000 scale map.

Prey availability

Since pelicans are very intolerant of disturbance I avoided handling birds to obtain food samples. Their indiscriminate feeding technique (Whitfield & Blaber (1979b) and Din (1979) stated that Great White Pelicans take fish of appropriate sizes much in proportion to the species composition present) allowed me to assess prey availability from data on the fish size and species composition in the utilised water bodies (Millard & Scott 1953; Talbot 1954; Middlemiss 1974; Hamman et al. 1977; Noble & Hemens 1978; Ratte 1978; Gaigher & Thorn 1980; Grindley et al. 1980; Heydorn & Grindley 1981). Species which are unavailable to pelicans owing to their depth distribution were distinguished from those likely to have been pelican prey. Maximum prey sizes taken by Great White Pelicans were reported by Berry et al. (1973), Berruti (in litt.) and Middlemiss (1974). Only fish below the mean of these three estimates were considered to be potential pelican prey.

Since many of the water bodies used by pelicans have not been surveyed for their fish populations I used the detailed data from Seekoevlei (freshwater lake), Sandvlei (estuarine lake) and Botrivier (riverine lagoon) to represent these three habitat types; I believe these to be typical of their habitat types since casual observations at other sites indicate that the same dominant fish species are present.

Computing energy expenditures

Collection of activity budget data and breeding data is described in detail in Chapters 4 and 5. Fish consumption by the pelican population was estimated over a period of one year using a bioenergetics model adapted from Furness & Cooper (1982). Limitations of this approach are discussed by Furness (1982). In applying the model to the study population of pelicans there were few difficulties since detailed data were readily available for all the most important parameters. The pelican population was assumed to consist of 600 adults of which 200 pairs bred, laying 1.75 eggs per nest and making 1.33 breeding attempts per pair per year (Chapter 5). Annual adult mortality was taken to be 20%, first year mortality 41% and mortality of chicks at fledging 10% (Strait & Sloan 1974). I assumed that pelicans first bred when 3 years old (Brown et al. 1982). Incubation takes 35 days and chick rearing 75 days (Brown et al. 1982). Hatching success was calculated to be 75% and fledging success 41% in order that the population should have a zero rate of increase in the model. Adult masses were taken to be 11.5 kg for males and 7.6 kg for females (Din & Eltringham 1977). Mean egg mass is 177 g (derived from Brown & Urban 1969 assuming initial egg density of 1.04 g/cm^3). I have assumed that pelicans fly at 45 km/hr and that 80% of flying time is spent in flapping flight and 20% in gliding flight. These values are a compromise between data presented by Feely (1962) and Pennycuick (1972) and also take account of the situation in the southwestern Cape Province where the breeding site is an offshore island (Dassen Island) so that soaring flight is difficult for birds commuting between colony and feeding areas. Also, since the population is rather small, flock sizes tend to be small so that there is limited scope for energy savings through flock formation, which allows a greater proportion of gliding flight (O'Malley & Evans 1982a, 1982b). The weighted average distance (weighted in proportion to numbers using each site) from breeding colony to feeding vleis (water bodies) was calculated to be 110 km and I added a further 1.5 km to this to allow for initial circling to gain height at the start of each flight. Mean inter-vlei distance was calculated at 11 km. All nonbreeders were assumed to be on the feeding vleis rather than visiting the colony, and breeders were estimated to visit the feeding sites from the colony 0.5 times per day per pair between initial arrival at the colony and the 28th day after hatching, once per day per pair between days 28 and 42, and 0.6 times per day per pair between day 43 and chick fledging (L.H. Brown, pers. comm.).

Activity budgets at feeding vleis were derived from Chapter 5. The mean calorific value of fish was taken to be 4 kj/g wet weight, computed from published values for the main prey species (Cummins & Wuycheck 1971: Marais & Erasmus 1977; Ratte & Hanekom 1980; Whitfield 1980). A review of fish species known to be included in Great White Pelican diet elsewhere in Africa (Whitefield & Blaber 1979b) suggests that this value is probably appropriate for the species' food in this and other parts of the continent. Chick growth was assumed to be logistic and to follow the equation:

$$Wt = \frac{12\ 000}{1 + 59e^{-0.115t}} \quad (g)$$

derived from Portman (1937).

Food utilization efficiency was taken to be 80% (Kendeigh et al. 1977) and the bioenergetics equations used were derived from

Kendeigh et al. (1977) and were as follows:

Existence $0^{\circ}C$ $17.33W^{0.5444}$ kj/day
$30^{\circ}C$ $4.47W^{0.6637}$ kj/day

Using temperature data in Schulze (1972) I interpolated linearly between these extremes.

Flapping flight $M = 1.395W^{0.67}$ kJ/hr
Gliding flight $M = 0.091W^{0.7347}$ kJ/hr
Chick daily budget $M = 5.661W^{0.814}$ kJ/day
Egg production $M = 5.439$ (egg wt) x 100/73 kJ/egg

I carried out a sensitivity analysis to discover which parameters most influenced model output; for this Great White Pelican population the estimate of annual consumption is most sensitive to the values of population size, adult body mass, food utilisation efficiency, calorific value of prey fish, flight costs and time spent in flight. The first four of these parameters are accurately known (within 5%) but flight costs and time spent flying are less certain. However, flight represents only about 14% of the total energy budget (see below) so that even rather large errors in my estimates will not have too great an influence on the overall calculation.

Results

Available prey

Fish species in the utilised water bodies are listed in Table 6.1. From the availability of suitable fish prey (Fig. 6.1) it is clear that Great White Pelican predation is largely of *Cyprinus carpio* and *Oreochromis mossambicus* in lakes. *Liza*

Table 6.1. Fish species of water bodies in the southwestern Cape region utilised by Great White Pelicans; all species representing at least 1% of the total gill-net catch (by numbers) are given (data sources Hamman et al. (1977); Ratte (1978) and Gaigher & Thorne (1980)); species unavailable to pelicans are given in parentheses

	Seekoevlei (freshwater lake)	Sandvlei (estuary)	Botrivier (riverine lagoon)
Number of fish caught:	12 624	8 478	12 636
Fish species	%	%	%
Cyprinus carpio	53.6	0.3	0.0
Oreochromis mossambicus	46.4	0.1	0.0
Liza richardsoni	0.0	82.2	23.2
Lithognathus lithognathus	0.0	5.1	9.4
Mugil cephalus	0.0	5.8	2.6
Hepsetia breviceps	0.0	0.0	44.2
Rhabdosargus globiceps	0.0	5.1	0.0
Gobius spp.	0.0	0.0	8.1
(*Galeichthyes feliceps*)	0.0	0.0	5.4
Gilchristella aestuaris	0.0	0.0	4.6
25 other species	0.0	1.1	2.5

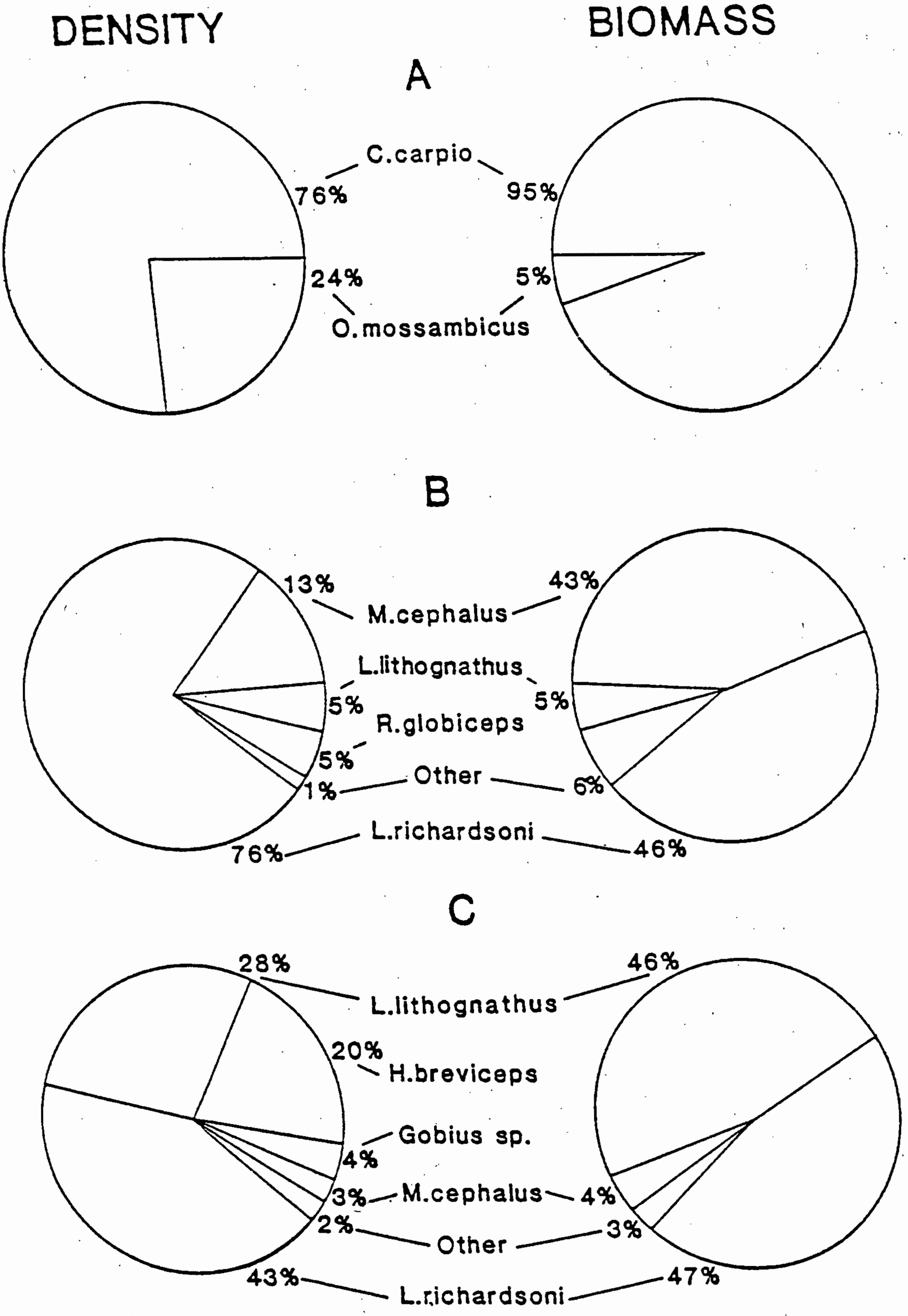

Fig. 6.1. Estimated availability of prey fish species to Great White Pelicans in the southwestern Cape Province in terms of fish numbers or density, and fish biomass in the water systems. A: Seekoevlei (freshwater lake), B: Sandvlei (estuarine lake), C: Bot River (riverine lagoon).

richardsoni and Mugil cephalus in estuaries, Liza richardsoni and Lithognathus lithognathus in riverine lagoons. The species of fish which, for reasons of their depth distribution, are unavailable to pelicans, represent only a very small fraction of the total fish populations (Table 6.1). However, some fish are outside the preferred size range and so the composition of Fig. 6.1, which accounts for the observed size classes as well as species composition, is not quite identical to the composition by numbers, as given in Table 6.1. In general, most of the fish production in each type of water body is available to pelicans as food.

Energy requirements

Weekly energy requirements for different aspects of the total budget are shown in Fig. 6.2. The overall annual energy requirement of the population was 7.4×10^8 kJ. Assuming a calorific value of 4 kJ g^{-1} (see methods), this is equivalent to 184 tons of fish.

Of the total annual energy budget, 69% is required for adult existence, 17% for chicks, 9% for flight between and at feeding sites, and 5% for flights between the breeding colony and feeding sites.

Impact on fish stocks

The total surface areas and shore lengths of utilised water bodies in the southwestern Cape Province and Rwenzorie are presented in Table 6.2. Although the pelican population at Rwenzorie is very much larger than that in the southwestern Cape, the utilised water area at Rwenzorie is also very much larger.

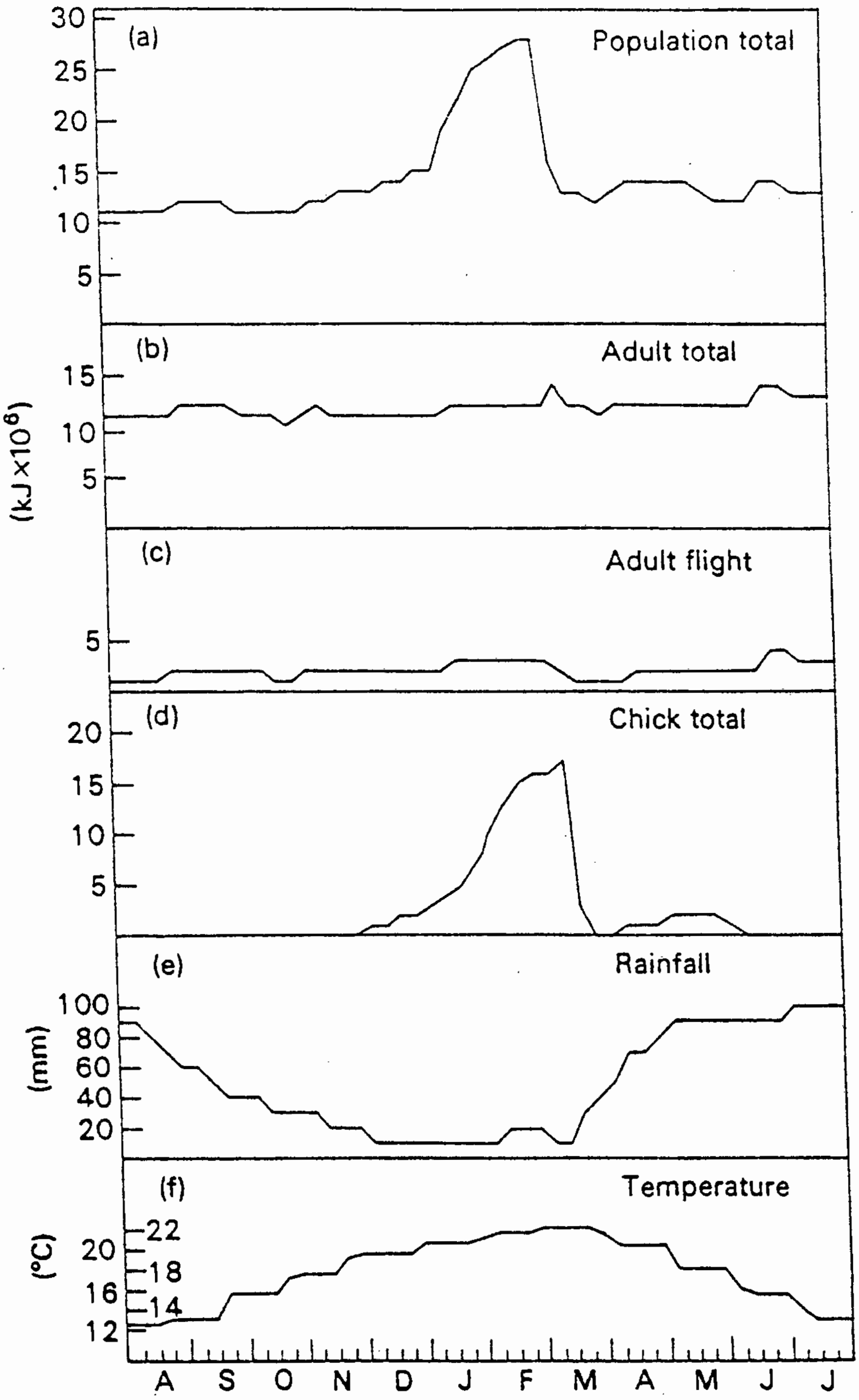

Fig. 6.2. Weekly values of Great White Pelican energy requirements for (a) population total, (b) adult total, (c) adult flight, (d) chicks (all expressed as kJ x 10^6) and variation in (e) rainfall and (f) mean ambient temperature; last two parameters obtained from long-term averages from meteorological office records.

Table 6.2. Physical parameters, Great White Pelican densities and estimated fish consumption in the southwestern Cape region and Uganda

	Surface area (km^2)	Length of shoreline (km)	Pelican density		Estimated fish consumption $kg\ km^{-2}\ year^{-1}$	
			pelicans per km^2	pelicans per km of shoreline	my data	Din (1979)
Southwestern Cape	74	427	8.1	1.4	2 500	
Rwenzorie	930	323	1.9	5.3	580	766

Din (1979) estimated that each Great White Pelican at Rwenzorie consumed 1 009g fish per day. My estimate for the southwestern Cape population suggests an average daily consumption per adult of only about 840g. The apparent difference may be due to the crude estimate of fish consumption used by Din (10% of body weight per day) and to inaccuracies in my calculations, or may reflect a real difference in the activity budgets of birds in the two populations. I have estimated the annual consumption of fish per square kilometer assuming my own figure for fish consumption to apply to both populations, and for comparison have also used Din's figure for Rwenzorie (Table 6.2). Because of the much smaller area of water used by the southwestern Cape population, the density of pelicans is greater in that region, so the energy demand per km^2 of water body is also greater (western Cape 2 500 Kg fish km^{-2} yr^{-1} vs. Rwenzorie 580 or 766 Kg fish km^{-2} yr^{-1}).

Discussion

Din & Eltringham (1974) multiplied the numbers of Great White Pelicans counted at periodic intervals by an assumed pro capita daily fish consumption and the number of days between census counts. Their estimate of daily food consumption by individual pelicans was obtained by weighing the stomach contents of a sample of birds and allowing a correction factor for the amount of time which would have remained that day for further feeding. Berruti (1983) was interested in fish consumption by a wide variety of species, including the Great White Pelican, and he estimated individual daily consumption by multiplying the estimated Standard Metabolic Rate (Lasiewski & Dawson 1967) by a factor of four to allow for the various additional costs of free living. Both these methods may be subject to criticisms.

Using stomach contents or other field estimates of daily food intake is highly unreliable and studies on the same species can provide widely differing results. For example, estimates of daily fish consumption by guillemots (*Uria aalge*) and *Uria lomvia*) vary over a 10-fold range according to different workers (Furness 1984). Brown & Urban (1969) and Din (1979) suggest that Great White Pelicans consume each day a quantity of fish approximately equal to 10% of their body mass. This value is within the range quoted by a number of other authors for fish-eating birds. Bowmaker (1963) suggests that Long-tailed cormorants *Phalacrocorax africanus* have a daily intake of 14% of body mass. Love (1983) suggests that Sea eagles *Haliaeetus albicilla* consume the equivalent of 9% of body mass per day, though Golden eagles *Aquila chrysaetos* take only 5% per day (Fevold & Craighead 1958). Variations between these estimates will be due not only to difficulties in measuring these values directly, but also to differences in the energy allocation patterns between species, and within species between seasons, populations, and breeders or non-breeders.

Similarly, Berruti (1983) could have chosen a factor of two or three rather than four to allow for increased costs of free-living over Standard Metabolism. The correct factor will depend on several things, including the particular activity budget of the birds in question.

The total consumption of 7.4×10^{8} kJ by the southwestern Cape population of, on average, 600 Great White Pelicans, plus their chicks, can be expressed as an average of 1.2×10^{6} kJ per individual per year, accounting for the provisioning of chicks as well as maintenance. This figure may be converted to a daily requirement of 840 g (wet weight) of fish, which represents 8.8% of the mean body weight of adult males and females. This is not very different from the estimate of 10% used by Din (1979). The Standard Metabolic Rate of Great White Pelicans under thermoneutral conditions can be derived from equation 5.5 in Kendeigh et al. (1977). This gives a mean daily energy expenditure of males and females of 1 682 kJ. Thus Berruti's (1983) use of 4BMR (Basal Metabolic Rate) to estimate energy consumption equates with a daily food intake of 1.68 Kg, or 17.6% of mean body weight. This is twice as high as my estimate based on a detailed study of activity budgets and integrative bioenergetics calculation. The use of 4BMR is not without precedent. Wolff et al. (1975) and Summers (1977) used this factor to estimate energy consumption by shorebird communities in two estuarine studies carried out outside the breeding season. My analysis shows that, over the year, 2BMR would be a more appropriate factor to use for Great White Pelicans. In fact, 4BMR appears to be about the maximum sustainable working level which any bird can achieve (Drent & Daan 1980) and is normally only reached during chick-rearing.

Where data allow analysis using an integrative bioenergetics approach this is clearly to be preferred since it accounts for details of the breeding performance and activity budgets of the population concerned. Where such details are lacking, a preliminary assessment may be reasonably made using an assumed daily consumption per adult of 10% of body mass, or of between 2 and 3 BMR. Twice the BMR may be more appropriate for studies covering the whole year or outside the breeding season, while 3 BMR may apply to the breeding season, when the work rates of birds are generally highest.

This study has shown that the energy budget of the Great White Pelican population of the southwestern Cape Province is largely determined by the costs of adult existence, since relatively little time is spent in flight. The breeding season is timed to coincide with the time of year when costs of adult existence and flight between feeding sites are at their lowest level (Fig. 6.2). Adult energy costs of moving between feeding sites are highest in June-September, when rainfall is at a maximum, so that water levels at foraging sites are high. With the rise in temperature and drying out of water bodies in October-November Great White Pelican foraging conditions improve (Chapter 5) and breeding begins as foraging flight costs are at a minimum. Ecological theory generally suggests that birds breed at a time which maximises the availability of food for the growing young (Lack 1966), and the tendency for Great White Pelicans to breed when water levels are low and foraging costs are correspondingly low fits with this general theory, since a reduced energy expenditure by adults in foraging will allow a greater energy allocation to the young.

How can I assess the impact of the pelican population on its food supplies? The annual production of fish in sub-tropical environments is generally around 10-20 g m^{-2} yr^{-1}, or 10 000-20 000 Kg km^{-2} yr^{-1} (Gerking 1978). Few studies of annual fish production in water bodies utilised by Great White Pelicans have been published, so it is difficult to give an accurate assessment of the proportion of the production taken by the pelicans. My figures suggest that the energy demand in the southwestern Cape Province (2 500 Kg fish km^{-2} yr^{-1}) is likely to represent between 10% and 25% of annual fish production. Predation by Great White Pelicans at Rwenzorie is clearly less

(580 Kg fish km^{-2} yr^{-1} according to my calculations applied to that population). Berruti (1983) showed that Great White Pelicans were responsible for about 80-90% of fish predation by birds at Lake St Lucia. His 4BMR estimate of their consumption suggests that they require 50 kJ m^{-2} yr^{-1}. If I correct this to a more likely 25 kJ m^{-2} yr^{-1} (2BMR) this represents about 6 000 Kg km^{-2} yr^{-1}, or 30-60% of annual fish production of the utilised areas of the lake. However, the deepest parts of the lake were ignored in Berruti's calculations and, while these may not be used for foraging pelicans, fish production in these areas may be utilised by pelicans if these fish move into shallower waters. There is clearly need for more accurate data on the quantities of fish produced in lakes used by pelicans, but the implication of these three studies is that Great White Pelicans take large quantities of the production of species such as Mullet and Carp. In the southwestern Cape Province and at Lake St Lucia freshwater stocks are of negligible importance for human food, but provide sport angling facilities. According to Noble & Hemens (1978) sport angling in South Africa lands a total of only 15 tons of fish annually, so that freshwater fish stocks are not heavily utilised and there is no conflict of interests between man and birds. However, Din (1979), using an assumed consumption per individual of 10% of body mass per day, which agrees fairly well with my findings, estimated that pelican consumption at Rwenzorie represented about 12% of the fish yield to man. Since the pelicans at Rwenzorie were apparently consuming only about one quarter as much fish per unit area as those in the southwestern Cape Province (Table 6.2), it is possible that the establishment of a human fishery in areas used by the Cape Province pelicans would lead to competition for this resource.

The Great White Pelican is assigned 'Red Data' status (Brooke 1984) in South Africa, since it breeds only at a small number of sites, and requires the use of a number of freshwater feeding areas. Successful conservation of this species may be aided by a clearer understanding of its trophic importance in freshwater food webs. This study suggests that it is a major consumer of fish, and that the quantity consumed may vary considerably between sites (Table 6.2). However, the analysis of pelican numbers in relation to surface area and shore length (Table 6.2) suggests that the total shore length may be as important a parameter as the surface area of the water body. Great White Pelicans at Rwenzorie may be unable to achieve the population density and fish consumption per km^2 found in the southwestern Cape Province because they feed on a lake with a much smaller shoreline in relation to its surface area (Table 6.2).

SUMMARY AND SYNTHESIS

As I suggested in the INTRODUCTION, the ecology and biogeography of African waterbirds differ strikingly from those of birds with non-aquatic habitats. In Chapter 1, I show that waterbirds partition Africa much more coarsely (i.e. have fewer avifaunal zones), and exhibit a longitudinal rather than a latitudinal gradient in species diversity (number of species), with higher diversity in the east. Moreover, I identify several geographically localized environmental events of ancient and/or recent origin (e.g. through habitat modification by modern man), which may have been, and continue to be, refugia for African waterbirds during persistent xeric conditions. However, present-day variation in the availability and quality of waterbird habitats are also major factors controlling the distribution, diversity and abundance of waterbirds in Africa. The subregion dominated by tropical rainforest is low in waterbird habitat diversity and quality, but temporally relatively uniform. The subregion dominated by savanna, is generally richer in waterbird habitat, but it is spatially and temporally much more variable. The relatively xeric zones in northeastern and southwestern Africa are both low in waterbird habitat diversity. However, the northeast arid zone is apparently characterized by more predictable fluctuations in waterbird habitat resources. This is possibly because climatic variation in this zone is more seasonal, and therefore more predictable, than the erratic climatic pattern in the southwestern zone.

In my southern African sub-continental analysis (Chapter 2), I study the east-west diversity gradient in much greater detail.

The eastern zone is characterized by relatively reliable, highly diverse waterbird habitat; whereas, the more xeric western zone is noted for its ephemerally superabundant waterbird habitat resources. Not unexpectedly, waterbird diversity and endemism are low in these relatively xeric areas. However, the east-west decline in waterbird diversity is not as steep as that for non-aquatic birds. Moreover, it is also not as steep for mobile waterbirds as it is for essentially sedentary waterbirds. This apparent incongruence is explained by the ability of mobile waterbirds to exploit ephemerally superabundant resources in dramatically fluctuating aquatic ecosystems, e.g. pans (seasonal ponds with no outflow) and vleis (flattish stretches of rivers with marshy vegetation and seasonally standing water) in the western half of southern Africa.

These conclusions are supported by the results of my ecosystem and species-level research. Long-term studies of the waterbird community structure at Rondevlei Bird Sanctuary (Chapter 3) and of seasonal variation in dispersion of the Great White Pelican <u>Pelecanus</u> <u>onocrotalus</u> (Chapter 4) show that highly mobile waterbirds respond rapidly to fluctuations in wetland habitat availability and suitability. Correlations between waterbird abundance and abiotic environmental variables are mediated through the effects of the latter on habitat and prey availability. Rainfall and water level have a marked negative influence on habitat availability, and higher water and ambient temperatures promote prey density. Thus, the results presented in Chapters 1-4 emphasize the need for the conservation of wetland biotope diversity and temporal succession, as opposed to individual waterbodies, waterbird species or groups of economically important species (e.g. ducks).

Moving to the species level aspect of this thesis, results of Chapters 4 and 5 reinforce conclusions based on the broad-scale studies in the first three chapters. The Cape Great White Pelican population and its effective conservation depend on the availability of spatio-temporally highly diverse water biotopes (e.g. natural and man made lakes, rivers and estuarine lagoons). In fact, unlike other pelican populations studied to date, the southwestern Cape population cannot rely on a few major water systems. For a large fraction of the year, these pelicans scatter among a number of small, irregularly utilised water systems. Therefore, ideally, all of these water bodies within the range of the pelicans should be maintained, whether utilised regularly or irregularly.

There is a need for an ecologically sound management policy for the southwestern Cape Great White Pelican population. It is a 'Red Data' species (Brooke 1984). It is also a major predator on fish stocks, and therefore is in potential competition with other piscivorous species, including man. The estimate, in Chapter 6, of the energy flow mediated through this discrete population of pelicans could be an important factor underpinning such a policy. This estimate could also be applied in studies of large and overlapping pelican populations elsewhere in Africa.

In conclusion, there is an urgent need for further, detailed studies of Africa's waterbirds and their habitats. Hopefully, I have shown that a better understanding of the biogeography and community ecology of African waterbirds can help scientists to understand key processes which sustain wetland ecosystems and consequently help conservation departments and the private sector to manage them effectively. The research comprising my thesis is only a crude beginning. Future studies of African (and other) wetlands clearly require an ecosystem approach focusing on key abiotic and biotic factors, and waterbirds should feature prominently in the latter.

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