POPULATION GENETICS, BEHAVIOURAL ECOLOGY AND MANAGEMENT OF THE GREYWING FRANCOLIN *FRANCOLINUS AFRICANUS*

by

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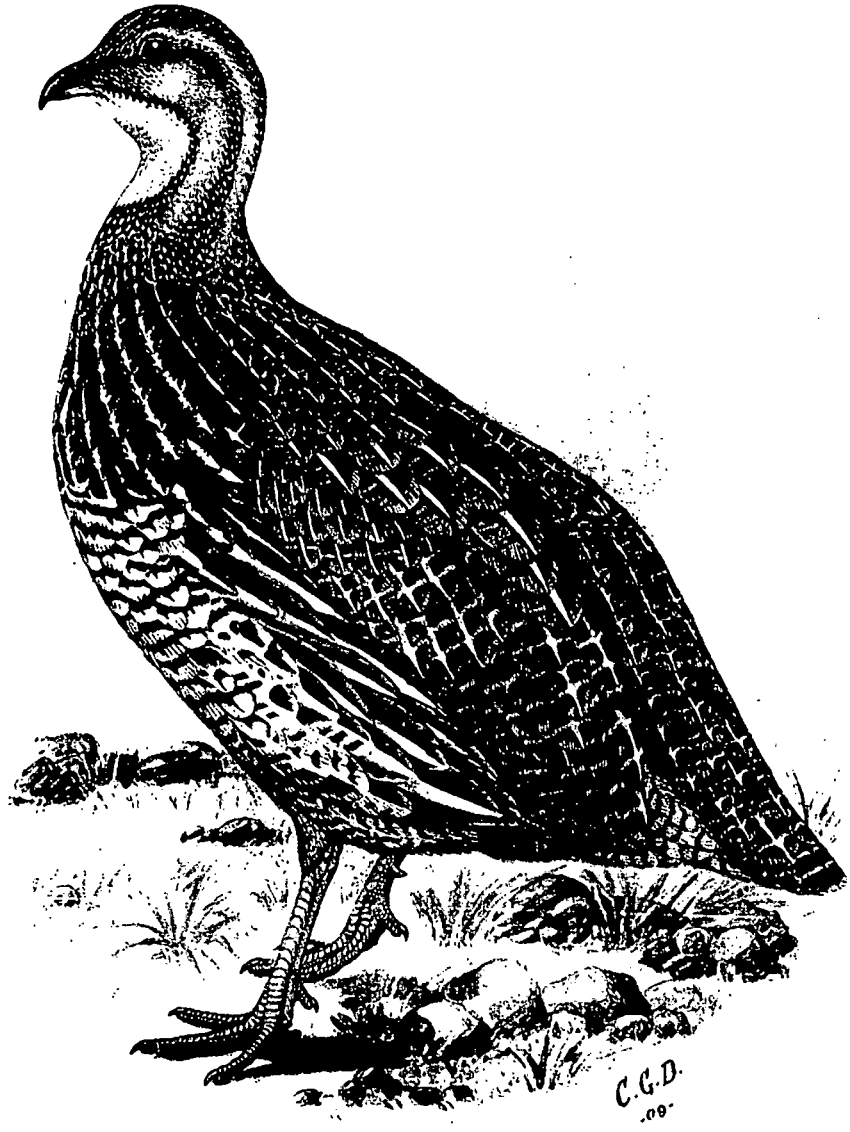
Submitted in fulfillment of the degree of Doctor of Philosophy

in the Faculty of Science (Department of Zoology),

University of Cape Town

August 1992


C.G.D.

DECLARATION

This thesis reports the results of original research I conducted under the auspices of the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, between 1988 and 1992. All assistance that I received has been fully acknowledged. This work has not been submitted for a degree at any other University.

Signed by candidate

Robin M. Little

To Lynn, my family,

my pointers and those special Greywing

Gremlin

'They live to run in search of Greywing'

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ACKNOWLEDGEMENTS

This study was made possible by the FitzPatrick Institute and the supporters of the Greywing Partridge Research Project. Peter Johnson was a constant source of enthusiasm and energy, and generated invaluable support for the project from farmers, hunters and gamebird enthusiasts. John and Sheryl Broster receive my dearest thanks for their hospitality, assistance and friendship toward myself and my family throughout our stay on the Stormberg. John's Greywing hunting operation formed the nucleus of most of the field projects underpinning this research.

I am also grateful to the people of the Stormberg for their hospitality and support, and to the farmers on whose properties I roamed - this area has as part of its heritage the 'heart' of Greywing country. The hunters who visited the Stormberg during the study gallantly endured my scrutiny of their hunting activities, and graciously tolerated my dissection of their prized quarry, I thank them for their valuable contributions. My family and I are indebted to Sandy and Non Stretton and Charles and Lyn Pope for their friendship and delightful accommodation during the study.

Dr Mike Mentis introduced me to the splendour of English pointers and the magic of Greywing Francolin. Many hours have been spent with my dogs, Gremlin, Hailey and Casual, and other canine friends, Doctor, Higgins, Bruce and Tess, working the hilltops for the pleasure of finding a covey of Greywing. I love them all for those splendid times. Other friends in the field were Luke Bell and Robert Stretton, both of whom have a special affection for the Greywing.

I am grateful to the South African Nature Foundation, the Foundation for Research Development (Post-graduate Bursary), the Bob Blundell Memorial Fund, the Percy FitzPatrick Memorial Trust, the University of Cape Town's Research and Equipment Committees and SASOL for financial aid. I am particularly grateful to The African Gamebird Research, Education and Development Trust for funding my appointment as Gamebird Research Officer at the FitzPatrick Institute.

I thank all my collaborators who offered their skills, expertise and laboratory assistance: Dr Roy Earlé (Department of Parasitology, Faculty of Veterinary Science, University of Pretoria, Onderstepoort), Dr Faadiel Essop (FitzPatrick Institute, University of Cape Town), Prof. Rob Gous (Department of Animal Science and Poultry Science, University of Natal, Pietermaritzburg), Dr Stewart Grant (Department of Genetics, University of the Witwatersrand) and Prof. Anna Verster (Department of Parasitology, Faculty of Veterinary Science, Onderstepoort). Stewart Grant also acted as supervisor of the genetic sections of my research and contributed meaningful discussion on theory of population genetics and population ecology. He also provided laboratory facilities within the Department of Genetics, University of the Witwatersrand, which enabled me to undertake research on the population genetics of Greywing.

I am grateful to Rob Leslie for writing a program to calculate spatial autocorrelation statistics, and to René Navarro for assistance with statistical interpretation of the growth models. Andrea Plös helped with graphics for various figures.

My wife, Lynn, deserves special praise for enduring many hours packaging and labeling genetic tissue and worm samples on cold Stormberg nights, and monotonous days measuring young Greywing, scribing while I counted arthropods, or volumetrically measuring crop contents while I muttered seemingly meaningless conversation about the glory of the Greywing. I will long remember her cartoons of Greywing prey items on the field-sheets illustrated during times of boredom and frustration.

I am grateful to Debbie Davies (Department of Animal Science and Poultry Science, University of Natal, Pietermaritzburg) and the staff at Allerton Regional Veterinary Laboratory for laboratory analysis of the nutritional contents of Greywing diet.

Special thanks are conveyed to Richard Brooke, Prof. Mike Gilpin, Dr Stewart Grant, Casper Heÿl, Dr Peter Hudson, Joris Komen, Dr Mike Mentis, Dr David Parkin and Prof. Anna Verster for constructive criticism of various chapters of my thesis.

Finally, I am particularly grateful to Prof. Tim Crowe for his support and continuous encouragement, guidance and friendship.

Little, R.M. 1992. Population genetics, behavioural ecology and management of the Greywing Francolin Francolinus africanus. PhD thesis, FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa. vi + 249 pp.

Abstract: This study investigates the population genetics and behavioural ecology of the Greywing Francolin, Francolinus africanus, and identifies factors which influence the distribution and abundance of this important gamebird. It also develops scientifically sound management strategies which should allow the maintenance of populations at levels which will produce sustained and economically viable hunting yields as a co-product of agriculture.

Examination of genetic variability based on allozymes disclosed estimates of average within-population heterozygosity higher than that for most birds, and for all other galliformes for which data are available. Thus, Greywing apparently have a high degree of population stability and large effective population sizes. Indirect estimates of migration and several significant allele-frequency differences between nearby coveys suggest that there is a greater degree of genetic subdivision among Greywing populations than among populations of other birds. However, although the data suggest that populations are genetically differentiated on a large geographical scale, they also indicate that there is considerable dispersal, which produces outbred subpopulations on a fine geographical scale. Greywing therefore have a wealth of genetic variability that may 'buffer' populations against environmental changes, responsible hunting and/or short-term demographic bottlenecks. They also appear to

undergo sufficient migration so that recruitment from adjacent populations will ensure population stability in hunted areas.

The timing of breeding in the Greywing is strongly correlated with the initiation of annual rains in the summer-rainfall, grassland regions of Natal, Lesotho and the eastern parts of the Orange Free State and Cape Province. However, in the winter-rainfall, Fynbos Biome of the southwestern Cape Province, the Greywing's nesting period is contracted and follows immediately after the cessation of the rainy season. The main causes of nest failure in Greywing populations on the Stormberg Plateau were predation by small carnivores and crows, and destruction by management fires. In order to minimize the effects of hunting on Greywing reproductive output, the hunting season should be from 15 April to 31 July in the summer-rainfall region and from 1 April to 30 June in the winter-rainfall region (currently 1 April-15 July in the Cape Province and 31 May-31 August in Natal). For the same reason, grasslands in the summer-rainfall region should not be burned later than the end of August.

Growth and development of young Greywing is rapid, with linear body measurements and plumage development approaching asymptotic values within 12 weeks. Sexual dimorphism was not significant in the development of young Greywing, and body mass was too variable to be reliable as an estimator of age. Linear body measurements and moult patterns are recommended for accurate age estimation of Greywing up to 12 weeks, with primary feather replacement reliable for aging at least up to 20 weeks. These techniques will be used to age birds in hunting bags for estimating annual variation in production and reproductive success.

Calling is strongly correlated with the annual social cycle, remaining at high levels from August to April. Calling was most frequent at sunrise, and was negatively correlated with wind speed. Comparison of calling frequency and population density showed that call counts (especially during March-April) can be used to estimate changes in year-to-year population density, as well as within-season variation among areas.

Greywing were not equally distributed over the land surface. As was reported by Mentis & Bigalke (1981a) for Greywing populations in the Natal Drakensberg, inherent landscape features, e.g. ridges, shelves, slopes and valleys, also influenced habitat partitioning of Greywing on the Stormberg Plateau. Furthermore, vegetation structure (i.e. successional stage of grasslands) is the primary factor influencing distribution of Greywing populations (Mentis 1992; Chapter 6), and annual variation in summer and autumn arthropod abundance is the primary diet-related influence on abundance of Greywing.

Most Greywing hosted helminths, and infestation was independent of host-sex. Although no pathological conditions were found, high overall prevalence, and seasonal peaks in worm burdens could pose potential threats to Greywing populations. Particularly if these parasites are density dependent on the host population, and Greywing numbers are increased by manipulative management, as was displayed by Red Grouse Lagopus lagopus populations in Scotland and northern England (Hudson 1986).

Investigation of the haematozoan parasites of Greywing again showed no evidence of pathogenic effects. However, the presence of Plasmodium juxtanucleare in 11% of Greywing examined might contribute to mortality rates because most of the infected birds

showed chronic infection. This parasite species has not previously been recorded in southern Africa.

Analysis of commercial Greywing hunting effort, efficiency and impact on Greywing populations showed that hunter effort and skill were not significantly different between years, and that hunter satisfaction was significantly correlated with the number of Greywing seen. Furthermore, comparison of the mean population density of areas shot at progressively higher percentage off-take showed significant reduction of the population in the year following the hunt, where above 50% of the population was removed. Therefore, for sustainable, economically viable hunting, groups of between four and seven hunters should be offered 50-65 Greywing per hunt, and populations should be hunted only once per season, removing no more than 50% of a covey.

Investigation of the effects of hunting on population and genetic structure suggests that although annual density cycles for hunted and unhunted Greywing populations were similar, hunted populations experienced a 'pulse' of immigration immediately after hunting and bred earlier. Nevertheless, average levels of allozyme heterozygosity for hunted and unhunted populations were identical ($\underline{H}$ = 0,076). Furthermore, the hunted populations displayed similar levels of outbreeding to those for unhunted populations. Therefore, although a 'pulse' of local immigration followed hunting, which apparently results in relatively fewer migrants into unhunted populations, I conclude that the effect of hunting at present levels of offtake (40-50% of the population) on Greywing Francolin populations has no apparent long-term influence on their genetic structures.

GENERAL INTRODUCTION

INTRODUCTION

It is evident that major changes have occurred in land-use and farming practices in South Africa during the last century, and that even more dramatic changes are in the making for land-use practices (Huntley et al. 1989). Recent publications provide evidence of the concern for developing a strategy for land-use as an accountable and goal-oriented industry within the 'new' South Africa's economy (Mentis 1989, 1990a, 1990b). Sustained agriculture and land-use, in general, must be designed around as profitable and viable a combination of co-products as can be utilized. Furthermore, for certain widespread, but low-density species, e.g. the White Pelican Pelecanus onocrotalus (Guillet 1985), many raptors (Accipiterformes) and cranes (Gruidae) (D. Allan pers. comm.), private landowners need to make an ever-increasing contribution to environmental conservation, if South Africans are to see their present biota persist through the next century.

Gamebird management and habitat improvement as a profitable co-product of agriculture can promote the conservation of wild biota and provide landowners with additional income necessary to maintain quality of life in the future South Africa. Realization of economic viability of gamebirds as a sustained yield will ensure the stability of gamebird populations, their habitat, and other non-target, sympatric taxa in the long-term, an achievement not always possible by 'pure' conservation.

The Greywing Francolin, Francolinus africanus Stephens 1819, (often called Greywing or Greywing Partridge) is a highly prized, southern African gamebird which inhabits montane grassland in the

Drakensberg range and woody communities in the western and southern Cape Province of South Africa (Fig. 0.1). Most of the Greywing's range is agricultural land, of which, in the eastern Cape, almost all is used for domestic livestock production. These privately owned grasslands could be managed for both wildlife production and agriculture if sufficient incentive and wisdom were created to unite the two industries. In order to manage these lands for wildlife, the basic ecological requirements of the species concerned and their socio-economic potential require examination.

The population biology and management of Greywing Francolins have been studied by Mentis (1973) and Mentis & Bigalke (1973, 1979, 1980, 1981a, 1981b) in an ecological context in the 'conserved' grasslands of the Natal Drakensberg. The present study was conducted primarily on privately owned land on the Stormberg Plateau ($31^{o}15'$ S; $26^{o}30'$ E), eastern Cape Province, South Africa, under commercial stock farming, and in situations in which Greywing have been hunted regularly over the last century. Therefore, these results provide essential comparative data useful for assessment of the effects of agriculture and hunting on this economically important gamebird. Greywing populations on the Stormberg co-exist with commercial livestock production, and have recently contributed economically to the district's farming community as a co-product of agriculture. Commercial rough-hunting of this species was established as a seasonal boost to farming revenue and since 1989 has been the largest source of outdoor recreational revenue in this area.

The objectives of this thesis are to investigate the population genetics and behavioural ecology of Greywing Francolin

populations within the agricultural grasslands of the Stormberg, and to present guidelines for management of Greywing Francolin in southern Africa.

The thesis is divided into ten chapters within four sections. The first section (Chapters 1 & 2) is an investigation of the geographical range, taxonomic status, evolutionary stability and population structure of the Greywing. The second section (Chapters 3-5) deals with aspects of behavioural ecology (breeding biology, calling behaviour and growth and development) which have relevance to either management of Greywing populations or assessment of variation in population density and age estimation. The third section (Chapters 6-8) focuses on influences on population regulation and presents the potential effects of habitat, diet and parasites (helminth and haematozoan) on Greywing distribution and abundance. The final section (Chapters 9 & 10) presents analysis of the hunting strategy and the effects of hunting on Greywing populations.

THE PRINCIPAL STUDY AREA

Location

Although published and unpublished information are summarized from various geographical areas within the range of the Greywing Francolin, the principal study area (unless otherwise indicated within the thesis) is located within the Molteno and Dordrecht magisterial districts of the eastern Cape Province, South Africa, between 31° S & 31°30' S and 26°15' E & 27° E and extends over approximately 1 800 km^2 (Fig. 0.1). Brief descriptions of the study area relevant to various chapters are included before the methods section of those chapters.

Topography

The principal study area covers most of the Stormberg Plateau and ranges in elevation from about 1 600 m a.s.l. to around 2 000 m a.s.l. The landscape comprises an undulating plateau, with shallow valleys, adjacent slopes, shelves of sedimentary substrata and ridge tops often capped with igneous substrata. The sedimentary substrata are made up of the Stormberg group which contains three distinctive lithostratigraphic units: the Molteno, Elliot and at the top the Clarens Formations. These are capped by the igneous Drakensberg Volcanics composed of tholeiitic basalts (Truswell 1977).

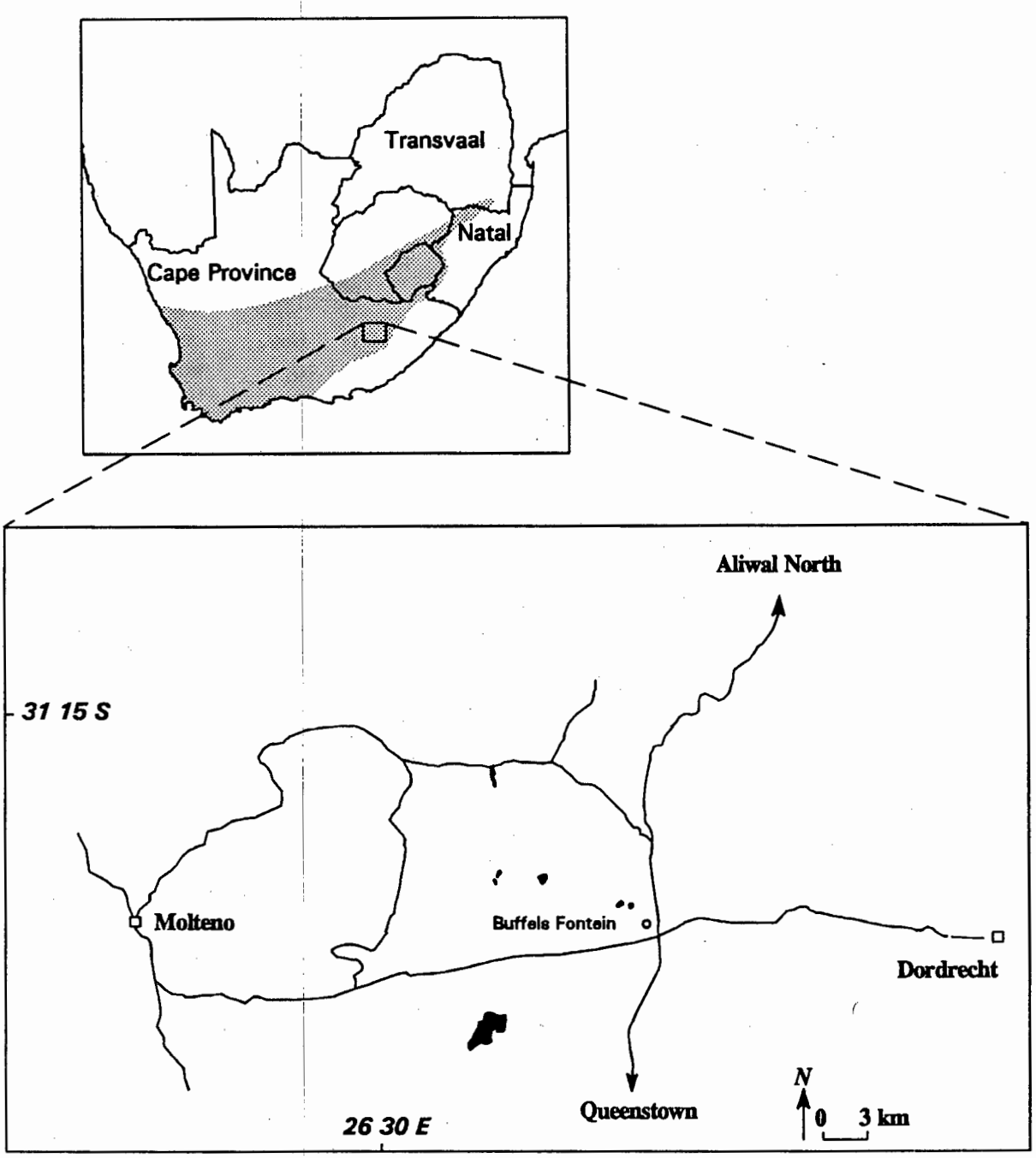


Figure 0.1. Range of the Greywing Francolin (stippled, Maclean 1985) and location of the principal study area.

Climate

The climate is mild to cold, with mild summers and cold winters (Fig. 0.2). Rain falls mostly during the summer months (November-March) and averages 542 mm per year (100 year average, 1885-1984; Anon. 1885-1990) (Fig. 0.2). Schulze & McGee (1978) disagree, in general, with the adequacy of fitting Köppen's climatic classification (Köppen & Geiger 1936) to the Acocks vegetation types (Acocks 1975). However, they agree that for the Stormberg the montane sweetveld biotope suitably fits the Köppen classification Cwb (temperate, with dry winters and the warmest months below 22^{o}C).

Snow and frost are common and severe during the winter months. Detailed rainfall, temperature, humidity, day length, cloud cover and wind speed records are presented in Chapters 3, 5 & 8. These data were recorded at Buffels Fontein farm (31^{o}22' S; 26^{o}42'E), an Agro-Meteorological weather station (#6029 Agricultural Meteorological Section, Grootfontein), located within the study area, 31 km east of Molteno (Fig. 0.1).

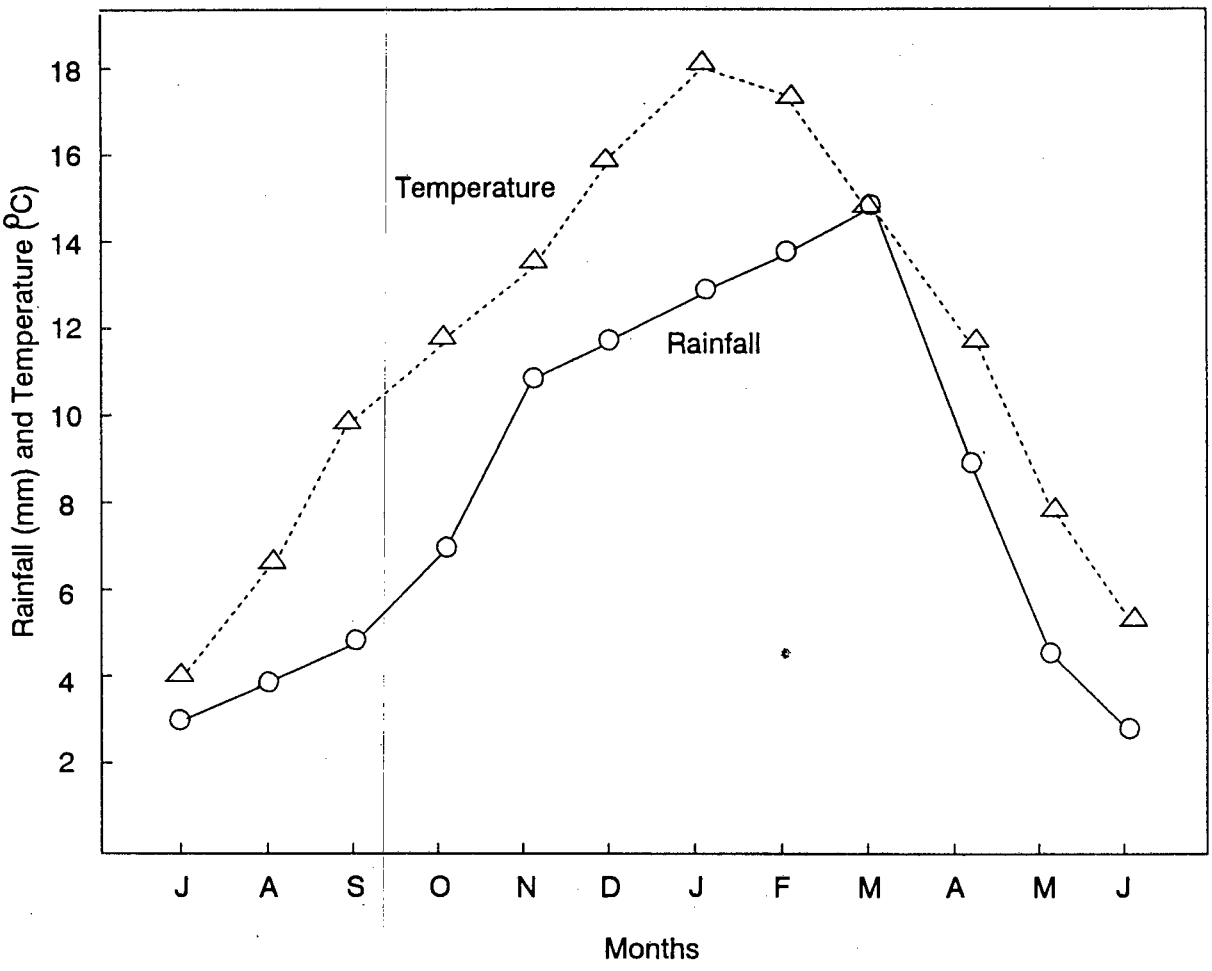


Figure 0.2. Distribution of mean monthly rainfall and temperature for the principal study area (Anon. 1885-1990).

Flora

The vegetation of the Stormberg is typical of the Afromontane Region (White 1978), characteristically of the lower slopes of highest mountains and the upper slopes of lesser mountains. At high elevation, as on the Stormberg, grasses and Cyperaceae become physiognomically dominant where the soil is shallow or the drainage is impeded.

Acocks (1975) placed the vegetation of this area in the Stormberg Plateau Sweetveld (veld type 59): a transitional stage between Themeda-Festuca Alpine Veld (veld type 58) and Karroid Merxmuellera Mountain Veld (veld type 60). Areas of relatively deep soils are dominated by Themeda/Tetrachne grasslands with Merxmuellera spp. dominant at higher elevations, on shallower soils. On degraded surfaces with extensive soil loss, invasion by Karroid False Fynbos is eminent. The grasslands of the region, as in most of the southern sub-continent can be regarded as highly modified. The domestic livestock grazing regime has generally resulted in selective grazing of more palatable grasses, causing an increase of less palatable species such as Elionurus muticus, Aristida diffusa and Eragrostis spp. In areas where grazing has removed the decreaser species (e.g. Themeda triandra and Tetrache dregei), particularly by continuous sheep grazing, species such as Karroochloa purpurea and Pentaschistis microphylla now dominate. The farmers of the region use presence of T. dregei as an indicator of good quality veld.

Fauna

The fauna of the Stormberg Plateau is typical of the montane grasslands of eastern South Africa. Distinct seasonality with short summers and harsh winters result in a fauna with seasonal fluctuations in both species richness and population densities.

Domestic livestock are the major large herbivores. Blesbuck Damaliscus dorcas phillipsi, Springbuck Antidorcas marsupialis and Black Wildebeest Connochaetes gnou have been 're-introduced' on some farms. Indigenous ungulates have been reduced to remnant populations of Grey Rhebuck Pelea capreolus, Mountain Reedbuck Redunca fulvorufula and Steenbuck Raphicerus campestris, of which the Grey Rhebuck is most common.

Small-mammals are well represented by colonies of fossorial Red Meerkat Cynictis penicillata, Suricate Suricata suricatta and Striped Ground Squirrel Xerus erythropus. The family Mustelidae is further represented by the Striped Polecat Ictonyx striatus, White-naped Weasel Poecilogale albinucha and Cape Clawless Otter Aonyx capensis. Other members of the family Viverridae recorded during the study were the Water Mongoose Atilax paludinosus and Cape Grey Mongoose Herpestes pulverulentus. The African Wild Cat Felis libyca was seen regularly in the study area, whereas the Caracal Felis caracal was scarse. Although the family Canidae has been heavily persecuted, Black-backed Jackal Canis mesomelas still persist, and the two foxes, Cape Vulpes chama and Bat-eared Otocyon megalotis, are common. Other small mammals recorded in the study area are the Rock Dassie Procavia capensis, Spring Hare Pedetes capensis, Porcupine Hystrix africaeaustralis, Red Rock Hare Pronolagus crassicaudatus and scrub hares Lepus sp.

The avifauna of the Stormberg is also typical of montane grasslands of southern Africa. A total of 187 species were recorded in the study area during 1988-1991, and another 72 species have been recorded by W.S. Stretton (unpubl. data) during 1956-1990 (Little 1992). Of the 187 species recorded during the study period, nine are listed by Brooke (1984) as threatened in southern Africa and 44 species are endemic to southern Africa (Clancey 1986). Twenty-four species are regarded as vagrants to the Stormberg, 50 species are migrants, and 113 are resident species, of which breeding was confirmed for 54 species. Of the 72 additional species, 44 were recorded on less than 10 occasions during 1956-1990, and another three species, the Bald Ibis Geronticus calvus, Cape Vulture Gyps coprotheres and Redwing Francolin Francolinus levaillantii, are regarded as recently absent from the Stormberg (Little 1992).

Comparison of the Stormberg avifauna with that of the avifauna of the Natal Drakensberg described by Little & Bainbridge (1988) shows a large overlap: 143 species were recorded in both the communities. However, four major differences exist. Firstly, a lack of forest species on the Stormberg. Of the 103 Natal Drakensberg species which were not recorded on the Stormberg 62 species (60%) are forest/woodland species. The apparent absence of these species on the Stormberg is presumably due to historic climatic and fire impact in this area as opposed to the milder climate and greater occurrence of fire refuge sites in the Natal Drakensberg 'little berg' system. Secondly, a greater richness in wetland bird species (e.g. South African Shelduck Tadorna cana, Cape Shoveller Anas smithii and Maccoa Duck Oxyura maccoa), and abundance (grebes, ducks, waders and warblers), on the

Stormberg, probably because of the greater number of farm dams on the Stormberg. Thirdly, more short-grassland birds (e.g. larks, korhaans, bustards and coursers) on the Stormberg, undoubtedly due to the higher grazing pressure of this area. Finally, more pronounced than in the Natal Drakensberg system is the invasion of Karoo species on the Stormberg. Species such as Karoo Robin (Erythropygia coryphaeus), Layard's Titbabbler (Parisoma layardi), Titbabbler (P. subcaeruleum), Longbilled Crombec (Sylvietta rufescens), and Ludwig's Bustard (Neotis ludwigii) are regular species of the Stormberg (Little 1992).

Land-use

Primary land-use in the area is livestock production, including various range methods of cattle and sheep management. Cultivation is confined primarily to fodder crops of small area in valleys.

Fire does not play a major role in the veld management of this area. Although some farmers use fire irregularly, little documented records of burns could be located. In a number of degraded areas, as mentioned above, where Pentzia globulus and other karoo species occur, burning might assist in restoring palatable grass species.

SECTION ONE

POPULATION RANGE AND GENETICS

CHAPTER 1

THE RANGE AND STATUS OF THE GREYWING FRANCOLIN

FRANCOLINUS AFRICANUS

Francolinus africanus Stephens, 1819. Shaw's General Zoology, Volume 11, part 2, p. 323; Cape Province.

Distribution

Horsbrugh (1912) described the range of the Greywing Francolin as "generally distributed through the Cape Colony and the upper and more elevated parts of Natal and locally through the Orange River Colony and the southern Transvaal". Hall (1963) stated that, "it is found in the grasslands of the mountains of the southern Transvaal, Orange Free State and Cape Province, reaching Natal on the high spurs of the Drakensberg", and argued that, "McLachlan & Liversidge (1957:94) show an overlap in the ranges of F. shelleyi and F. africanus in the southern Transvaal but I cannot substantiate this, the most northerly specimens of africanus recorded being from Potchefstroom and Wakkerstroom, 100 miles south of shelleyi at Pretoria, and in rather different country". Crowe et al. (1986) describe the range of F. africanus as an "endemic resident from W, SW, E and NE Cape Province to SW and E Orange Free State, Lesotho, SE Transvaal and highlands of Natal".

Taxonomy and phylogeny

There has also been considerable discussion in the literature on the taxonomy and phylogentics of the Greywing. Clancey (1986)

reported that, "F. africanus had on occasion been deemed to be conspecific with certain East African forms, but as those are spatially remote and differ markedly in plumage pattern, it is better dealt with as a South African endemic centred on the southern aspects of the austral arid zone, east of which it ranges as far north as the south-eastern Transvaal highveld. Crowe et al. (1992) suggested that F. africanus forms a superspecies with F. streptophorus, F. levaillantii, F. levaillantoides F. shelleyi, F. psilolaemus and F. finschi. Hall (1963) formulated eight assemblages within the genus Francolinus and placed psilolaemus, shelleyi, africanus, levaillantoides, levaillantii and finschi in her Red-winged Group. She commented that, "the degree of divergence and the relationship between shelleyi and its three neighbours, africanus, whytei and uluensis varies only slightly, but is just sufficient to treat africanus as a species and the other three as conspecific. Based on similarities in mitochondrial DNA (mtDNA) structure, Crowe et al. (1992) clustered levaillantoides, shelleyi and africanus as distinct species within the Red-winged Group, but found that sequence divergence in mitochondrial DNA between this group and levaillantii was sufficient to isolate levaillantii.

Within F. africanus, Sclater (1912) suggested that perhaps three races could be recognized from within southern Africa. Mackworth-Praed (1922) recognized these three races, designating them as F. africanus subspp. 1,2 and 3. Clancey (1957) formally separated these alleged races into two taxa, proposing the name F. a. proximus for the populations of the Drakensberg Mountains. He commented that, "the birds from Wakkerstroom are quite

different-looking from those of the Cape". Based on plumage colour and marking, Clancey (1967) described the distribution of these two subspecies as "western and south-western Cape from northern Little Namaqualand south to the Peninsula, thence eastwards through the southern mountains and the Karoo districts to the eastern Cape, and extending north to Griqualand West, the western Orange Free State, and probably, the south-western Transvaal (for F. a. africanus), grading into the following subspecies (F. a. proximus) to the east of its range" in "the Drakensberg montane system of the north-eastern Cape, including Griqualand East, high western and Upper Natal, Lesotho, adjacent highland areas of the Orange Free State, and the Drakensberg of the south-eastren Transvaal and western Swaziland" (Fig. 1.1).

Hall (1963) acknowledged slight local variation within the range of F. africanus, but suggested that it is not great enough to warrant the recognition of any subspecies, stating that proximus (Clancey 1957) is therefore placed in the synonymy. Crowe et al. (1992) suggested that structural variation in mtDNA within F. africanus is not significant (sequence divergence between two individuals collected at Ceres and Molteno = 0,3%).

Since F. africanus is endemic to southern Africa (Clancey 1986), and that this species has become increasingly sought after as a commercial co-product of agriculture (Little 1990), it is the responsibility of landowners, hunters and conservationists to manage this resource on a sustainable basis. For the management and utilization of game species, and from a perspective favouring the conservation of biotic diversity, it is necessary to identify the fundamental units of biodiversity for the Greywing. In other words, is it necessary to manage F. africanus populations at

subspecies level or as one essentially homogeneous unit?

The objectives of this chapter are to investigate geographical genetic variation within F. africanus.

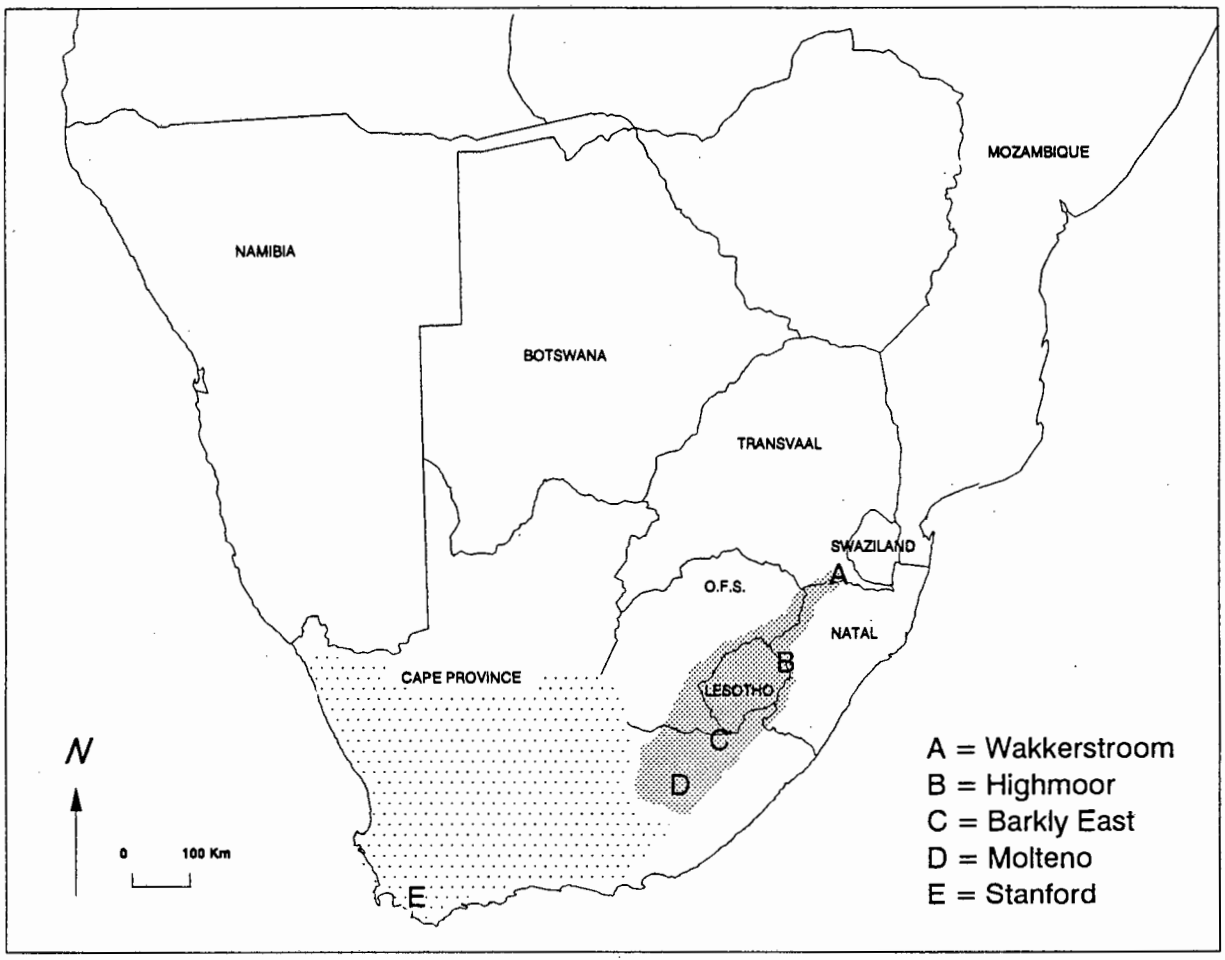


Figure 1.1. Range of *Francolinus africanus africanus* (light stipple) and *F. a. proximus* (dark stipple) (Clancey 1967), and location of populations sampled for analysis of geographic variation.

METHODS

mtDNA

Heart, liver and muscle tissue were sampled from nine individuals: two from near Wakkerstroom (27°20'S; 30°00'E) in the southern Transvaal, one at Highmoor State Forest (29°20'S; 29°30'E) in the Natal Drakensberg, two near Barkly East (30°55'S; 27°40'E) on the foothills of southern Lesotho, two near Molteno (31°25'S; 26°50'E) in the northeastern Cape, and two near Stanford (34°20'S;19°40'E) in the southwestern Cape (Fig. 1.1).

Mitochondrial DNA was isolated and purified using a combination of the methods of Cummings et al. (1987) and Smith et al. (1971) with modifications. Frozen tissue was cut into small pieces, resuspended in 4,5 x volume of extraction buffer (100 mM Tris-HCl, pH 7,4, 150 mM NaCl, 20 mM EDTA, 10% (w/v) sucrose) and centrifuged at 1 000 x g for 10 minutes at 4°C. The pellet was resuspended in 3 x volume of extraction buffer, homogenized for 25 seconds in a blender and centrifuged at 1 000 x g for 10 minutes at 4°C. The supernatant was filtered through cheesecloth to remove residual fat particles before being centrifuged at 10 000 x g for 15 minutes at 4°C. The mitochondrial pellet was resuspended in 4 ml of STE buffer (100 mM NaCl, 10 mM Tris-HCl, pH 8,0, 1 mM EDTA). All manipulations up to this stage were performed at 4°C while subsequent steps were performed at room temperature. The mitochondrial suspension was incubated for 10 minutes at 20°C in 1% (w/v) SDS to allow for lysis of the mitochondrial cell walls. The mixture was then made 1,0 M in CsCl and left for 10 minutes at room temperature. The solution was then centrifuged at 10 000 x g for 15 minutes at 20°C and to

the supernatant ethidium bromide and CsCl was added and density-gradient centrifugation was performed at 50 000 rpm for 18 hours at 20°C (Maniatis et al. 1989). Supercoiled mtDNA was purified as described by Maniatis et al. (1989).

Purified mtDNA from each animal was incubated with 9 six-base-pair-recognizing restriction endonucleases, namely Asp718, BamHI, BclI, EcoRI, HindIII, HpaI, NcoI, NheI, and PvuII. Restriction endonuclease digestions were performed at 37°C for 2 hours using a buffer designated KGB (McClelland et al. 1988). Restriction fragments were end-labeled with ^{32}P-dCTP and separated by agarose gel electrophoresis.

With Nei & Li's (1979) method, sequence divergence in mtDNA (δ) is related to F (proportion of shared restriction fragments) by the relationship $F = P^4/(3-2P)^3$, where: $P = e^{-rlt}$ with r = number of nucleotides per restriction site, l = the rate of nucleotide substitution per unit time (t) and $\delta = 2\ lt = -(2/r)\ \log_e P$. Although δ cannot be calculated directly from the above formula (even when F is known), it is simple to calculate F for given values of δ. The relationship between δ and F was therefore constructed graphically for values of δ ranging from 0,01 to 2,5 in steps of 0,01 (cf. Essop et al. 1991).

Allozyme electrophoresis

Heart, liver and muscle tissue were sampled from 657 Greywing collected: 19 at Highmoor State Forest, 11 near Barkly East, 618 near Molteno, and nine near Stanford (Fig. 1.1).

Standard electrophoretic methods with 12% starch gels were used to assay allozyme variation at 31 protein-encoding loci (Harris &

Hopkins 1976; Chapters 2 & 10). Nei's unbiased genetic distance (Nei 1978) was calculated between all pairs of samples and the UPGMA cluster analysis was applied to the matrix of distance to produce a phenogram.

RESULTS

mtDNA

Twenty seven identical mtDNA fragments were observed per individual. The sequence divergence between the individuals was 0,0. Therefore, there were no differences in mtDNA structure within or between populations.

Allozyme electrophoresis

Average sample heterozygosities were: Highmoor = 0,079; Rhodes = 0,078; Molteno = 0,070; Stanford = 0,103; (SD = 0,03 throughout). The average Nei's (1978) genetic distance among the four geographically separated populations sampled was 0,02 (SD = 0,01). The most genetically similar populations were those from Barkly East and Stanford ($\bar{D}$ = 0,008), and the Natal Drakensberg and Molteno populations were the most divergent ($\bar{D}$ = 0,036) (Table 1.2). The results of the UPGMA cluster analysis of genetic distances (Fig. 1.2) did not show meaningful clustering of the samples according to geographical location. The resulting phenogram (Fig. 1.2) suggests that populations from Rhodes and Stanford are sister taxa of most recent origin, followed by the Molteno and Natal Drakensberg populations.

Table 1.1. Matrix of Nei's (1978) identities (I) upper half matrix and standard unbiased genetic distances ($\bar{D}$) lower half matrix, among *F. africanus* populations.

	F. africanus populations			
	Natal Drakensberg	Barkly East	Molteno	Stanford
Highmoor	-	0,981	0,965	0,975
Barkly East	0,019	-	0,988	0,992
Molteno	0,036	0,013	-	0,982
Stanford	0,026	0,008	0,018	-

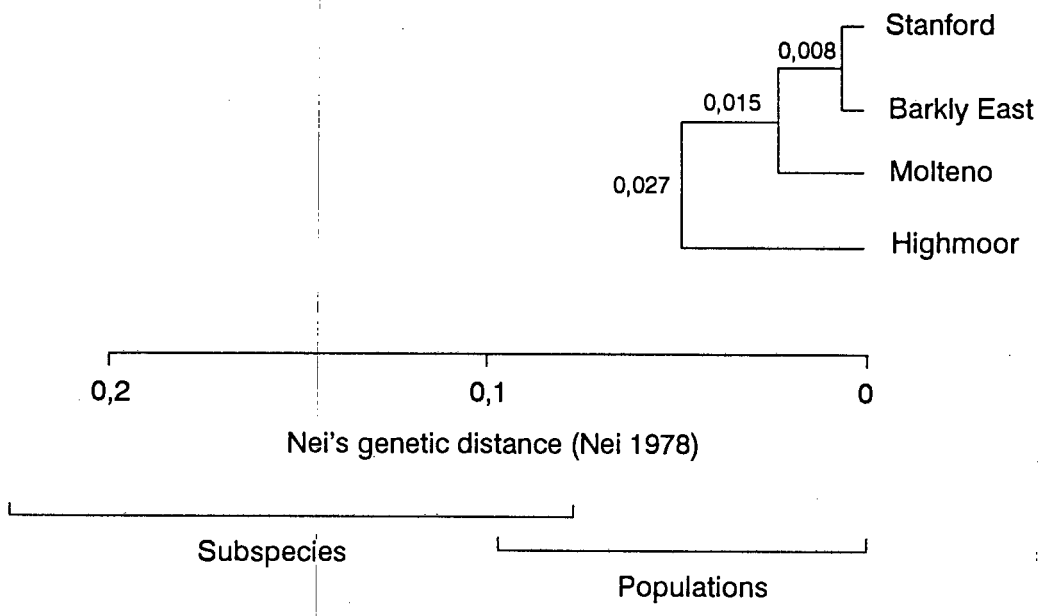


Figure 1.2. Phenogram of UPGMA of Nei's unbiased genetic distance for four geographically separated Greywing Francolin populations.

DISCUSSION

Intraspecific comparisons of birds tend to yield mtDNA nucleotide sequence divergence (δ) values less than 1,0 (Shields & Helm-Bychowski 1988). The lack of mtDNA divergence among Greywing Francolin populations (δ = 0,0) may be attributable to the preliminary investigation of only nine endonucleases. However, the results of Crowe et al. (1992) for single Greywing from Ceres (33°15'S; 18°45'E) and Molteno based on 14 endonucleases showed only a one fragment difference (= 0.3% sequence divergence).

Applications of multilocus protein electrophoresis in this study yielded an average genetic distance ($\bar{D}$) of 0,02 (SD = 0,01), four times higher than, and toward the top of the range of genetic differentiation for subpopulations of birds ($\bar{D}$ = 0,0048; range = 0,0-0,0214; Barrowclough 1980). However, the lack of a correlation between genetic and phenotypic (subspecies) differences does not support the partitioning of the Greywing into more than one taxon. The allozymic variation may be attributable to a panmictic megapopulation effect on nucleotide divergence, with the influence of relatively highly structured subpopulations and local philopatry (Grant & Little 1992; Chapter 2) on allelic genetic distances between populations.

Conclusions

Genetic distances between Greywing Francolin samples reflected by allozymes were discordant with geographical arrangements of samples, probably indicating that this species acts as a panmictic megapopulation within its range. Therefore, although

geographical differences were found in timing of breeding (Little & Crowe in press a; Chapter 3) and other regional differences in habitat and diet preferences are apparent (Mentis & Little 1992; Chapter 6) which might require flexibility in management, the species can be regarded as one unit in the 'currency' of conservation biology.

CHAPTER 2

POPULATION STRUCTURE AND GENE FLOW

Status: in press. How sedentary are Greywing Francolins Francolinus africanus? Evolution 46(5). co-author: W.S. Grant.

SUMMARY

Phasianids are considered to be sedentary birds with limited dispersal so that populations may be expected to show genetic isolation by distance. To test this, we examined genetic variability in 618 Greywing Francolins Francolinus africanus at 24 localities over a 1 500 km^2 area. We subdivided the samples to measure genetic population structure among localities separated by 6-60 km, and among coveys separated by 0,1-6 km. Thirteen (43%) of 30 allozyme loci were polymorphic, and heterozygosity ranged from 5,3 to 8,5% over 24 localities and averaged 7,0%, a value much larger than that found for other phasianids. Significant allele-frequency heterogeneity was detected among localities and among coveys at several localities for several loci. Mantel's test, however, showed that there was no correlation between geographical distance and the allele-frequency difference between localities for all but one allele. Although spatial autocorrelation was detected with Moran's I and Geary's c for two alleles, the geographical patterns of I in

correlograms of 18 independent alleles showed a "crazy-quilt" pattern of allele-frequency patches. This shows that the isolation-by-distance model of subpopulation structure is inappropriate for these birds. Individuals, therefore, appear to disperse far beyond neighbouring populations. "Private-allele" and F_{ST} estimates of migration under the island model were 8-9 individuals between localities each generation. Allele-frequency heterogeneity, large amounts of gene flow, and the general lack of spatial autocorrelation imply that the small, socially-structured populations of Greywing are subject to high rates of turnover, founder effects, and random drift.

INTRODUCTION

The relative importances of natural selection, migration and random genetic drift in the microevolutionary processes in birds are still largely unknown. Migration is thought to act as a cohesive force reducing the tendency of populations to diverge genetically from one another by random drift and selection. As migration (natal and breeding dispersal) increases, incompletely isolated subpopulations begin to act as a single population and this retards the loss of genetic variability by random drift. Dispersal can also enhance a species' ability to colonize vacant habitats or to expand into new areas. All of these processes can ultimately influence the rate of evolutionary change (Mayr 1963; Templeton 1980) and the probability of surviving major environmental and climatic shifts (Jablonski 1986).

Previous studies of allozymic variability show that there is relatively little genetic divergence among conspecific populations of birds, presumably because of the homogenizing effect of gene flow (Avise & Aquadro 1982; Barrowclough 1983). The analysis of geographical patterns of allozyme variability to understand microevolutionary processes, however, depends to a large extent on sampling design. Most studies of birds are based on small samples from a few localities, with the result that only large allele-frequency differences on geographic scales of hundreds to thousands of km can be detected. With the exception of Parkin & Cole (1984), there are no studies with large numbers of samples on a small geographical scale that can be used to measure the effects of dispersal and social behaviour on the genetic structure of bird populations.

Greywing Francolins, Francolinus africanus, are sedentary phasianids endemic to southern Africa (Clancey 1985) and extend from the montane grasslands of the eastern highlands of Transvaal and Natal Provinces, through the arid Karoo to the warm temperate ecosystem of the southwestern Cape (Crowe et al. 1986). These birds are found in disturbed patches on shallow soils in grassland habitats (Mentis & Bigalke 1981a) and are organized into small social units, coveys, consisting of two to four adults, the broods of the year, plus recent immigrants. Adults attempt to mate annually, and mated pairs appear to be monogamous throughout a breeding season (Little & Crowe in press a; Chapter 3). Greywing Francolins are ideal for studying the effects of dispersal on a small geographical scale because they are sedentary, and because hunting in the eastern Cape Province provides a source of samples.

In this study, we examine patterns of allozyme variation within and among 24 populations of Greywing Francolins located over a 1 500 km^2 area on the Stormberg Plateau, South Africa. The large numbers and sizes of our samples permit tests for genetic differences among coveys separated from each other by hundreds of meters and among localities separated by six to 60 km. We used Wright's F statistics and spatial autocorrelation analysis to infer population structure from allozyme variability. If populations are isolated from one another by distance, as expected for a sedentary bird, there should be positive autocorrelation between nearby populations and negative autocorrelation between more distantly-separated populations (Sokal & Wartenberg 1983). Although our analyses detected a significant degree of microgeographic allele-frequency

heterogeneity, the frequency surfaces do not fit an isolation-by-distance model.

MATERIALS AND METHODS

Collection of Samples

We collected 618 birds from 24 localities within a 1 500 km^2 area on the Stormberg Plateau (Fig. 2.1). Birds were hunted on open grasslands subdivided by ravines and rocky buttes and stocked with cattle and sheep. The samples included all birds taken in hunts from mid-April to the end of July 1989. A hunt at a locality covered about 10 km^2 and lasted about six hours with three to seven hunters with at least two English pointers. Two localities (Fig. 2.1; 11 & 13) were hunted again after one week to measure the error in estimating allele frequencies from a single sample. Heart, liver and skeletal muscle were dissected from the birds, frozen in liquid nitrogen no later than six hours after collection, and stored at -75^{o}C for up to six months until electrophoresis.

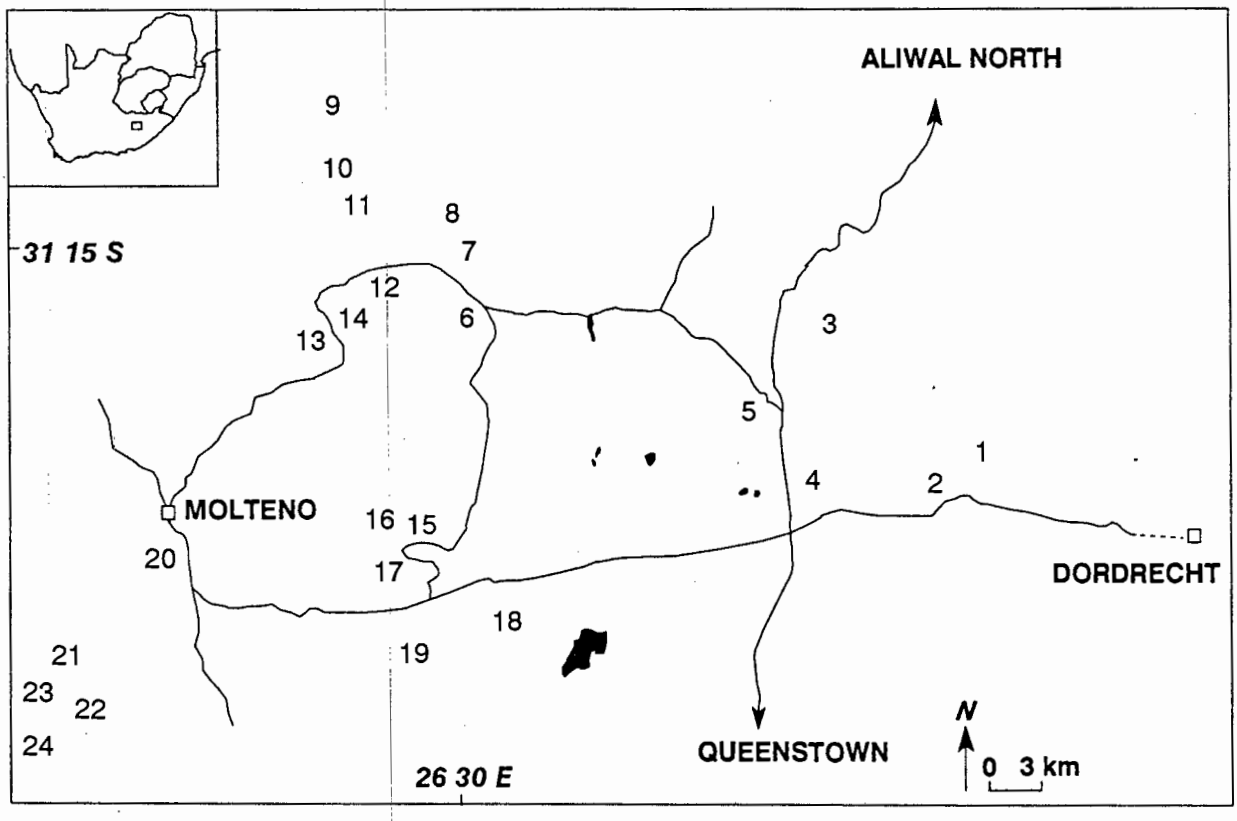


Figure 2.1. Localities of Greywing Francolin populations sampled for population genetic analysis on the Stormberg Plateau, South Africa.

Electrophoresis

Soluble proteins were extracted by homogenizing individual tissues with an equal volume of 0,1 M Tris HCl, and by centrifuging this mixture at 1000 X g for 5 minutes. Proteins in the clear supernatant were electrophoresed overnight in 11% starch gels at 4°C. Gels were sliced into 4 or 5 slabs, which were stained for specific enzymes (Harris & Hopkinson 1976). We used the following buffer-isozymes combinations (locus abbreviation and Enzyme Commission number) with heart [H], liver [L], or breast muscle [M] to resolve the gene products of 30 presumptive loci. A discontinuous tris-citrate, lithium-borate buffer, pH 8,7 (Ridgway et al. 1970) resolved isozymes of aconitase (Aco-1 [H]; 4.2.1.3), alcohol dehydrogenase (Adh [L]; 1.1.1.1), aspartate aminotransferase (Aat-1 [H], Aat-2 [H]; 2.6.1.1), creatine kinase (Ck-A [M], Ck-B [H]; 2.7.3.2), glucosephosphate isomerase (Gpi [H]; 5.3.1.9), lactate dehydrogenase (Ldh-A [M], Ldh-B [H]; 1.1.1.27), phosphoglucomutase (Pgm-1 [H], Pgm-2 [H]; 2.7.5.1), sorbitol dehydrogenase (Sdh [L]; 1.1.1.14), and superoxide dismustase (Sod [L]; 1.15.1.1). A Tris-citrate buffer, pH 6.9 (Whitt 1970) resolved the products of adenosine kinase (Ak [H]; 2.7.4.3), glyceraldehydephosphate dehydrogenase (Gap-1 [M]; 1.2.1.12), glycerol-3-phosphate dehydrogenase (G3p-1 [M], G3p-2 [H]; 1.1.1.8)., isocitrate dehydrogenase (Idh-A [H], Idh-B [L]; 1.1.1.42), malate dehydrogenase (Mdh-A [M], Mdh-B [H]; 1.1.1.37), malic enzyme (Me [H]; 1.1.1.40), and phosphogluconate dehydrogenase (Pgd-1, Pgd-2 [H]; 1.1.1.44). A Tris-Borate-EDTA buffer, pH 8.6, (Markert and Faulhaber 1965) resolved mannosephosphate isomerase (Mpi [H]; 5.3.1.8), nucleoside

phosphorylase (Np [L]; 2.4.2.1), and peptidases (Pep-A [H], Pep-B [L]; 3.4.11.-; Pep-D [H]; 3.4.13.9).

We used the patterns of gene expression in related taxa and the presumed subunit structures of the isozymes as guidelines for interpreting gel-banding patterns. When evolutionary nomenclature for a locus could not be inferred from tissue expressions and substrate, we numbered multiple loci by the mobilities of their products, beginning with the most anodal isozyme. Alleles were designated by their electrophoretic mobilities relative to the most common allele, which was designated 100. We ran some phenotypes side-by-side on the same gel to distinguish between similar phenotypes in different samples.

Statistical analyses

We tested for allele-frequency differences at two nested levels: coveys and localities. We subdivided localities into coveys when at least six birds were taken from a covey. The remaining birds at a locality were pooled into a single unit and used in the contingency-table analyses but not in the analysis of inbreeding. These samples contained 11,6 birds on average (SD = 6,0; n = 41 units). Samples from 24 localities averaged 25,7 birds. We used the G-test (Sokal & Rohlf 1981) and a two-way contingency-table analysis to test a null hypothesis of no frequency differences among coveys within a locality and among localities. Since tests were made for eight polymorphic loci, Aat-1, Mpi, Pep-A, Pep-B, Pep-D, Pgd, Pgm-1 and Pgm-2, we used Cooper's (1968) modification to account for the increase in type

I error (rejecting a null hypothesis when it is true) with repeated tests of the same hypothesis. We used a rejection criterion that was associated with a probability of α/n, where n was the number of repeated tests (number of polymorphic loci). Thus, the overall probability of rejecting HO by chance was

$$P = 1 - (1 - (0,05/n))n \approx 0,05.$$

Agreement with Hardy-Weinberg proportions was assessed by F with Levene's (1949) correction for small samples, and by the log likelihood-ratio test (G-test) for goodness of fit (Sokal & Rohlf 1981). Because of small sample sizes, the genotypes for loci were pooled into three classes, AA, AX, and XX where A is the most common allele and X is any other allele, and retested. A departure was considered significant if both the unpooled and pooled tests were significant. Levene's correction had the effect of increasing the apparent levels of inbreeding.

F_{IS}, the average F_{ISi} over all samples, F_{ST}, the standardized variance of allele frequencies among samples, and F_{IT}, inbreeding in the individual relative to the total population, were calculated for 20 independent alleles at 8 loci according to equations (1-4) in Weir & Cockerham (1984) and are related by

$$(1 - F_{IT}) = (1 - F_{IS})(1 - F_{ST}).$$

The null hypothesis, $F_{ST} = 0$, was tested for each allele with

$$X^2 = 2NF_{ST}; \quad d.f. = n - 1$$

(Workman & Niswander 1970). The null hypothesis, $F_{IS} = 0$ was tested with

$$X^2 = NF_{IS}^2; \quad d.f. = 1$$

(Li & Horvitz 1953), and the null hypothesis, $F_{IT} = 0$ was tested with

$$t = |F_{IT}\sqrt{N}|; \quad d.f. = \text{infinity}$$

(Brown 1970). Locus heterozygosities were estimated by calculating the expected proportions of heterozygotes with random mating, $h = 1 - \Sigma p_i^2$, where p_i is the frequency of the ith allele for a locus. Average sample heterozygosity, H, is the mean over all loci including monomorphic loci.

The association between geographical distance and allele-frequency differences between localities was tested with Mantel's standardized correlation coefficient, r, (Mantel 1967; NTSYS Exeter Software, New York). The significance of r was tested with a t-test under the null hypothesis that allele frequencies were randomly distributed among localities. We estimated an average random r based on 250 random frequency-sample permutations for comparison with the observed r.

We used Moran's I and Geary's c (Cliff & Ord 1981; Sokal & Oden 1978) to test for spatial autocorrelation among samples with 20 alleles. The significances of I and c were tested with the standard-normal testing procedures outlined in Sokal & Oden (1978) and Jumars *et al.* (1977) with an H_o of a random arrangement of allele frequencies over the study area. One-tailed tests were used because, under the alternative hypothesis of isolation by distance, we expected positive autocorrelation between nearby localities and negative autocorrelation between distant localities. The expected value of Moran's I when there is no geographic structure is $-1/(n - 1)$, where n is the number of localities. Positive values of Moran's I indicate that values of a variable at nearby localities are similar, and large negative values indicate that the values are unusually dissimilar. Geary's c is 1,0 when the values of a variable are

randomly distributed, less than 1,0 when there is positive spatial autocorrelation and greater than 1,0 when there is negative autocorrelation. We first searched for overall autocorrelation with a Gabriel-connected binary distance matrix, then with the inverse of the distance in km between localities. We then tested for autocorrelation between localities in 12, five-km distance classes with Moran's $\underline{I}$ and present these results as correlograms. Distance classes were defined by Euclidean distances measured on a 1:250 000 scale map.

We used three indirect methods to estimate migration among localities. First, the graphical method of Slatkin (1981) yielded a qualitative (low, medium and high) measure of gene flow. Second, since the lack of spatial autocorrelation suggested a lack of isolation by distance among localities, we felt justified in using the island model of migration (Wright 1951) to estimate the number of migrants $\underline{Nm}$ between localities from

$$\underline{F}_{ST} = 1/(1 + 4\underline{Nm}).$$

We calculated the number of migrants directly, $\underline{Nm}_i$, from the average $\underline{F}_{ST}$ over 20 alleles and indirectly, $\underline{Nm}_i^*$, with a jackknife procedure (Weir 1990) in which one allele at a time was dropped from the average of $\underline{F}_{ST}$. A 95% confidence interval was calculated from the variance of these estimates. Third, we used the average frequency of "private" alleles and the equation

$$\underline{Nm}_p = {}_{10}\,[\log_{10}(p(1) + 1{,}1/-0{,}58)]$$

to estimate the number of migrants between localities, $\underline{Nm}_p$ (Slatkin & Barton 1989). We also calculated a jackknifed estimate, $\underline{Nm}_p^*$, with this method. The second and third methods estimate the number of migrants, $\underline{Nm}$, between each locality that

successfully breed in the new population each generation.

RESULTS

Genetic Variability

We examined 250 individuals for all enzymes, then examined only polymorphic loci in the remaining samples. Allelic frequencies of 13 loci estimated for 24 localities appear in Appendix 2.1. Five isozymes (Mpi, Pep-A, Pep-B, Pgm-1, and Pgm-2) had banding patterns that were consistent with a monomeric subunit construction; five enzymes (Aat-1, Gpi, Idh, Pep-D, and Pgd-1) appeared to have a dimeric structure; and three enzymes (Ldh-1, Ldh-2, and Sdh) appeared to have a tetrameric structure. Of the 30 loci examined, 13 (43%) showed at least some polymorphism and 8 (27%) were polymorphic with a 0,95 common-allele-frequency criterion. Average heterozygosities for all loci (including monomorphic loci) for the 24 localities ranged from 0,053 to 0,085 and averaged 0,070 (SD = 0,009).

We hunted two localities twice, a week apart, and found no significant differences in allele frequencies between the two samples at each locality. Each of the 24 localities in the study area had been hunted at least once in previous seasons, but, since natural mortality is as high as hunting mortality (Chapters 9 & 10), the results of this study are unlikely to be different for unhunted populations. On average, 44,5% (SD = 8.4%; N = 24) of the birds seen on a hunt were included in a sample.

Allele-frequency heterogeneity

We tested for allele-frequency heterogeneity among the 24 localities with a contingency-table analysis and found significant overall heterogeneity for Mpi ($P < 0,01$), Pep-A ($P < 0,05$), Pep-D ($P < 0,01$), Pgd-1 ($P < 0,001$) and Pgm-1 ($P < 0,05$), after correction for multiple tests. We then subdivided the samples from each locality into coveys, when this was possible, and tested for allele-frequency differences on a small geographical scale. There was significant heterogeneity among coveys at eight localities before correction for multiple tests. After correction, there were significant differences among or between coveys at localities 11, 12 and 18 for Pgm-2 ($P < 0,05$), at localities 16 and 22 for Pgd ($P < 0,01$), at localities 18 ($P < 0,05$) and 22 ($P < 0,01$) for Aat-2.

F Statistics

Allele-frequency heterogeneity on one geographic scale should produce deviations from Hardy-Weinberg proportions on a larger scale of sampling (Wahlund's effect). We therefore pooled all of the localities and found a deficit of heterozygotes as expected with a weak Wahlund's effect ($F = 0,025$; n.s.; $N = 618$). Within localities, however, there was a nonsignificant excess of heterozygotes, on average ($F = -0,014$; average $N = 25,7$). Eight localities, 1, 2, 3, 4, 9, 13, 15 and 22, showed significant departures from Hardy-Weinberg proportions for at least one locus (Appendix 2.1). These loci included Aat-2, Pep-B, Pgd-1, and Pgm-1. There was also an excess of heterozygotes, on average, for 24 covey samples with at least six birds ($F = -0,030$; average $N = 7,7$). For these samples, we found significant departures

from Hardy-Weinberg proportions in one covey at locality 19 for Pgm-2 ($P < 0,05$), and another at locality 21 for Pgd-1 ($P < 0,05$). Genotypic proportions in these samples most likely reflect Mendelian segregation in only a few matings. Although most of the young of the year and some adults disperse soon after the winter hunting season, juveniles may remain in their natal areas until the following year.

F_{ST}, F_{IS}, and F_{IT} are shown in Table 2.1 for 20 variable alleles. Values of F_{ST}, a measure of allele-frequency divergence among populations, varied from 0,014 to 0,066 and averaged 0,030 (eq. 10, Weir & Cockerham 1984). Nine of the 20 alleles showed significant geographical heterogeneity. Values of F_{IS}, inbreeding relative to the subpopulation, varied from -0,058 to 0,162 and averaged 0,022. Only a single allele, Pgd-1^{100}, showed a significant overall deficit of heterozygotes within localities. Values of F_{IT}, inbreeding relative to the total population, varied from -0,026 to 0,205 and average 0,051. Three alleles, Aat-1^{40}, Pgd-1^{100}, and Pgd-1^{115} showed significant positive values of F_{IT}.

Spatial autocorrelation

We used Mantel's statistic to test each variable allele for correlation with geographical distance and with the reciprocal of distance. Tests with Euclidean distances emphasize regional patterns, whereas tests with reciprocals of distance increase the power of the test to detect local patterns. We found significant correlation between allelic frequencies and geographical distance for only Pep-A^{108} ($r = 0,25$; $P < 0,05$) (Table 2.2).

Table 2.1. Wright's F-statistics for eight polymorphic loci in Greywing Francolins. Statistics calculated according to equations (1) in Weir and Cockerham (1984), SD = standard deviation of allelic frequency.

Locus	Allele	Average frequency	SD	FST	FIS	FIT
Aat-2	- 20	0,24	0,076	0,021	0,031	0,051
	-100	0,70	0,079	0,019	0,015	0,034
	-140	0,06	0,049	0,033*	0,074	0,104**
Mpi	110	0,07	0,059	0,043**	-0,015	0,029
	100	0,92	0,058	0,033*	-0,017	0,017
Pep-A	108	0,03	0,036	0,031*	-0,022	0,010
	100	0,94	0,043	0,023	-0,020	0,004
Pep-B	120	0,08	0,054	0,028	0,026	0,053
	100	0,85	0,058	0,016	-0,043	-0,026
	80	0,06	0,044	0,026	0,011	0,037
Pep-D	80	0,07	0,058	0,043**	-0,008	0,035
	100	0,83	0,085	0,039**	-0,058	-0,017
	112	0,11	0,088	0,066***	-0,009	0,058
Pgd-1	115	0,17	0,083	0,036**	0,059	0,093*
	100	0,69	0,118	0,051**	0,162***	0,205***
	70	0,11	0,051	0,016	0,039	0,054
Pgm-1	100	0,97	0,031	0,023	0,039	0,062
	60	0,02	0,023	0,019	-0,007	0,012
Pgm-2	100	0,80	0,067	0,018	-0,005	0,013
	80	0,16	0,056	0,014	0,012	0,025
Average over loci				0,030	0,022	0,051

*P < 0,05, **P < 0,01, ***P < 0,001

Table 2.2. Mantel's standardized correlations for overall geographic structure on allele-frequency differences between samples, Moran's I and Geary's c autocorrelation coefficients for Gabriel-connected pairs of samples and for pairs connected by the reciprocal of geographic distance (km). Degrees of freedom for t-test of Mantel's standardized r are infinity.

		Mantel's test							
		Distance (km)		Reciprocal		Moran's I		Geary's c	
Locus	Allele	r	t	r	t	Gabriel	Reciprocal	Gabriel	Reciprocal
Aat-2	-140	0,23	1,85	-0,18	1,88	0,45**	0,13**	0,54**	0,76
Mpi	110	-0,16	1,50	0,16	1,94	0,41	0,32	1,33	1,19*
Mpi	100	-0,09	1,00	0,11	1,50	0,41*	0,09	1,40*	1,11
Pep-A	108	0,25*	2,21	0,05	0,62	0,18	0,03	0,68	0,78*
Pgm-1	100	0,03	0,30	-0,07	0,86	0,22	0,06*	0,90	1,06
Pgm-1	60	0,08	0,66	-0,04	0,49	0,14	0,07**	0,95	1,08

*P < 0,05, **P < 0,01

The results of the autocorrelation analysis of individual alleles fell into two categories. Some alleles showed significant overall spatial autocorrelation or significant autocorrelation at one or more of the distance classes, but did not show any clear geographical pattern in the correlograms (Fig. 2.2). For example, with the Gabriel-connected binary distance matrix, there was positive autocorrelation for $\underline{Mpi}^{100}$ with Moran's $\underline{I}$ (0,041; $P < 0,05$), but negative autocorrelation with Geary's $\underline{c}$ (1,40; $P < 0,05$). The correlogram of Moran's $\underline{I}$ over 12 distance classes, however, showed a "crazy-quit" pattern in which positive and negative autocorrelation alternated between adjoining distances classes (Fig. 2.2). This apparently random pattern also appeared for several other alleles.

The allele-frequency distributions of two alleles, however, showed significant overall autocorrelation and geographical structure in their correlograms. $\underline{Pgm\text{-}1}^{100}$ showed significant autocorrelation between the reciprocal of the distance and local deviations from the mean ($\underline{I} = 0,06$; $P < 0,05$). The correlogram showed strong positive autocorrelation between localities separated by less than 5 km, negative autocorrelation between localities separated by 10-15 km, but no pattern at larger distance classes (Fig. 2.3). The overall results for $\underline{Aat\text{-}2}^{-140}$ showed positive autocorrelation over short distances (reciprocal of distance: $\underline{I} = 0,13$; $P < 0,01$), and long distances (Gabriel network: $\underline{I} = 0,45$; $P < 0,01$; $\underline{c} = 0,54$; $P < 0,01$). The correlogram indicated a "depression" in the allele-frequency surface; there was significant positive autocorrelation over short distances, negative autocorrelation at intermediate

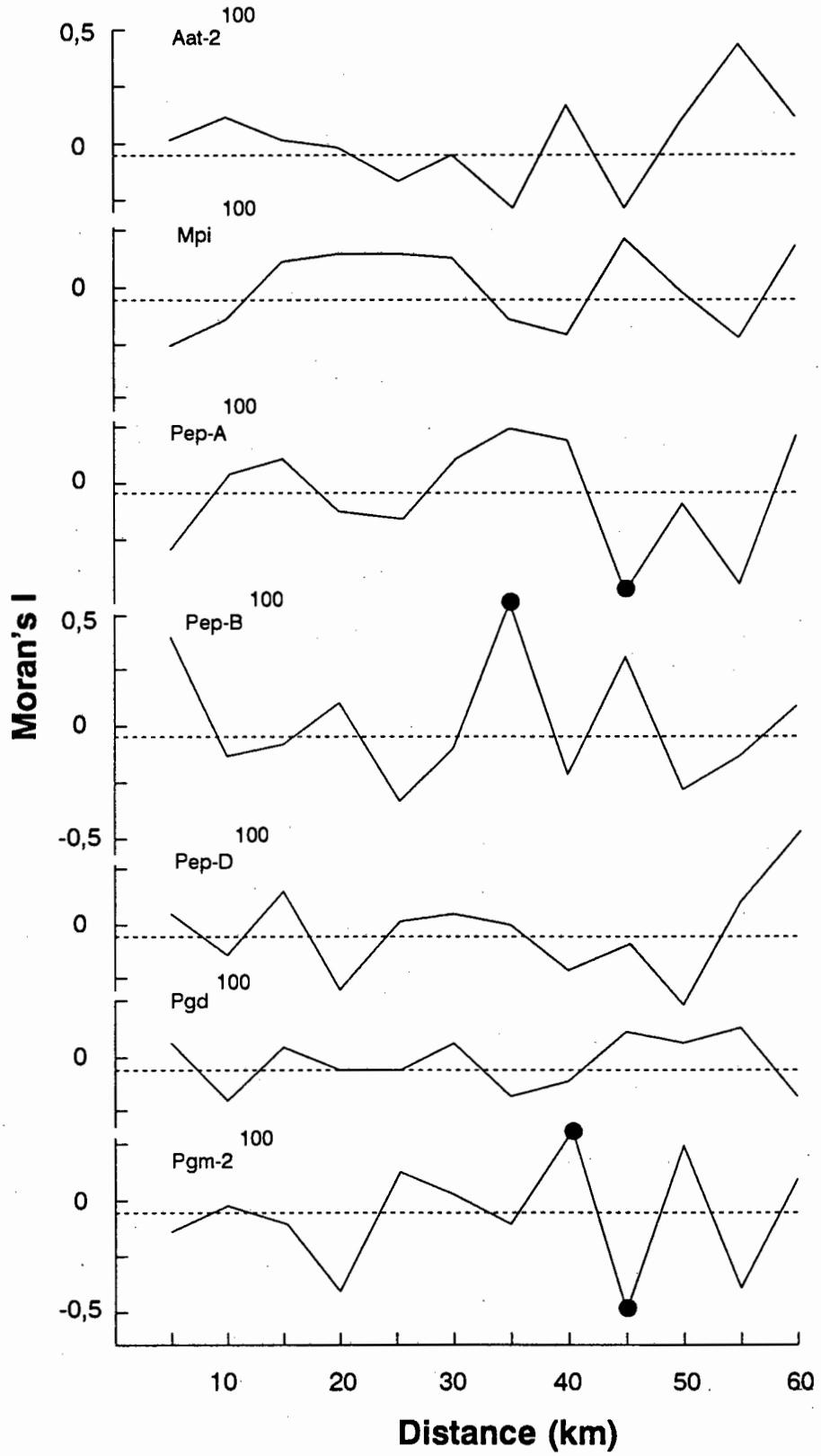


Figure 2.2. Moran's I for seven alleles in Greywing Francolin, over 12 five-km distance classes. These alleles show a random "crazy-quilt" distribution over the study area. The solid circles indicate significant ($P<0,05$) values of I.

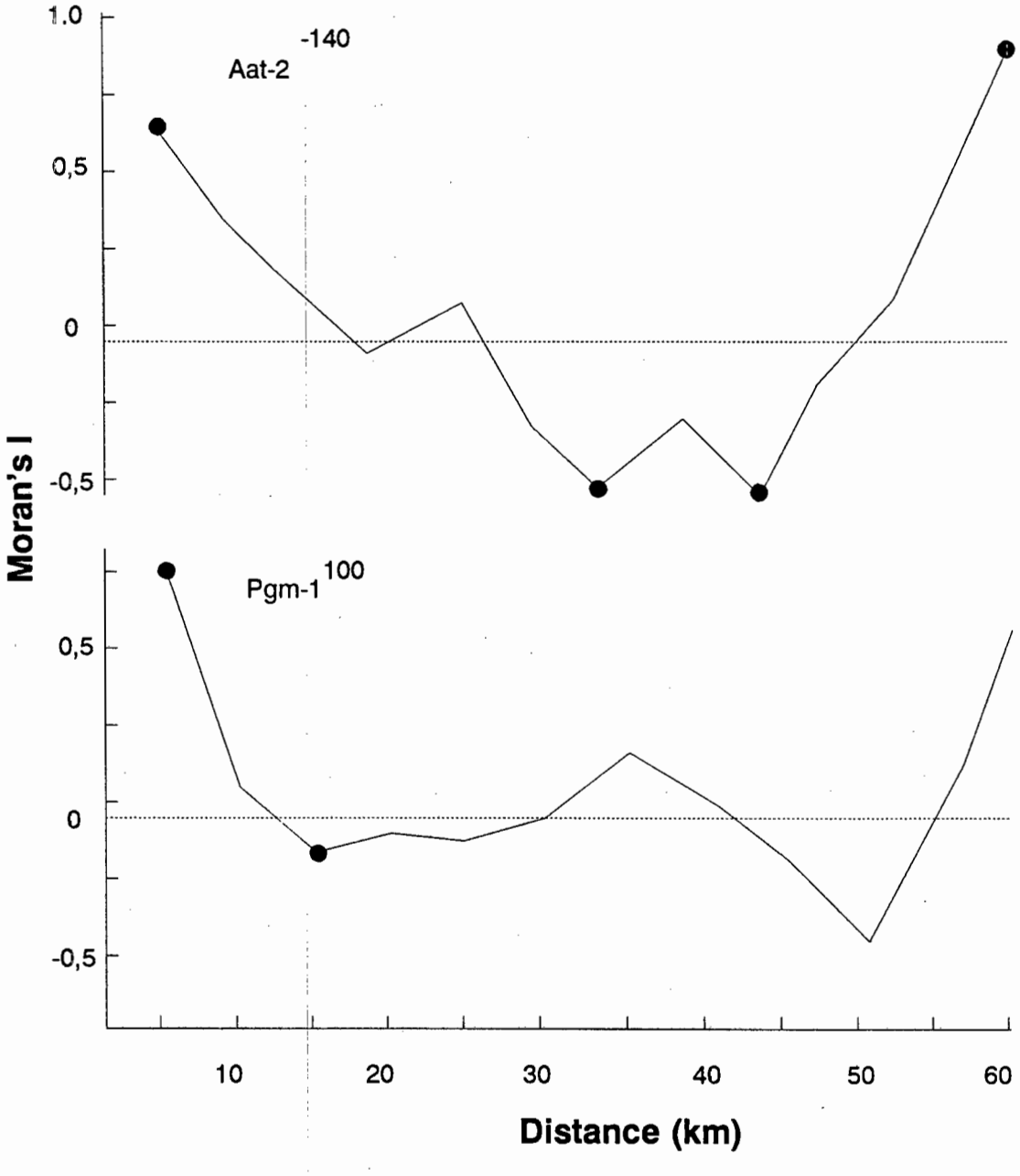


Figure 2.3. Moran's I for Aat-2^{-140} and Pgm-1^{100} over 12, five km distances classes in Greywing Francolin. These alleles show apparent geographic structure over the study area. The solid circles indicate significant (P<0,05) values of I.

distances of 30-50 km and positive autocorrelation in the largest distance class. These autocorrelations arose from high allele-frequencies in peripheral populations and low frequencies in the central populations.

We also tested for spatial autocorrelation among the $\underline{H}$s at each locality. If subpopulations are more stable or larger in some areas, then these populations may share larger amounts of genetic diversity. Tests for autocorrelation with a Gabriel network and $\underline{H}$, the arcsine transformation of $\underline{H}$, and the natural log of $\underline{H}$, however, showed negative, nonsignificant autocorrelation for both $\underline{I}$ and $\underline{c}$.

Estimates of migration

Since these results suggested that there was a general lack of isolation by distance, we used three methods of estimating migration that assume the island model of migration. First, the graph of conditional average allele frequencies, $\underline{p}(\underline{i})$, in the 24 localities (Fig. 2.4) yielded a concave curve typical of high levels of gene flow. Comparison of this curve with curves in the simulation study of Slatkin (1981, p. 327) for the island model suggests that $\underline{Nm}$ is about 2,5 individuals between localities. Second, the "private"-alleles method yielded estimates of $\underline{Nm}_p$ = 9,1 and $\underline{Nm}_p{}^*$ = 8,9 (95% C.I.: 8,4-9,3). Third, Wright's equation and $\underline{F}_{ST}$ gave estimates of $\underline{Nm}_i$ = 8,1 and $\underline{Nm}_i{}^*$ = 8,4 (95% C.I.: 8,3-8,5).

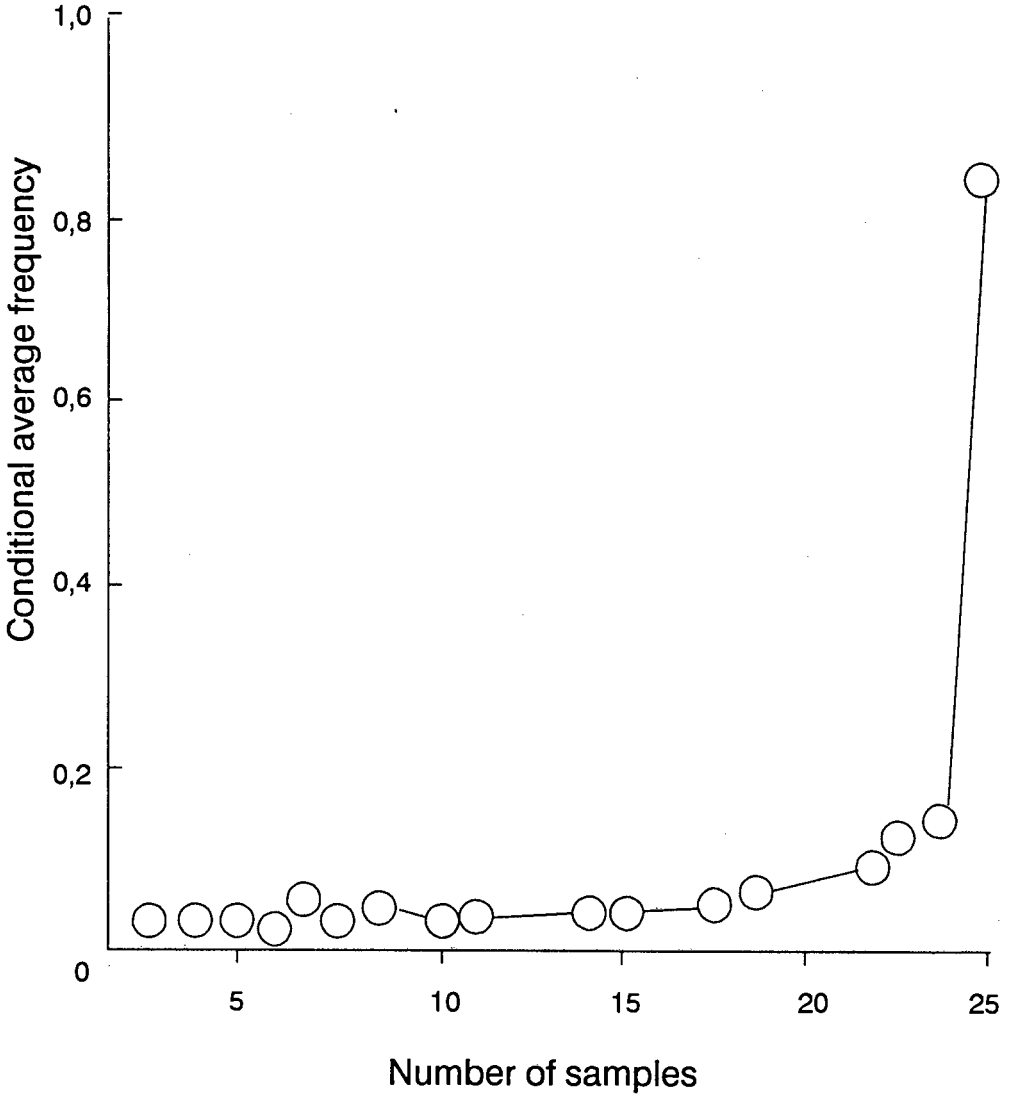


Figure 2.4. Distribution of conditional average allele frequencies (Slatkin 1981) in Greywing Francolin.

DISCUSSION

Genetic differences among subpopulations arise when there is a sufficient reduction in gene flow to allow local subpopulations to diverge from one another through random drift and natural selection. We can use allozyme variability indirectly to estimate migration only when local selective forces have a small influence on allelic frequencies; otherwise, this approach would produce a biased estimate of the gene flow between subpopulations. Several studies, however, have shown that electrophoretically-detectable variation in birds appears to be neutral or nearly neutral to selection (Barrowclough et al. 1985). The similarity in the estimates of population divergence with different alleles in our study also suggests that selection is not important over the extent of the study area. We therefore, assume that the geographical patterns of allozyme variants chiefly reflect random genetic drift and migration (Lewontin 1974).

One measure of population structure is the amount of variation harboured within a subpopulation. If Greywing Francolins are subdivided into small, isolated subpopulations, then within-population genetic variability would eventually be lost through random drift. Our estimate of average heterozygosity ($\underline{H}$ = 0,070), however, is somewhat larger than estimates of $\underline{H}$ in other phasianids, which are sedentary birds. Although estimates of $\underline{H}$ in birds in general range from 0,0 to 0,307 and average 0,065 for 79 species, the mean $\underline{H}$ for 11 species of phasianids, is only 0,035 (range 0,0 - 0,075) (Evans 1987). The large value of $\underline{H}$ in Greywing Francolins of the Stormberg Plateau implies both that

population size may be larger than expected for a sedentary bird and that this population may have had a long, unbroken history without severe population bottlenecks.

The large number of individuals and extensive sampling of localities over a small area allowed us to examine the fine-scale geographical structure of Greywing populations in some detail. We searched for population structure in several ways. The first was to test for allele-frequency heterogeneity over the study area with a contingency-table analysis and with F_{ST}. We found significant levels of geographical heterogeneity on scales both of a few hundred meters to six km and on a scale of tens of km for about half of the polymorphic loci.

Second, we examined subpopulation structure by measuring inbreeding on different geographical scales. We first viewed the Stormberg subpopulations as a single unit, then subdivided the samples into progressively smaller geographical units. We interpreted the inbreeding coefficient, F, at a particular level to reflect the degree of panmixis among populations on that geographical scale. What we found was a weak, but nonsignificant deficit of heterozygotes on a large scale over the entire study area and a nonsignificant excess of heterozygotes on a microgeographic scale. The deficit of heterozygotes on a large scale reflects Wahlund's effect that results from including genetically-differentiated populations in the same sample. The excess of heterozygotes on a small scale, in contrast, reflects the sampling of outbred, extended family units. Thus two opposing forces influence the genetic structure of Greywing populations. On the one hand, subdivision into socially-

structured coveys tends to produce small-scale geographical differences among subpopulations and, on the other, dispersal tends to homogenize allele frequencies over short distances.

Although these results demonstrate the presence of allele-frequency heterogeneity and give some indication of genetic patch size, they do not distinguish between different models of population structure, as both isolation-by-distance and island-like migration can produce similar values of F_{ST} and F_{IS}. We therefore used Mantel's test and spatial autocorrelation analysis to distinguish between these two classic models. Since Greywing are sedentary, we expected limited dispersal to produce allozyme-frequency patterns that would reflect isolation by distance. Mantel's statistic, however, indicated that there was no correlation between geographical distance and allele-frequency differences between samples. The isolation-by-distance model also predicts that contiguous populations should show positive autocorrelation and non-contiguous populations should show negative autocorrelation because of the homogenizing influence of gene flow between neighboring populations. Although Moran's I and Geary's c indicated that there was positive autocorrelation for two alleles on a small scale, the correlograms for the remaining 18 alleles showed a random, "crazy-quilt" pattern of autocorrelation in which there was little allele-frequency similarity between neighboring populations. We interpret this to mean that dispersal is not limited to neighbouring or nearby populations as expected with isolation by distance.

Patterns for Aat-2^{-140} and Pgm-1^{100}, however, that showed geographically-meaningful patterns. The pattern of autocorrelation for Aat-2^{-140} suggested a "depression" in its

frequency over the study area. The frequency of this allele tended to be higher in peripheral localities so that frequencies in nearby localities (0-15 km) as well as those in widely-separated localities (55-60 km) showed positive autocorrelation. Frequencies at localities separated by intermediate distances (25-50 km), on the other hand, showed negative autocorrelation. Frequencies of Pgm-1^{100} also showed positive autocorrelation over short distances (0-5 km) and negative autocorrelation over intermediate distances (10-25 km), but did not show any pattern of autocorrelation over larger distances. The patterns for these two alleles were not congruent with each other. One explanation for these patterns may be that the two alleles are under some kind of selection or are linked to loci under selection. Alternatively, the shapes of the correlograms may be due to a chance arrangement of allelic frequencies in populations experiencing random drift and frequent founder effects.

We interpret both the presence of genetic heterogeneity and the general lack of autocorrelation to indicate that there is no diffusion-like spread of alleles through Greywing populations. Instead, allele-frequency surfaces show a mosaic pattern that appears to reflect random drift in small populations, founder effects and haphazard dispersal beyond neighbouring populations. Population structure may therefore be better, but not exactly, represented by the classic island model of migration (Wright 1943).

We then used three methods of estimating dispersal that assume the island model of migration. Slatkin's (1981) graphical method for estimating gene flow showed a strongly concave curve and

points to large amounts of gene flow between populations of Greywing, as is generally observed in birds (Barrowclough 1983). This graphical method, however, is largely insensitive to measuring anything but gross differences in gene flow between taxa. Both "private-allele" and F_{ST} estimates of the number of migrants between populations were very similar and suggested that, on average, 8-9 birds effectively migrated between each pair of localities each generation. Such a level of migration, however, was not anticipated for "sedentary" Greywing Francolins. In spite of the large amount of gene flow, random drift and founder effects in small socially-structured populations still appear to be important in producing heterogeneous allelic frequencies on a small geographical scale.

In conclusion, the high rates of migration suggest that the Stormberg subpopulations of Greywing act more or less as a single population extending over at least 1 500 km^2. High values of sample heterozygosity suggest that the Stormberg Greywing populations have been stable for a long period of time and that genetic diversity has accumulated in spite of small subpopulation sizes. Nonetheless, high rates of population turnover and subdivision into socially-structured coveys leads to temporary founder effects and genetic drift, which produce a mosaic of small-scale genetic patches.

Appendix 2.1. Allele frequencies for 14 polymorphic loci in Greywing Francolin.

		Locality																				
Locus	Allele	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Aat-2	- 20	0,20	0,29	0,29	0,21	0,30	0,36	0,35	0,17	0,09	0,20	0,19	0,23	0,25	0,17	0,25	0,10	0,27	0,20	0,30	0,26	0,13
	- 40	-	-	-	-	-	-	0,01	-	0,02	-	0,05	-	-	-	-	-	0,03	-	-	-	-
	- 50	-	-	-	-	0,02	-	-	-	-	-	-	-	0,02	-	-	-	-	0,02	-	-	-
	-100	0,70	0,63	0,64	0,79	0,64	0,64	0,63	0,77	0,84	0,77	0,76	0,75	0,69	0,74	0,69	0,87	0,67	0,71	0,65	0,70	0,67
	-140	0,10	0,08	0,07	-	0,04	-	0,01	0,06	0,05	0,03	-	0,02	0,04	0,09	0,06	0,03	0,03	0,07	0,05	0,04	0,20
N		10	12	34*	28	25	26	49	15	28	32	29	30	28*	36	26	15	15	28	20	23	20
Gpi	80	-	-	-	-	-	-	-	-	-	-	0,02	-	-	0,01	-	-	-	0,05	0,03	-	-
	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,03	-	-	-	-
	-100	1,00	1,00	1,00	1,00	1,00	1,00	0,99	1,00	1,00	1,00	0,97	1,00	1,00	0,99	1,00	1,00	0,97	0,95	0,97	1,00	1,00
	-200	-	-	-	-	-	-	0,01	-	-	-	0,02	-	-	-	-	-	-	-	-	-	-
N		10	12	34	28	25	26	49	15	28	32	30	30	29	39	26	15	15	26	20	23	20
Idh-A	-100	1,00	1,00	0,99	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00
	-120	-	-	0,01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N		10	12	34	28	25	26	49	15	28	32	30	30	29	39	26	15	15	28	20	23	20
Ldh-A	110	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,02	-	-	-	-	-	-
	100	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	1,00	0,98	1,00	0,98	0,91	1,00	0,96	0,93	1,00	1,00	1,00	1,00	1,00
	0	-	-	-	-	-	-	-	-	-	0,02	-	0,02	0,09	-	0,02	0,07	-	-	-	-	-
N		10	12	34	26	25	26	49	14	26	32	30	30	29	39	26	15	15	28	20	23	20
Ldh-B	100	1,00	1,00	1,00	1,00	1,00	1,00	0,99	1,00	1,00	1,00	1,00	1,00	1,00	0,99	1,00	1,00	1,00	1,00	1,00	1,00	1,00
	-1000	-	-	-	-	-	-	0,01	-	-	-	-	-	-	0,01	-	-	-	-	-	-	-
N		10	12	34	28	25	26	49	15	26	32	30	30	29	39	26	15	15	28	20	23	20
Mpi	110	-	0,04	0,10	0,04	-	0,19	0,14	0,03	0,05	0,16	0,03	-	0,07	0,04	0,15	-	-	0,07	0,03	0,15	-
	107	-	-	-	0,02	-	-	-	-	-	-	-	0,02	0,02	-	-	-	0,07	-	-	-	-
	100	1,00	0,96	0,90	0,94	0,98	0,81	0,86	0,97	0,95	0,82	0,97	0,98	0,89	0,96	0,85	0,97	0,86	0,93	0,97	0,85	1,00
	93	-	-	-	-	0,02	-	-	-	-	0,02	-	-	0,02	-	-	0,03	0,07	-	-	-	-
N		10	12	34	28	25	26	49	15	28	32	29	30	28	38	26	15	15	28	20	23	20
Pep-A	108	-	0,13	0,09	0,11	0,04	-	0,04	-	0,02	-	-	0,05	-	0,08	0,02	-	0,07	0,02	0,05	0,02	-
	100	1,00	0,88	0,89	0,89	0,94	1,00	0,95	0,97	0,98	0,94	0,98	0,85	0,88	0,92	0,94	1,00	0,90	0,98	0,92	0,98	1,00
	92	-	-	0,02	-	0,02	-	0,01	0,03	-	0,06	0,02	0,10	0,12	-	0,04	-	0,03	-	0,03	-	-
N		10	12	34	28	25	26	49	15	28	32	30	30	29	39	26	15	15	28	20	23	20
Pep-B	140	-	0,04	0,02	-	-	0,02	-	0,07	0,02	-	-	0,02	-	0,03	-	-	-	-	-	0,02	0,03
	120	0,15	-	0,13	0,07	0,06	0,02	0,09	0,03	0,05	0,03	0,17	-	0,12	0,09	0,11	0,13	0,13	0,05	0,20	0,13	0,08
	104	-	-	0,03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	100	0,85	0,88	0,72	0,89	0,82	0,96	0,88	0,90	0,93	0,86	0,83	0,88	0,86	0,83	0,83	0,77	0,83	0,84	0,80	0,72	0,88
	80	-	0,08	0,10	0,04	0,12	-	0,03	-	-	0,11	-	0,10	0,02	0,05	0,06	0,10	0,03	0,11	-	0,13	0,03
N		10	12	34	28	25	26	48	15	28	32	30	30	29	38	26	15	15	28	20	23	20
Pep-D	120	-	-	-	-	0,02	-	-	-	0,02	-	-	-	-	-	-	-	-	-	-	-	-
	112	0,03	0,04	0,03	0,04	0,10	0,19	0,01	0,03	0,29	0,03	0,10	0,10	0,09	0,24	0,06	-	0,07	0,11	0,25	0,11	-
	100	0,70	0,83	0,88	0,91	0,80	0,81	0,89	0,94	0,70	0,86	0,90	0,75	0,88	0,73	0,87	1,00	0,93	0,88	0,65	0,82	0,75
	80	-	0,13	0,09	0,05	0,08	-	0,09	0,03	-	0,11	-	0,15	0,03	0,03	0,08	-	-	0,02	0,08	0,07	0,25
	70	-	-	-	-	-	-	0,01	-	-	-	-	-	-	-	-	-	-	-	0,02	-	-
N		10	12	34	28	25	26	49	15	28	32	30	30	29	37	26	15	15	28	20	23	20

Appendix 2.1, Continued

Pgd-1	140	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,02	-	-	-	-	-	0,03
	120	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	115	0,10	0,08	0,12	0,18	0,16	0,06	0,14	0,13	0,13	0,03	0,18	0,12	0,06	0,15	0,12	0,13	-	0,09	0,05	0,07	0,16
	110	-	-	-	-	-	-	-	-	0,02	-	0,05	-	-	-	-	-	-	-	0,03	-	0,03
	100	0,60	0,88	0,74	0,66	0,60	0,87	0,70	0,73	0,62	0,63	0,42	0,60	0,87	0,67	0,54	0,73	0,86	0,73	0,85	0,76	0,50
	80	0,10	-	-	0,05	-	-	-	-	0,02	-	0,03	-	-	-	0,08	-	0,07	-	-	-	0,03
	70	0,20	0,04	0,15	0,11	0,24	0,08	0,15	0,13	0,21	0,34	0,32	0,28	0,07	0,18	0,24	0,13	0,07	0,18	0,08	0,17	0,25
	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N		10*	12	34	28*	25	26	49	15	28	32	30	30	27*	38	26*	15	15	28	20	23	20
Pgm-1	120	-	-	0,06	0,02	-	-	-	-	-	-	0,02	-	0,02	0,02	0,02	0,03	-	-	-	-	-
	100	1,00	1,00	0,94	0,98	1,00	0,98	0,96	1,00	1,00	0,98	0,92	0,95	0,98	0,91	0,96	0,90	1,00	0,98	1,00	1,00	1,00
	60	-	-	-	-	-	0,02	0,04	-	-	0,02	0,07	0,03	-	0,07	0,02	0,07	-	0,02	-	-	-
	50	-	-	-	-	-	-	-	-	-	-	-	0,02	-	-	-	-	-	-	-	-	-
N		10	12	34	28	25	26	49	15	28	32	30	30	29	38	26	15	15	28	20	23	20
Pgm-2	140	-	-	-	-	-	-	-	-	0,02	-	-	-	-	-	-	-	-	-	-	-	-
	115	0,05	0,08	0,02	0,11	-	0,04	0,06	0,04	0,04	-	0,05	-	0,09	0,01	0,06	-	-	0,04	0,13	0,02	-
	100	0,90	0,75	0,82	0,73	1,00	0,87	0,80	0,78	0,76	0,92	0,76	0,82	0,80	0,84	0,79	0,87	0,71	0,70	0,70	0,85	0,75
	80	0,05	0,17	0,16	0,16	-	0,10	0,14	0,18	0,19	0,08	0,19	0,18	0,11	0,15	0,15	0,13	0,29	0,27	0,15	0,13	0,25
	70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,03	-	-
N		10	12	34	28*	25	26	49	14	27*	32	29	30	28	39	26	15	14	28	20	23	20
Sdh	10	-	-	0,03	-	-	-	0,01	-	-	0,03	0,05	0,05	0,02	0,08	0,02	-	-	0,05	0,03	0,07	-
	-100	1,00	1,00	0,97	1,00	1,00	1,00	0,99	1,00	1,00	0,97	0,95	0,95	0,98	0,92	0,98	1,00	1,00	0,95	0,98	0,94	1,00
N		10	12	34	28	25	26	49	15	28	32	30	30	29	39	26	15	15	28	20	23	20

N is number of birds in sample.

* Significant departure from Hardy-Weinberg proportions, 0,05 > P > 0,01.

** Significant departure from Hardy-Weinberg proportions, P < 0,01.

SECTION TWO

POPULATION AND BEHAVIOURAL ECOLOGY

CHAPTER 3

BREEDING BIOLOGY

Status: in press. The breeding biology of the Greywing Francolin Francolinus africanus and its implications for hunting and management. S. Afr. J. Zool. co-author: T.M. Crowe.

SUMMARY

We studied the breeding biology of the Greywing Francolin Francolinus africanus on the Stormberg Plateau of the eastern Cape Province, South Africa during 1988-1991. Timing of breeding, nesting behaviour, clutch size, egg size, and clutch survival rates were recorded and compared with published and unpublished information from Natal, the eastern Orange Free State and southwestern Cape Province. The Greywing breeds during the austral summer throughout its range, with peak laying activity during August-November. However, the nesting period is contracted in the southwestern Cape, where it starts about one month earlier and ends three months earlier than in the eastern Orange Free State and the eastern Cape, where laying was recorded from August to March. The Greywing's breeding season is more consistently positively correlated with measures of environmental variation in the summer rainfall region than in the winter rainfall region. Flushed single birds were the best indicators

of nesting sites. Clutches were incubated by hens only. Mean clutch size was 5,5 (SD = 1,2) and mean egg dimensions were 39,9 mm x 30,1 mm (SD = 1,9 & 0,9). Incubation period was 21,7 days (SD = 0,5), hatching success (the probability that eggs present at hatching time actually produced living young) was 90% and clutch survival rate (the probability that a clutch will survive 21,7 days of incubation) was 31%. Hunting seasons for the Greywing should be from 15 April to 31 July in the summer rainfall region and from 1 April to 30 June in the winter rainfall region. Veld burning should cease at the end of August throughout the Greywing's range so that disturbance of breeding birds is minimized.

INTRODUCTION

The nesting habits and breeding season of the Greywing Francolin, Francolinus africanus, have been discussed by Gilfillan (1908), Clancey (1967), Winterbottom (1968, 1971), Mentis (1973), Mentis & Bigalke (1980), Maclean (1985) and Crowe et al. (1986). Clancey (1967) suggested that Greywing populations in the eastern, southern and western Cape Province breed significantly earlier than populations from Lesotho, Natal and the extreme eastern Cape. Liversidge (1987) also reported that the Greywing breeds earlier in the southwestern Cape Province, where rain falls predominantly in the austral winter (May-August), than elsewhere within its range, where the onset of breeding coincides with the initiation of the rains of the austral summer. Therefore, if reproduction in the Greywing is influenced by rainfall, as is the case in the Helmeted Guineafowl, Numida meleagris (Crowe 1978; Crowe et al. 1986), significant variation would be expected between the timing of breeding in populations from winter and summer rainfall regions. The Greywing is a popular and commercially important gamebird (Mentis & Bigalke 1985a; Johnson & Wannenburgh 1987; Hickman 1988), and should any significant variation occur in its breeding season, it will be necessary to time the hunting season and certain management activities (e.g. veld burning) to coincide with its non-breeding season to minimize their impact on population losses and trends. Furthermore, for sustainable hunting of Greywing it is necessary to have information on their annual productivity.

The objectives of this study are to investigate the variation

in timing of breeding in three geographic regions within the range of this species, and to estimate the clutch size, incubation period, hatching success and clutch survival rates of the Greywing populations from commercially-grazed grasslands of the Stormberg Plateau in the eastern Cape Province, i.e. at the extreme southwestern range of F. a. proximus (Clancey 1957). Comparative published and unpublished breeding information for Greywing populations from conservation areas in Natal, and from the eastern Orange Free State and a range of areas from the southwestern Cape Province were obtained. These data, plus various measures of environmental variation and availability of food were used to determine: 1) timing of breeding in relation to environmental and other variables, 2) breeding biology and nesting success, and 3) implications for hunting and management.

STUDY AREA AND METHODS

Most of our observations on the breeding biology of the Greywing were made on farms on the Stormberg Plateau (31°15' S; 26°30' E), in the eastern Cape Province of South Africa during 1988-1990 (Figure 3.1). Additional observations were made on the timing of egg-laying in the eastern Cape, and gonad size and pairing behaviour of Greywing from the southwestern Cape, during 1991. The Stormberg study area is dominated by open grasslands ranging in elevation from 1 700 m to 2 000 m above sea level. Greywing populations within the study area are subjected to annual hunting at 35%-40% removal levels. However, significant alteration of the results of this study by hunting is unlikely,

because these socially-structured populations display naturally high rates of turnover (Grant & Little 1992, Chapter 2) and little between-population variation in demography or genetics between hunted and unhunted populations, at these levels of offtake (Little et al. in review, Chapter 10).

Greywing reproduction was monitored by measuring gonadal development and by observing the timing of pairing and egg-laying. Testis and ovarian follicle size were measured for Greywing shot monthly during July 1988-December 1990. For male birds, gonad size was the anterio-posterior length of the larger testis (usually the left one) and for females, the diameter of the largest follicle. Greywing were classified as adult if they had a rounded tenth primary, or juvenile (< one year) if this feather was pointed (Little & Crowe in press b, Chapter 4). The percentage of coveys comprised of two birds reflect pairing rates. The presence of chicks was estimated by advancing the nesting curve for Greywing by one month, i.e. about 10 days longer than the 20-23 day incubation period for most francolin species studied to date (Crowe et al. 1986).

We compared our results with measures of reproductive condition and pairing behaviour of Greywing populations from Giant's Castle Game Reserve, Natal Drakensberg (29°15'S; 29°30'E) (Mentis 1973; Mentis & Bigalke 1980) and with unpublished nest records from a range of sites in the southwestern Cape and eastern Orange Free State (Nest Record Card Scheme of the Southern African Ornithological Society) (Figure 3.1).

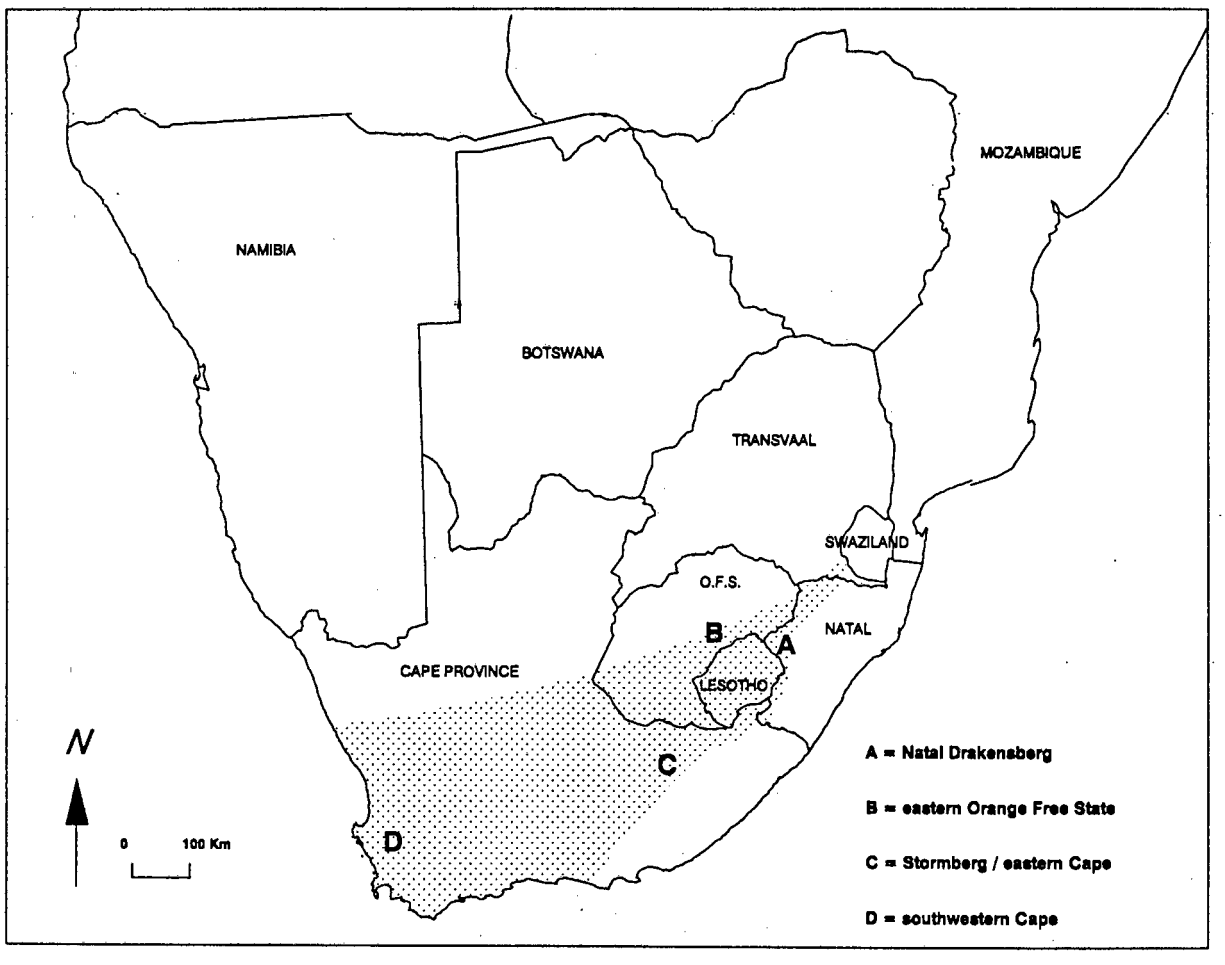


Figure 3.1. Range of the Greywing Francolin (stippled; Maclean 1985) and location of study areas (A-D).

We used the multiway frequency tables: log-linear model (4F) from the BMDP statistical package (Dixon et al. 1990) to test the hypothesis of independence, and departures from expectations, of nesting times in the three geographical regions. BMDP-4F tests for independence of the rows and columns (regions and months) using a likelihood-ratio chi-square (G-statistic), and also tests for levels of adjusted standardized deviation (ASD) from expected values at each cell (in this case number of nests per region per month). Adjusted standardized deviates are significant if the absolute value is greater than $t_{\infty,0,05}$=1,96 (Everitt 1977).

Simple correlation analyses were done between seasonal variation in pairing, follicle size, nesting and the presence of chicks for the three regions and measurements of monthly rainfall, ambient temperature, day length and the availability of arthropod food, to investigate relationships between Greywing breeding and environmental variation.

Environmental variables were extracted from the Agro Climatical Reports (Anon. 1983-1991) for the farm Buffels Fontein (31°22'S; 26°42'E) in the eastern Cape and from the Weather Bureau (Anon. 1979) for Cedara (29°32'S; 30°17'E) in Natal and D.F. Malan Airport (33°58'S; 18°36'E) in the southwestern Cape. Day length was the number of hours between standardized sunrise and sunset for Buffels Fontein, Cedara and D.F. Malan (CSIR 1973).
Variation in arthropod numbers in the eastern Cape was recorded monthly using a 0,25 m^2 quadrant. Arthropods were counted for one minute per quadrant, at 30 quadrants about 2 m apart, per survey. Two surveys were conducted per month, on calm clear days and between 10h00 and 15h00. Data on availability of arthropods were extracted from Earlé (1981) and Siegfried (1969) for Natal

and the southwestern Cape, respectively.

We measured eggs and examined nests on site. Nest dimensions were the mean of two diameters within the lining of the nest bowl and depth, from a horizontal line across the top of the bowl to the floor of the bowl. Clutch size was the largest number of eggs in the nest during incubation. Egg length was measured with Vernier calipers along the longitudinal axis, and egg width across the widest part of the egg. Incubation period was the number of days from the laying of the last egg in a clutch to the hatching of that egg (Campbell & Lack 1985).

Nesting success was determined using methods described by Mayfield (1975) and Johnson (1979). Hensler & Nichols (1981) suggest that the measure of nest success proposed by Mayfield (1975) is a maximum likelihood estimator.

RESULTS

Timing of breeding

There was highly significant geographical variation in the timing of nesting of Greywing between Natal, the eastern Cape and the southwestern Cape (G = 34,4, df = 16, P = 0,005; Table 3.1).

Table 3.1. Monthly distribution of Greywing Francolin nest records for the eastern Cape (eCape), eastern Orange Free State (eOFS) and southwestern Cape (swCape).

Region	Months												
	J	A	S	O	N	D	J	F	M	A	M	J	Total
eOFS[2]		2	2	4	6	1	1	3[+]	2[+]				21
eCape[1]	[-]	5	11	12	7	4	1		1				41
swCape[2]	6[+]	9	13	10	6	3							47
Total	6	16	26	26	19	8	2	3	3				109

[-] negative significant deviation (ASD>1,96, P=0,05).
[+] positive significant deviation (ASD>1,96, P=0,05).
[1] this study.
[2] Nest Record Card Scheme of S.A.O.S.

Natal

Gonadal development of adult Greywing from Natal was greatest during July-December (Mentis 1973; Mentis & Bigalke 1980). Furthermore, the frequency of paired Greywing was greatest during September-December (Fig. 3.2a). Although there are few nesting data available for Natal, data for 21 nests from the nearby eastern Orange Free State indicate that nesting peaks there during October-November (Table 3.1). There was significantly more nesting activity during February-March in the eastern Orange Free State (ASD = 3,6 & 2,1 respectively, $P < 0,05$) than in the eastern and southwestern Cape. Measurements of monthly pairing behaviour, follicle size and the presence of chicks were significantly positively correlated with environmental variables (Table 3.2).

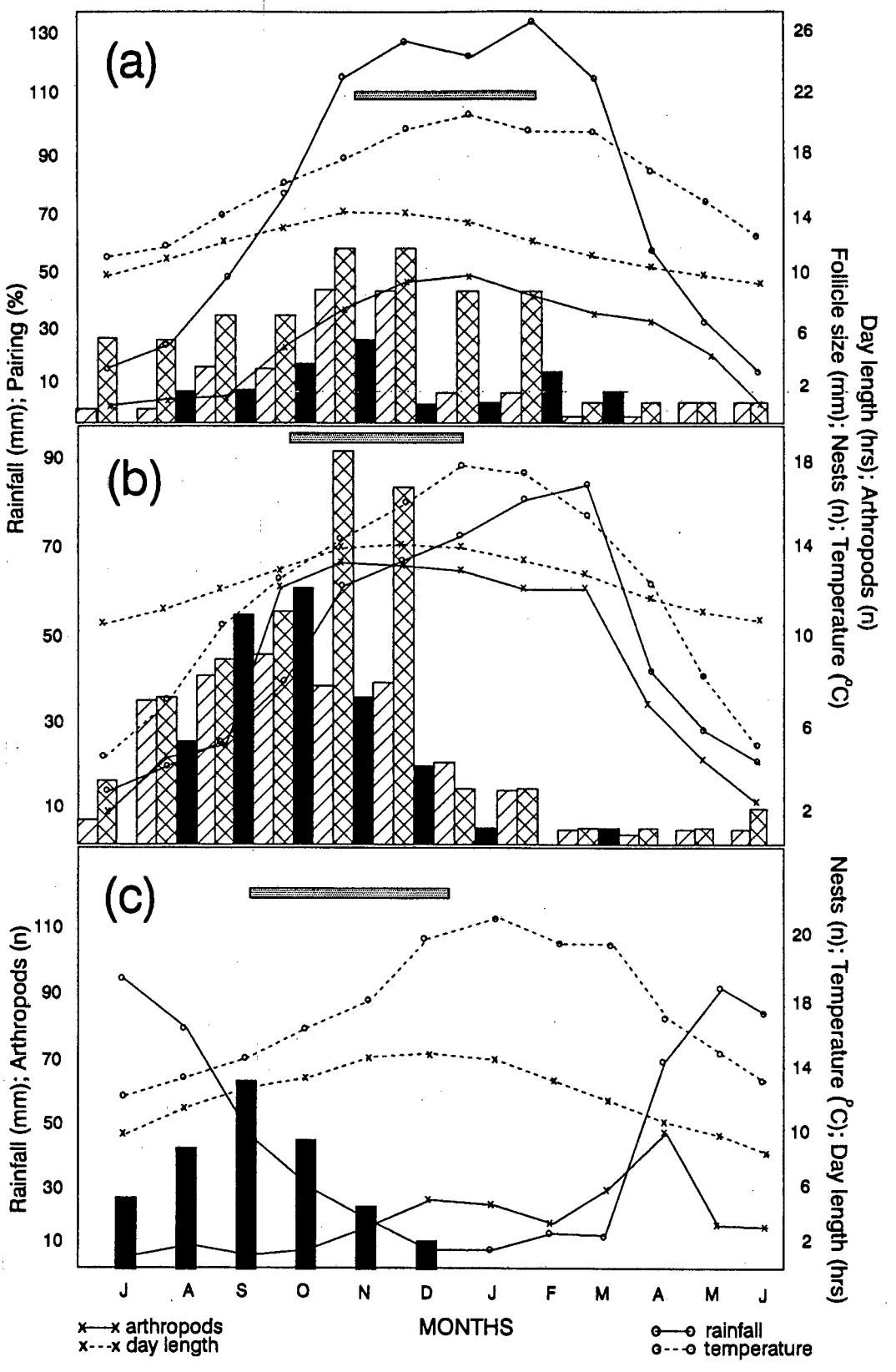


Figure 3.2. Reproductive activity of Greywing Francolin (vertical bars) and environmental variables (lines) for a) Natal/eastern Orange Free State b) eastern Cape Province, and c) southwestern Cape Province. Hatched bars = pairing frequency, cross hatched bars = mean follicle diameter, solid bars = nests; horizontal stippled bars = peak chick 'windows'.

Eastern Cape Province

As with Greywing from Natal, the gonads of 929 Greywing from the eastern Cape, examined during July 1988-March 1990, showed greatest adult reproductive activity during July-December (Table 3.3). Adult males had enlarged testes (>10 mm) between July and March, and the testes of juvenile males were not significantly different from those of adults during September-November (P = 0,43, Mann-Whitney U-test). Gonadal development in adult females peaked during August-December (Fig. 3.2b), and follicle size of juvenile females was greatest during August-October (Table 3.3).

Gonadal development in 89 Greywing measured during July-December 1990 showed testicular development similar to that for 1988-1989. However, follicle size of adults was significantly greater for birds collected in August 1990 ($\bar{x}$ = 38,0 mm; SD = 1,0; n = 3 vs 6,7 mm; P < 0,01, Mann-Whitney U-test). The onset of egg-laying was also earlier in 1990 (in early August) than in the two previous seasons.

Egg-laying in 1991 commenced in late August, before the start of the spring rains and following a dry winter, despite the lowest August temperatures in nine years (mean minimum temperature = -5,1^{o}C; SD = 6,4), nearly 3,0^{o}C colder than the 1983-1990 mean minimum temperature.

All two-bird coveys collected during August-March (n = 10) consisted of a male and a female in breeding condition. The incidence of such pairing was greatest during August-December (Fig. 3.2b). Incubating birds were observed during August-March, but excluding February, and the majority of nests (73%; n = 41) were found during September-November (Table 3.1; Fig. 3.2b).

Although Greywing nests were recorded during January-March,

this extension of the breeding season was not significantly different from the general pattern for the three regions (Table 3.1; ASD = 0,4, -1,4 and -0,2 respectively; $P > 0,05$). However, the potential for early nesting in the eastern Cape was suggested by a significant negative deviation from expected in July, i.e. the model expected to detect breeding in July in the eastern Cape (ASD = -2,0; $P < 0,05$). Indeed, on 26 July 1991 a hen in breeding condition (3 follicles > 10 mm in diameter) was shot on the Stormberg Plateau.

The monthly incidence of follicle size and the presence of chicks were usually significantly positively correlated with monthly temperature, rainfall, day length and arthropod availability. Correlations with pairing and nesting were not significant (Table 3.2).

Southwestern Cape Province

Pairing frequency for Greywing populations from the southwestern Cape during August (33%; n = 6 coveys) was similar to that for the eastern Cape (35%), and the mean follicle size for 18 females from these populations was not significantly different ($P > 0,05$, Mann-Whitney U-test) from that of the eastern Cape for April (1,8 mm), June (2,7 mm), August (5,3 mm) and November (17,6 mm) (Table 3.3). However, nest record cards (n = 47) from the southwestern Cape indicate that nesting peaks during August-October (Table 3.1; Fig. 3.2c), and that there is significantly earlier nesting in the southwestern Cape, i.e. during July (ASD = 2,9; $P < 0,05$), than in the eastern Cape and eastern Orange Free State. There were no significant

correlations between our measurements of Greywing breeding activity and environmental variables in the southwestern Cape (Table 3.2).

Table 3.2. Correlation coefficients (r) for monthly breeding activity of Greywing Francolin and monthly environmental variables (July-December).

Correlation variables	Regional Statistics Natal r	eCape r	swCape r
Pairing vs			
Temperature	0,91 *	0,60 ns	-
Rainfall	0,96 **	0,43 ns	-
Day length	0,95 **	0,58 ns	-
Arthropods	0,93[1]**	0,57 ns	-
Follicle size vs			
Temperature	0,90 *	0,96 **	-
Rainfall	0,95 **	0,98 **	-
Day length	0,95 **	0,97 **	-
Arthropods	0,93[1]**	0,92 **	-
Nesting vs			
Temperature	0,54 ns	0,37 ns	-0,53 ns
Rainfall	0,48 ns	0,17 ns	0,23 ns
Day length	0,53 ns	0,36 ns	-0,35 ns
Arthropods	0,42[1]ns	0,37 ns	-0,78[2]ns
Chicks vs			
Temperature	0,92 **	0,82 *	0,48 ns
Rainfall	0,95 **	0,77 ns	-0,69 ns
Day length	0,95 **	0,84 *	0,63 ns
Arthropods	0,93[1]**	0,89 *	0,10[2]ns

*=significant at P<0,05.
**=significant at P<0,01.
ns=not significant (P>0,05).
[1]arthropod availability data from Earlé (1981).
[2]arthropod availability data from Siegfried (1969).

Table 3.3. Monthly variation in gonadal size of Greywing Francolin (Stormberg: July 1988 - March 1990).

		Months											
		J	A	S	O	N	D	J	F	M	A	M	J
Male (testis length, mm)													
Ad	$\bar{x}$	12,5	13,6	14,6	14,3	15,5	16,2	13,7	11,9	13,3	9,4	8,0	8,5
	SD	3,7	1,8	2,7	1,5	1,8	2,6	2,3	1,9	2,0	2,3	1,6	2,0
	n	69	17	7	4	11	5	10	9	9	47	80	78
J	$\bar{x}$	9,5	9,4	14,6	13,3	13,0	6,0	5,5	10,0	6,8	5,8	6,5	6,9
	SD	3,9	2,7	0,9	4,3	-	0,0	1,3	-	1,5	2,0	1,1	1,1
	n	45	11	5	4	1	2	4	1	5	17	32	34
Female (follicle diameter, mm)													
Ad	$\bar{x}$	3,0	6,7	8,5	10,8	18,5	17,3	3,4	2,6	1,3	1,2	1,2	1,5
	SD	2,1	6,8	9,1	9,8	18,2	17,2	1,3	1,3	0,5	0,4	0,5	0,6
	n	44	20	8	5	4	4	5	7	4	22	47	32
J	$\bar{x}$	1,1	3,1	3,0	3,3	1,0	-	1,0	1,3	1,1	1,1	1,0	1,1
	SD	0,9	4,2	0,0	0,5	0,0	-	-	0,5	0,3	0,4	0,0	0,3
	n	57	17	3	4	2	-	1	4	9	28	36	59
Tot n		215	65	23	17	18	11	20	21	26	114	195	203

Ad = adult.
J = juvenile (first-year).

Nesting, clutch size and incubation

Of 41 nests examined on the Stormberg during the study period, all but two were found by searching areas from where single birds had flushed. One nest was located by pointing dogs during 73 hours of searching, and the other was located by random searching (effort not recorded). Nests were all situated on the ground, under the canopy of a grass tuft, with the exception of one, which was placed in a lucerne Medicago sativa land. Greywing nests are scrapes in the earth lined with grass and occasionally feathers. Mean nest dimensions measured from eight nests were 16,9 cm diameter (SD = 0,3; range = 16,5-17,5) by 4,8 cm deep (SD

= 1,0; range = 3,5-6,5).

Mean clutch size for the eastern Cape was 5,5 eggs (SD = 1,2; range = 4-8; n = 38), and was not significantly different between years (1988/89 $\bar{x}$ = 5,45; SD = 1,6; n = 11; 1989/90 $\bar{x}$ = 5,25; SD = 0,9; n = 12; 1990/91 $\bar{x}$ = 5,80; SD = 1,0; n = 15; P > 0,05, t-test). Mean egg size was 39,93 mm x 30,11 mm (SD = 1,9 & 0,9; range = 37,2-44,6 x 28,3-32,1; n = 101). Egg coloration was consistent with the descriptions by Maclean (1985) and Crowe et al. (1986), i.e. yellowish brown, sometimes speckled with brown and slate. Mean incubation period for 13 eggs from two wild clutches was 21,7 days (SD = 0,5), while three eggs of known laying date, incubated in an electronic incubator, hatched at 21 days. Clutches were incubated by the hen only, usually with the paired male close to the nest site.

Nest success

The clutch survival rate, hatching rate and the survival per egg-day were calculated for 21 nests from the Stormberg study period (Table 3.4; Appendix 3.1). The hatching rate (i.e. the probability that eggs present at hatching time actually produce living young) was 44 young/49 eggs which equals a hatching probability of 0,898. That is, about 10% of the eggs present at hatching did not hatch. Nine clutches were lost during 172 nest-days of incubation, the rate of clutch loss was therefore 9/172 = 0,052 per nest-day, and the clutch survival rate was 1 - 0,052 = 0,948 per nest-day. Thus, the probability that a clutch will survive 21,7 days of incubation is $0,948^{21,7}$ = 0,31. The variance of Mayfield's estimator of clutch survival per nest-day

($\underline{s}$) using the method of Johnson (1979) is:

$$\text{Var}(\underline{s}) = [(172)^3/(172 - 9)9]^{-1}$$
$$= 2{,}883(10^{-4}),$$

and the standard error (the square root of the variance) = $1{,}698(10^{-2})$. The 95% confidence limits for $\underline{s}$, calculated as the estimated value ± 2 standard errors, gives the boundary at 0,914 to 0,982 (usually: $\bar{x} \pm 2SD/\sqrt{n}$).

The overall mortality per egg-day from seven eggs lost individually during incubation, where the exposure was 899 egg-days was $7{,}8(10^{-3})$ per egg-day. Therefore, the survival was 0,992 per egg-day, and the probability of an egg surviving the incubation period without the entire clutch being destroyed was 0,84.

The mortality per egg-day for the eight clutches which persisted until hatching was $3/671 = 4{,}5(10^{-3})$. Thus, the probability of an egg surviving the incubation period in a persisting nest was 0,907.

Table 3.4. Nest success rates (as percentages) calculated for 21 Greywing Francolin clutches from 1988-1990 on the Stormberg Plateau.

Success Rate	Breeding season		
	1988/89	1989/90	Cumulative
Number of nests	10	11	21
Clutch success:			
Mortality/nest-day	10,26	1,06	5,23
Survival/nest-day	89,74	98,94	94,77
Survival/21,7 days	9,55	79,29	31,39
Egg success:			
Overall:			
Mortality/egg-day	1,21	0,41	0,78
Survival/egg-day	98,79	99,59	99,22
Survival/21,7 days	76,72	91,46	84,40
Persisting/nests:			
Mortality/egg-day	0,76	0,25	0,45
Survival/egg-day	99,24	99,75	99,55
Survival/21,7 days	84,79	94,80	90,73
Hatching success:			
Mortality/season	25,00	5,41	10,20
Survival/season	75,00	94,60	89,80

DISCUSSION

Timing of breeding

The Greywing Francolin has a prolonged breeding season (August-March) in the summer rainfall region (i.e. the eastern Cape Province and Natal/eastern Orange Free State) and a contracted breeding season which begins significantly earlier (July-December) in the winter rainfall region. In the Stormberg study area, annual variation in August temperature appeared to have no effect on the timing of breeding. However, above-average winter rainfall during June 1990 did appear to induce earlier egg-laying in August 1990. The view that food availability is the chief ultimate factor influencing the onset of breeding (Marshall 1951;

Nix 1976) and that breeding in gamebirds is timed to take advantage of a seasonal flush of arthropods (Potts 1986) is not supported by the negative relationship between laying, and the weak positive relationship between chick-rearing phase, and arthropod availability in the southwestern Cape. Thus, it appears that the seasonal variation in suitable breeding conditions in the southwestern Cape create a relatively small acceptable time 'window' for breeding in that region which necessitates both early onset and cessation of breeding. In the summer rainfall region, however, Greywing breed when temperature, rainfall, day length and arthropod availability are increasing or peaking. The alternative for Greywing from the southwestern Cape would be to breed when there is maximum arthropod availability at the start of the rainy season (i.e. March-April). However, this is a time during which temperature is decreasing and winter rainfall is increasing. Since the survival of young gamebirds may be poor under cold and wet conditions (Pedersen & Steen 1979; Potts 1986) chick survival would be low.

The biological implications of this breeding pattern pose two, as yet unanswered, questions. First, is the Greywing capable of the same reproductive success in the winter rainfall region as it is in the summer rainfall region? Second, if not, is reduced reproductive success in the winter rainfall region a result of inadequate arthropod availability? If so, this less-than-optimal breeding strategy may lead to reduced populations and hence its low utilization for hunting in that area.

Clutch and egg size

Mean clutch and egg sizes in this study were consistent with those in other studies for this species, except for the upper range of clutch size, which was less than that reported by Gilfillan (1908), Maclean (1985) and Crowe et al. (1986). These authors suggest that larger clutches may result from two hens laying in the same nest, a behaviour which was not observed during this study.

Mean Greywing clutch size is less than that of nine species of northern hemisphere quails and partridges (Johnsgard 1988), but is similar to that of ten other southern African francolin species (Crowe et al. 1986). Lack (1968) suggested that smaller clutch sizes, characteristic of tropical partridges, may reflect either reduced amounts of nutritious foods, shorter diurnal foraging periods, or longer nesting seasons making it more feasible to raise two or more broods per season. No evidence was found during this study to support the multiple-broods hypothesis for the Greywing, despite previous circumstantial evidence of 'old' hens raising more than one brood per season (Mentis & Bigalke 1980). Indeed, parents stayed with their chicks throughout the breeding season, and chicks of different sizes and ages were never observed with only one pair of adults. However, we suggest that the apparently extended breeding season, particularly in the summer rainfall region, would allow successful re-nesting after failure of the first clutch.

Nest success

Nesting losses for the Greywing were as highly variable between years as for most other gamebirds (Johnsgard 1988). However, the

between-year difference in nesting success would be reduced if corrections were possible for the disturbing influence of sampling during the 1988/89 season. Nevertheless, the cumulative nesting success of 31,4% for the Stormberg is not significantly different from the mean of 40,7% (SD = 18,1) reported by Johnsgard (1988) for several studies of northern hemisphere quails and partridges. During the 1988/89 season, we visited nests daily, and hens were flushed from the nest at each visit. This may have contributed to the higher predation rate and one case of nest desertion during the first season. Visits to nests were not made as frequently, and hens were flushed less often, during the 1989-1990 breeding season.

Although we recorded high seasonal variation in hatching rate, the cumulative egg-failure rate of Greywing closely matches the egg-failure rates of less than 10% for three gamebird species reported by Johnsgard (1988).

Individual egg losses were low (i.e. when eggs were lost to predation either all the eggs were taken or the nest was deserted). Therefore we used Mayfield's (1975) assumption that the product of the probabilities of hatching success and clutch survival will give the probability that an egg present at the start of incubation produces a chick. This probability for Greywing is 0,90 x 0,31 = 0,28. Thus, the mean clutch size of 5,5 eggs x 28% probability of chick production = $\pm$2 chicks hatched per pair per season, on average. Mentis & Bigalke (1980) report an average annual turnover of birds in a population of 50% for the Natal Drakensberg populations. We recorded adult: juvenile ratios of 55-60%:40-45% in non-breeding (winter)

populations on the Stormberg during this study (Little et al. in review; Chapter 10). These production levels suggest that our estimates of chick production are conservative.

Regional and seasonal differences may be found in the rates of nest success, particularly where influenced by different levels of predation. During this study, two nests were preyed on by crows (Corvus spp.), three by small carnivores and one by a common egg-eater (Dasypeltis scabra). Greywing egg-shells located in the grassland indicated additional predation by crows and snakes. We suggest that nest predation by small carnivores and crows is possibly the major cause of nest failure on the Stormberg Plateau, and that the high incidence of losses of entire clutches is attributable to this cause [as found by Myrberget (1985a) for Willow Grouse Lagopus lagopus lagopus]. However, further study is required on the effects of predator removal on the nesting success of the Greywing before this can be tested fully.

Other causes of nest failure observed during this study were destruction by management fires (one case in August and two cases in September), human disturbance (one) and trampling by sheep (one).

Management implications

The management implications of a geographically variable breeding season in the Greywing create the need for regional differences in the timing of hunting. We suggest that the hunting season for the Greywing should be from 15 April to 31 July in the summer rainfall region and from 1 April to 30 June in the winter rainfall region (presently 1 April-15 July in the Cape

Province, and 31 May-31 August in Natal).

Although previous literature reports that a fine-scale fire mosaic maintains high densities of grassland francolins (Mentis & Rowe-Rowe 1979; Mentis & Bigalke 1981b), it has been suggested that late spring burning is detrimental to the reproductive success of these grassland francolins (Little & Bainbridge 1988). The common practice of burning grasslands shortly after the first spring rains usually encroaches into the breeding season of Greywing Francolin. We therefore recommend that grasslands in the summer rainfall region be burned not later than the end of August.

Appendix 3.1. Nest success data for 24 Greywing Francolin nests recorded during 1988/89 and 1989/90.

Nest no.	Incubation: Egg-days	Incubation: Nest-days		Days before hatching: 21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
1/88	17	4	*					5		4				0											
2/88	2	1	*								4	0													
3/88	2	1	*								4	0													
4/88	5	2	*								5		0												
5/88	4	1	*								4	4													
6/88	151	21	*	8								7	7	7	7	7	7	7	7	7	7	7	7	7	5/2
7/88	0	0																							?/2
8/88	40	9	*	5	5	5	5	5	5	5	5	5	0												
9/88	0	0							7																
10/88	113	21	*	6	6	6	6	6	6	6				5	5	5	5	5	5	5	5	5	5	5	4/1
11/88	67	12	*			8	7		6	6	6	6	6	6			2								
12/88	11	6	*					4				1		0											
1/89	90	20	*		5																			4	3/1
2/89	9	2	*	5	4	4																			
3/89	112	16	*						7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6/1
4/89	65	13	*									5	5	5	5	5	5	5	5	5	5	5	5	5	5/0
5/89	48	8	*														6	6	6	6	6	6	6	6	6/0
6/89	40	8	*														5	5	5	5	5	5	5	5	5/0
7/89	0	0							5																
8/89	24	4	*											6	6	6	6	6							
9/89	52	13	*									4	4	4	4	4	4	4	4	4	4	4	4	4	4/0
10/89	35	7	*					5	5	5	5	5	5	5	5										
11/89	60	10													6	6	6	6	6	6	6	6	6	6	6/0
12/89	12	3	*							4	4	4	4												
Total	899	172	*																						44/5

* = clutches used for calculation of nest success rate.

Nest no.	Comments	Nest no.	Comments
1/88	destroyed by predator	1/89	hatched
2/88	" fire	2/89	deserted, (?)
3/88	" fire	3/89	hatched
4/88	" unknown	4/89	"
5/88	" human disturbance	5/89	"
6/88	hatched	6/89	"
7/88	predated nest found	7/89	location of nest lost
8/88	destroyed by predator	8/89	clutch to incubator
9/88	location of nest lost	9/89	hatched
10/88	hatched	10/89	not re-visited
11/88	destroyed by predator	11/89	hatched - captive
12/88	" unknown	12/89	clutch to incubator

CHAPTER 4

GROWTH AND PLUMAGE DEVELOPMENT

Status: in press. The use of morphometrics and development of plumage in estimating the growth rate and age of Greywing Francolin Francolinus africanus. Ostrich 63. co-author: T.M. Crowe.

SUMMARY

Morphometrics and the developmental stages of plumage in captive-reared Greywing Francolin, Francolinus africanus, to 150 days of age were studied to determine patterns of growth and their utility in estimating age. There were no significant differences between sexes for body mass or linear body measurements for juvenile Greywing. Male spurs became sufficiently large (> 1mm) for reliable sexing only after 70-77 days. Linear body measurements of juveniles approached adult values within 91 days, and asymptotic values were reached at 136 days. The high amount of variation observed in body mass limited its use to age birds. Gompertz and logistic (but not von Bertalanffy) models fitted the growth data well. Plumage developed rapidly, with distinct natal, juvenal and near-adult (at 49-56 days) phases. The growth and replacement of remiges was sequential and similar in moult pattern and fledging to that of new world quails (Odontophorinae) and partridges (Perdicini). Flutter-flight was recorded at 14-21

days and juvenal primaries were full grown at 77-84 days. Juvenile wing loading values were greater than adult values before 14-21 days, and thereafter declined below those of adult values until 136 days. We suggest that growth curves for the linear body measurements, and the replacement of primary feathers, as well as contour plumage moult, can be used simultaneously to estimate the age of young Greywing up to the age of 84-91 days, when asymptotic measurements are approached. For birds 84-140 days old we suggest that the primary moult is the most reliable estimator of age.

INTRODUCTION

Although the morphometrics of all southern African terrestrial gamebirds in the order Galliformes have been summarized by Clancey (1967), Maclean (1985) and Crowe et al. (1986), there is little information about their growth rates and patterns of development. Siegfried (1966) and Heÿl (1988) studied growth, plumage development and moulting behaviour for the Helmeted Guineafowl Numida meleagris coronata and the Cape Francolin Francolinus capensis, respectively, and Mentis & Bigalke (1980) assumed that immature Greywing Francolin, Francolinus africanus, retained the outermost juvenal primary feathers (which have pointed tips) during their first winter.

In this chapter we present growth curves of body mass, wing length, wing area, tarsal length and culmen length for the Greywing Francolin, and describe the development of plumage and behaviour in this species. These results are valuable for comparison of growth patterns between Greywing and other species, and to determine if growth or plumage, or both, are useful in estimating the ages of Greywing Francolin.

METHODS

Rearing of chicks

Greywing Francolin chicks were obtained from eggs of wild clutches which were incubated in an electronically controlled incubator. Chicks were removed from the incubator within 24 hours after hatching and housed in an indoor electrically-heated brood-box for 28 days, after which the chicks were moved to a

brood-room (heated at night only) until 70-84 days of age. Thereafter, chicks were housed in outdoor portable pens or permanent aviaries.

The chicks were fed on 22% protein poultry growing mash for the first 70 days, after which a minimum 700 g/kg grain (maize, wheat and sorghum seed) crush was added to the mash. Both food and water were provided ad libitum. Chicks were also fed either termites or earthworms, and either lucerne or clover, two or three times daily.

Chicks were individually marked with coloured plastic leg rings (celluloid split and Darvic coil). Three ring sizes (4,0 mm, 6,0 mm and 8,0 mm) were used and changed at 42-56 days (4,0 mm to 6,0 mm), and at 70 days (6,0 mm to 8,0 mm).

Development of calling and flight behaviour was recorded at irregular intervals.

Morphometrics

All body measurements were taken at about seven-day intervals after hatching until 150 days of age. Wild adult birds were measured during the first six months of 1990 for comparison with growth values of captive-reared birds. The adult bird measurements were not tested for sexual dimorphism because of the lack of dimorphism displayed by the captive-reared birds.

Body mass was measured with a triple-beam Ohaus balance to the nearest 0,1 gram. Birds beyond the flutter-flight age (14-21 days) were weighed in a cloth bag. Wing length was recorded as the chord from the carpal joint to the tip of the longest primary, with the wing bent at the carpal joint but not

flattened. Wing area was measured from the tracing of one wing, using a Geographic Information Systems digitizing program (Anon. 1990a), and doubled for the area of both wings. Tracings were made with the wing extended and flattened over a sheet of paper so that the leading edge formed as straight a line as possible. Wing loading was calculated as (a) mass loading [body mass divided by wing area (g/cm^2)], and (b) linear loading [the cube root of body mass divided by the square root of wing area ($g^{0,33}/cm$)] (Jaksić & Carothers 1985). Tarsal length was measured from the intertarsal joint to the foot-pad with vernier calipers. Exposed culmen length was also measured with vernier calipers.

The growth of four chicks about 112 days of age was retarded by a severe necrotizing and exudative typhlitis of the caecum as a result of Histomonas meleagridis infestation (R.A. Earlé pers. comm.). Therefore, only data from chicks which showed no retardation in their growth were used in analyses.

Curve fitting

We fitted three sigmoidal growth models (Ratkowsky 1983) to the data sets:

1. Gompertz, $f = A \exp(- \exp(-K(age - I)))$

2. Logistic, $f = A/(1 + \exp(-K(age - I)))$

and 3. von Bertalanffy, $f = A\ (1 - \exp(-K(age - I)))^3$.

Ricklefs' (1967) graphical method of fitting equations to growth curves was used to obtain an initial estimate of growth rate (K) for each growth model. The estimated value for the inflection point (I), for each data set was read from a plot of the actual data. Asymptotic values (A) were fixed as the highest

value recorded per variable which did not change significantly over a period of 14 days.

Growth models were fitted using the derivative-free nonlinear regression program (AR) from the BMDP statistical package (Dixon et al. 1990) with fixed A values and floating K and I values. BMDP-AR estimates the parameters of nonlinear functions by a least squares method with a pseudo-Gauss-Newton iterative algorithm.

The goodness of fit of a particular model to the growth data was measured by three criteria: (i) the smallest deviation between the growth inflection point visually determined from a plot of the data and the point fixed by the model, (ii) random distribution of residuals over time (no autocorrelation of residuals), and (iii) the smallest residual sum of squares (RSS) for the estimated parameter values.

Plumage development

Distinct temporal changes in natal, juvenal and immature contour plumage are briefly described as a gross means of estimating age. Development and moult sequence of the remiges were recorded at seven-day intervals after hatching until 150 days of age. Moult of immature (F2) P9 and P10 feathers was observed until 280 days of age. Primary and secondary feather scores were calculated separately for the development of the set of juvenal (F1) and the (F2) generations of these feathers. Feather vanes were clipped to facilitate such recognition. Primary remiges were numbered descendantly from P1-P10, from proximal to distal. The secondaries were numbered ascendantly

from S1-S16, from distal to proximal. Feather growth indices similar to those used by Heÿl (1988) were:

0 = no feather (for juvenile primary development) or old feather remaining (during post-juvenal moult).

1 = feather absent from follicle or new feather in pin.

2 = sheath broken, but 1/3 or less of fully grown feather.

3 = more than 1/3 but less than 2/3 of fully grown feather.

4 = more than 2/3 but with blood in the shaft.

5 = fully grown new feather.

RESULTS

Behaviour

The first incomplete advertisement calls were heard at 7 days, near adult-like calls at 56 days and adult-like calls (pip-pip-pip pi-pip wipleeu ...) at 70 days of age. The first record of an antiphonal reply (pipeeu ...) to the advertisement call was at 140 days of age. Flight was observed as flutter-flight of 2-3 m at age 14-21 days, before which chicks preferred to crouch to avoid detection. Normal adult flight of about 20 m was recorded at 84 days. Captive chicks 98 days old which were unfamiliar with raptors reacted to a Redbreasted Sparrowhawk, Accipiter rufiventris, which flew past the aviaries, by fleeing into grass cover and crouching.

Morphometrics

There were no significant differences in body measurements (body mass (BM), wing length (WL), wing area (WA), tarsal length (TL) and culmen length (CL)) between male and female juvenile

Greywing (P > 0,05; t-test). Male spurs became sufficiently obvious (> 1mm) for reliable sexing only after 70-77 days. Mean body measurements of newly hatched Greywing chicks varied in proportion to mean adult measurements, with BM and WA less than 5% of mean adult values, and TL and CL over 30% of mean adult size (Tables 4.1 & 4.2).

Table 4.1. Growth of young Greywing Francolin.

Age (days)		Body Mass (g)			Wing length (mm)			Tarsus length (mm)			Culmen length (mm)		
	n	Mean	SD	%	Mean	SD	%	Mean	SD	%	Mean	SD	%
1	14	11,4	1,5	2,5	16,4	1,0	10,5	12,8	0,7	35,4	7,2	0,7	30,3
7	5	16,4	2,6	3,7	28,2	6,9	18,0	14,3	1,8	39,5	9,2	0,7	38,7
14	9	29,6	5,9	6,6	54,6	7,9	34,9	15,5	1,0	42,8	10,3	0,8	43,3
21	10	45,3	8,9	10,1	78,7	6,5	50,4	17,9	1,7	49,5	11,9	0,8	50,0
28	10	59,5	12,1	13,3	92,5	8,4	59,2	19,8	1,9	54,7	13,8	1,2	58,0
35	10	76,3	18,1	17,0	105,6	7,3	67,6	23,3	2,6	64,4	15,6	1,1	65,6
42	9	110,2	23,3	24,6	118,4	5,5	75,8	26,1	2,8	72,1	17,0	1,2	71,4
49	9	137,9	30,4	30,8	124,3	6,9	79,5	28,4	3,3	78,5	17,8	1,0	74,8
56	9	165,2	35,8	36,9	134,6	9,9	86,1	30,2	3,0	83,4	18,6	1,1	78,2
63	9	193,4	39,5	43,2	141,9	6,8	90,8	31,4	2,8	86,7	19,6	1,0	82,4
70	9	216,9	41,7	48,4	145,8	6,2	93,3	33,4	2,7	92,3	20,3	1,1	85,3
77	9	232,6	42,9	51,9	147,4	5,8	94,3	33,8	2,2	93,4	21,1	1,3	88,7
84	9	251,8	45,3	56,6	148,0	4,6	94,7	34,7	2,0	95,9	22,3	1,6	93,7
91	9	256,1	44,7	57,2	148,7	4,5	95,1	34,9	1,3	96,4	22,7	1,5	95,4
98	9	262,4	40,7	58,6	148,8	4,4	95,2	35,1	0,9	97,0	22,8	1,4	95,8
105	5	293,0	51,6	65,4	149,8	5,5	95,8	34,9	1,0	96,4	22,6	1,7	95,0
112	4	-	-	-	152,0	2,8	97,3	35,5	1,0	98,1	22,7	1,3	95,4
136	3	463,3	20,2	103,4	160,3	0,6	102,6	36,6	1,9	101,1	23,5	0,4	98,7
150	3	463,2	19,9	103,4	160,3	0,6	102,6	36,5	1,9	100,8	23,5	0,4	98,7
Adult[1]		448,0 (n = 322)	29,6		156,3 (n = 302)	2,7		36,2 (n = 152)	1,5		23,8 (n = 153)	1,0	

[1]Adult measurements recorded from wild birds during 1 January-9 June 1990.
Body mass was not measured at 112 days of age.
% = percent of mean adult values.

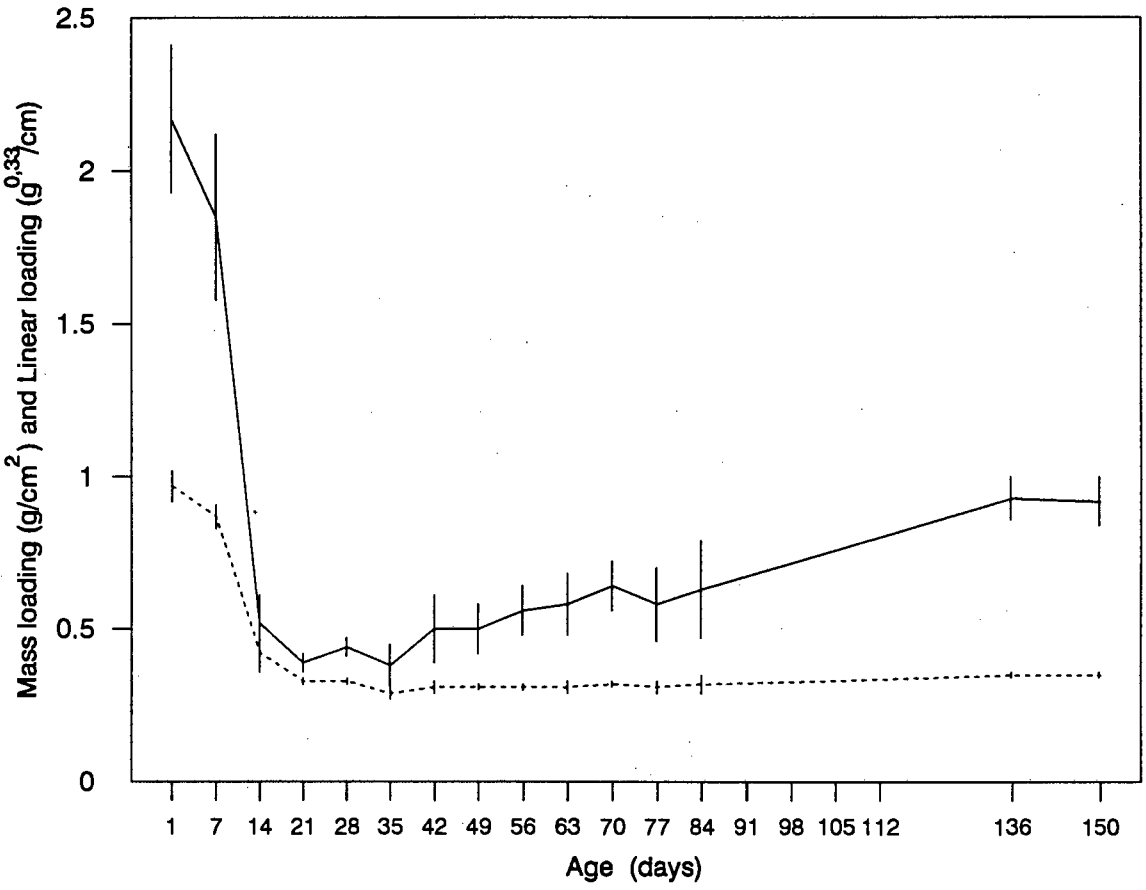


Figure 4.1. Wing loading of young Greywing Francolin (solid line = mass loading, broken line = linear loading). Vertical lines display one standard deviation.

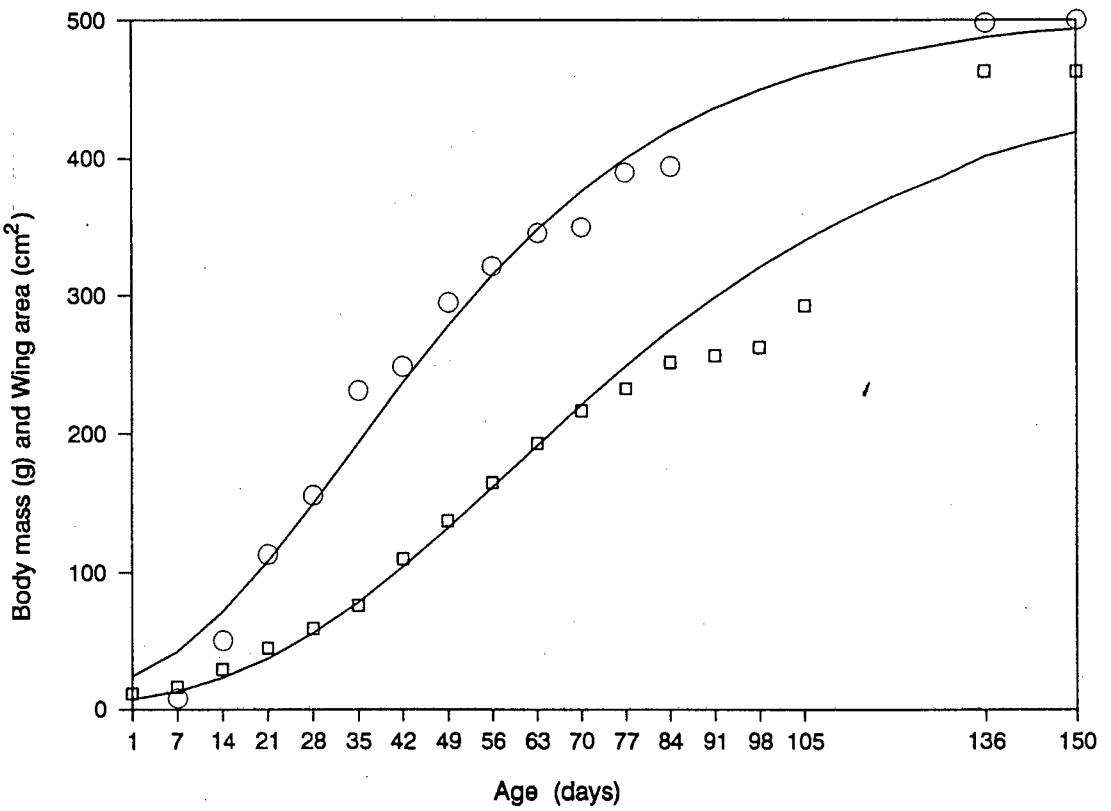


Figure 4.2. Body mass (squares) and wing area (circles) of young Greywing Francolin.

Mean adult dimensions were approached (i.e. within 95%) within 91 days of age, except BM which was only 57% at 91 days (Table 4.1), and WA which was 77% of adult size at 84 days (Table 4.2). Tarsal and culmen growth was relatively slow after 91 days of age, actual asymptotic values were reached for all five variables only at 136 days. In these analyses the data for both sexes were pooled.

Wing area increased rapidly, particularly over the first 21 days, causing mean wing loading values, which were higher than those of adult values before 14 days, to drop below mean adult values at 14-21 days (Table 4.2, Fig. 4.1). Thereafter, until 136 days, mean juvenile wing loading remained below the mean adult value.

Table 4.2. Wing area and wing loading statistics of young Greywing Francolin (n = 3).

Age (days)	Wing area (cm^2)			Mass loading (g/cm^2)		Linear loading ($g^{0,33}/cm$)	
	Mean	SD	%	Mean	SD	Mean	SD
1	5,8	0,6	1,1	2,17	0,24	0,97	0,05
7	8,1	0,1	1,6	1,85	0,27	0,87	0,04
14	50,5	24,3	9,9	0,52	0,09	0,42	0,06
21	113,5	25,4	22,2	0,39	0,03	0,33	<0,01
28	155,5	31,6	30,4	0,44	0,03	0,33	<0,01
35	230,9	9,5	45,2	0,38	0,07	0,29	0,02
42	248,8	2,4	48,7	0,50	0,11	0,31	0,02
49	295,6	18,3	57,8	0,50	0,08	0,31	0,01
56	320,6	19,9	62,7	0,56	0,08	0,31	0,01
63	344,7	7,6	67,5	0,58	0,10	0,31	0,02
70	349,2	21,2	68,3	0,64	0,08	0,32	0,01
77	388,9	1,4	76,1	0,58	0,12	0,31	0,02
84	393,4	7,3	77,0	0,63	0,16	0,32	0,03
136	502,8	24,8	98,4	0,93	0,07	0,35	0,01
150	503,0	25,4	98,4	0,92	0,08	0,35	0,01
Adult[1]	511,0	26,5		0,86	0,06	0,34	0,01

[1]Adult measurements collected from 32 wild birds (17 males & 15 females) during 19 April-20 May 1990.
% = percent of mean adult wing area.

The Gompertz model fitted marginally better than the logistic model for BM, WL and WA, whereas, the logistic model had the best fit for TL and CL (Table 4.3). Although the RSS value for the logistic model was lower than that for the Gompertz model for the fit of BM data, the Gompertz model was chosen because the other two descision criteria fitted better for that variable. The von Bertalanffy model fitted the data poorly for all five body measurements, and these results are therefore not presented. The growth curve equations found to fit the data best, their equivalent growth rate predictions, and their statistical significance are summarized in Table 3. All curves were sigmoidal (Figs. 4.2 & 4.3).

Table 4.3. Comparisons of Greywing Francolin growth curves with theoretical models.

Model	Parameter	Morphometric variables				
		Body mass	Wing length	Wing area	Tarsal length	Culmen length
Gompertz	K	**0,025**	**0,046**	**0,034**	0,032	0,031
	A	**463**	**160**	**503**	36,6	23,5
	I	**58,00**	**16,34**	**33,65**	7,36	6,87
	r^2	0,976	0,994	0,980	0,980	0,995
	RSS	4815,3	184,8	6318,1	17,6	1,7
Logistic	K	0,041	0,062	0,048	**0,042**	**0,039**
	A	463	160	503	**36,6**	**23,5**
	I	73,58	25,75	46,58	**20,12**	**19,69**
	r^2	0,984	0,979	0,954	0,992	0,996
	RSS	3135,0	591,9	14297,9	7,4	1,4

K = predicted growth rate; A = fixed asymptote;
and I = predicted inflection point.
r^2 = pseudo R-square.
RSS = residual sum of squares.
Bold values indicate model with best fit.

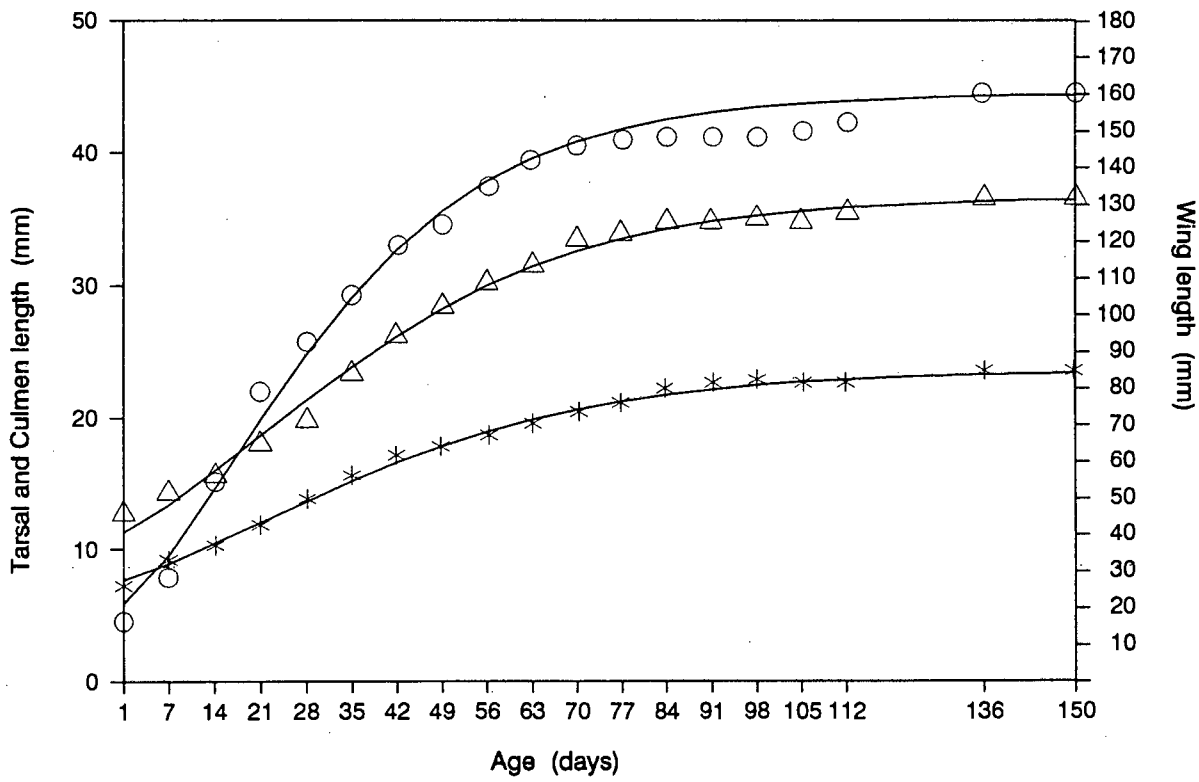


Figure 4.3. Wing (circles), tarsal (triangles) and culmen (crosses) lengths of young Greywing Francolin.

Plumage development

Plumage developes rapidly, with three distinct phases from natal down to juvenal and immature patterns and finally, to near-adult appearance at about 49-56 days of age (Table 4.4; Fig. 4.4). The growth and replacement of juvenal primary remiges are sequential and descending, with wave moult occurring from 28-35 days until after the moult of juvenal P10.

Table 4.4. Stages of plumage development of young Greywing Francolin.

Age	Plumage description
1-10 days	True downy plumage.
14 "	Downy head pattern, rectrices & remiges emerged.
21 "	Downy head pattern, body becoming quail-like, back chevron still bold.
28 "	Downy head pattern, start 'scruffy' stage, back chevron moulting.
35 "	Head pattern moult, but striping still apparent.
42 "	Head pattern moult, striping less apparent.
49 "	Near-adult plumage, end 'scruffy' stage.
56 "	Near-adult plumage.

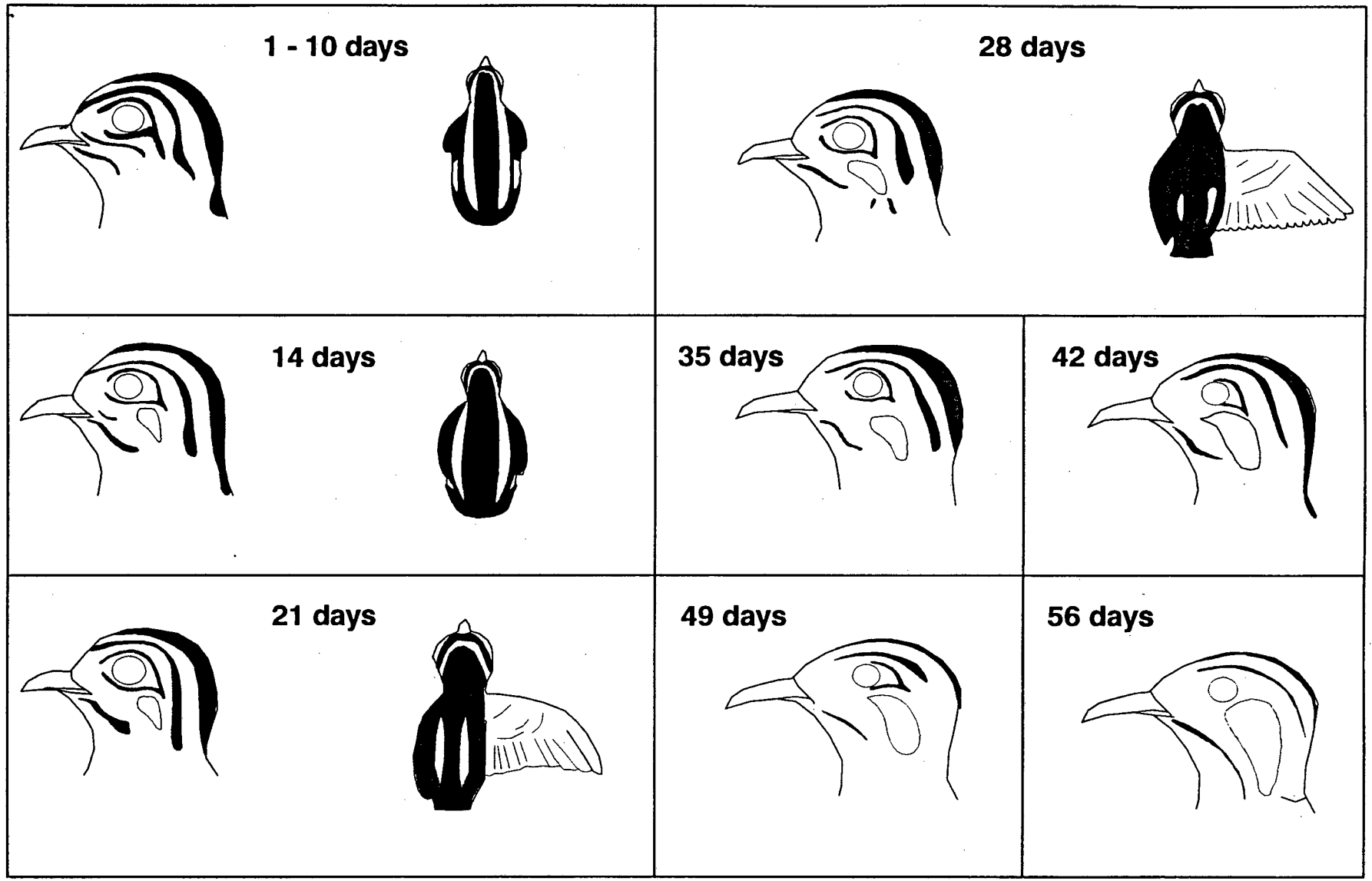


Figure 4.4. Stages of head pattern and back-chevron plumage development in young Greywing Francolin.

At hatching, the innermost seven juvenal (F1) primaries are present as functionless pins, emerging to release the feather vanes in a few days. P8 appears between 7-14 days, with P9 emerging between 21-28 days and P10 appearing between 28-35 days of age. By 77-84 days, P10 is fully grown, completing the set of juvenal primary feathers (Fig. 4.5).

P1 is lost in the post-juvenal moult at 28-35 days. In this moult feathers sequentially replace the F1 generation primaries with the immature (F2) generation until P8 is lost at 140-147 days (Fig. 4.5). P9 was replaced between 136 and 226 days (n = 3), and P10 (still pointed) persisted beyond 280 days of age (n = 2), as assumed by Mentis & Bigalke (1980). No significant differences in the mean ages of post-juvenal primary moult were found between males and females (P > 0,05; Mann-Whitney U-Test).

The juvenal (F1) secondaries 3-12 were present as pins at hatching. S2 emerged between 7-14 days, whereas S1 emerged only between 14-21 days. By day 56, S1 was distinctly pointed and longer than the other secondaries. Post-juvenal moult began with S3 and by day 126 the pointed S1 still persisted and was shorter than the other secondaries. The complete set of immature (F2) secondaries appeared after day 140.

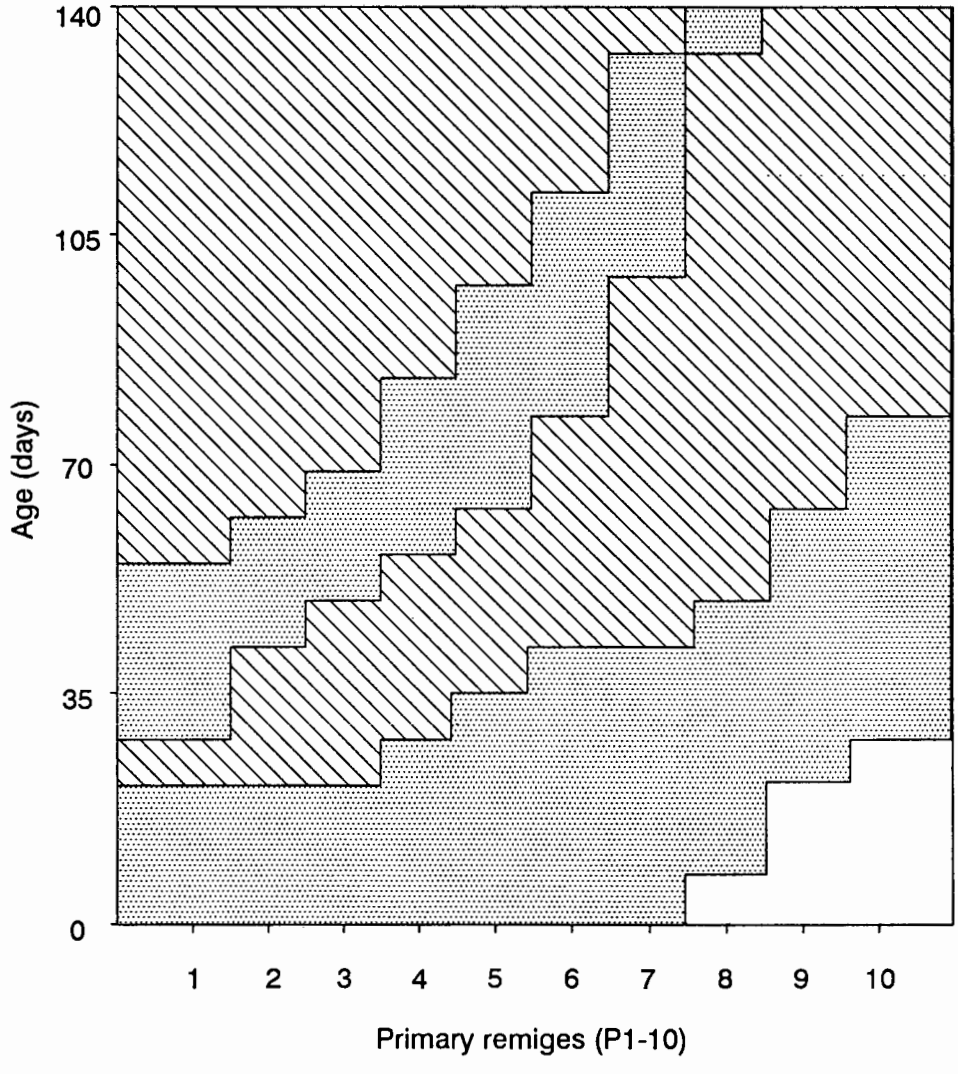


Figure 4.5. Primary feather growth and replacement in young Greywing Francolin. Dotted shading = periods of growth, hatched shading = non-growing stages.

DISCUSSION

Morphometrics

Both empirical growth curves and theoretical growth curves were included in this paper. This was done because although empirical data may be sufficient to assess the suitability of growth curves for aging of a species, it is necessary to have growth rate (K) values provided by standardized models for comparative research. Examples of such comparative research are: (i) comparison between species, (ii) comparison between different groups within a species (e.g. between this study and any future study on wild Greywing chicks), and (iii) comparison between the growth rates of different body parts within the same species.

Comparison of our body mass growth rate (K = 0,025, Gompertz model) for Greywing Francolin with those reported by Ricklefs (1973) for other avian species confirm that precocial species develop more slowly than altricial species (O'Connor 1984). Moreover, the rate of increase in body mass of Greywing Francolin, was less than that of most phasianids reported by Ricklefs (1973) including Ringnecked Pheasant, Phasianus colchichus, Grey Partridge, Perdix perdix, and Common Quail, Coturnix coturnix. However, Greywing had a growth rate that was similar to Red Junglefowl, Gallus gallus, and domestic poultry, G. g. var. domesticus, but was greater than that of the large Common Turkey, Meleagris gallopavo.

Although Siegfried (1966) and Heÿl (1988) did not fit growth models to their data, some comparison can be gleaned from their results by the use of percentage values relative to adult body mass at similar ages. Both the Helmeted Guineafowl and the Cape

Francolin apparently show weight gain that is similar to Greywing, attaining about 33% of adult body mass in 56 days. However, both species increased in body mass for a longer period than Greywing, only attaining ±80% of the adult body mass by day 140, whereas Greywing had already attained adult size in all five measurements by day 136. These results, plus a growth rate higher than for the Common Turkey, are not surprising, considering that Ricklefs (1973, 1979) proposed that birds growth rates are inversely related to adult body mass.

Both Siegfried (1966) and Heÿl (1988) reported sexual dimorphism in body mass from 42 to 56 days for Helmeted Guineafowl and Cape Francolin, respectively, and significant differences between sexes in adults, whereas our results for Greywing showed no significant sexual dimorphism in young birds. The only external morphological criterion for sexing young Greywing are the single male spurs which become obvious only after 70-77 days of age.

Wing length growth rate ($\underline{K}$ = 0,046, Gompertz model) was higher than the growth rates for other variables recorded for Greywing. The resulting pattern of mass loading and linear loading with age might suggest a modified confirmation of Lack's (1968) predator avoidance theory as a determinant of growth patterns. Wing loading in young Greywing drops below the mean adult value at 14-21 days, before which time chicks are reluctant to flush to escape from terrestrial predation. Lower wing loading values presumably mean less effort in take-off and in flight, and thus less effort in predator avoidance through flushing. Therefore, we suggest that energy might be channelled into wing and flight

feather growth as a trade-off in early growth rate over other morphometric variables. Clearly, the relatively large initial tarsal and culmen length indicate that terrestrial mobility and feeding are important activities, at least within the first 14-21 days.

Plumage development

The growth and replacement of Greywing Francolin juvenal remiges were sequential, and similar in moult pattern and fledging to that of new world quails (Odontophorinae) and partridges (Perdicini) (Demmers & Garton 1980; Johnsgard 1988). The sequence of moult is also similar to that of the Cape Francolin (Heÿl 1988). However, Greywing retain the outer juvenal primary feather (P10) beyond at least 280 days, and therefore beyond the about 140 days reported for wild Cape Francolin.

Age determination

Sexual dimorphism was lacking in young Greywing, making the sexing of Greywing by external criteria before the age of 70-77 days unreliable. For this reason data for both sexes were pooled.

Body mass was too variable to be reliable to estimate age. Measurement of linear growth and stages of plumage replacement are more reliable for aging young Greywing. We suggest that growth curves for the linear body measurements (Figs. 4.2 & 4.3), the moulting stages of primary feathers (Fig. 4.5), and the contour plumage moult (Table 4.4; Fig. 4.5), can be used to age young Greywing up to 84-91 days of age, when asymptotic sizes are

approached. For birds of 84-140 days, primary moult is the most reliable estimator of age. We therefore confirm Ricklefs' (1968) suggestion that morphological criteria other than body mass are more stable and may depend less on the bird's nutritional state.

The fitting of regression models to the growth of primaries replaced during the post-juvenal moult, as described by Demers & Garton (1980) for Grey Partridge, might also increase accuracy of aging young Greywing Francolin. However, lengths of juvenile primaries were not recorded in this study.

Mentis & Bigalke's (1980) use of the retention of the outer, pointed primary as an indication of first year birds is consistent with our findings up to 280 days of age. Therefore, this is a reliable assumption, at least up to 280 days.

There were no data for wild chicks of known age. Wing, tarsal and culmen lengths of captive-reared Cape Francolins differed significantly from those of wild young at 140 days (Heÿl 1988). However, a less than 5% difference existed between young captive-reared Greywing and wild adults at this age. We therefore suggest that captive-reared Greywing chicks grow faster than Cape Francolin chicks reared under similar conditions, or that their growth rates correspond more closely to those of wild chicks up to 140 days of age, or both.

We still view the aging of young Greywing as a procedure of estimation, and caution that variation in environmental conditions may create variability in growth, limiting the statistical confidence placed on our aging methods.

CHAPTER 5

CALLING BEHAVIOUR

Status: in press. Vocal behaviour of Greywing Francolin Francolinus africanus can be used to estimate population density. Ostrich 63. co-author: T.M. Crowe.

SUMMARY

Four common calls of the Greywing Francolin, Francolinus africanus, are described acoustically, and their functions discussed. Data from 166 crepuscular call count surveys (2 472 counts) and 540 diurnal call counts were analysed to investigate the temporal and meteorological effects on calling activity, and to assess the use of call counts as an index of between year and between area variation in population density. Calling remained at high levels from August to April during the breeding season. Calling was most frequent at sunrise and sunset. Calling frequency and the number of calling coveys were significantly higher at sunrise than at sunset. Calling was concentrated in the 30 minute periods straddling sunrise and sunset, and peaked during the 15-minute periods before sunrise and before sunset. Calling activity was negatively correlated with wind speed and positively correlated with relative humidity. Calling was spuriously negatively correlated with seasonal variation in Greywing population density and strongly positively correlated

with between year and between area variations in population density. We therefore suggest that call counts collected during March-April could be used to index annual change in the population density in a particular area from year to year, as well as within-season variation among areas.

INTRODUCTION

The Greywing Francolin, Francinus africanus, is endemic to southern Africa (Clancey 1986) and is common to abundant in its preferred habitat, montane grassland above 1 800m above sea-level (Mentis & Bigalke 1981a). It appears to be a sedentary species with the same covey being found in the same area over at least four years (RML unpubl. data). This philopatric behaviour should allow the cost-effective monitoring of the population density of this species through the assessment of some relatively easy-to-measure index (e.g. calling activity).

Measures of vocal activity have been used elsewhere to estimate the density of gamebird species (e.g. Kimball 1949; McGowan 1953; Brown & Smith 1976; March & Church 1980; Rotella & Ratti 1986). However, very little is known about the vocal behaviour of the Greywing Francolin other than brief descriptions of its advertisement (presumably territorial) call and suggestions that this call is given primarily at dawn and dusk (Gilfillan 1908; Wolff & Milstein 1976; Newman 1983; Maclean 1985; Crowe et al. 1986; Milstein & Wolff 1987; Ginn et al. 1989).

Our objective was to determine if calling activity was directly related to population density and to determine when call counts that are to be used as a population index should be conducted. In this chapter we describe several common vocalizations of the Greywing Francolin, and the behavioural context(s) in which they are given, and report on seasonal, crepuscular and diurnal variation in the frequency of advertisement calls. We analyse effects of weather on calling, and examine relationships between calling activity, social behaviour and population density.

STUDY AREA AND METHODS

Study areas

From mid-January 1989 to mid-January 1990, and during spring (October-November) 1990 and autumn (March-May) 1991, Greywing advertisement calling was monitored along a 30 km transect in Greywing habitat on the Stormberg Plateau of the eastern Cape Province (31°15'S; 26°30'E), South Africa (Fig. 5.1). Data from surveys in two areas during April 1991 in northern Lesotho (29°10'S; 28°25'E) were also included in the analyses.

Vocalization recording and description

Greywing vocalizations were recorded from free-ranging birds (advertisement and flush calls) and from captive birds (alarm and chick/juvenile calls), using a Sony TC-D5 PRO II stereo cassette recorder and Sennheiser K3 microphone with a Sennheiser ME88 microphone head. Recorded calls were analysed, and sonograms produced, using the Farallon Computing Incorporated, MacRecorder Sound System (Anon. 1990b) on an Apple Macintosh micro-computer. Representative calls were selected by visual examination for clarity. Whenever possible, the behavioural context of calls was noted.

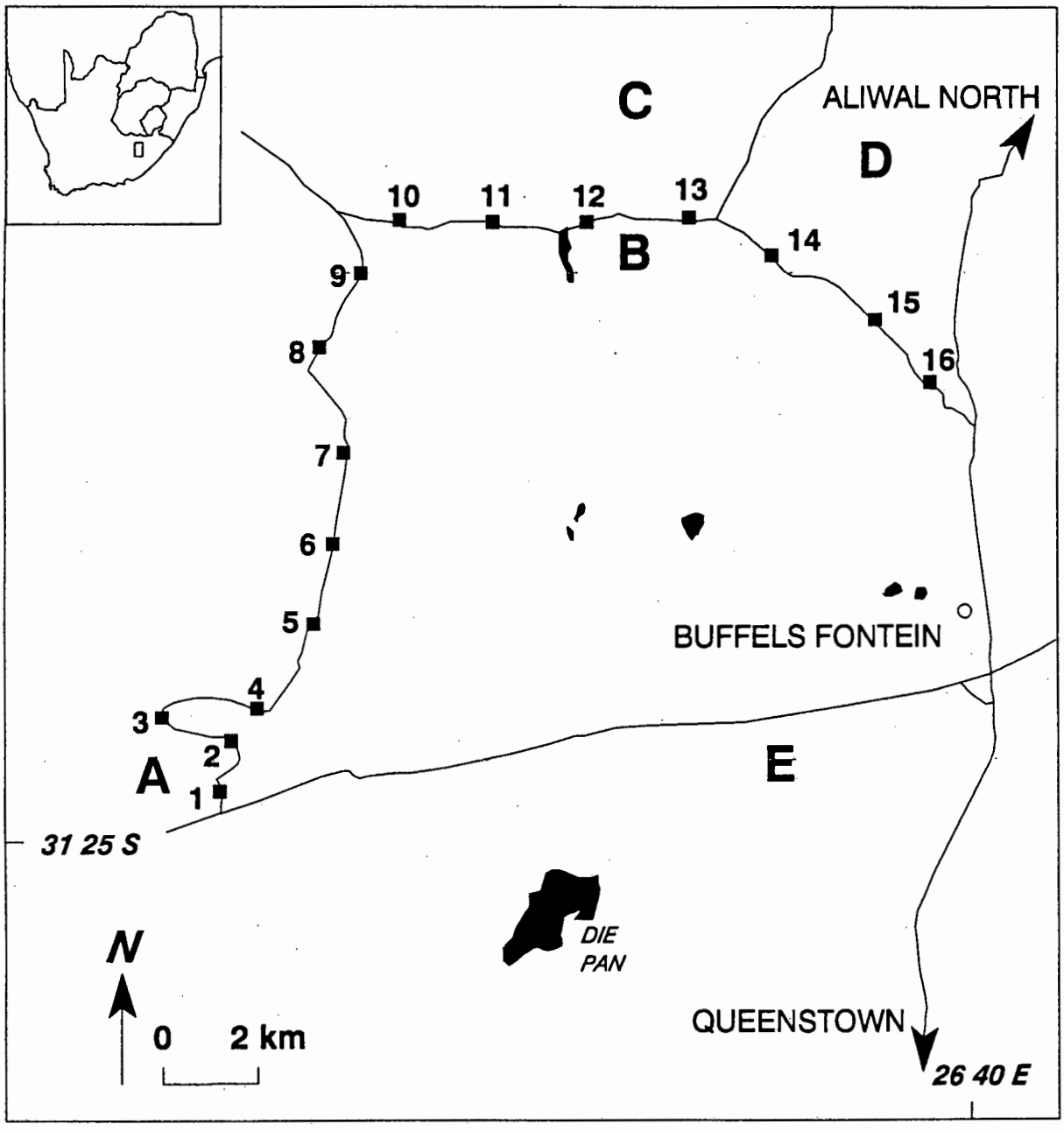


Figure 5.1. Map of the Stormberg study area with the call count survey route, listening stations (1-16), and Greywing Francolin population density census plots (A-E).

Advertisement call surveys

Five complete dawn and dusk surveys (i.e. 16 stations per survey, Fig. 5.1) of Greywing advertisement calling were made each month from mid-January 1989 to mid-January 1990. Thus, during this one-year study, 120 complete crepuscular surveys were made, comprising 1 920 counts. Listening stations were spaced 2 km apart (i.e. > the 1,6 km used by Rotella & Ratti 1988) to avoid recounting the same birds. Greywing were seen regularly between listening stations on the Stormberg Plateau. An additional 540 counts were made opportunistically at other times throughout daylight hours. Listening station counts were conducted over four minutes, as has been done successfully with the Grey Partridge, Perdix perdix (Rotella & Ratti 1986), and Northern Bobwhite Quail, Colinus virginianus (Robel et al. 1969).

For each count, two measures of Greywing advertisement calling activity were recorded; (i) the number of wi-pleeu.... and pipeeu.... components heard; both components of the call were counted, as our preliminary observations suggested that two birds gave these calls antiphonally, and (ii) the number of sites (coveys) from which we heard calling; i.e. the number of identifiable locations where birds (coveys) occurred. Call sites were easily distinguished because there was a large distance between them and because the number of calling coveys at a listening station was usually small (see Results).

Survey methods were similar to those used for other upland gamebird species (Rotella & Ratti 1988). Complete surveys were initiated one hour before sunrise (SR) and sunset (SS), using CSIR Tables (Anon. 1973) to correct for seasonal variation in the time of SR and SS (Appendix 5.1). The duration of surveys was

about two hours. The order of the stations (1-16 vs. 16-1) was alternated as recommended by March & Church (1980) and Rotella & Ratti (1988). Surveys were not conducted when mean wind speed exceeded 24 km per hour because of wind noise. Wind speed and direction, ambient temperature, relative humidity, percentage cloud cover and time of sampling relative to locally-corrected SR and SS were recorded at Buffelsfontein Farm ($31^{o}22'S$; $26^{o}42'E$) for each survey.

Opportunistic diurnal counts were recorded by hour in relation to local mean monthly noon, i.e. the mid-point between local sunrise and local sunset of the middle day of each month. Complete surveys and opportunistic counts were summarized as the monthly mean, standard deviation, coefficient of variation and median call frequency and number of calling coveys for the two hours straddling SR and SS, and for ten hours (spring, summer and autumn) and eight hours (winter) straddling local noon.

An additional 20 surveys (10 SR and 10 SS) were conducted during October-November 1990, and 22 surveys (12 SR and 10 SS) during March-May 1991. Counts from four surveys (2 SR and 2 SS) at two different areas in Lesotho were also included in the analyses. Two observers simultaneously made nine surveys on the Stormberg during March-May 1991 to assess the magnitude of observer bias in recording Greywing calls. Because no calling was recorded during the periods 60-30 minutes before SR, and 30-60 minutes after SS, all surveys conducted during spring 1990 and autumn 1991 were reduced to twelve listening stations.

Median tests have traditionally been used for analysis of variation in calling frequency (Rotella & Ratti 1986), however,

we used mean calling frequency because there was low variation between mean and median values (see Results). We mostly used nonparametric methods (Mann-Whitney U-test) to test differences in distribution between samples, however, the Statistical Graphics System (Anon. 1986) provides for two-sample analysis (t-test) where equal variance is not assumed; in such cases we report an adjusted value for degrees of freedom.

Variation in population density, and aspects of social behaviour

Greywing population density was estimated on a monthly basis in five areas adjacent to the call-count survey route (Fig. 5.1) using the flush-and-count method with the assistance of at least two pointing dogs (Mentis & Bigalke 1985b). The mean searching time, along transects, within each of the five census areas were 150,3 mins. (SD = 13,6), 114,3 mins. (SD = 10,4), 151,0 mins. (SD = 14,3), 142,9 mins. (SD = 8,7), and 173,4 mins. (SD = 7,5)(n = 12 counts). We censused Greywing population density concurrently with the spring (1990) and autumn (1991) call counts.

Information on the Greywing's social behaviour (pairing vs grouping) was extracted from Little & Crowe (in press a; Chapter 3) for comparison with temporal variation in population density and calling activity.

RESULTS

Vocalizations

Insufficient numbers of calls were recorded to measure average duration or frequency ranges, or to make conclusive statements regarding the behavioural contexts of the calls. However, four

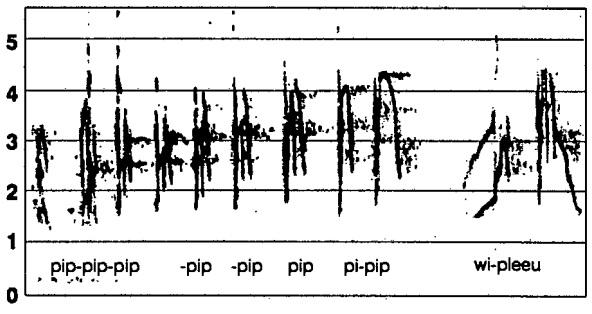
vocalizations commonly used by Greywing were recorded.

The advertisement call comprises at least two components which may be rendered as pip-pip-pip pi-pip wi-pleeu (Fig. 5.2a) and pipeeu (Fig. 5.2b). This call is given by members of localized, undisturbed coveys in their territories, and by members of a covey while reassembling after being flushed. The wi-pleeu phrase of the first component is usually repeated in series and is often 'punctuated' antiphonally by a second bird in the covey giving a series of pipeeu components. The pip-pip-pip pi-pip wi-pleeu component was observed only from male birds, whereas the pipeeu component was given by both males and females. A male bird was seen giving both components of the call.

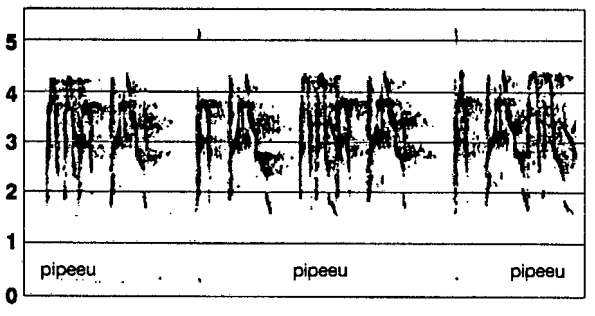
The flush call is given by birds in flight, and may be rendered as an excited pre-pre-pre-pre-preeu-preeu-preeu-preeu (Fig. 5.2c).

The alarm call is a guttural aspirated poch poch with occasional higher pitched notes, all repeated in series for as long as the birds are distressed (Fig. 5.2d). This call was given in three contexts: on detection of an intruder (e.g. a human), preceding the wi-pleeu component of the advertisement call, and by both parents when separated from their chicks.

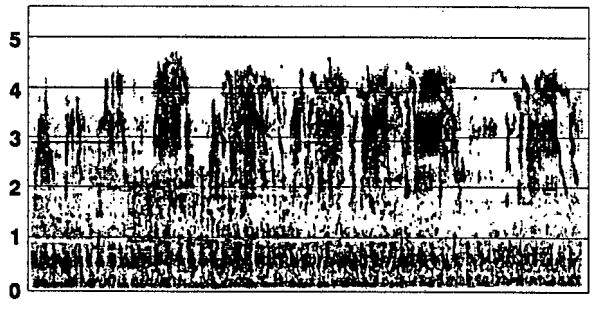
The chick or juvenile call was recorded only for young reared in captivity without parents. It was used mostly as a contact call between chicks as they moved about their cage. It may be rendered as a clear and high pitched, chic chic chic.... (Fig. 5.2e). Chicks also attempted the advertisement call, as early as their first week, usually when separated from other members of the brood (Fig. 5.2e).



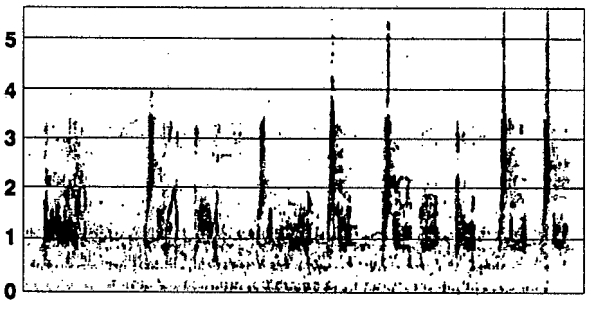
a



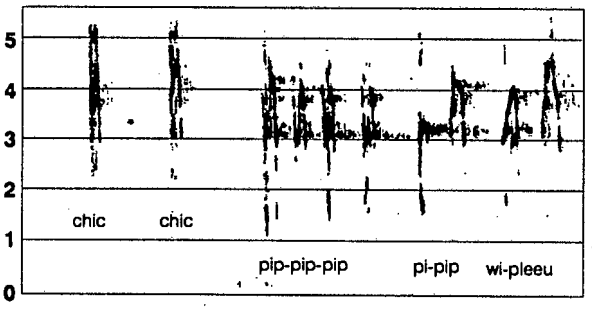
b



c



d



e

Figure 5.2. Sonograms of Greywing Francolin calls: a) advertisement call, b) antiphonal phrase, c) flush call, low frequency noise (<1,5 kHz) are wing beats, d) alarm call, e) chick contact and advertisement call. Y-axies = frequency (0-5,5 kHz), x-axies = time (0-2,9 seconds).

Temporal variation in advertisement calling

Greywing give the advertisement call throughout the year, with peak calling during spring through to autumn (August-April). Throughout the year, the frequency of calls and the number of calling coveys were significantly higher ($P < 0,01$; Mann-Whitney U-test) for the crepuscular periods (one hour either side of SR and SS) than for the remaining daylight hours (Table 5.1; Fig. 5.3). However, the calling frequency and the number of calling coveys were significantly greater ($P < 0,001$) at SR than at SS, and the majority of calls and calling coveys were recorded during the 60 minute period straddling SR, with peak activity during the 15 minute period prior to SR (Fig. 5.4). Sunset calls peaked during the 15 minute period before SS throughout the year (Fig. 5.5).

Effects of weather

Greywing tended to call more frequently, and from more coveys, both at SR and at SS, when there was a northerly wind than when there was a southerly wind (Table 5.2; Appendix 5.2). However, this difference was significant ($P = 0,03$; Mann-Whitney U-test) only for the number of SR calls per survey. There were no significant correlations between calling activity and ambient temperature, or between calling activity and cloud cover ($r < 0,2$; $P > 0,05$; $n = 120$). However, there was a positive correlation ($P < 0,001$; $n = 120$) between relative humidity and the frequency of calling ($r = 0,51$) and number of calling coveys ($r = 0,47$) at SR, but not at SS ($r = 0,09$ and $0,15$; $P > 0,05$). There was a negative correlation ($r = -0,32$ to $-0,52$; $P < 0,001$) between wind speed and calling activity, both at SR and SS.

Table 5.1. Greywing Francolin advertisement calling activity and population density during January 1989 - January 1990.

Number of calls per survey

	Sunrise				Sunset				Daylight[1]				Density (birds/km^2)		
	Mean[2]	S.D.	C.V.	Median	Mean	S.D.	C.V.	Median	Mean	S.D.	C.V.	n	Mean	S.D.	C.V
July	216,4	90,7	0,42	179	3,4	7,6	2,24	0	1,6	7,1	4,44	52	14,74	4,8	0,3
August	154,8	151,2	0,98	109	55,0	61,5	1,12	43	0,6	2,9	4,83	42	11,38	3,4	0,2
September	243,2	98,2	0,40	241	37,6	39,8	1,06	21	1,4	6,5	4,64	31	9,93	3,5	0,3
October	125,2	137,6	1,10	77	18,1	18,2	0,97	8	4,0	6,8	1,70	26	10,19	3,5	0,3
November	148,0	74,3	0,50	170	57,4	57,8	1,01	38	0,0	0,0	-	31	9,20	2,5	0,2
December	96,8	55,2	0,57	87	37,6	26,0	0,69	47	0,4	1,6	4,00	42	9,16	1,8	0,1
January	201,1	126,8	0,63	221	43,2	41,5	0,96	24	1,4	4,0	4,00	31	7,87	3,3	0,4
February	203,8	129,7	0,64	250	39,2	44,9	1,15	20	-	-	-	-	8,90	2,7	0,3
March	344,8	140,6	0,41	251	63,0	83,1	1,32	12	0,4	1,7	4,25	66	9,65	3,6	0,3
April	273,6	113,3	0,41	314	77,0	70,5	0,92	50	3,1	11,5	3,71	81	10,46	3,1	0,3
May	261,6	149,5	0,57	323	48,2	45,9	0,95	59	0,8	5,0	6,25	62	16,72	7,4	0,4
June	124,4	136,6	1,10	79	33,4	30,2	0,90	38	2,4	10,7	4,46	62	15,83	4,8	0,3

Number of call sites per survey

	Sunrise				Sunset				Daylight[1]			
	Mean	S.D.	C.V.	Median	Mean	S.D.	C.V.	Median	Mean	S.D.	C.V.	n
July	9,6	4,2	0,44	8	0,2	0,5	2,50	0	0,1	0,3	3,00	52
August	9,6	7,0	0,73	7	3,6	3,0	0,83	3	0,1	0,1	1,00	42
September	18,0	5,4	0,30	16	3,6	3,3	0,92	3	0,1	0,4	4,00	31
October	9,8	9,5	0,97	5	2,6	1,3	0,50	2	0,4	0,7	1,75	26
November	11,6	5,4	0,47	11	4,2	4,1	0,98	2	0,0	0,0	-	31
December	9,2	4,8	0,52	8	2,4	1,8	0,75	2	0,1	0,3	3,00	42
January	12,8	7,0	0,55	17	3,4	3,4	1,00	2	0,1	0,3	0,30	31
February	13,0	4,8	0,37	13	3,0	2,9	0,97	2	-	-	-	-
March	17,0	6,1	0,36	14	3,6	3,4	0,94	3	0,1	0,3	0,30	66
April	13,2	5,7	0,43	15	3,2	2,4	0,75	3	0,2	0,5	2,50	81
May	14,0	7,1	0,51	17	2,4	1,8	0,79	3	0,2	0,8	4,00	62
June	7,2	7,5	1,04	5	1,2	0,8	0,67	1	0,1	0,5	5,00	62

[1]All median values were 0, i.e. >50% of the data points = 0 within each month.
[2]Sample sizes for all sunrise and sunset entries were 15.
Sunrise = period from 1 hour before to 1 hour after actual sunrise.
Sunset = period from 1 hour before to 1 hour after actual sunset.
Daylight = period from 1 hour after sunrise to 1 hour before sunset.

Table 5.2. The effect of wind direction on Greywing Francolin crepuscular calling activity.

	Sunrise		Sunset	
	Northerly wind	Southerly wind	Northerly wind	Southerly wind
n	48	5	31	29
Number of calls per survey				
Mean	199,6*	76,4*	53,7	31,0
SD	124,9	68,1	57,9	31,0
Number of call sites per survey				
Mean	12,1	7,8	3,1	2,4
SD	6,6	5,5	3,0	2,2

*P<0,05; Mann-Whitney U-test.

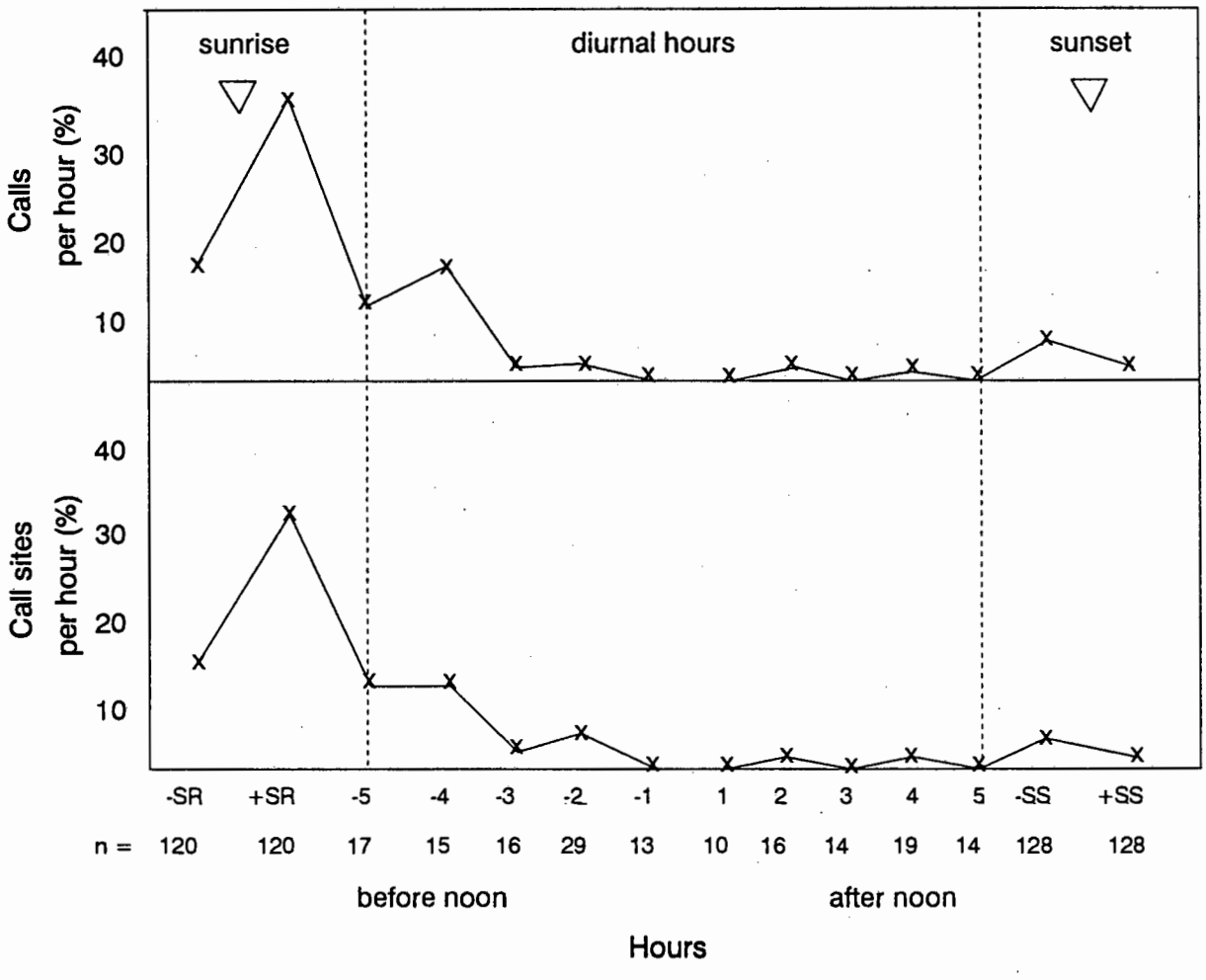


Figure 5.3. Frequency distributions of mean Greywing Francolin calling activity recorded for the crepuscular and the diurnal hours during autumn at the Stormberg study site. Autumn is the recommended call count survey season. (% = proportion of total number over the 14 hours, SR = sunrise, SS = sunset, n = number of counts per hour).

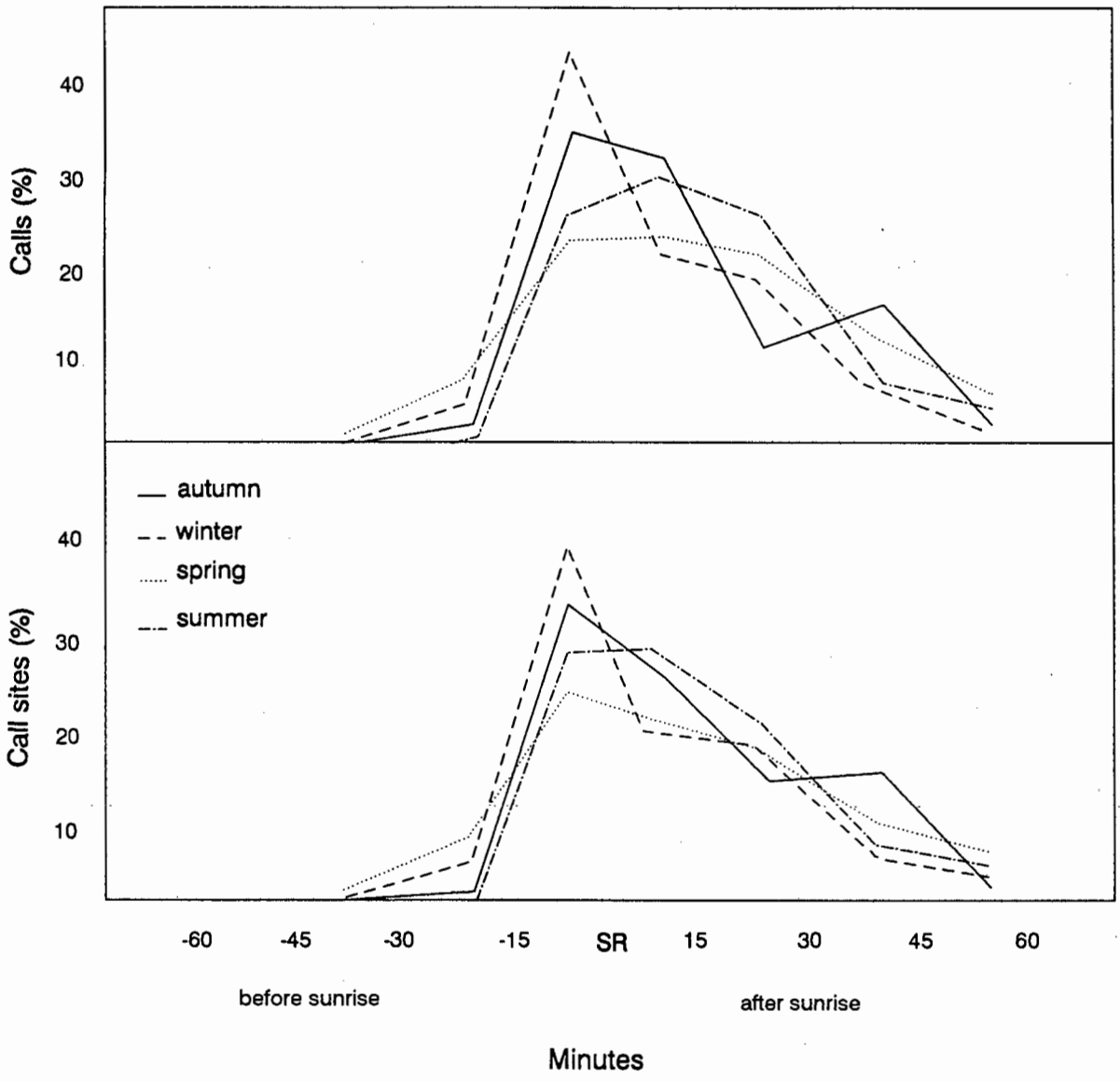


Figure 5.4. Frequency distribution of mean Greywing Francolin calling activity recorded per 15-minute sector before and after sunrise. (% = proportion of total number heard over the eight 15-minute listening periods, SR = sunrise, n = 15 surveys per season).

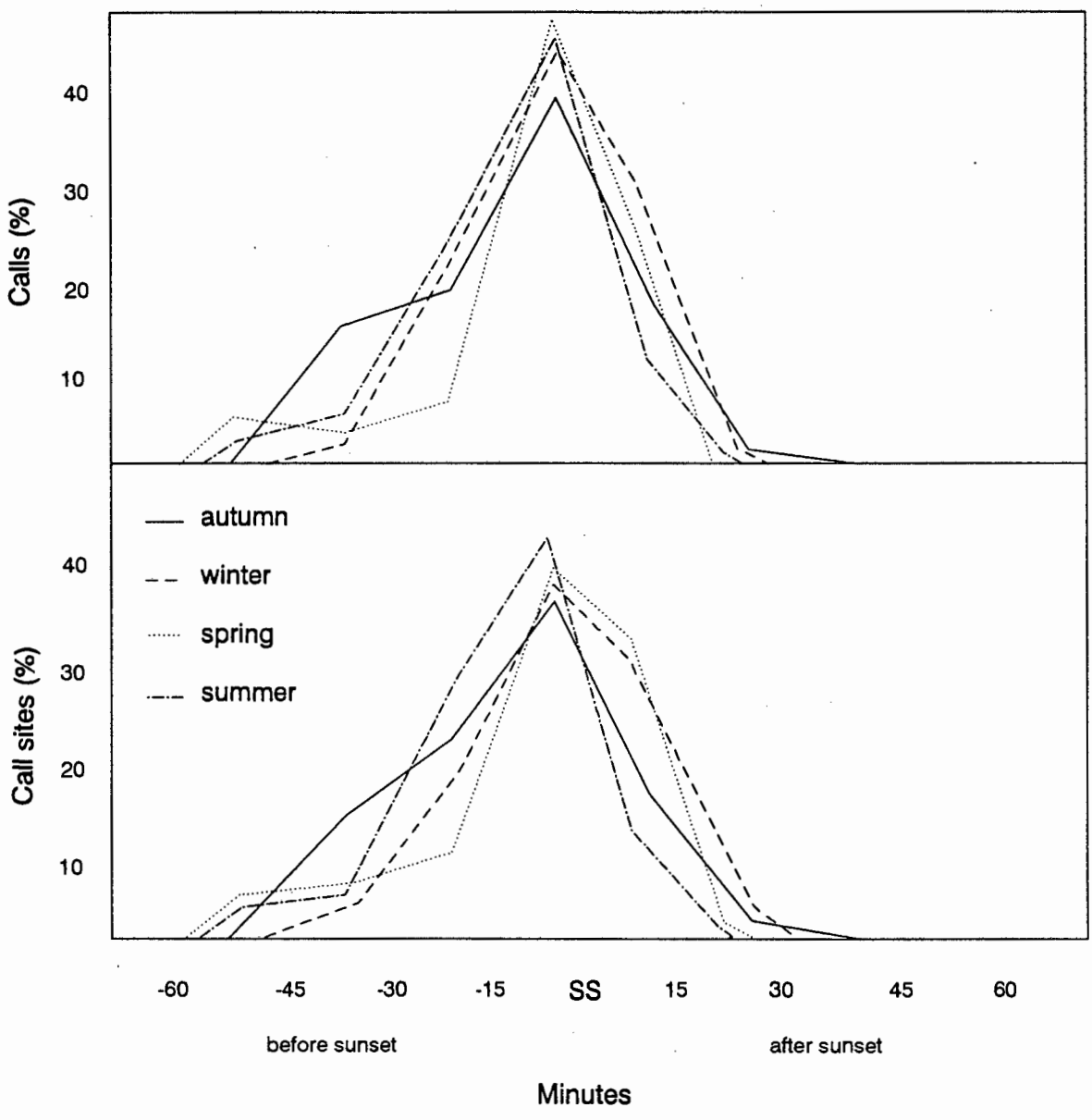


Figure 5.5. Frequency distribution of mean Greywing Francolin calling activity recorded per 15-minute sector before and after sunset. (% = proportion of total number heard over the eigth 15-minute listening periods, SS = sunset, n = 15 surveys per season).

Relationship between advertisement calling and population density, and social behaviour

Mean and median values for number of calls per survey per month, and number of call sites per survey per month were positively correlated (Table 5.1; r = 0,79 to 0,91). The only significant correlation between seasonal measures of advertisement calling and Greywing population density was between the mean number of calling sites at SS and mean Greywing density (r = -0,70; P < 0,01) (Table 5.1). The period of high Greywing population density and low number of coveys calling at SS corresponds with the overlap period of high social activity (i.e. when less than 10% of the coveys are pairs) (Fig. 5.6).

There were no significant differences in the mean number of calls and mean number of calling sites recorded per year on the Stormberg study site (P > 0,05; t-test) (Table 5.3); with these comparisons of the variation in mean population density was not significant (P > 0,05; t-test). However, the mean number of autumn SR calls and calling sites per survey were both significantly positively correlated with mean population density for a wider data-set (r = 0,96; P < 0,05 and r = 0,96; P < 0,05 respectively) (Fig. 5.7). These data were obtained from four independent areas/periods, i.e. two from different years on the Stormberg, and two from different areas within the same season in Lesotho (Table 5.4).

Nine data-sets recorded simultaneously by two observers on the number of calls per survey (r = 0,98; P < 0,001), and the number of calling sites per survey (r = 0,98; P < 0,001) were strongly correlated.

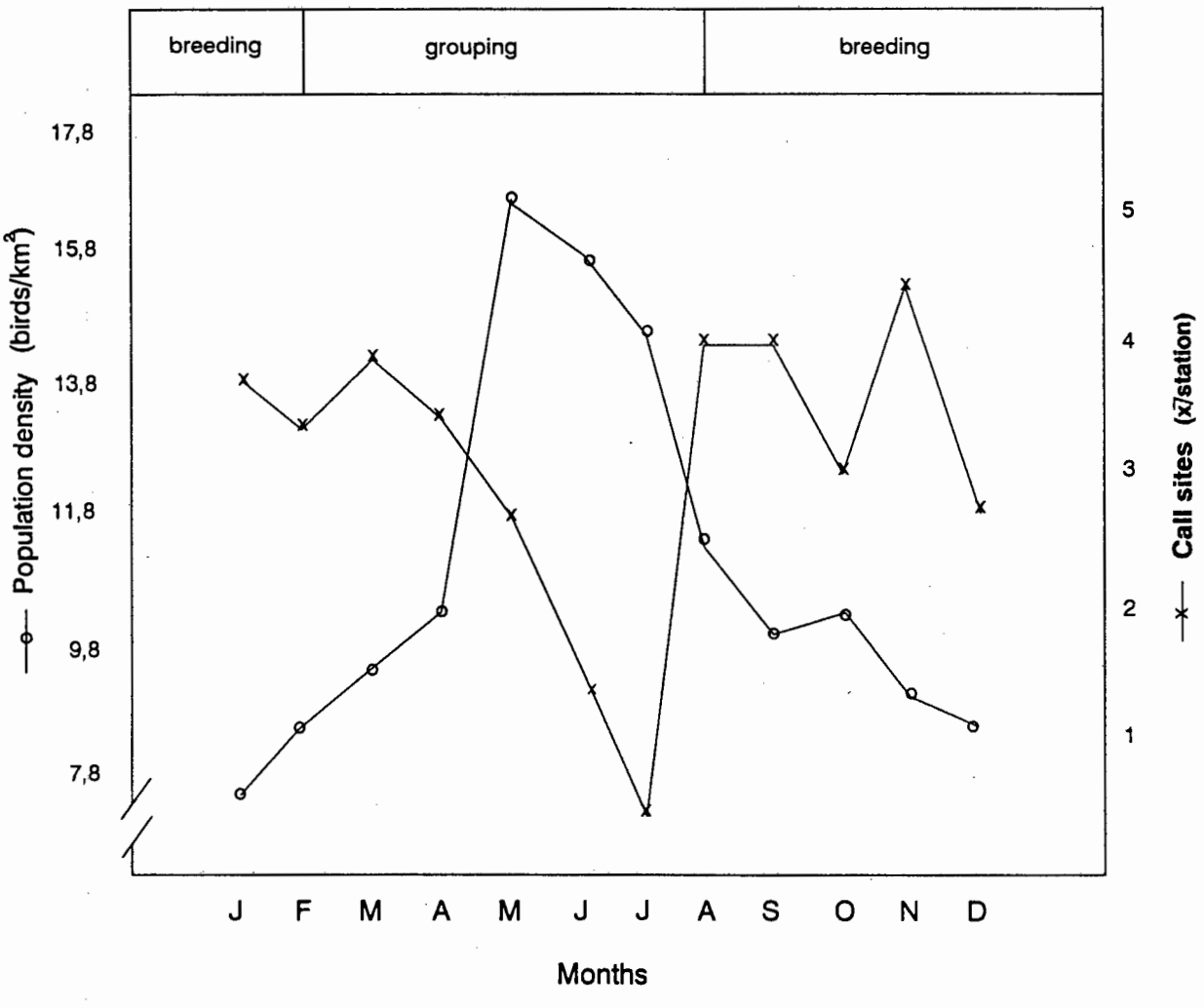


Figure 5.6. Temporal variation in Greywing Francolin population density, mean sunset call site activity and social behaviour (breeding = >10% of coveys are pairs).

Table 5.3. Comparison of Greywing Francolin calling activity and population density between different years for the Stormberg study site; mean number of calls and call sites per survey, ±1 standard deviation.

	Spring				Autumn			
	1989	1990	D.F.[1]	P	1989	1991	D.F.[1]	P
SR Calls	136,6 ± 104,9	102,7 ± 72,2	16,0	0,41	293,3 ± 130,9	379,7 ± 261,5	15,4	0,27
SR Sites	10,7 ± 7,4	6,8 ± 3,1	12,1	0,14	14,7 ± 6,1	15,8 ± 9,8	17,6	0,72
SS Calls	38,1 ± 45,2	17,0 ± 19,6	12,3	0,19	62,7 ± 64,4	118,3 ± 121,6	12,4	0,15
SS Sites	3,4 ± 3,0	1,8 ± 2,1	16,3	0,19	3,1 ± 2,5	6,2 ± 7,5	10,3	0,15
Density[2]	9,7 ± 3,0	8,7 ± 2,6	9,2	0,52	10,2 ± 3,2	11,1 ± 2,1	11,6	0,58

[1]degrees of freedom adjusted for data with unequal variance; p>0,05; t-test.
[2]population density = birds/km^2.

Table 5.4. Greywing Francolin autumn sunrise calling activity and population density in the Stormberg and Lesotho study areas (mean number of calls ±1 standard deviation).

Area/year	Calls	Call sites	Density[1]
Stormberg 1989	293,3 ± 130,9	**14,7 ± 6,1	10,2 ± 3,2
Stormberg 1991	379,7 ± 261,5	15,8 ± 9,8**	*11,1 ± 2,1*
Lesotho 1 1991	192,0 ± 35,7	**3,0 ± 0,7**	*6,4 ± 0,7
Lesotho 2 1991	220,5 ± 91,0	10,5 ± 2,7	7,8 ± 0,7*

[1]population density = birds/km^2.
Asterisks in same column indicate significant variation between samples; *P<0,10; **P<0,05; Mann-Whitney U-test.

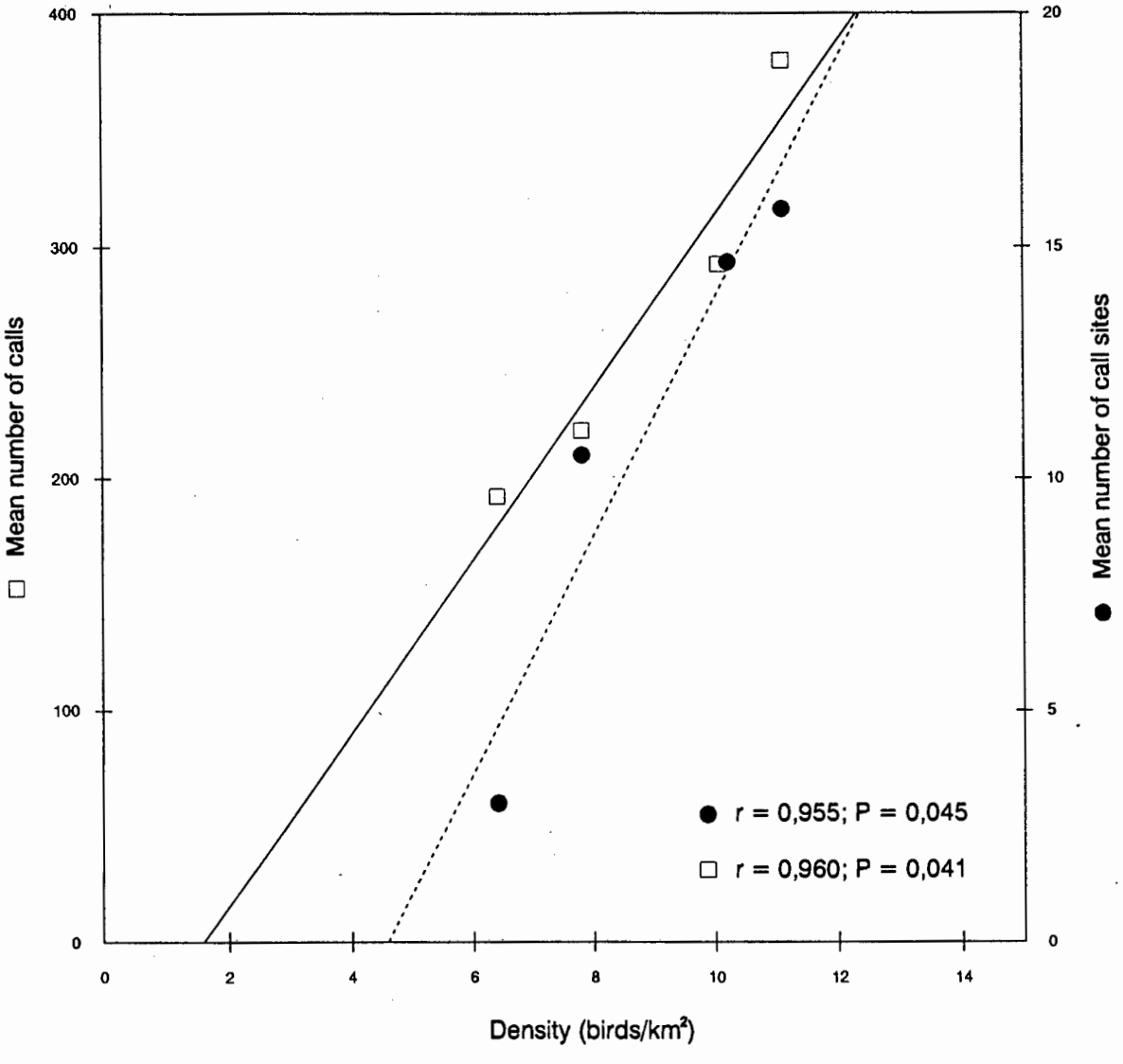


Figure 5.7. The regression of the number of Greywing Francolin calls and call sites recorded at sunrise during autumn in the Stormberg and Lesotho, on the index of population density in these two areas.

DISCUSSION

Vocalizations

The description of the acoustic structure and functions of vocalizations of the Greywing is still incomplete. The difficulties involved in observing Greywing behaviour under natural conditions, because of their anthropomorphic and secretive nature, dictate that such research must be done on captive birds. Nevertheless, we have discovered that the so-called advertisement call is used for more than territorial advertisement. Our statement that the main component of the advertisement call was given only by males must be viewed with caution. This is because only birds behaving territorially were observed in the wild, and not regrouping individuals, and also because we could not sex chicks attempting the advertisement call. More detailed studies of temporal (seasonal and diurnal) and geographical variation of this call may reveal further functional variation, especially in its role in reproductive isolation from the parapatric Redwing Francolin, F. levaillantii (Crowe et al. 1986).

Temporal variation in advertisement calling

As with the Grey Partridge (Rotella & Ratti 1986), there is marked diurnal variation in advertisement calling in the Greywing. Moreover, as in the Grey Partridge, calling decreases during the late autumn and winter months (May-July) and increases with the onset of the breeding season. However, unlike most bird species (Armstrong 1963), Greywing advertisement calls continue at high levels throughout the spring, summer and autumn. We

suspect that this persistence in calling is due to the strong year-round territorial behaviour of this gregarious francolin.

The crepuscular nature of advertisement calling activity confirms the opinions of previous researchers, but our data showed a higher bias toward sunrise calling activity than was previously suggested. We hypothesize that sunrise peaks in Greywing advertisement calling function primarily to reaffirm territory ownership at the onset of the day, whereas the relatively subdued calling at sunset, may serve to gather covey members to their terrestrial sleeping sites. This would result in a minimal amount of 'advertisement' to diurnal avian predators, and diurnal and nocturnal mammalian predators.

Effects of weather on calling activity

The apparent negative effects that the wind, especially after sudden shifts from the more common northwesterly to southerly wind, has on Greywing advertisement calling is probably due to a combination of the effects on the birds' physiology (cold winds exacerbating the effects of low morning temperatures, e.g. -1 to -13^{o}C in winter) and the attenuation effects on vocal signals. On the other hand, humidity may stimulate calling indirectly because of the 'triggering' effect that precipitation has on the onset of reproductive activity in South African gamebirds (Crowe & Siegfried 1978; Berry & Crowe 1985). Indeed, during the 1990 breeding season, egg-laying was one month advanced over the preceding two seasons as a result of unusually early rains in July.

Relationship between advertisement calling and population density

The negative correlation between Greywing advertisement calls and population density at sunset is primarily an artifact of the marked drop in calling during May-July. The drop in calling activity during May-July corresponds with Greywing families coalescing to form large coveys, and a period of peak population density. They presumably abandon pair territories and shift from feeding, in part, on uniformly distributed arthropods to feeding at localized patches of underground corms and roots (Mentis & Bigalke 1981a; Chapter 6), hence the reduced need for territorial advertisement. There is no significant correlation between any measure of Greywing advertisement calling and their population density if the data for these three months are excluded from the analyses ($r < 0,20$). Thus, Greywing advertisement calling cannot be used as a reliable measure of month-to-month variation in population density in a particular study area.

However, strong positive correlations between early morning call count data and estimates of population density for different years and areas, suggest that call counts could provide a useful index of Greywing population density.

Management implications

To be of use to managers of Greywing hunting operations (which are conducted during May-July on the Stormberg), surveys should be conducted during January-April. This appears to be a suitable period for counting, because Greywing numbers increase during this period. Since the Greywing breeding season on the Stormberg extends from August to as late as March, we recommend that calling surveys be conducted during March-April to give the best

assessment of relative changes in population density from year to year. To achieve reliable estimates of relative bird density we suggest that at least five counts be done per site per season. It is strongly suggested that the fieldwork be confined to the early morning hours when advertisement calling activity is at a peak. To reduce variation caused by census methods, we suggest that calls not be counted on days when the wind is southerly and when relative humidity is low. However, it would be premature to employ this index routinely without at least several years of data collection during periods of population increase and decline to test its applicability for estimating year-to-year population variation.

Appendix 5.1. Times of sunrise, sunset and mid-month noon for the Stormberg.

Standardized sunrise and sunset times for the Stormberg (31°15'S; 26°30'E) extracted from the CSIR tables (1973).

Times are given as a three figured number, the first is the hour, the other two the minutes. Two columns are listed per month, the first are daily sunrise times (a.m.), the second are daily sunset times (p.m.).

Standard time of local apparent noon is the time midway between sunrise and sunset. The noon time listed for each month is the mid-month local noon time calculated from the middle day (the 15th, except February the 14th, day) of each month.

Date	Month											
	Jan.		Feb.		March		April		May		June	
1	514	721	541	714	603	649	624	611	643	539	703	520
2	514	721	542	713	604	648	625	610	644	538	704	520
3	515	721	543	712	604	647	625	608	644	537	704	519
4	515	721	544	711	605	646	626	607	645	536	704	519
5	516	722	545	711	606	645	627	606	646	535	705	519
6	517	722	546	710	607	644	627	605	647	534	705	519
7	517	722	546	710	608	643	628	604	648	533	706	519
8	518	722	547	709	608	641	628	603	648	532	707	519
9	519	722	548	708	609	640	629	602	649	531	707	519
10	520	722	549	708	610	638	630	600	650	531	707	519
11	521	722	550	707	611	637	631	559	651	530	708	519
12	522	722	550	706	611	636	631	558	651	529	708	519
13	522	722	551	705	612	634	632	557	652	529	709	519
14	523	721	552	704	613	633	633	556	652	528	709	519
15	524	721	553	704	613	633	633	555	653	527	709	519
16	525	721	554	703	614	632	634	554	653	527	709	519
17	526	721	554	702	615	630	634	553	654	526	710	519
18	527	720	555	701	616	629	635	552	655	526	710	519
19	528	720	556	659	616	628	636	551	656	525	711	519
20	529	720	557	658	617	627	636	550	656	525	711	520
21	530	720	558	657	617	625	636	548	657	524	711	520
22	631	719	559	656	618	624	637	547	657	524	711	520
23	532	719	559	655	618	623	638	546	658	523	711	520
24	533	719	600	654	619	622	639	545	658	523	712	521
25	534	718	601	653	619	620	639	544	659	522	712	521
26	535	718	602	652	620	618	640	543	700	522	712	521
27	536	718	602	651	621	617	641	542	700	521	712	522
28	537	717	603	650	622	616	641	541	701	521	712	522
29	538	717	603	650	622	614	642	541	702	521	712	522
30	539	716	-	-	623	613	643	540	702	520	712	522
31	540	715	-	-	623	612	-	-	703	520	-	-
NOON	1222		1228		1223		1214		1210		1214	

Appendix 5.1, continued

Date	Month											
	July		Aug.		Sept.		Oct.		Nov.		Dec.	
1	712	523	701	539	631	557	554	615	519	636	503	702
2	712	523	700	540	630	558	553	616	518	637	503	703
3	712	523	700	541	629	559	552	616	518	638	503	704
4	712	524	659	541	628	559	551	617	517	639	503	705
5	712	524	658	542	627	600	549	617	516	640	503	706
6	712	525	658	542	626	600	548	618	515	641	503	707
7	712	525	657	543	624	601	547	618	514	641	503	707
8	712	526	656	543	623	601	546	619	514	642	503	708
9	712	526	655	544	621	602	545	620	513	643	503	709
10	711	527	654	544	620	603	543	621	513	644	504	709
11	711	527	653	545	618	604	542	622	512	645	504	710
12	711	528	652	546	617	605	540	622	511	646	504	711
13	711	528	651	546	616	605	539	623	510	647	504	711
14	710	529	650	547	615	605	537	624	509	648	505	712
15	710	529	649	548	614	606	536	624	508	649	505	713
16	710	530	648	548	612	606	535	625	508	650	505	713
17	710	530	647	549	610	607	533	626	507	651	506	714
18	710	531	646	550	609	607	532	627	507	652	506	715
19	709	531	645	550	608	608	531	627	506	653	507	715
20	709	532	644	551	607	609	530	628	506	653	507	716
21	708	533	643	552	605	609	529	628	506	654	508	716
22	708	533	642	552	604	610	528	629	505	655	508	717
23	707	534	641	552	603	611	527	630	505	656	509	717
24	707	534	640	553	602	611	527	631	505	657	509	718
25	706	535	639	553	600	612	526	632	504	658	510	718
26	705	535	638	554	559	612	525	633	504	658	510	719
27	705	536	637	554	558	613	524	633	504	659	511	719
28	704	537	636	555	557	614	523	634	504	700	511	719
29	703	537	635	555	556	614	522	635	504	701	512	720
30	702	538	634	556	555	615	521	635	504	701	513	720
31	701	538	632	556	-	-	520	636	-	-	513	720
NOON	1219		1218		1210		1200		1158		1209	

Appendix 5.2. Call count and meteorological data for the Stormberg study area during January 1989-January 1990.

Sunrise surveys:

Month[1]	Calls #	Sites #	Wind (360°)	Wind (km/hr)	Temp. (°C)	Humid. (%)	Cloud (%)
1	151	14	-	0,0	15	75	10
1	13	1	315	8,4	14	72	40
1	344	19	315	0,0	9	90	0
1	221	13	45	0,0	11	83	60
1	276	17	315	0,0	12	87	30
2	45	6	135	6,6	11	91	100
2	94	11	315	12,0	14	86	100
2	275	17	-	0,0	11	87	100
2	250	13	315	0,0	8	90	40
2	355	18	315	0,0	8	92	50
3	233	13	270	0,0	4	91	0
3	244	11	-	0,0	4	92	0
3	516	22	-	0,0	1	97	0
3	251	14	315	0,0	5	93	20
3	480	25	0	0,0	9	97	20
4	120	5	315	0,0	4	89	40
4	329	17	315	0,6	11	86	80
4	314	15	315	0,0	2	96	10
4	199	10	45	0,0	8	97	70
4	406	19	315	0,0	3	98	10
5	433	22	-	0,0	-2	98	0
5	66	7	315	6,0	6	80	10
5	336	17	315	0,0	-3	90	10
5	323	18	315	0,0	0	97	60
5	150	6	-	0,0	-1	98	100
6	7	1	135	1,2	2	95	100
6	300	17	315	0,0	-10	95	0
6	0	0	315	1,8	-8	88	0
6	79	5	315	0,6	2	77	10
6	236	13	315	0,0	-9	95	0
7	301	13	-	0,0	-9	95	0
7	179	8	315	3,6	-5	82	0
7	159	5	315	0,0	-9	94	0
7	119	7	315	4,8	-1	82	100
7	324	15	315	6,0	-1	90	30
8	379	18	315	0,0	-13	95	0
8	231	16	315	0,0	-6	92	0
8	48	5	315	18,0	7	55	60
8	109	7	315	4,2	-1	85	10
8	7	2	315	15,0	3	65	0
9	241	16	315	0,0	-13	95	0
9	373	26	315	0,0	-4	98	0
9	304	21	315	0,0	1	90	20
9	160	14	225	0,0	-5	92	20
9	138	13	225	0,0	-2	96	0
10	14	3	315	14,4	9	28	0
10	2	1	315	0,0	-7	88	10
10	212	18	0	0,0	-2	93	20
10	321	22	0	0,0	-2	93	0
10	77	5	315	0,0	1	87	0
11	79	8	315	6,0	12	93	100
11	189	13	45	6,0	9	85	10
11	238	20	45	0,0	11	92	100
11	170	11	270	0,0	9	50	60
11	64	6	0	6,0	11	55	0
12	123	10	45	0,0	8	92	10
12	32	5	225	2,4	11	85	100
12	87	8	90	0,0	6	90	0
12	66	6	315	12,0	15	63	10
12	176	17	315	0,0	10	85	100

Sunset surveys:

Date month	Calls #	Sites #	Wind (dir)	Wind (km/hr)	Temp. (°C)	Humid. (%)	Cloud (%)
1	51	4	270	6,6	27	24	20
1	24	1	315	4,8	26	28	70
1	21	1	135	0,0	18	40	10
1	8	2	135	7,2	20	40	10
1	112	9	135	0,0	21	30	20
2	4	1	315	14,4	26	32	10
2	0	0	135	21,6	18	47	10
2	11	3	270	5,4	19	50	70
2	20	1	135	18,0	13	85	80
2	114	8	225	9,6	15	50	40
2	47	2	135	14,2	17	77	50
3	193	6	270	0,0	17	40	0
3	0	0	225	4,8	25	20	10
3	100	8	315	0,0	17	80	100
3	12	1	180	3,6	22	40	60
3	10	3	180	0,0	20	40	10
4	50	3	180	12,6	19	45	100
4	32	2	270	3,0	17	50	90
4	158	6	315	4,2	18	33	0
4	145	5	315	0,0	12	58	50
4	0	0	315	6,0	17	33	40
5	112	5	315	0,6	12	55	10
5	0	0	315	10,8	14	45	10
5	63	3	225	12,0	12	40	20
5	59	3	315	0,0	11	43	80
5	7	1	315	7,2	12	45	10
6	52	1	225	6,6	6	43	0
6	6	2	135	3,6	2	65	0
6	0	0	225	3,6	13	28	0
6	38	1	315	4,8	10	44	0
6	71	2	315	1,2	12	33	0
7	0	0	315	0,0	5	35	0
7	0	0	315	3,0	8	40	0
7	0	0	315	12,0	9	40	10
7	0	0	315	11,4	6	45	10
7	17	1	315	4,8	8	40	10
8	43	5	135	0,0	4	65	0
8	14	1	315	13,2	16	30	80
8	158	8	315	6,0	13	35	10
8	3	1	315	14,4	12	40	0
8	57	3	315	1,2	7	28	0
9	47	4	225	2,4	0	60	10
9	21	3	225	4,8	6	90	90
9	103	9	315	0,0	13	45	0
9	7	1	135	9,6	12	24	10
9	10	1	225	0,0	10	20	10
10	45	4	225	0,0	10	30	0
10	31	4	315	3,0	14	20	0
10	5	1	315	0,0	15	20	10
10	5	2	270	2,4	17	26	10
10	8	2	135	12,0	14	65	10
11	138	10	315	0,0	17	70	80
11	7	1	135	13,2	13	85	90
11	96	7	315	7,2	19	45	50
11	8	1	225	1,8	15	30	40
11	38	2	315	3,6	17	30	0
12	61	5	135	0,0	18	50	80
12	0	0	135	6,0	11	87	90
12	22	2	135	6,6	15	55	10
12	47	3	135	7,2	18	55	20
12	58	2	135	12,0	18	65	40

†January (1)-December (12).

SECTION THREE

POPULATION REGULATION

CHAPTER 6

DISTRIBUTION AND DIET

Status: in review. The distribution of the Greywing Francolin, Francolinus africanus, on the Stormberg Plateau, eastern Cape Province, South Africa in relation to diet and substrata. Ostrich. co-authors: R.M. Gous & T.M. Crowe.

SUMMARY

Previous research indicates that Greywing Francolin, Francolinus africanus, in 'pristine' grasslands are isolated on areas over igneous substrata and are highly qualitatively selective in their diet, but are more widespread in grazed grasslands. This study examines whether this variation in dispersion and ecology is a result of quantity and/or quality of diet, or because of veld structure. We studied quantitative and qualitative aspects of the diet of Greywing Francolin populations, and the distribution and status of these populations over various land-form types and substrata on the Stormberg Plateau, eastern Cape Province, South Africa. We conclude that, within the montane grassland areas of the range of the Greywing Francolin, veld structure is the primary factor influencing distribution of Greywing Francolin populations, and that annual variation in summer and autumn arthropod abundance is the primary diet-related influence on abundance of Greywing Francolin.

INTRODUCTION

Various authors have reported that shortage of certain food types are potential limiting factors of southern African gamebirds (Crowe 1978, 1984; Mentis et al. 1975; Winterbach & Oosthuizen 1992), and may also affect body size (Penzhorn et al. 1991).

Mentis & Bigalke (1981a) reported that Greywing Francolin, Francolinus africanus, in the "pristine" grasslands of the Natal Drakensberg only occupied patches of sparse, short grass above 1 840 m a.s.l. on igneous substrata only, and had a more selective diet and shorter gut length than the partially sympatric Redwing Francolin, F. levaillantii. The habitat in that area is montane grassland (Themeda-Festuca alpine veld; Acocks 1975), managed under a policy which includes light grazing by wild herbivores and extensive biennial burning, hereafter termed 'conservation'. Recently, Mentis & Little (1992) investigated the interaction of these two francolins under a change of management from farming practices, with moderate to heavy grazing and frequent burning to a policy of 'conservation', and found an apparent partial displacement of Greywing Francolin by Redwing Francolin, and the establishment of Redwing Francolin where no francolins previously occurred. However, Greywing Francolin in the southern Drakensberg also persisted over sedimentary substrata. Mentis & Little's (1992) explanation for these findings was that soils of the southern Drakensberg are possibly less weathered than those to the north, and that therefore food plants on sedimentary substrata may reach the sufficiently high nutritive levels apparently required by Greywing Francolin.

To test these hypotheses: that quantity and quality of diet influence the distribution of Greywing Francolin, we investigated the diet and distribution of Greywing on the Stormberg Plateau, eastern Cape Province, South Africa. Land on the Stormberg is privately owned, and has been moderately to heavily grazed by commercial livestock (hereafter termed 'farming') for at least the past 150 years (W.S. Stretton pers. comm.). Fire has not been of frequent occurrence in this region. Although Redwing Francolin have been recorded recently in neighbouring areas (e.g. near Ugie (31°20'S; 28°15'E), RML pers. obs.), none have been recorded on the Stormberg (Little 1992). Therefore, without partial competition with Redwing Francolin (Mentis & Bigalke 1981a), and under 'farming' management practices, we would expect Greywing to be found over both sedimentary and igneous substrata, but that populations over igneous substrata should procure higher quantity and quality food, and be more abundant than populations over sedimentary substrata.

METHODS

Study area

The Stormberg Plateau (31°15'S; 26°30'E) is dominated by open montane grasslands, ranging in elevation from 1 700 m to 2 000 m above sea level. These grasslands are transitional from Themeda-Festuca alpine veld to Karroid Merxmuellera mountain veld, and are generally Themeda-dominated veld on black, peaty soil, often invaded by Karroid False Fynbos (Acocks 1975). The climate is cold and dry in winter (10-18°C), with minimum temperatures

regularly below -10°C, and mild temperature maxima (22-30°C) in summer. Rain falls mostly during the austral summer and averages 542 mm per year (Anon. 1984). The study area is stocked with cattle and sheep.

Distribution of Greywing

During June-July 1988, the land-form type (valley bottom, valley side, shelf or ridge top) and geological substratum (sedimentary or igneous) were recorded at the site from which each covey was flushed. Time spent searching for Greywing on different land-form types was also recorded. This was not done for the different substrata, because of the uncertainty of, or relatively wide, transition zones in places. However, where hunts were on areas of homogeneous substratum (i.e. predominantly sedimentary or predominantly igneous substrata), this was noted. Greywing population density was estimated with pointing dogs (Mentis & Bigalke 1985b).

Collection of diet samples

We collected crop contents from 788 Greywing during June 1988-March 1990. Crops were removed from birds hunted commercially during April-July, and from smaller samples during the rest of the year. Crop contents were stored in plastic bags and frozen for subsequent analysis at -20°C. Samples were labeled according to date and time of collection, sample site, Greywing sex, age and population density, and various morphological measurements (body mass, length of small intestine). Birds were aged as adult or juvenile (first year) by examination of the stage of moult of the remiges (Little & Crowe in press b; Chapter 4).

Analysis of crop contents and nutrition

Crops were later thawed, and the contents weighed and separated into eight food type classes (corms, rhizomes, leaves, buds, fruits, seeds, arthropods and grit). Food items were counted, and measured volumetrically by the water displacement method (to the nearest 0,01 ml) per food class. Crop contents were saved for later nutritional analysis.

Moisture content, protein and gross energy content of the diet were measured for each bird. Neutral detergent fibre, and the proportion of eight minerals (Ca, P, Mg, K, Na, Cu, Zn and Mn) in the diet of Greywing were measured for each population sampled.

Monthly variation in arthropod abundance was recorded by counting arthropods within a 0,25 m^2 quadrat for one minute. This procedure was repeated 30 times per survey, with about two meters between quadrat sites. Two surveys per substratum type (igneous or sedimentary) were done each month, on the nearest calm and clear day to the 10th and 20th days of each month, and between 10h00 and 15h00.

Statistical analysis

We used various statistical programs within the BMDP software package (Dixon et al. 1990) to analyze the data at different levels. The detailed data description program (2D) was used to summarize the overall composition of the diet by food class and either number or volume of food items. We then used the bivariate (scatter) plot program (6D) to, (i) compare crop contents and nutrition with population density and body mass for the winter months (April-August), and (ii) compare crop mass,

crop volume and total number of items in the crop with the time of day that birds were collected (09h00-17h00). The two-way analysis of variance program (7D) was used to test for variation in the composition of diet between sexes, ages and season over the two substrata. These data were first run including both age classes, and then run independent of age-class, after it was found that most variation was due to differences between age classes. We then re-ran the analysis excluding season to increase sample sizes. Finally, we used the stepwise regression program (2R) to compare the relationships between diet (crop volume and crop mass) and nutrition (moisture content, protein, gross energy, neutral detergent fibre, and the eight minerals) with Greywing population density during autumn-spring (April-August).

RESULTS

Distribution of Greywing

More Greywing were flushed from sites on ridge tops and shelves than on valley slopes and valley bottoms (Table 6.1). On hunts, during June and July 1988, 100 coveys were flushed from sites on sedimentary substrata and 80 from sites on igneous substrata. The hunting effort over these two substrata is unknown. However, mean population densities on four areas of predominantly sedimentary substrata were not significantly different from mean population densities on four areas of predominantly igneous substrata, censused in 1988 and 1989 ($P > 0,05$, t-test) (Table 6.2). Greywing population densities on the Stromberg (Tables 1 &

2) were as high as populations of both Greywing and Redwing in the Natal Drakensberg (Mentis & Bigalke 1981; Mentis & Little 1992).

Table 6.1. Frequency of Greywing Francolin flushed from four land-form types.

Land-form type	Time (mins.)	Number coveys	Coveys/ minute	Number birds	Birds/ minute	Density[1] (birds/ha)
Valley bottom	758	14	0,019	87	0,115	0,066
Valley side	398	6	0,015	50	0,126	0,070
Shelf	608	17	0,028	146	0,240	0,113
Ridge top	1 533	61	0,040	415	0,271	0,125
Total	3 297	98		698		

[1]estimated density; Mentis & Bigalke method (1985b).

Table 6.2. Comparison of mean population densities of Greywing Francolin between four areas over sedimentary substrata and four areas over igneous substrata.

Year	Sedimentary substrata $\bar{x}^1$	SD	Igneous substrata $\bar{x}^1$	SD	p^2
1988	0,101	0,04	0,115	0,02	0,54
1989	0,096	0,01	0,129	0,04	0,18

[1]mean population density (method: Mentis & Bigalke 1985b).
[2]comparison of two sample means, t-test.

Greywing diet

Above-ground plant parts (leaves, buds, fruits and seeds) were more plentiful (58,5%) than underground storage organs of plants (corms and rhizomes, 36,5%) in the diet of Greywing. However, by volume, corms and rhizomes comprised 78,0% of the diet (Fig. 6.1).

Greywing were seasonally selective in the gross food types taken. Winter diet, of both sexes and both ages, was mostly underground storage organs of geophytes, mainly of the genus Mariscus (family Cyperaceae), while arthropods were most important during the summer. The proportion of arthropods in the diet dropped off sooner on sedimentary than on igneous substrata for both adults and juveniles (Figs. 6.2 & 6.3).

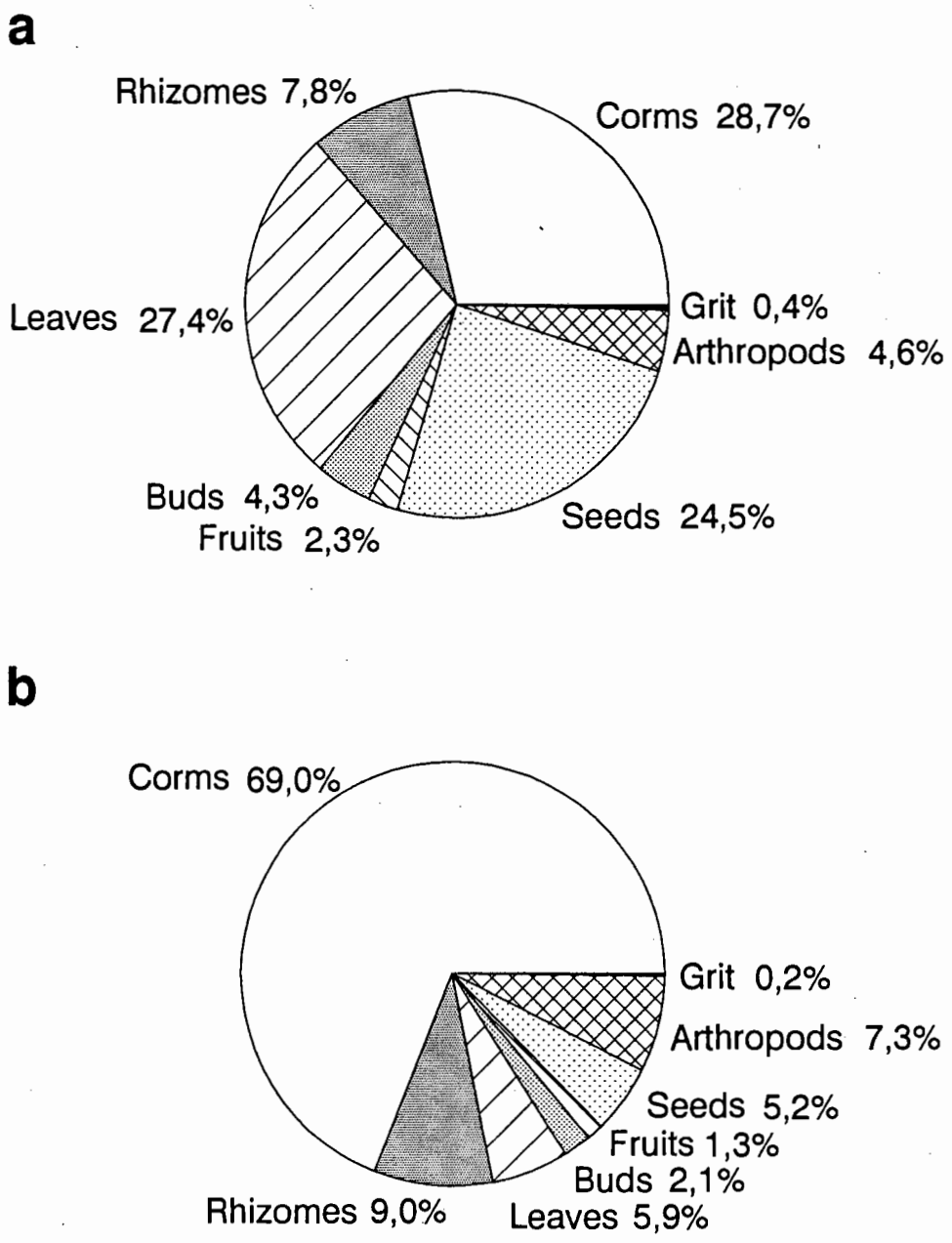


Figure 6.1. Frequency distribution of Greywing Francolin food types within the crop recorded throughout the year on the Stormberg, a = number of food items per food type, b = volume of food items per food type (N = 751 crops examined).

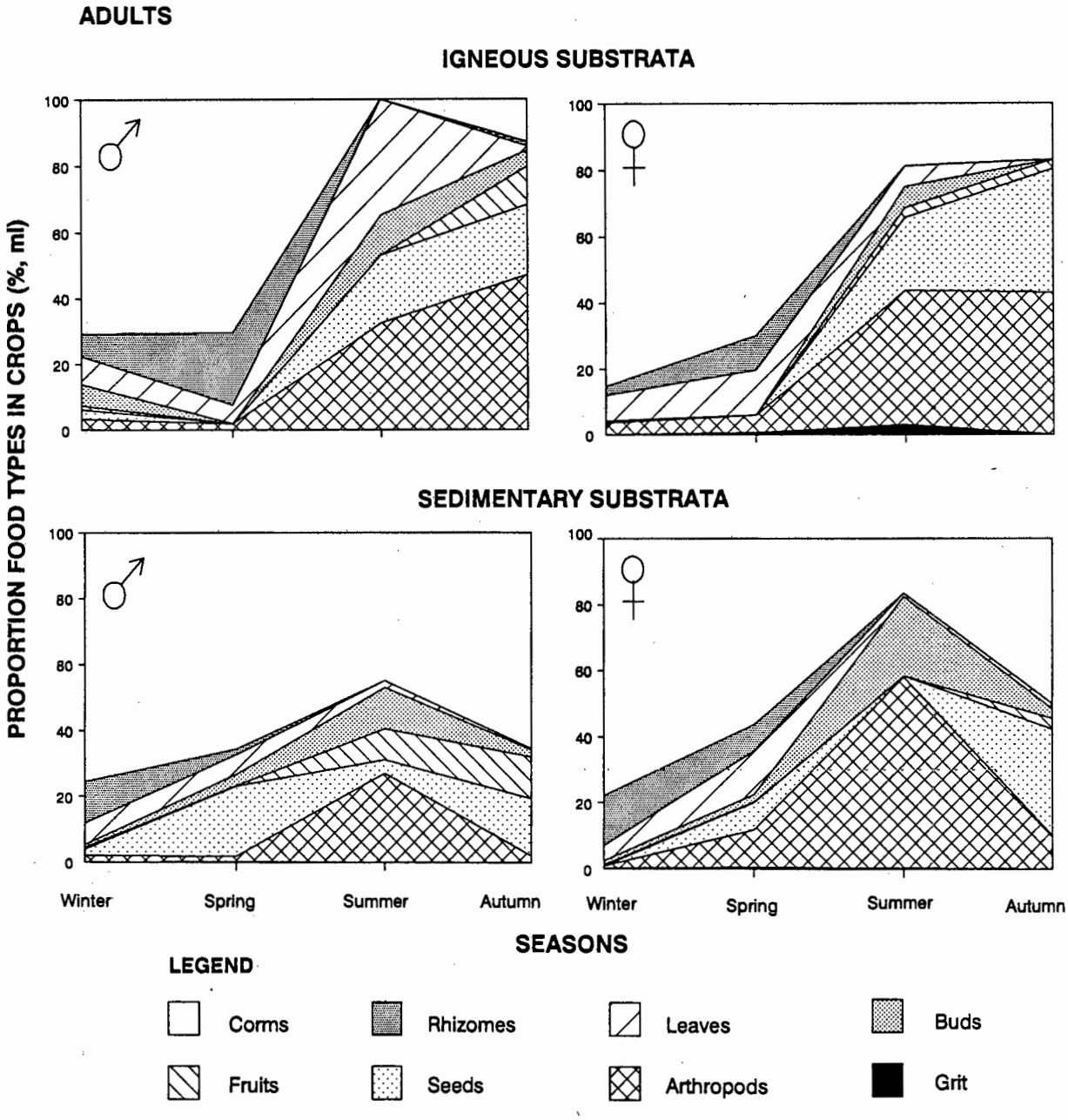


Figure 6.2. Seasonal distribution of proportion of food types, by volume, within the crops of adult Greywing Francolin collected on the Stormberg.

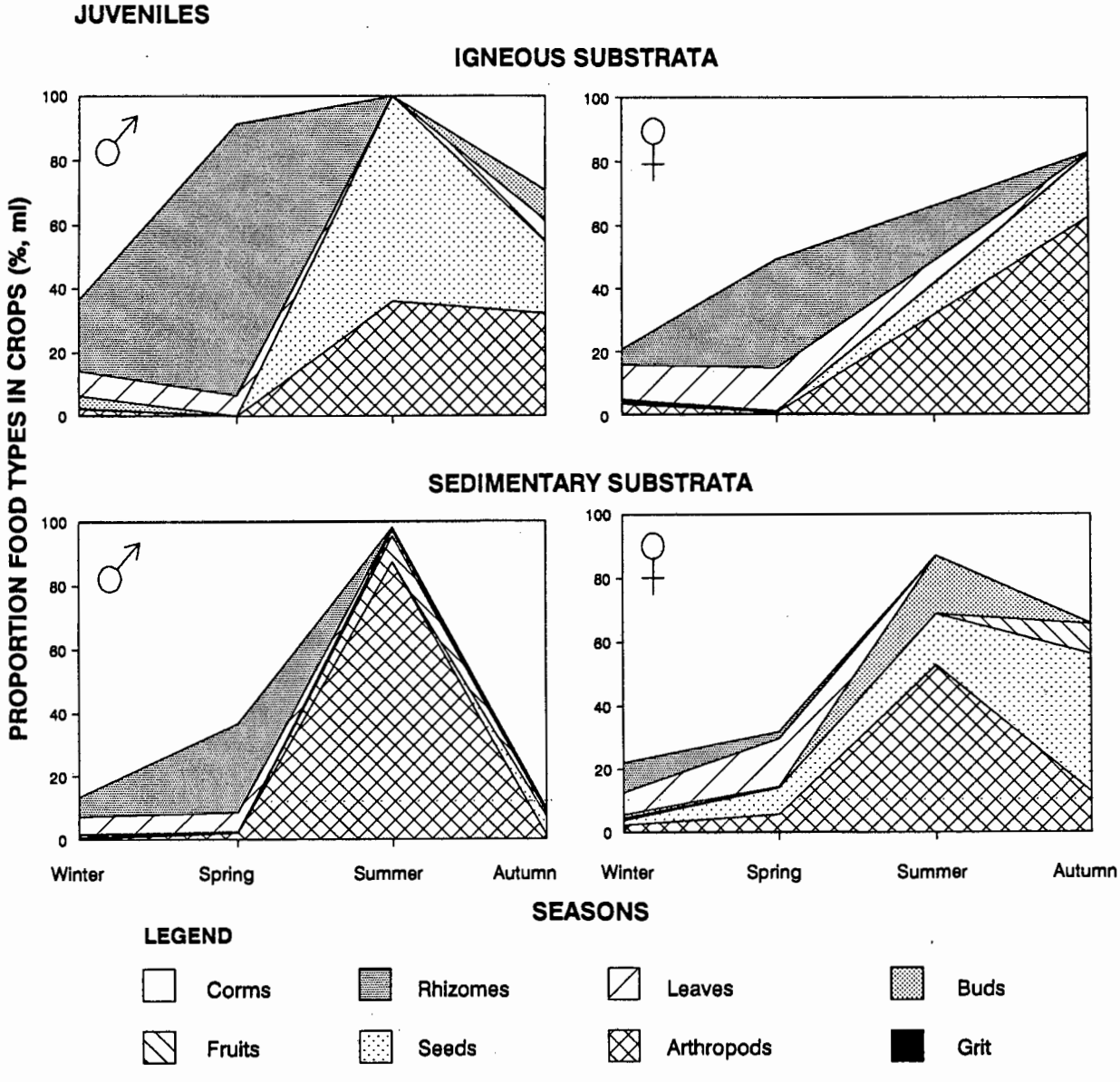


Figure 6.3. Seasonal distribution of proportion of food types by volume, within the crops of juvenile (<1 year old) Greywing Francolin collected on the Stormberg.

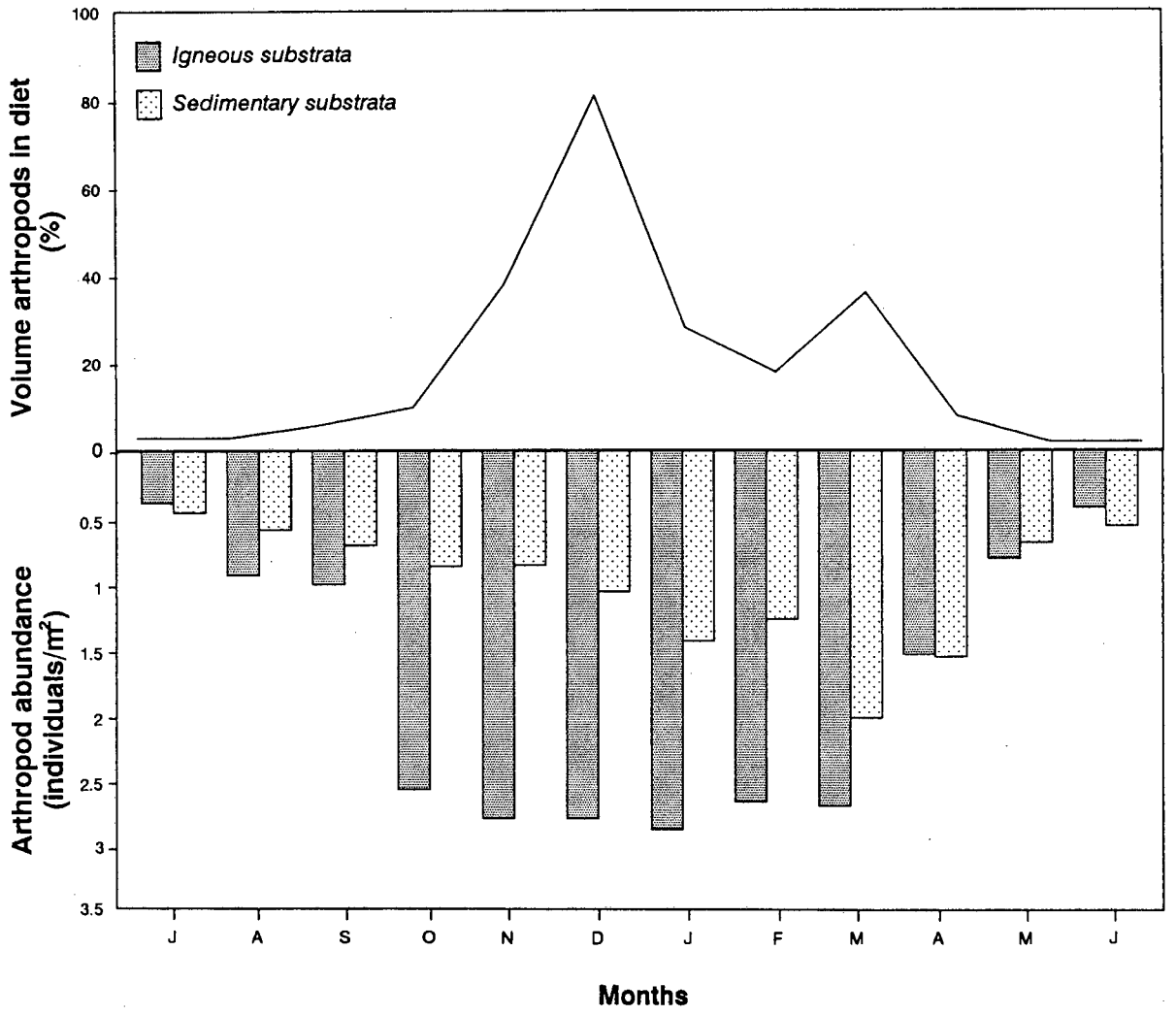


Figure 6.4. Comparison of mean monthly volume of arthropods in the diet of Greywing Francolin with mean monthly arthropod abundance over igneous and sedimentary substrata on the Stormberg.

Monthly frequency distribution of arthropods in the diet of Greywing was significantly correlated with monthly arthropod abundance over igneous substrata ($r = 0,71$; $P < 0,01$), but was not significantly correlated with monthly arthropod abundance over sedimentary substrata ($r = 0,40$; $P = 0,20$). Furthermore, arthropods were more abundant over igneous than over sedimentary substrata ($P = 0,03$; t-test) (Fig. 6.4). Seeds were generally an important part of the autumn diet of Greywing of both ages.

Time of day when Greywing were collected was significantly correlated with mean crop mass ($r = 0,43$; $P < 0,001$; $n = 471$), mean crop volume ($r = 0,42$; $P < 0,001$; $n = 446$) and mean number of food items in the crop ($r = 0,16$; $P < 0,001$; $n = 446$).

Comparison of quantity and quality of Greywing diet with Greywing morphometrics and distribution

Correlations of mean crop volume, crop mass and nutrition of Greywing diet with mean body mass and population density of Greywing were mostly not significant ($P > 0,05$) (Table 6.3). Only potassium was significantly negatively correlated with Greywing body mass ($r = -0,45$; $P = 0,02$).

Furthermore, various morphometric and diet variables were also mostly not significantly different over igneous or sedimentary substrata (Table 6.4). However, mean body mass of adult males was significantly higher over igneous substrata than those collected over sedimentary substrata ($P < 0,05$), mean volume of corms in juvenile male crops over sedimentary substrata were significantly higher than those over igneous substrata ($P < 0,05$), and mean protein content of the diet of adult males over igneous substrata was significantly higher than those over

sedimentary substrata ($P < 0,01$).

Juvenile Greywing over sedimentary substrata had significantly higher arthropod, and protein, content during summer than juvenile birds over either sedimentary or igneous substrata in winter or spring ($P < 0,001$, Bonferroni test). Furthermore, juvenile Greywing over igneous substrata, collected during autumn, also had higher arthropod and protein content, than birds over sedimentary or igneous substrata in winter or spring ($P < 0,001$, Bonferroni test) (Appendixes 6.1 & 6.5).

Adult Greywing showed a similar pattern, with adult males over igneous substrata in summer also having significantly higher mean protein content in the diet than birds over sedimentary and igneous substrata in winter and spring ($P < 0,001$) (Appendixes 6.3 & 6.4). Greywing of both age and sex classes contained more arthropods and protein in their diet over igneous substrata in autumn than those over sedimentary substrata in the same season (Appendixes 6.1-6.4).

Furthermore, stepwise regression of diet and nutrition, with Greywing population as the dependent variable, was only significant for one step, when protein was isolated as having the highest correlation with population density ($r = 0,53$; $P < 0,05$).

Table 6.3. Bivariate correlation coefficients, probability values and sample size for comparisons between winter diet and nutrition, and body mass and population density of Greywing Francolin.

	Body mass (grams)			Population density (birds/ha)		
	r	P	n^1	r	P	n^2
Crop volume	0,12	0,58	26	-0,23	0,20	33
Crop mass	0,18	0,37	28	-0,23	0,18	35
Moisture content	0,32	0,10	28	-0,18	0,31	35
Protein	0,07	0,71	28	-0,12	0,49	35
Gross energy	-0,26	0,18	28	0,05	0,80	35
Neutral detergent fibre	-0,26	0,18	28	0,01	0,95	35
Calcium (Ca)	-0,01	0,97	28	-0,32	0,07	34
Phosphorous (P)	-0,26	0,17	28	-0,26	0,14	34
Magnesium (Mg)	0,19	0,34	28	-0,16	0,36	34
Potassium (K)	-0,45	0,02*	28	0,10	0,95	34
Sodium (Na)	0,19	0,37	25	-0,02	0,91	26
Copper (Cu)	0,11	0,57	28	-0,24	0,17	34
Zinc (Zn)	0,20	0,30	28	-0,26	0,13	34
Manganese (Mn)	-0,13	0,55	25	0,14	0,44	31

*significant correlation, $P<0,05$.

[1] = number of birds sampled.

[2] = number of populations sampled.

Table 6.4. Mean morphometric, diet, and nutrition values (±1 standard deviation) for Greywing Francolin collected over sedimentary and igneous substrata.

	Sedimentary				Igneous			
	Male		Female		Male		Female	
	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n
Small intestine length (cm)								
Adult	70,2±5,5	59	72,2±6,6	32	70,3±5,2	43	71,2±7,0	18
Juvenile	67,6±7,1	16	66,7±9,3	17	68,5±6,2	18	68,8±8,3	23
Body mass (g)								
Adult	450,6±32,3	157	428,6±26,9	81	464,1±26,0*	69	430,6±30,0	45
Juvenile	404,2±61,5	56	378,1±72,8	72	431,9±46,1	42	396,4±45,5	55
Crop volume (ml)								
Adult	4,4±3,8	147	5,7±5,0	73	4,2±4,7	70	3,9±3,1	46
Juvenile	5,5±5,5	46	5,5±4,5	64	3,7±3,7	42	4,0±3,1	55
Crop mass (g)								
Adult	5,7±5,0	154	7,1±5,7	78	5,3±5,5	69	5,0±3,8	45
Juvenile	7,1±6,5	52	7,0±6,0	72	4,9±4,7	40	5,1±3,9	52
Corms volume (ml)								
Adult	3,1±3,4	147	3,6±4,6	73	2,6±3,5	70	2,9±2,8	46
Juvenile	4,3±5,6*	46	3,9±3,8	64	1,8±2,3	42	2,6±2,7	55
Invertebrate volume (ml)								
Adult	0,2±0,7	147	0,6±1,5	73	0,4±1,2	70	0,3±0,8	46
Juvenile	0,3±1,0	46	0,3±0,6	64	0,3±0,9	42	0,5±1,1	55
Number of food items								
Adult	92,6±144,5	147	113,0±156,5	73	104,3±175,4	70	74,2±80,6	46
Juvenile	83,8±89,8	46	136,6±170,7	64	75,8±86,3	42	76,9±94,5	55
Protein (%)								
Adult	9,9±7,0	144	10,6±7,6	73	14,6±11,1**	60	10,7±9,0	39
Juvenile	8,4±8,5	47	10,1±7,6	69	11,2±8,8	35	12,8±12,7	47
Gross energy (%)								
Adult	16,1±2,0	124	16,3±2,3	65	16,9±2,1	48	16,0±1,3	32
Juvenile	16,1±2,4	41	16,2±2,0	59	16,4±1,6	29	16,6±1,7	42

Significantly different means, **P < 0,01, *P < 0,05, Bonferroni test, between same sex only.

DISCUSSION

Greywing on the Stormberg Plateau used the same land-form types as they do throughout the Natal Drakensberg. However, on the Stormberg, they occurred at similar densities over both substrata types. Furthermore, the density of Greywing populations over both igneous and sedimentary substrata on the Stormberg is similar to that for both Greywing and Redwing Francolin taken together in the Natal Drakensberg (Mentis & Bigalke 1981a; Mentis & Little 1992). This might be the case because either (i) soils over both substrata on the Stormberg have similar nutrient levels, as suggested by Mentis & Little (1992) for the southern Drakensberg, or (ii) the elevational difference between sedimentary and igneous substrata is relatively small on the Stormberg, with few areas below 1 840 m a.s.l., or (iii) the grazing of these grasslands has created a relatively open veld structure that allows food plants of Greywing to flourish.

The diet and feeding pattern of Greywing on the Stormberg Plateau are similar to those of Greywing described by Mentis (1973) and Mentis & Bigalke (1981a) for the 'conserved' grasslands of the Natal Drakensberg, except that plant types differed from the predominantly Iridaceous corms eaten by the Drakensberg birds. The similarity in both quantitative and qualitative nature of the diet of Stormberg populations compared with populations of the 'pristine' grasslands of the Natal Drakensberg suggests that energy levels of diet are adequate for successful existence of the species.

Although slightly more birds were found over igneous than over

sedimentary substrata, and body mass was slightly higher over igneous than over sedimentary substrata, little significant evidence was found to suggest that quantity and/or quality of Greywing diet on the Stormberg had any profound effect on the population distribution or morphometrics of Greywing. The strength of these results might however be weakened by the unknown degree of overlap of Greywing home range size and scale of igneous/sedimentary sustrata mozaic.

However, the higher arthropod and protein content of the diet of Greywing populations over igneous substrata than over sedimentary substrata in autumn may be significant in the survival of chicks, particularly when spring and early summer rains are delayed, thus causing either deferred egg laying or failure of first broods in that season.

Conclusions

The lack of substantial evidence that nutrition of Greywing diet affects either Greywing distribution or body size (body mass or gut length), and the fact that Greywing appear to be as abundant over both substrata as francolins in the Natal Drakensberg (Mentis & Bigalke 1981a; Mentis & Little 1992), suggest that quantity and/or quality of food is not the determining factor of Greywing population distribution in montane grasslands. However, evidence that Greywing abundance is similar over both substrata only when the grasslands are moderately grazed by domestic stock ('farming') (Mentis & Little 1992; This study) indicates that food plants of Greywing might be dependent on successional stage and/or veld structure of these grasslands. We therefore suggest that in the montane grassland areas within

the range of the Greywing, veld structure is the primary influence on Greywing population distribution (i.e. number of coveys).

Furthermore, although food plants, which are eaten during most of the year (April-October), apparently do not determine Greywing abundance, they might determine Greywing home range distribution. Moreover, evidence suggests that arthropod abundance may affect the annual reproductive success and therefore population size of Greywing. We suggest that the influence on reproductive success of variation in quantity of arthropods in the diet of Greywing between substrata types and between years, depending on timing of early summer rains (Little & Crowe in press a; Chapter 3), is the primary diet-related influence on Greywing population abundance (i.e. numbers of individuals per covey).

Appendix 6.1. Within and between season comparison of arthropod content of diet for first-year Greywing Francolin (N = 207) sampled on sedimentary and igneous substrata.

	Winter				Spring				Summer				Autumn			
	Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
$\bar{x}$ =	0,0	0,1	0,1	0,1	0,1	0,4	0,0	0,0	1,9	1,2	0,5	0,0	0,1	0,5	2,5	2,6
SD =	0,0	0,2	0,2	0,5	0,2	1,0	0,0	0,0	2,7	0,9	0,6	0,0	0,2	0,7	2,5	1,6
n =	27	45	33	36	10	9	4	10	5	3	2	1	4	7	3	8
1									**						**	**
2									**						**	**
3									**						**	**
4									**						**	**
5									**						**	**
6									**						**	**
7									**						**	**
8									**						**	**
9	**	**	**	**	**	**	**	**					**			
10																
11																**
12																*
13									**						**	**
14															**	**
15	**	**	**	**	**	**	**	**					**	**		
16	**	**	**	**	**	**	**	**			**	*	**	**		

significantly different means; *P<0,05, **P<0,01; Bonferroni test.
1 = ♂ on sedimentary substratum in winter - 16 = ♀ on igneous substratum in autumn.

Appendix 6.2. Within and between season comparison of protein content of diet for first-year Greywing Francolin (N = 198) sampled on sedimentary and igneous substrata.

	Winter				Spring				Summer				Autumn			
	Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
$\bar{x}$ =	6,9	9,0	9,0	8,7	6,8	7,1	7,5	7,1	46,0	40,1	21,6	-	5,7	13,4	31,5	37,9
SD =	2,8	4,8	5,5	5,8	2,7	4,4	1,1	1,4	3,9	11,6	0,0	-	2,9	9,2	12,3	14,1
n =	31	53	28	33	10	8	3	7	2	2	1	0	4	6	3	7
1									**	**		-			**	**
2									**	**		-			**	**
3									**	**		-			**	**
4									**	**		-			**	**
5									**	**		-			**	**
6									**	**		-			**	**
7									**	**		-			**	**
8									**	**		-			**	**
9	**	**	**	**	**	**	**	**			*	-	**	**		
10	**	**	**	**	**	**	**	**				-	**	**		
11									*			-				
12	-	-	-	-	-	-	-	-	-	-	-					
13									**	**					**	**
14									**	**					**	**
15	**	**	**	**	**	**	**	**					**	**		
16	**	**	**	**	**	**	**	**					**	**		

significantly different means; *P<0,05, **P<0,01; Bonferroni test.
1 = ♂ on sedimentary substratum in winter - 16 = ♀ on igneous substratum in autumn.
- = no data.

Appendix 6.3. Within and between season comparison of arthropod content of diet for adult Greywing Francolin (N = 343) sampled on sedimentary and igneous substrata.

	Winter				Spring				Summer				Autumn			
	Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
$\bar{x}$ =	0,1	0,0	0,2	0,1	0,1	0,8	0,1	0,3	1,2	4,0	0,3	0,3	0,1	0,6	1,6	2,1
SD =	0,2	0,1	0,6	0,4	0,2	1,2	0,2	0,6	1,8	3,4	0,4	0,5	0,2	1,1	2,2	2,3
n =	104	45	52	29	16	14	6	10	17	6	5	5	10	8	13	3
1									**	**					**	**
2									**	**					**	**
3									**	**					**	*
4									*	**					**	*
5									*	**					**	*
6										**						
7										**						
8										**					*	
9	**	**	**	*	*					**						
10	**	**	**	**	**	**	**	**	**		**	**	**	**	**	
11										**						
12										**						
13										**					**	
14										**						
15	**	**	**	**	**			*		**			**			
16	**	**	*	*	*											

significantly different means; *P<0,05, **P<0,01; Bonferroni test.
1 = ♂ on sedimentary substratum in winter - 16 = ♀ on igneous substratum in autumn.

Appendix 6.4. Within and between season comparison of protein content of diet for adult Greywing Francolin (N = 323) sampled on sedimentary and igneous substrata.

	Winter				Spring				Summer				Autumn			
	Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous		Sedimentary		Igneous	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
$\bar{x}$ =	9,5	8,0	10,7	8,9	6,6	11,2	6,3	9,5	20,2	28,1	27,6	10,6	7,6	11,3	29,0	38,1
SD =	5,6	3,0	7,2	5,2	3,2	6,0	1,5	7,5	12,5	14,3	13,9	0,0	5,6	5,3	11,2	17,6
n =	107	46	47	27	15	14	6	10	12	6	3	1	10	7	10	2
1									**	**	**				**	**
2									**	**	**				**	**
3									**	**	**				**	**
4									**	**	**				**	**
5									**	**	**				**	**
6									*	**	**				**	**
7									**	**	**				**	**
8									*	**	**				**	**
9	**	**	**	**	**	*	**	*					**			*
10	**	**	**	**	**	**	**	**					**	**		
11	**	**	**	**	**	**	**	**					**	*		
12																*
13									**	**	**				**	**
14										**	*				**	**
15	**	**	**	**	**	**	**	**					**	**		
16	**	**	**	**	**	**	**	**	*			*	**	**		

significantly different means; *P<0,05, **P<0,01; Bonferroni test.
1 = ♂ on sedimentary substratum in winter - 16 = ♀ on igneous substratum in autumn.

CHAPTER 7

INTESTINAL HELMINTHS

Status: in prep. Variation in intestinal helminth infestation of the Greywing Francolin, Francolinus africanus. Ostrich. co-authors: A. Verster & T.M. Crowe.

SUMMARY

We recorded prevalence and intestinal worm burdens for 312 Greywing Francolin, Francolinus africanus, on the Stormberg Plateau, eastern Cape Province, during April 1989-December 1990. Most Greywing (86,2%) had helminths in their small intestine or caeca. Nematodes were confined to the caeca and were more prevalent than cestodes. The prevalence and number of cestodes in the small intestine were highest during September-February and peaked during November-December. Caecal nematodes were present in high numbers throughout the year with two peaks during June-August and November-January. Helminth infestation was independent of host-sex. The prevalence of cestodes was significantly higher in juvenile Greywing than in adults during the austral winter (May-July). The number of cestodes was consistently, but not significantly, higher in juveniles than in adults. Prevalence and worm burdens of caecal nematodes were independent of host-age. Greywing body mass, length of small intestine and population density were not significantly

correlated with worm burdens. Although no pathological conditions were found, the high overall prevalence of helminths, and seasonal peaks in cestode and nematode burdens could pose potential threats to Greywing populations.

INTRODUCTION

The high prevalence of gastrointestinal helminths in poultry, and the deleterious effects on the health of these hosts was recognized at least sixty years ago (Baker 1930). Recently, observations supported by experimental work have shown that parasites can directly reduce the condition, survival and reproductive output of wild game species while indirect effects can lead to reduced competitive ability of the host and vulnerability to predators (Hudson 1986; Hudson & Dobson 1988). Hudson (1986) suggested that the combined effects of malnutrition and parasite burden will influence the condition of the bird and, together, these affect breeding output. Furthermore, parasites adversely affect male secondary sex characters, and females prefer unparasitized rather than parasitized males in the Red Jungle Fowl, Gallus gallus (Zuk, Thornhill, Ligon & Johnson 1990). It is therefore surprising that few ecological studies have concentrated on the role of parasites in regulating gamebird numbers (Hudson 1988). Except for studies by Rowan (1971) and Markus (1974) on the relationships of avian distribution patterns and arthropod-borne disease, very little is known about the influence of endoparasites on the distribution and abundance of African birds.

The Greywing Francolin, Francolinus africanus, is a highly prized gamebird in the eastern highlands of southern Africa (Mentis & Bigalke 1985a; Johnson & Wannenburgh 1987). Present hunting levels are not based on reproductive success and actual population size (Mentis & Bigalke 1980, 1985a). It is therefore beneficial to the management of Greywing populations to

understand which population regulatory factors have most impact on these populations, and how these factors function.

In this chapter we, 1) estimate the proportion of the Greywing population carrying parasites (prevalence) and the number of parasites per host within these Greywing populations (worm burdens), 2) compare the prevalence and worm burdens with season, host-sex and host-age, 3) correlate the prevalence and worm burdens with body mass and length of small intestine of Greywing, and 4) examine the relationship between Greywing population density and helminth parasitism to assess the potential influence of parasite burdens on annual Greywing production.

METHODS

Study area

Greywing Francolin were collected on various farms on the Stormberg Plateau (31°15'S; 26°30'E), eastern Cape Province, South Africa. The plateau is dominated by open montane grasslands ranging in elevation from 1 700 m to 2 000 m above sea level. These grasslands are transitional from Themeda-Festuca alpine veld to Karroid Merxmuellera mountain veld, and are generally Themeda-dominated veld on a black, peaty soil, often invaded by Karroid False Fynbos (Acocks 1975). The climate is cold and dry in winter (10-18°C), with minimum temperatures regularly below -10°C, and mild temperature maxima (22-30°C) in summer. Rain falls mostly during the austral summer with a mean of 542 mm per year (Anon. 1984). The study area is stocked with cattle and sheep.

Sampling and analysis

Between April 1989 and December 1990, intestineal tracts were collected from 312 freshly killed Greywing Francolin. During the Greywing hunting season (April-July) the samples were obtained from hunting bags and from August to March from birds collected by myself. The birds were sexed, mass measured and their age determined before the intestinal tracts were removed. Sex was determined by inspection of the gonads. Birds were aged as either adult or first year, according to moult of the tenth primary (Little & Crowe in press b; Chapter 4). Body mass was measured to the nearest five grams using a Pesola spring scale. Intestinal tracts were measured according to (Leopold 1953), labeled individually, and frozen at -20^{o} C until examination.

At a later stage the intestines were thawed, separated into gizzard, small intestine and caeca, and opened for the recovery of the helminths. The ingesta was examined with the aid of a stereo-microscope, and the helminths counted and removed for identification. Although samples were collected over 21 months, counts were pooled per month to increase sample size.

The data were analyzed to determine the overall prevalence of the helminths, the seasonal abundance of cestodes and nematodes and the influence of sex and age on the worm burdens. The population density of the Greywing Francolins was estimated as described by Mentis & Bigalke (1985b), and this with the body mass correlated with the worm burdens.

RESULTS

The Greywings were infested with cestodes belonging to three genera (Ascometra sp., Raillietina sp. and Hispaniolepis sp.) and one caecal nematode (Subulura sp.). Tremtodes were present in the small intestine of two birds.

A high proportion of Greywing Francolin (86,2%; 269/312) were parasitized by helminths, either in the small intestine or the caeca. Only 45,2% (141/312) were infested with cestodes, while nematodes were present in the caeca of 76,9% (240/312).

The prevalence of intestinal cestodes in Greywing was highest during September-February, peaked during November-December (92,3% & 90,0% infestation, respectively), and was lowest in May (9,8% infestation). Whereas, the prevalence of nematodes in the caeca remained high throughout the year (76,9% overall infestation), with two peaks during June-August and November-January (Table 7.1).

Cestode burdens in the small intestine peaked during November-January whereas, nematode infestation in the caeca peaked during June-August and November-January (Table 7.1). The prevalence and intensity of intestinal helminths showed a significant positive correlation with both cestodes ($r = 0,76$; $P = 0,004$) and nematodes ($r = 0,71$; $P = 0,01$).

Table 7.1. Seasonal abundance of cestodes and nematodes in Greywing Francolin, Francolinus africanus.

		Cestodes			Nematodes		
		Infested	Numbers		Infested	Numbers	
Date	n	%	Range	$\bar{x}\pm SD$	%	Range	$\bar{x}\pm SD$
July	52	34,6	0-8	0,5±1,4	84,6	0-106	11,9±18,2
August	25	44,0	0-6	0,4±1,3	88,0	0-60	9,1±13,5
September	29	75,9	0-6	1,2±1,4	82,4	0-31	5,0±6,6
October	21	81,0	0-30	5,1±8,0	42,9	0-8	1,2±2,5
November	13	92,3	1-100	12,8±29,0	92,3	0-26	8,2±8,1
December	10	90,0	0-37	11,6±14,2	100,0	0-95	16,8±29,2
January	13	84,6	0-38	10,6±12,9	92,3	0-120	23,5±39,0
February	11	81,8	0-2	1,4±0,8	72,7	0-14	3,7±4,3
March	19	47,4	0-3	0,6±0,8	21,1	0-5	0,7±1,6
April	18	27,8	0-7	0,7±1,7	77,8	0-8	2,5±2,5
May	41	9,8	0-1	0,1±0,2	63,4	0-12	2,2±3,1
June	60	23,3	0-3	0,2±0,5	91,7	0-86	11,9±17,6

Although there were no significant differences in the seasonal prevalence of nematode infestations between sex or age classes ($P > 0,05$; Fisher's exact test), juvenile Greywing had significantly higher prevalence of cestodes during May-July than adults ($P = 0,009$; two-tailed Fisher's exact test) (Table 7.2).

The mean seasonal burdens of nematodes did not differ significantly between sex or age classes of Greywing, nor between sexes for cestode infestations ($P > 0,05$; Mann-Whitney U-test). However, juveniles had consistently higher burdens of cestodes

than adults, although the differences were not significant (P > 0,05; Mann-Whitney U-test) (Table 7.2).

Table 7.2. Seasonal prevalence of helminths in Greywing Francolin, Francolinus africanus.

	November-January			February-April			May-July			August-October		
	Birds		Worm burden	Birds		Worm burden	Birds		Worm burden	Birds		Worm burden
	Positive			Positive			Positive			Positive		
Host	n	%	$\bar{x}$±SD	n	%	$\bar{x}$±SD	n	%	$\bar{x}$±SD	n	%	$\bar{x}$±SD
Cestodes												
Male	28	89,2	9,9±12,2	30	43,3	0,5±0,7	79	13,9	0,3±1,0	44	52,3	2,6±6,0
Female	8	87,5	18,0±34,2	18	55,6	1,3±1,7	74	16,2	0,2±0,7	31	67,7	1,3±1,6
Adult	29	89,8	8,0±10,5	31	48,4	0,7±0,9	112	7,2**	0,2±0,8	52	55,8	1,8±4,7
Juvenile	7	85,7	26,9±35,5	17	47,1	0,9±1,7	41	41,4**	0,7±1,0	23	65,2	2,7±4,8
Nematodes												
Male	28	92,9	14,6±27,9	30	60,0	2,5±3,4	79	78,5	7,9±12,1	44	65,9	6,9±11,5
Female	8	100,0	21,4±31,6	18	80,0	1,3±1,9	74	85,1	10,9±19,1	31	64,5	2,8±3,7
Adult	29	93,3	15,7±27,3	31	61,3	2,5±3,2	112	80,4	7,7±12,7	52	69,2	5,7±10,5
Juvenile	7	100,0	18,0±35,1	17	41,2	1,4±2,3	41	85,4	13,7±22,0	23	56,5	3,9±5,7

** P<0,01; Fisher's exact test.

There were no significant correlations between worm burdens and body mass (P > 0,05) in males and females (Table 7.3), nor between length of small intestine and cestode loads (r = -0,16; P = 0,55) or nematode loads (r = 0,03; P = 0,91), for the winter months (May-July). Neither were there any significant correlations between mean worm burdens and Greywing population density in males and females (range = 7,55-19,23 birds per km^2; n = 10 populations) for the same period (P > 0,05).

Table 7.3. Comparison between sex-related worm burdens and body mass for adult Greywing Francolin collected during May-July.

	n	Mass $\bar{x}\pm SD$	Cestodes $\bar{x}\pm SD$	r	P	Nematodes $\bar{x}\pm SD$	r	P
Male	69	460,3±26,8*	0,26±1,04	-0,06	0,64	7,99±12,70	-0,06	0,61
Female	43	424,5±22,0*	0,05±0,21	-0,25	0,11	7,23±12,84	-0,04	0,79

*P<0,001; t-test.

DISCUSSION

Intestinal helminth communities in Greywing are partitioned similarly to those in Helmeted Guineafowl, Numida meleagris, (Crowe 1977) and Bobwhite Quail, Colinus virginianus (Moore & Simberloff 1990), whereby cestodes are confined to the small intestine and nematodes inhabit the caeca.

Although the mean prevalence of helminth infestation in Greywing is high (86,2%), this rate of infection is lower than the 100% prevalence of three species of helminths in the Bobwhite Quail (Kellogg & Prestwood 1968; Moore, Freehling, Horton & Simberloff 1987), and maximum prevalence of infestation in the Helmeted Guineafowl (99,5%, Crowe 1977; 100%, Vercruysse, Harris, Bray, Nagalo, Pangui & Gibson 1985).

Furthermore, mean worm burdens in Greywing are significantly lower than that of Red Grouse, Lagopus lagopus scoticus, (range = 2 032-8 996 Trichostrongylus tenuis/bird, Hudson 1986), and of Bobwhite Quail (range = 0-153 cestodes & 0-465 nematodes/bird, Kellogg & Prestwood 1968) and (mean = 98,1 helminths/bird, Moore & Simberloff 1990). However, Kellogg & Prestwood (1968) concluded that the prevalence and worm burdens were higher in

high density host populations, and Hudson (1986) showed that both parasite burdens and the effect of parasitism are density-dependent on the host population.

Therefore, we conclude that although worm burdens are relatively low in the Greywing, this species presently exists at relatively low densities, and therefore the high prevalence of infestation might indicate a potential increase in worm burdens if Greywing density become greater.

The seasonal peaks of helminth infestation are probably due to environmental influences on free-living stages, and/or different endo-habitat requirements of the parasites. The summer peak in cestodes is probably related to the switch in feeding behaviour from underground storage organs of plants in winter to arthropods in summer (Mentis & Bigalke 1980; Little & Crowe in review; Chapters 3 & 6), because the life cycle of cestodes involves an intermediate host. The two peaks in caecal nematodes cannot be explained.

The peaks in helminth infestation have potential biological implications on the well-being of Greywing. Cestodes peak during November-December, coinciding with the peak breeding season of the Greywing (Little & Crowe in press a; Chapter 3), and therefore could influence body condition, reproductive capacity and predator evasion of breeding birds. Nematodes peak during June-July, when Greywing are at their highest population densities, immediately before the socially induced annual population decline (Mentis & Bigalke 1980). Therefore, helminth infestation might already be density-dependent, and contributing to regulation of populations in high Greywing density areas.

Moore et al. (1987) attributed the apparent independence of

host-sex, and occasional bias in host-age to prevalence and worm numbers to the social behaviour of seasonally gregarious Bobwhites, which form mixed-sex, and mixed-age coveys, and therefore are assumed to be equally exposed to parasite propagules. Greywing behave similarly, forming mixed age and sex coveys soon after breeding and remaining in these social groups until the onset of the breeding season (Mentis & Bigalke 1980; Little & Crowe in press a; Chapter 3). Furthermore, chicks of precocial phasianids, including Greywing, develop rapidly and start independent foraging away from the nest-site within their first day of life (Little & Crowe in press b; Chapter 4), thus being exposed to parasites from a significantly earlier age than that of altricial species. Therefore, we assume that Greywing are also equally exposed to parasite propagules, irrespective of age or sex. However, various authors, including Crowe (1977) suggest that higher burdens in juvenile gamebirds than in adults might be attributed to lower resistance to infection in younger birds.

Crowe (1977) concluded that the lack of gross pathological conditions in Guineafowl infested with helminths indicates that infection is at a tolerable level. We also found no sign of pathological condition, and furthermore, found no significant correlations between Greywing body mass or small intestine length. The apparent lack of significant correlation between helminth burdens and Greywing population density might be due to the buffering effect of a broad range of definitive hosts in the study area, as was suggested for two species of helminths (Aproctella stoddardi and Dispharynx nasuta) in populations of

Bobwhite Quail (Davidson, Kellogg, Doster & Moore 1991). However, high overall prevalence of infestation, and timing of seasonal peaks in both cestode and nematode infestation, particularly during the laying season of the Greywing (August-November, Little & Crowe in press a; Chapter 3) and pose potential threats to Greywing populations.

CHAPTER 8

HAEMATOZOAN PARASITES

Status: (1) 1991. Occurrence of Plasmodium juxtanucleare in Greywing Francolin. S. Afr. J. Wildl. Res. 21:30-32. co-authors: G.F. Bennett, R.A. Earlé & F.W. Huchzermeyer.

(2) in press. Haematozoa of Greywing Francolin Francolinus africanus from the Stormberg, eastern Cape Province, South Africa. S. Afr. J. Wildl. Res. co-authors: T.M. Crowe & R.A. Earlé.

(3) in review. Mortality caused by histomoniasis in young Greywing Francolin. S. Afr. J. Wildl. Res. co-authors: T.M. Crowe, R.A. Earlé & F.W. Huchzermeyer.

SUMMARY

We examined blood smears collected from 251 Greywing Francolin, Francolinus africanus, from the Stormberg Plateau, eastern Cape Province, during January-December 1990. The monthly infection rate of Greywing Francolin by blood parasites averaged 37,8% (95/251; range = 27,9 - 63,6). Microfilariae, Plasmodium juxtanucleare, Leucocytozoon macleani and L. peaolopesi were the commonest of eight haematozoan parasites recorded. Adult Greywing Francolin had higher prevalence of blood parasites (54%) than juveniles (<1 year old; 21%). P. juxtanucleare might

contribute to mortality rates of Greywing Francolin. Infection by L. macleani and L. peaolopesi were distinct temporally. Peak prevalence of Leucocytozoon spp. appeared to be related to timing of annual rainfall because of the dependence of their vectors on running water for breeding. Levels of haematozoan infection in Greywing Francolin are not sufficiently high to have macroscopically visible effects on the quality of the meat of this important gamebird.

INTRODUCTION

Although most blood parasites hosted by wild populations of birds are largely regarded as benign, some species such as Leucocytozoon simondi have long been known to cause high mortalities in anatids (Chernin 1952; Kocan 1968; Bennet et al. 1976). Furthermore, Markus (1974) supported earlier suggestions by Warner (1968) and Rowan (1971) that arthropod-borne disease is a possible factor limiting the distributions of birds. Recent evidence has shown that a variety of haematozoan microparasites can have detrimental effects on their hosts, both under intensive conditions such as in aviaries and in wild populations (Gardiner, Jenkins & Mahoney 1984; Atkinson & Forrester 1987; Simpson 1991; Earlé, Bastianello, Bennett & Krecek 1992). Because the tissue infection by these parasites (in particular Haemoproteus sp.) can cause extensive muscle necrosis in the vertebrate host (Becker 1959), and because high parasitaemia by Plasmodium sp. and Aegyptianella sp. is expected to cause anaemia, it is undesirable for gamebirds to host pathogenic levels of these parasites. Under such conditions, general body condition of the host and especially the quality of meat can be affected seriously.

The prevalence of blood parasites in southern African gamebirds is poorly known (Earlé, Horak, Huchzermeyer, Bennett, Braack & Penzhorn 1991). Individuals from only three species, Greywing Francolin Francolinus africanus, Swainson's Francolin F. swainsonii and Helmeted Guineafowl Numida meleagris, have been examined in fair numbers (Bennett, Earlé, du Toit, Hester & Huchzermeyer 1992). Of these, only in the Helmeted Guineafowl were the data spread over a 12-month period to give some

indication of seasonal variation in the occurrence of the parasites (Earlé et al. 1991).

The aims of this study were, 1) to determine which blood parasites occurred in populations of Greywing Francolin on the Stormberg Plateau, eastern Cape Province, 2) to describe and explain seasonal variation in the abundance of these parasites and their dependence on sex and age classes in these francolin populations, and 3) to determine the potential influence of parasitaemia on Greywing Francolin populations, and on the quality of this species as a gamebird.

MATERIALS AND METHODS

We collected 251 blood smears from Greywing Francolin during January-December 1990. Blood was obtained from the hearts of freshly shot birds. The blood smears were air-dried and fixed with absolute methanol before being stained with 4% Giemsa solution for 50 minutes. Smears were examined microscopically and the blood parasites identified. The severity of each infection was quantified by counting the number of specific parasites and expressed as totals per 100 fields at either 200 (for microfilariae, Leucocytozoon and Trypanosoma) or 1 000 magnification (for all other parasites). Sex was determined by examination of the gonads, and age by inspection of the stage of moult of the tenth primary (adult = >1 year; Little & Crowe in press b; Chapter 4). Prevalence and intensity of infection were compared temporally, and with annual rainfall. Rainfall data were extracted from the Agro Climatic Reports (Anon. 1885-1990).

RESULTS

The prevalence of haematozoan parasites in the blood of Greywing Francolin ranged between 27,9% in April and 63,6% in February with an overall rate of 37,8%. Infected birds hosted on average 1,3 parasite species per individual (SD = 0,6), with 76% of infected birds hosting a single parasite species, 20% with two species, 3% with three species and only 1% with four species. Eight haematozoan parasites were identified (Table 8.1) of which four were common and the others occurred less frequently. Microfilariae were the most frequently seen parasites, followed by *Plasmodium juxtanucleare*, *Leucocytozoon macleani*, and *L. peaolopesi*. *Aegyptianella* sp., *Trypanosoma avium*, *Leucocytozoon* sp. and *Hepatozoon* sp. were recorded infrequently (Table 8.1). Adult Greywing had higher prevalence of blood parasites (54%) than juveniles (<1 year old; 21%).

Table 8.1. Prevalence of avian haematozoa in 251 Greywing Francolin examined from the Stormberg Plateau, eastern Cape.

Parasite species	No. of birds infected	% of birds infected	% of infected birds
Aegyptianella sp.	8	3,2	8,4
Hepatozoon sp.	1	0,4	1,1
Leucocytozoon macleani	28	11,2	29,5
Leucocytozoon peaolopesi	17	6,8	17,9
Leucocytozoon sp.	4	1,6	4,2
Microfilariae	40	15,9	42,1
Plasmodium juxtanucleare	28	11,2	29,5
Trypanosoma avium	6	2,4	6,3

Although P. juxtanucleare and microfilariae infected the birds throughout the year, few juvenile birds were parasitized by these species. Larger numbers of microfilariae were present during summer than during the rest of the year (March-August; Fig. 8.1).

The occurrence of L. macleani and L. peaolopesi was temporally distinct, with neither species being recorded during October-December (Fig. 8.1). Parasitism intensities for the four most commonly encountered parasites were calculated and expressed as the number of parasites per 50 000 erythrocytes (Fig. 8.1).

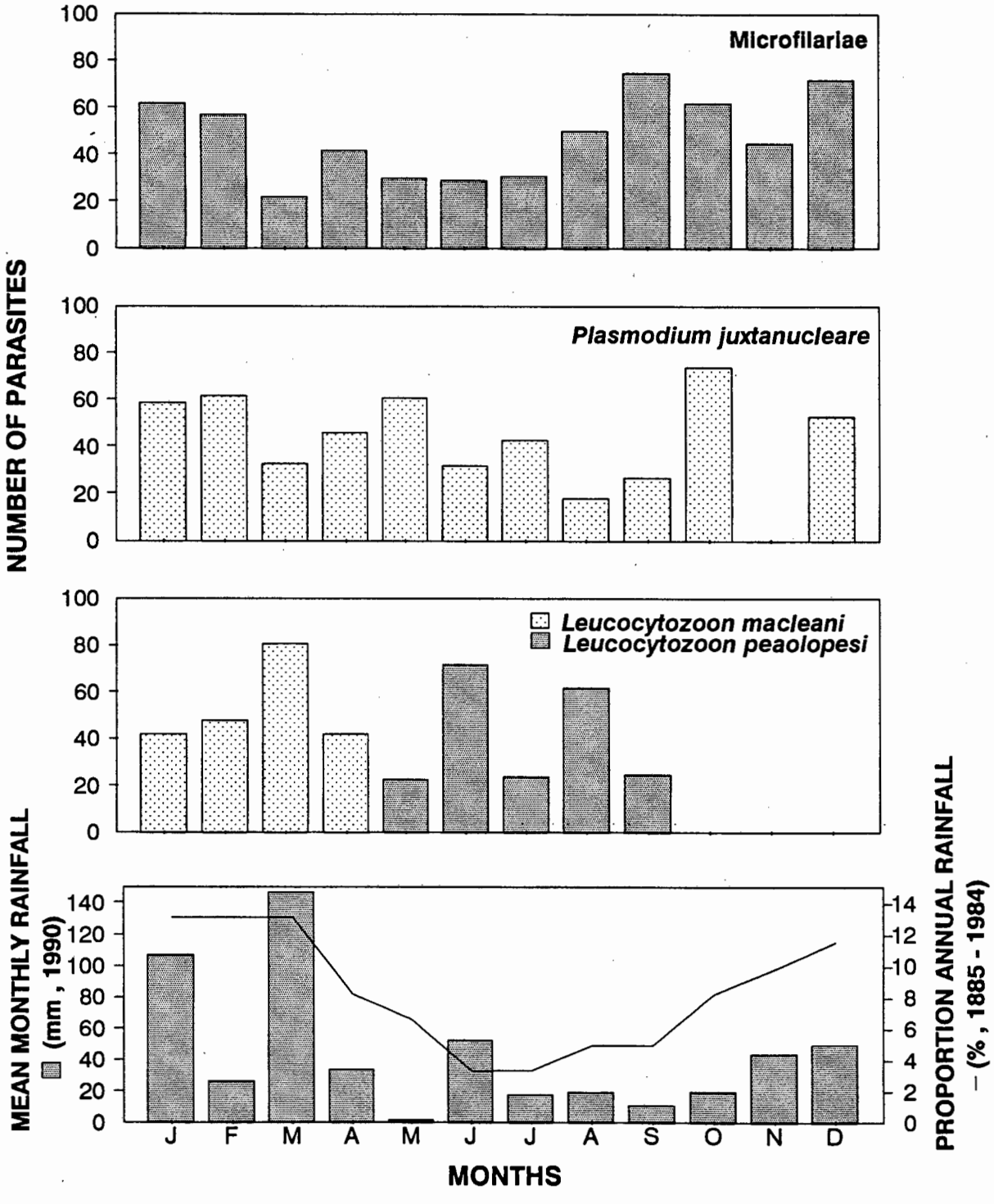


Figure 8.1. Fluctuations in infections of microfilariae, *Plasmodium juxtanucleare, Leucocytozoon macleani* and *L. peaolopesi* in Greywing Francolin from the Stormberg, during 1990 in relation to rainfall. Number of parasites = intensity per 50 000 erythrocytes.

DISCUSSION

The overall prevalence of avian haematozoa in Greywing Francolin is low compared with infestation levels in Helmeted Guineafowl (86%; Earlé et al. 1991) and in northern hemisphere anatids (76%; Bennett, Stotts & Bateman 1991). Reasons for this might be a combination of relatively low rainfall ($\bar{x}$ = 542 mm/annum) and cold winters (regularly below -10°C), on the Stormberg, which might reduce numbers of vectors.

Although P. juxtanucleare, which causes avian malaria, is transmitted by culicine mosquitoes, which are probably seasonal in occurrence, most of the infections by this haematozoan parasite were chronic and any indication of seasonality would be clouded. This species is said to be a severe pathogen (Becker 1959), and might contribute to Greywing mortality rates. However, Earlé, Huchzermeyer, Bennett & Little (1991) suggested that the South African strain, parasitizing the Greywing, does not pose a threat to domestic poultry.

Although recorded infrequently in this study, the detection of Aegyptianella sp. in Greywing Francolin is noteworthy. Only two species of avian Aegyptianella are known, both occurring in gallinaceous birds (domestic chickens Gallus gallus and Helmeted Guineafowl) in South Africa (Huchzermeyer et al. 1991). It is possible that the species found in the Greywing is a new species, but insufficient blood was collected during this study for isolation and further investigation of the taxonomy of this parasite.

Although microfilariae are also vector-dependent for transmission, and prevalence is a function of availability of

vectors, duration of infection or infestation, and/or persistence of detectable parasitaemia, little is known about the life cycle of these parasites. However, they possibly have an extended period of infection after transmission, and therefore are not seasonally dependent on time of infection, and thus occur throughout the year in the host. The apparently low prevalence of these worms in juvenile Greywing may be due to the time delay necessary for development within host tissue.

The striking feature of the prevalence of blood parasites in Greywing Francolin is that three Leucocytozoon species were recorded, and that the infestations by L. macleani and of L. peaolopesi were temporally distinct. Threlfall & Bennett (1989) reported that Leucocytozoon spp. appear to be host-family specific, with only one species usually being found in a host family. The separation in the timing of transmission suggests that these two parasites are transmitted by different species of blood sucking flies of the genus Simulium (black flies), the only known vectors of Leucocytozoon (Becker 1959; Bennett et al. 1992). The biology of these vectors, and the dependence of Greywing on open water, are poorly known. Nevertheless, it seems probable that L. macleani is transmitted by a Simulium sp. which breeds in running water during the summer months, when temporary fast flowing streams, charged by summer rainfall, are abundant and the parasite is transmitted by the adult flies from late summer to autumn (Fig. 8.1). During the colder, drier months of the year (i.e. when mean monthly rainfall is less than 8% of the annual precipitation) L. peaolopesi is probably transmitted by another Simulium sp. which breeds in the more permanent streams,

and the birds thus show infection by this species during winter. The absence of Leucocytozoon spp. during October-December is probably the result of low numbers or even the absence of suitable vectors (e.g. black flies) during these months. A reason for this might be high between-year fluctuations in the timing of rainfall (i.e. low predictability) during this period, which also affects the timing of breeding of the Greywing (Little & Crowe in press a; Chapter 3). The peak prevalence of Leucocytozoon spp. therefore seems to be associated primarily with timing of annual rainfall rather than with season per se (Earlé, Bennett, du Toit, de Swardt & Herholdt 1991).

High infection rates by Leucocytozoon spp. were recorded during winter (May-August), which includes most of the hunting season of the Greywing in this region (1 April-15 July; Anon. 1989). However, levels of Leucocytozoon infection are not sufficiently high to have any macroscopically visible effects (e.g. anaemia, splenomegaly or liver degeneration; Fallis, Davies & Vickers 1951), on the quality of the meat or liver to make it unacceptable to the hunter.

SECTION FOUR

HUNTING STRATEGIES AND SUSTAINABLE YIELD

CHAPTER 9

HUNTING EFFICIENCY AND HUNTING IMPACT

Status: in review. Hunting efficiency and the impact of hunting on Greywing Francolin populations. S. Afr. J. Wildl. Res. co-author: T.M. Crowe.

SUMMARY

Despite the Greywing Francolin's Francolinus africanus popularity as a gamebird, the effects of hunting on standing densities and long-term yields are not well documented. We recorded hunting effort, hunting efficiency and the impact of hunting on Greywing Francolin populations during 123 hunts conducted on various farms situated on the Stormberg Plateau during 1988-1991. Between-year variation in hunting effort and hunter skill was not significant. Hunter satisfaction was significantly positively correlated with the number of Greywing seen, and with hunter group size. Hunter skill was also significantly negatively correlated with hunter group size. There was no significant difference between removal levels with various hunting limits. However, populations from which more than 50% of the standing density was removed were significantly reduced in the year following the hunt. We conclude that, for sustainable, economically viable hunting, groups of between four and seven hunters should be offered between 50-65 Greywing Francolin per hunt, and that these populations be hunted only once per season, with hunters removing no more than 50% of a covey.

INTRODUCTION

Utilization of gamebirds by humans occurs in two major forms: subsistence and sport. Both forms have occurred and still occur in South Africa (Dixon 1978; Brooke 1987). Early in this century, large numbers of gamebirds were sold at markets, presumably for household use (Horsbrugh 1912).

Despite the Greywing Francolin's Francolinus africanus traditional and continued popularity as a gamebird (Gilfillan 1908, Horsbrugh 1912, Johnson & Wannenburgh 1987), the effects of varying intensities of hunting on standing densities and long-term yields are not well documented. Mentis & Bigalke (1985a) reported that populations of Greywing and Redwing F. levaillantii Francolins within state land in highland Natal could provide sustained hunting. They suggested that hunting intensity could be limited by restricting the number of hunters and dogs per hunting party, by controlling the duration of a hunt, and by allocating each party more land than can be hunted thoroughly with the resources at hand. More specifically, they reported that maxima of one day, three hunters and three dogs per party on a minimum of 400 ha did not decrease the density of francolin in the year following hunting.

Little et al. (in review; Chapter 10) found that, although a pulse of local immigration followed hunting, which apparently results in relatively fewer migrants in unhunted populations, the effect of hunting at present levels of offtake (40-50% of the population) on Greywing Francolin populations has no apparent long-term impact on their genetic structure.

The objectives of this study are to define a harvest strategy appropriate for the Greywing Francolin, and to assess the impact of varying intensities of hunting on standing densities and long-term yields.

METHODS

We recorded hunting effort, hunting efficiency and the impact of hunting on Greywing Francolin populations during 123 commercial hunts conducted on various farms situated on the Stormberg Plateau (31°15'S; 26°30'E), eastern Cape Province, South Africa, during 1988-1991. Hunting was done in the traditional fashion, with hunters (2-7) forming a line, and pointing dogs (2-6) ranging ahead. When a covey was located, the hunters approached the pointing dogs and the nearest hunter to the dog on point flushed the covey. Coveys were re-flushed, and shot at repeatedly, attempting to bag specific removal levels. Time spent hunting was recorded to the nearest minute, excluding breaks when dogs and hunters were inactive.

The number of birds per covey, number of shots fired (including 0 shots) and number of birds killed (including 0 killed) or lost were recorded at each flush occasion. Lost birds were birds either killed, or visibly hit by the shot, and not retrieved. The number of lost birds per hunt was included in the calculations of minutes per kill, shots per kill and percentage kill, but were excluded from the calculation of birds bagged.

Hunt routes were designed so that birds were not shot over the same ground within one day, and careful note was made of covey movements to prevent re-shooting of the same covey after the

prescribed removal level was achieved. Before the start of each hunt, hunters were informed of the intended offtake according to two removal levels: (1) shooting halted after 50% of the covey was shot, and (2) no limit. Hunts were held only once over each area of ground per season (year). However, during 1989, two areas were hunted twice each, with no bag limit.

The number of shots fired was not recorded during 1991, and all hunts during that year were limited to removal level 1 (shooting halted after 50% of the covey was shot). Furthermore, bird numbers were lowest during that year (see Results). For these reasons, data from 1991 were used for between-year analyses only.

RESULTS

Between-year variation in hunting effort (number of hunters and time spent hunting) per hunt was not significant, except for significantly fewer hunters per hunting group during 1988 than during 1989 (Table 9.1). Furthermore, the skill of the hunters (shots per kill) was not significantly different throughout the study period (Table 9.1). The number of hunters per hunting group was positively correlated with the mean number of shots fired per kill ($r = 0,96$; $P = 0,009$). However, the number of shots fired per hunter and the number of birds bagged per hunter were inversely related to hunter group size ($r = -0,97$; $P = 0,006$ & $r = -0,85$; $P = 0,03$ respectively) (Fig. 9.1).

Table 9.1. Mean hunting effort and hunting efficiency per hunt (±1 standard deviation) for 123 Greywing Francolin hunts during 1988-1991.

	Year							
	1988	P	1989	P	1990	P	1991	P
n	15		26		39		43	
Hunters	4,3±1,1	**	5,5±1,1	**	5,0±1,3		4,9±1,3	
Time	345,9±38,8		346,3±30,0		346,9±65,9		358,4±57,5	
Coveys	11,0±4,0	**	10,3±2,7	**	8,0±3,1	**	8,8±3,8	
Birds	75,9±25,5	*	81,3±26,0	**	60,7±24,5	** *	59,8±28,2	**
Shots	80,5±26,3	*	104,0±28,6	*	79,5±39,2[a]	*	nd	
Bag	27,9±10,0	**	31,9±11,2	*** **	24,2±10,8	** *	18,6±9,4	*** ** *
Birds/minute	0,22±0,07	** *	0,23±0,08	*** **	0,18±0,06	** *	0,16±0,07	*** **
Time/kill	13,5±5,4	**	11,4±3,5	*** **	15,7±7,0	** **	23,1±12,7	*** ** **
Shots/kill	2,9±0,6		3,2±0,8		3,0±1,0[a]		nd	
Bag/hunter	7,3±4,3	*** *	5,8±1,7	***	5,0±2,3	* *	3,9±1,9	*** *
Percent kill	38,3±5,0		41,9±8,9	***	42,5±7,8	***	33,4±9,0	*** ***

*P<0,05, **P<0,01, ***P<0,001; t-test.
Time/kill & shots/kill include lost birds.
Bag & bag/hunter exclude lost birds.
[a]sample size=22 hunts, not 39.
nd=no data.

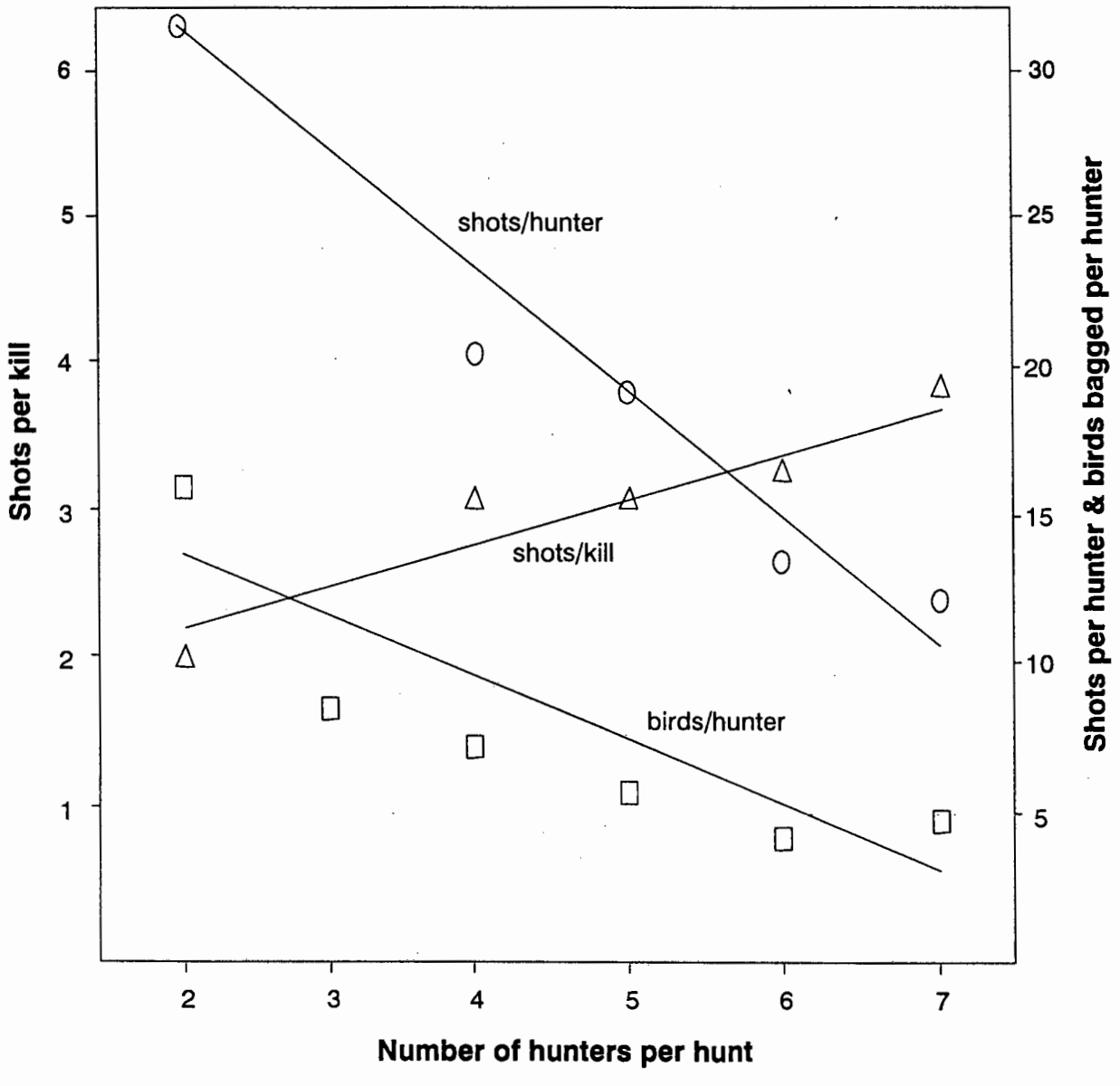


Figure 9.1. Comparison of hunter efficiency (shots fired per kill) and hunter satisfaction (shots fired per hunter and birds bagged per hunter) for various hunting group sizes.

The numbers of birds (and coveys) located, and thus birds per minute, differed significantly between years, with highest bird numbers recorded during 1989 and lowest numbers during 1991 (Table 9.1). Hunter satisfaction (number of shots fired and number of birds bagged) per hunt was significantly positively correlated with the number of Greywing seen ($r = 0,79$ & $0,82$ respectively; $P < 0,001$; $n = 63$ hunts), and the time per kill was significantly negatively correlated with the number of Greywing seen ($r = -0,72$; $P < 0,001$; $n = 63$ hunts).

The impact of hunting on standing densities (percent kill) was significantly greater during the two years of high population density (1989 & 1990) than during the year of lowest Greywing density (1991) (Table 9.1), but was not significantly correlated with the number of Greywing seen per hunt ($r = -0,17$; $P = 0,20$; $n = 63$). Moreover, there was no significant difference between removal levels when hunting was limited to removal of no more than 50% of a covey ($\bar{x}=41,6$; $SD=7,7$; $n=46$ hunts) and when no limit was placed on the hunting ($\bar{x}=41,5$; $SD=8,1$; $n=34$ hunts), during the hunting seasons of 1988-1990 ($P>0,05$; t-test). The two areas that were hunted twice during 1989 resulted in offtake levels of 54,2% and 56,6%. The proportion of lost birds ranged from 4,1% (18 lost from 436 hit) in 1988 to 7,0% (60 lost from 858 hit) in 1991, and averaged 5,4% (176 lost from 3 165 hit) for the four years.

Most coveys (59%) were flushed between two and four times, while 13% of all coveys were flushed once only and 28% were flushed more than four times during a hunt (Fig. 9.2). Coveys flushed more than six times per hunt were relatively large coveys (8-15 birds per covey). There was no significant difference

between the number of times a covey was re-flushed during limited hunting compared with non-limited hunting ($P > 0,05$; t-test).

Most coveys (61%) escaped without mortality on the first flush, and the maximum number of birds killed on the first flush was three (Fig. 9.2). However, at least one bird was bagged on 51% of re-flushes, and four birds were killed on one re-flush occasion (Fig. 9.2). Only 9,7% of all coveys (n = 165 coveys) escaped without any member of the covey being bagged during the hunt.

There was no significant difference between estimates of population density during the hunt and those of the following year at removal levels less than 50% ($P > 0,05$; t-test; n = 25 populations). However, populations from which more than 50% of the standing density were removed were significantly reduced in density in the year following the hunt ($P = 0,04$; t-test; n = 7 populations) (Table 9.2).

Table 9.2. Response of Greywing Francolin populations in the year after hunting (D_{i+1}) to removal at three levels during the year of hunting (D_i).

Removal levels	Response to hunting D_i	D_{i+1}	P	n
<40%	0,223±0,06	0,218±0,08	0,85	15
40-50%	0,216±0,05	0,198±0,06	0,45	10
>50%	0,255±0,11	0,158±0,03	0,04	7

D=estimate of abundance - birds/minute ±1 standard deviation.
P=significance level; t-test.
n=number of populations censused in year D_i and in year D_{i+1}.

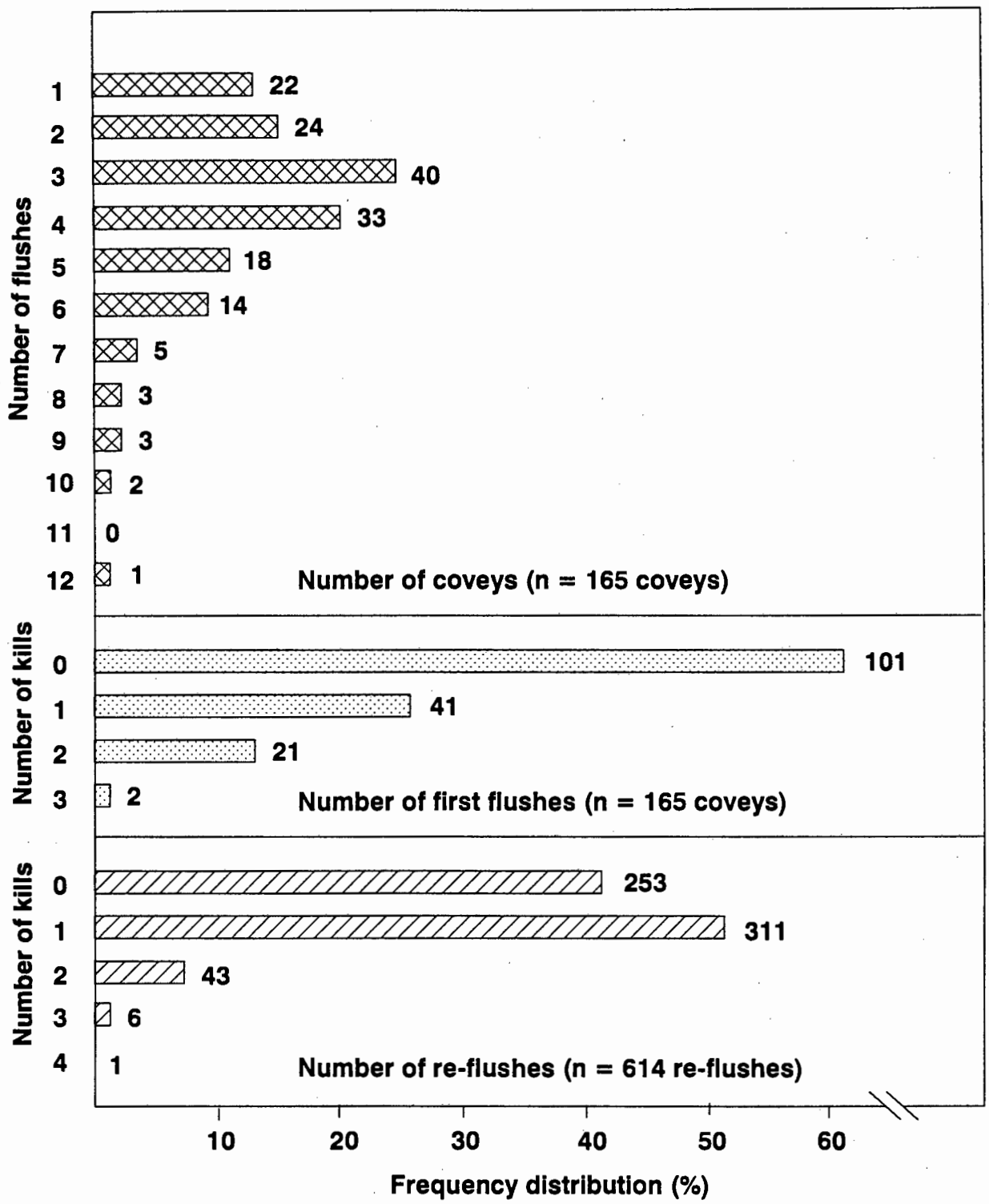


Figure 9.2. Frequency distribution of the number of times that coveys were flushed (cross-hatched bars), the number of birds killed at the initial flush of a covey (stippled bars) and the number of birds killed at each re-flush occasion (hatched bars).

DISCUSSION

The lack of between-year variation in hunting effort was a result of market forces rather than of experimental design. Experience has shown that hunting group sizes of between five and eight hunters satisfies the economic sustainability of commercial Greywing Francolin hunting (C.J. Broster, pers. comm.). While smaller groups may be more efficient, and thus more satisfied with the hunt, they pay a lower gross remuneration for the hunt. However, larger groups offer a greater reward, and although such groups have relatively lower hunting efficiency, they usually prefer the larger group size for social reasons.

While hunter-group size determines the gross socio-economics of the industry, the number of Greywing offered during the hunt determines the overall economic viability of the operation. The minimum bag size required for an economically viable hunt (i.e. hunter satisfaction) is between 20 and 25 birds per day (R.M. Little unpubl. data). With a mean percentage kill of about 40% per hunt, 50-63 Greywing per hunt must be available to the hunters.

Although limiting the offtake level did not result in a significantly lower removal rate, removal of more than 50% of the population (irrespective of limitation on hunting) resulted in a significant reduction of the population in the year following hunting. This is explained by the Greywing's apparently evasive escape behaviour. Few kills were made on the initial flush, presumably because of coveys flushing out-of-range of shooting or because hunters missed their quarry due to the uncertainty of where the birds would flush from. However, re-flushing resulted

in only 9,7% of all coveys escaping without loss. This increased mortality rate during re-flushes is probably due to birds sitting tighter and thus flushing within shooting range, and because hunters can personally mark the sites where birds land and thus anticipate the flush with more precision. However, allowing hunters no limit on their bag did not result in significantly more flush occasions. We therefore conclude that whatever the hunting effort, Greywing will evade most hunters after five to six re-flushes. However, the occasions when more than 50% of the population was killed were all recorded during non-limited hunts. Therefore, the possibility exists, on occasion, for over-hunting if uncontrolled.

Conclusions

1. At present market standards, socio-economic forces require that hunting groups of between four and seven hunters be offered between 50-65 Greywing Francolin per hunt for economically viable hunting.
2. For sustainable yield we suggest that populations of Greywing Francolin be hunted only once per season (year), and that hunters be allowed to remove no more than 50% of a covey.

CHAPTER 10

HUNTING IMPACT ON POPULATION AND GENETIC STRUCTURE

Status: in review. Does hunting affect the population and genetic structure of the Greywing Francolin Francolinus africanus? Cons. Biol. co-authors: W.S. Grant & T.M. Crowe.

SUMMARY

We studied hunted and unhunted populations of Greywing Francolin, Francolinus africanus, in the eastern Cape Province of South Africa to understand the effects of hunting on population and genetic structure. Greywing population density cycled annually for both hunted and unhunted populations. However, there was an apparent 'pulse' of immigration, and earlier reproduction, in the hunted populations immediately after the winter hunting season. Nevertheless, average levels of allozyme heterozygosity (H) for hunted and unhunted populations were both 0,076. Furthermore, the hunted populations displayed similar levels of outbreeding to those for unhunted populations. Therefore, although a 'pulse' of local immigration followed hunting, which apparently results in fewer immigrants in unhunted populations, we conclude that the effect of hunting at present levels of removal (40-50% of the population) on Greywing Francolin populations has no apparent long-term influence on their genetic structures.

INTRODUCTION

Previous researchers have measured the response of wild populations of game animals to hunting by comparing annual population dynamics with levels of annual removal (Mentis & Bigalke 1985a; Myrberget 1985b; Begon & Mortimer 1986). Although this approach can yield information on population size, age at maturity, mortality and age structure, it can not lead to an understanding of the genetic effects of hunting. Several studies have established that allozyme techniques can detect reductions in genetic diversity from the effects of man-made disturbances. For example, Baker & Moeed (1987) found that a reduction of mean number of alleles per locus and average heterozygosity was greatest in populations of introduced birds, and this was consistent with the theoretical predictions following founder effects. They concluded that, in the evolutionary short period of 100-120 years, bottlenecks and random drift have promoted genetic shifts equal to those between different subspecies of birds. Recently, Leberg (1991) used allozyme electrophoresis to determine that the genetic structure of populations of Wild Turkey, Meleagris gallopavo, which have undergone high levels of population fragmentation and bottlenecks as a consequence of anthropogenic activities, have higher levels of interpopulation differentiation than other birds. Furthermore, Ryman et al. (1981) concluded that the amount of genetic variation within populations can be reduced severely even within short periods of time as a result of improper hunting regimes. Their study emphasized that the switch from a natural to a man-influenced predatory regime changed the rates and patterns of gene flow

drastically. This influenced effective population size, and particularly, generation interval, which might be expected to lead to lower levels of genetic variability.

Because of their highly territorial and socially-structured behaviour (Crowe et al. 1986), the genetic structure of hunted and unhunted populations of francolin may differ. If gamebirds are hunted at levels which accelerate the loss of genetic variation within populations or increase the rate of gene flow between populations, we might expect to find significant differences in genetic heterogeneity between neighbouring populations of frequently hunted as compared to long unhunted populations. For example, if gene flow is significantly greater in hunted populations as a consequence of creating a larger than normal number of 'vacancies', genetic variation among these populations might decrease. If, however, hunting mimics natural annual mortality, i.e. removal of the annual surplus that would likely die from 'natural' causes anyway, then between-population gene flow should be similar in hunted and unhunted populations.

The Greywing Francolin, Francolinus africanus, has been hunted in the montane grasslands of eastern southern Africa for at least the past century (Gilfillan 1908). The Greywing is a highly prized gamebird (Mentis & Bigalke 1985a; Johnson & Wannenburgh 1987), and has been hunted commercially on the Stormberg Plateau ($31^{o}15'S$; $26^{o}30'E$) of the eastern Cape Province, South Africa, since 1982 (Little 1990). Mentis & Bigalke (1980) suggest that, because of the Greywing's high fecundity and natural decline in numbers before pairing in spring, this species can sustain annual hunting at about 50% of the autumn population. Furthermore,

based on studies of hunted populations of Greywing, Grant & Little (1992; Chapter 2) confirm that Greywing populations in the eastern Cape are subject to high rates of replacement, and random drift, and that the high rates of migration may buffer populations against local extinction.

In this study, we compare demography and genetic variation within and between hunted and unhunted populations of Greywing Francolin to test whether hunting has any affect on either aspect of this gamebird's biology. We show that, although both the levels of within-population heterozygosities and gene flow are the same in hunted and unhunted populations there are nonetheless differences in the population dynamics of these two groups.

STUDY AREA

We censused, and collected tissue from Greywing populations during 1988-1990 on the Stormberg Plateau in the eastern Cape Province of South Africa (31°15'S; 26° 0'E) (Fig. 10.1). The study area is livestock farmland, dominated by open montane grassland 1 700 m - 2 000 m above sea level. Rain falls seasonally, mainly during the austral summer (October-January), and averages 542 mm per annum (Anon. 1984).

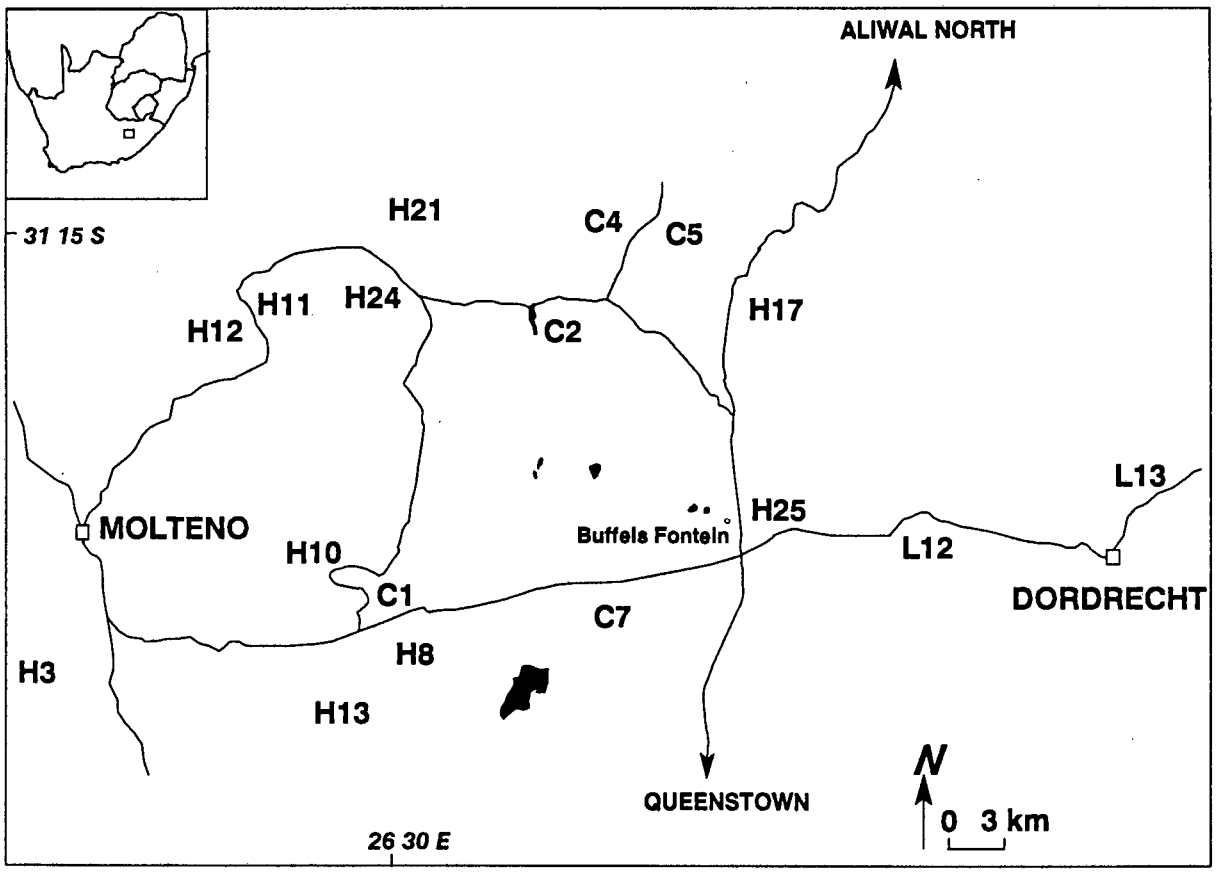


Figure 10.1. Locations of the study area, population census plots, and sampling sites used to compare variations in demography and genetic differentiation among hunted and unhunted populations of Greywing Francolin (H = hunted populations, C and L = unhunted populations).

METHODS

Population dynamics

We estimated the population densities of three regularly-hunted Greywing populations (H11, 13 and 17; Fig. 10.1) monthly, between January 1989 and December 1990, with pointing dogs and with the method of Mentis & Bigalke (1985b). During July 1988-December 1990, we estimated Greywing density for five historically-unhunted populations (C1, 2, 4, 5 and 7; Fig. 10.1). The hunted populations have each been shot once annually during the austral winter (May-July) since 1982. The average proportion of birds removed from the three populations in 1989 was 48,0% (SD = 12,3) and in 1990 was 45,6% (SD = 6,4). The number of hunters, number of Greywing seen and number of Greywing shot per hunt are listed in Table 10.1. We compared the population density curves visually and by correlation coefficient to quantify the trends.

Shot birds were sexed and aged during 1988-1991 for the hunted populations, and during 1990-1991 for the unhunted populations. Birds were sexed by inspection of the gonads, and aged by examination of the stage of moult of the remiges (Little & Crowe in press b; Chapter 4). We compared sex ratios and age-class frequencies for Greywing within hunted and unhunted populations using Fisher's exact test (Sokal & Rohlf 1981).

Table 10.1. The number of hunters, number of Greywing Francolin seen and number of birds removed for the three hunted populations which were censused during 1989 and 1990.

Year	Hunt	Number guns	Greywing seen	Greywing[1] shot	% removed
1989	H11	5	96	48+4	54,2
	H13	4	65	20+2	33,6
	H17	7	125	68+2	56,0
1990	H11	4	63	26	41,3
	H13	6	47	17+3	42,6
	H17	6	51	25+2	52,9

[1]Greywing shot = number of birds bagged plus number of birds shot but not retrieved.

Population genetics

We collected liver, heart and breast muscle tissue from 414 Greywings at 12 localities. Eight previously-hunted populations (H3, 8, 10, 11, 12, 21, 24 and 25; n = 208), and four historically-unhunted populations (C4, 5, L12 and 13; n = 145), were sampled during May-July of 1990 (Fig. 10.1). We resampled two of the historically-unhunted populations (C4 and L12; n = 61) during 1991. The previously-hunted populations had been hunted regularly for 3-10 years. On average 34,1% (SD = 5,1; 1988), 44,2% (SD = 11,5; 1989) and 42,1% (SD = 7,3; 1990) of the birds seen on a hunt were included in a sample. The historically-unhunted populations had not been hunted for at least the past 50 years.

Standard tissue collection and electrophoretic methods with 12% starch gels were used to assay allozyme variation at 31 protein-encoding loci (Grant & Little 1992; Chapter 2). We used the following isozymes (locus abbreviation and Enzyme Commission number) with heart [H], liver [L], or breast muscle [M] to resolve the gene products of 31 presumptive loci: aconitase (Aco-

1 [H]; 4.2.1.3), adenosine kinase (Ak [H]; 2.7.4.3), alcohol dehydrogenase (Adh [L]; 1.1.1.1), aspartate aminotransferase (Aat-1 [H], Aat-2 [H]; 2.6.1.1), creatine kinase (Ck-A [M], Ck-B [H]; 2.7.3.2), glucosephosphate isomerase (Gpi [H]; 5.3.1.9), glyceraldehydephosphate dehydrogenase (Gap-1 [M]; 1.2.1.12), glycerol-3-phosphate dehydrogenase (G3p-1 [M], G3p-2 [H]; 1.1.1.8), isocitrate dehydrogenase (Idh-A [H], Idh-B [L]; 1.1.1.42), lactate dehydrogenase (Ldh-A [M], Ldh-B [H]; 1.1.1.27), malate dehydrogenase (Mdh-A [M], Mdh-B [H]; 1.1.1.37), malic enzyme (Me [H]; 1.1.1.40), mannosephosphate isomerase (Mpi [H]; 5.3.1.8), nucleoside phosphorylase (Np [L]; 2.4.2.1), peptidases (Pep-A [H], Pep-B [L], Pep-C [L]; 3.4.11.-; Pep-D1, Pep-D2 [H]; 3.4.13.9), phosphoglucomutase (Pgm-1 [H], Pgm-2 [H]; 2.7.5.1), phosphogluconate dehydrogenase (Pgd-1, Pgd-2 [H]; 1.1.1.44), sorbitol dehydrogenase (Sdh [L]; 1.1.1.14), and superoxide dismustase (Sod [L]; 1.15.1.1).

We used the patterns of gene expression in related taxa and the presumed subunit structure of the isozymes as guidelines for interpreting gel-banding patterns. When evolutionary nomenclature for a locus could not be inferred from tissue expressions and substrate, we numbered multiple loci by the mobilities of their products, beginning with the most anodal isozyme. Alleles were designated by their electrophoretic mobilities relative to the most common allele, which was designated 100. We ran some phenotypes side-by-side on the same gel to distinguish between similar phenotypes in different samples.

We tested for allele-frequency differences at two nested levels: years and populations with a contingency-table analysis.

We used the G-test (Sokal & Rohlf 1981) and a two-way contingency-table analysis to test a null hypothesis of no frequency differences between years and among localities. Since tests were made for ten polymorphic loci, Aat-2, Mpi, Pep-A, Pep-B, Pep-C, Pep-D, Pgd, Pgm-1, Pgm-2 and Np, we used Cooper's (1968) modification to account for the increase in Type I error (rejecting a null hypothesis when it is true) with repeated tests of the same hypothesis. We used a rejection criterion that was associated with a probability of α/n, where n was the number of repeated tests (number of polymorphic loci). Thus, the overall probability of rejecting H_o by chance was

$$P = 1 - (1 - (0,05/n))^n \approx 0.05.$$

Agreement with Hardy-Weinberg proportions was assessed by F with Levene's (1949) correction for small samples, and by the log likelihood-ratio test (G-test) for goodness of fit (Sokal & Rohlf 1981). Because of small sample sizes, the genotypes for loci were pooled into three classes, AA, AX, and XX where A is the most common allele and X is any other allele, and retested. A departure was considered significant if both the unpooled and pooled tests were significant. Levene's correlation had the effect of increasing the apparent levels of inbreeding.

F_{IS}, the average F_{ISi} over all samples, F_{ST}, the standardized variance of allele frequencies among samples, and F_{IT}, inbreeding in the individual relative to the total population, were calculated for 21 independent alleles at 10 loci according to equations (1-4) in Weir & Cockerham (1984) and are related by

$$(1 - F_{IT}) = (1 - F_{IS})(1 - F_{ST}).$$

The null hypothesis, $F_{ST} = 0$, was tested for each allele with

$$\underline{X}^2 = 2\underline{N}\underline{F}_{ST}; \quad \underline{d}.\underline{f}. = \underline{n} - 1$$

(Workman & Niswander 1970). The null hypothesis, $\underline{F}_{IS} = 0$ was tested with

$$\underline{X}^2 = \underline{N}\underline{F}_{IS}^2; \quad \underline{d}.\underline{f}. = 1$$

(Li & Horvitz 1953), and the null hypothesis, $\underline{F}_{IT} = 0$ was tested with

$$\underline{t} = |\underline{F}_{IT}\sqrt{\underline{N}}|; \quad \underline{d}.\underline{f}. = \text{infinity}$$

(Brown 1970). Locus heterozygosities were estimated by calculating the expected proportions of heterozygotes with random mating, $\underline{h} = 1 - \Sigma p_i^2$, where p_i is the frequency of the $\underline{i}^{th}$ allele for a locus. Average sample heterozygosity, $\underline{H}$, is the mean over all loci including monomorphic loci.

We used two methods, which assumed the island model of migration (Wright 1951), to estimate migration among populations. First, we used

$$\underline{F}_{ST} \approx 1/(1 + 4\underline{N}\underline{m}).$$

to estimate the number of migrants $\underline{N}\underline{m}$ between populations. We calculated the number of migrants directly, $\underline{N}\underline{m}_i$, from the average $\underline{F}_{ST}$ over 21 alleles and indirectly, $\underline{N}\underline{m}_i{}^*$, with a jacknife procedure (Weir 1990) in which one allele at a time was dropped from the average of $\underline{F}_{ST}$. A 95% confidence interval was calculated from the variance of these estimates. Second, we used the average frequency of "private" alleles and the equation

$$\underline{N}\underline{m}_p = {}_{10}[\log_{10}(p(1) + 1{,}1/-0{,}58]$$

to estimate the number of migrants between populations, $\underline{N}\underline{m}_p$ (Slatkin & Barton 1989). We also calculated an indirect (jacknife) estimate, $\underline{N}\underline{m}_p{}^*$. These methods were used to estimate differences in the number of migrants, $\underline{N}\underline{m}$, between hunted and unhunted populations that successfully breed each generation.

RESULTS

Population dynamics

Annual Greywing population density cycled differently for regularly-hunted populations and for historically-unhunted populations ($r = 0,36$; $P > 0,11$; Fig. 10.2). Nevertheless, both sets of populations exhibited a post-breeding peak and a pre-breeding trough similar to that described by Mentis & Bigalke (1979, 1980) for Greywing from the Drakensberg in Natal. The major populational differences between hunted and unhunted populations were sharp decreases in the former during May-June in 1989 and during May and July in 1990. Indeed, when the immediate influence of hunting is excluded from the correlation (i.e. data for June-July 1989 and July-August 1990) the two curves are significantly positively correlated ($r = 0,65$; $P = 0,002$).

The other relatively minor difference between hunted and unhunted populations was that, in the former, the curve rose temporarily after hunting and then declined toward the annual trough (Fig. 10.2). Furthermore, in all three breeding seasons the hunted populations increased earlier than the unhunted populations (Fig. 10.2).

There was a consistent excess of males in all samples, but the ratio itself was not significantly different between years, or between hunted and unhunted populations within the same year ($P > 0,05$; two-tailed Fisher's exact test; Table 10.2). However, hunted populations contained a higher adult:juvenile ratio than unhunted populations during 1990 ($P = 0,014$; two-tailed Fisher's exact test; Table 10.2).

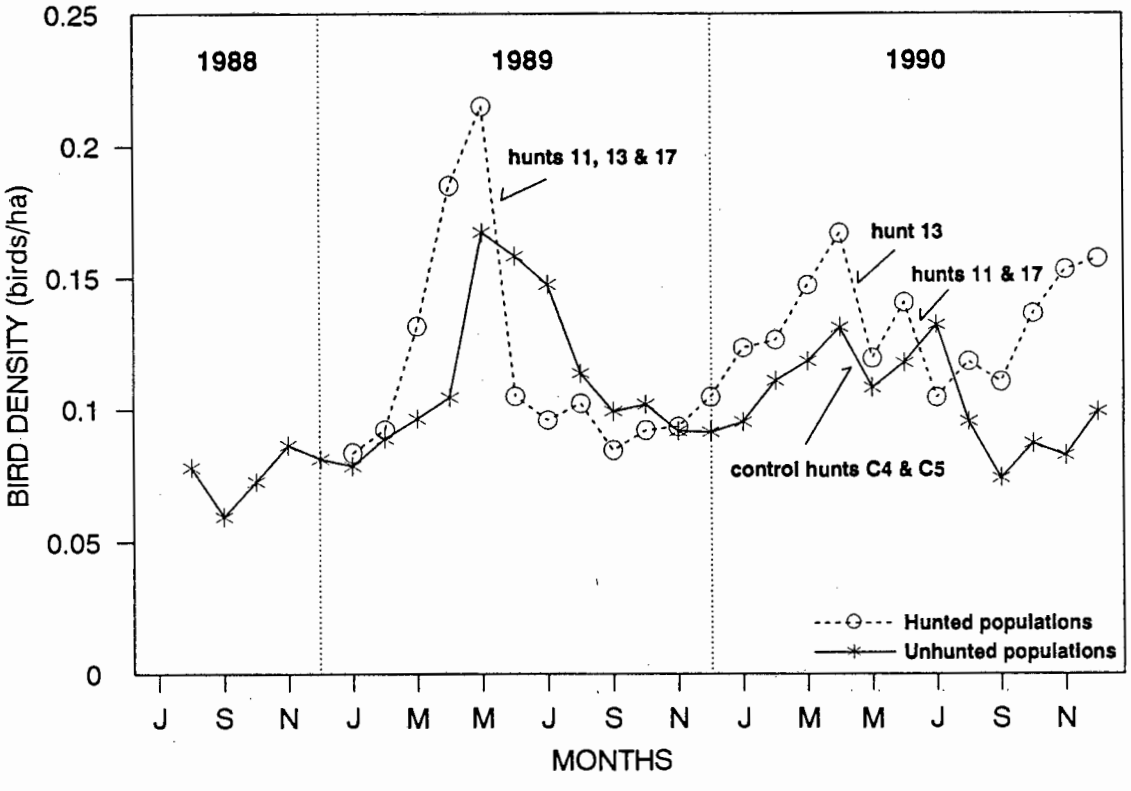


Figure 10.2. Population density curves for regularly hunted and historically unhunted Greywing Francolin populations.

Table 10.2. Variation in sex and age ratios between years and between hunted and unhunted population within years for Greywing Francolin. Mean (±1 standard deviation), total and ratio of males and adults are presented respective to females and juveniles (first-year birds).

Year	Hunted populations				Unhunted populations			
	Sex		Age		Sex		Age	
	male	female	adult	juvenile	male	female	adult	juvenile
1988								
$\bar{x}$	13,8±7,7	10,4±5,2	13,4±5,5	10,8±8,3				
total[1]	69,0	52,0	67,0	54,0				
ratio	1,33 : 1		1,24 : 1					
n[2]	5	5	5	5				
1989								
$\bar{x}$	14,4±5,4	13,8±4,8	16,1±4,2	12,0±4,8				
total	115,0	110,0	129,0	69,0				
ratio	1,04 : 1		1,34 : 1					
n	8	8	8	8				
1990								
$\bar{x}$	14,9±4,3	11,1±3,2	21,5±7,0	4,5±2,1	21,3±9,2	16,0±7,9	26,5±11,2	10,8±4,6
total	119,0	89,0	172,0	36,0*	85,0	64,0	106,0	43,0*
ratio	1,34 : 1		4,78 : 1		1,33 : 1		2,45 : 1	
n	8	8	8	8	4	4	4	4
1991								
$\bar{x}$	14,8±5,4	11,2±4,4			20,0±7,1	11,0±7,1	22,0±5,7	9,0±8,5
total	89,0	67,0			40,0	22,0	44,0	18,0
ratio	1,32 : 1				1,82 : 1		2,44 : 1	
n	6	6			2	2	2	2

[1] total = number of individuals collected.
[2] n = number of populations sampled.
* P<0,05, two-tailed Fisher's exact test.

Population genetics

Allelic frequencies of 17 polymorphic loci estimated for 12 localities are listed in Appendix 10.1. Of the 31 loci examined, 18 (58,1%) showed at least some polymorphism and 10 (32,3%) were polymorphic with the 0.95 common-allele-frequency criterion. Average heterozygosities for all loci (including monomorphic loci) for all 12 populations ranged from 0,052 to 0,093 and averaged 0,074 (SD = 0,022). A large proportion (95,9%) of the genetic variation was contained on average within samples, with

3,8% due to differences between populations, and only 0,3% due to differences between years in the hunted populations. The average heterozygosities for the eight previously-hunted populations ranged from 0,053 to 0,096 and averaged 0,076 (SD = 0,023), and for the six samples from historically-unhunted populations ranged from 0,066 to 0,087 and also averaged 0,076 (SD = 0,023). The proportion of genetic variation contained on average within samples was consistently high, both within the hunted populations (96,2%) and the unhunted populations (96,4%), with only 3,8% and 3,6% due to differences between populations, respectively. Three previously-hunted populations (H10, 11 and 24) and two historically-unhunted populations (C4 and 5) showed significant departures from Hardy-Weinberg proportions for at least one locus. These loci were Mpi, Np, Pep-A, Pgd-1 and Pgm-1.

Wright's F-statisticts (F_{ST}, F_{IS} and F_{IT} values) for 10 polymorphic loci are presented in Table 10.3 for 21 variable alleles. Values of F_{ST}, a measure of correlation of genes of different individuals in the same population ('coancestry'), varied from 0,016 to 0,054 and averaged 0,024 (eq. 10, Weir & Cockerham 1984). None of the 21 alleles showed significant geographical heterogeneity. Values of F_{IS}, the correlation of genes within individuals within populations ('inbreeding'), varied from -0,057 to 0,373 and averaged 0,035. Four alleles (Mpi^{100}, Pep-A^{100} and ^{120} and Pgd-1^{70}) showed significant overall deficits of heterozygotes within the populations sampled. Values of F_{IT}, correlation of genes within individuals relative to the total population, varied from -0,052 to 0,383 and averaged 0,058. The same four alleles which showed significant deficits of

heterozygotes also showed significant positive values of F_{IT}.

Wright's equation and F_{ST} gave estimates of Nm_i = 8,87 and Nm_i^* = 8,45 (95% C.I.: 8,27-8,63) for the hunted populations and Nm_i = 9,29 and Nm_i^* = 7,49 (95% C.I.: 7,04-7,94) for the unhunted populations. There were five private alleles in the samples from unhunted populations and eight alleles in samples from hunted areas. The "private"-alleles method of estimating migration rates yielded estimates of Nm_p = 7,34 and Nm_p^* = 7,20 (95% C.I.: 6,56-7,87) for the hunted populations, and Nm_p = 3,95 and Nm_p^* = 1,91 (95% C.I.: 0,0-3,96) for the unhunted populations.

Table 10.3. Wright's F-statistics for 10 polymorphic loci in Greywing Francolin. Statistics calculated according to equation (1) in Weir and Cockerham (1984).

Locus	Allele	Average frequency	SD[1]	F_{ST}	F_{IS}	F_{IT}
Aat-2	-100	0,71	0,086	0,029	-0,017	0,012
	-20	0,23	0,076	0,025	0,061	0,084
Mpi	100	0,91	0,063	0,039	0,234***	0,263**
Pep-A	100	0,96	0,036	0,026	0,227***	0,247**
	120	0,03	0,026	0,016	0,373***	0,383***
Pep-B	100	0,87	0,061	0,025	0,067	0,090
	80	0,08	0,034	0,009	-0,017	-0,008
Pep-C	80	0,03	0,027	0,020	0,071	0,089
	90	0,93	0,048	0,026	0,034	0,059
	100	0,03	0,020	0,008	-0,020	-0,012
Pep-D	100	0,77	0,065	0,017	-0,004	0,013
	115	0,14	0,067	0,029	-0,001	0,029
Pgd-1	100	0,76	0,095	0,042	0,038	0,078
	115	0,14	0,087	0,054	0,051	0,102
	70	0,07	0,045	0,022	0,138**	0,156*
Pgm-1	100	0,81	0,047	0,007	-0,033	-0,025
	85	0,15	0,039	0,005	-0,057	-0,052
	115	0,04	0,034	0,027	-0,031	-0,003
Pgm-2	100	0,96	0,034	0,024	0,034	0,057
	60	0,03	0,020	0,008	-0,017	-0,009
Np	70	0,91	0,034	0,007	0,069	0,075
Average over loci				0,024	0,035	0,058

[1] SD = standard deviation of allelic frequency.
*P<0,05, **P<0,01, ***P<0,001.

DISCUSSION

Population dynamics

The populational 'pulses' in Greywing numbers following either natural mortality or hunting, before the onset of the breeding season, indicate that there is a bout of immigration from neighboring populations. These 'pulses' were pronounced following earlier hunting of both hunted and previously unhunted populations during 1990. Ellison (1979 cited by Myrberget 1985b), suggested that, if hunting were concentrated within a relatively small part of a larger area, hunting losses might be compensated by immigration of younger birds during the following spring. A similar populational response might be expected in the Greywing, since there are high levels of natural replacement in Greywing populations due to immigration of first year birds into the population before the onset of the next breeding season (Mentis & Bigalke 1980). Therefore, the removal of adult birds by hunting appears to create 'vacancies', which are filled by less-dominant/younger birds immigrating from neighboring areas.

We expected a higher mortality of adult birds in hunted areas, because older birds tend to flush before young birds (Little 1989) thus presenting themselves to the hunters first. If these shot adults were replaced by young immigrant birds, it might be reasonable to expect lower adult:juvenile ratios in the hunted populations. However, sampling of the unhunted populations during 1990 followed a low reproductive season (i.e. higher adult:juvenile ratios, both in the hunted and unhunted populations than for the previous two seasons; $P < 0,001$; two-

tailed Fisher's exact test) and adult:juvenile ratios were significantly higher in the hunted populations than in the unhunted populations.

Unfortunately, reliable aging data were not available for the hunted populations during 1991, but the adult:juvenile ratios for the unhunted populations remained high. We therefore suggest that, in the Greywing, it is not necessarily a migration of young (first-year) birds into hunted populations, but possibly a movement of sub-dominant (adult and first-year) birds.

Whatever the case, it is reasonable to expect: (i) greater rates of replacement (immigration), and thus mixing of individuals, within the hunted populations, (ii) breeding pairs of adults to contribute less to future generations than those in unhunted populations, and (iii) higher average genetic heterozygosity within hunted populations.

The bias toward males in all populations is doubtfully a consequence of hunting. Firstly, because flushing sequence during the hunting season is not sex-biased (Mentis & Bigalke 1980; Little 1989). Secondly, because the male bias is probably due to predation on incubating hens (Little & Crowe in press a; Chapter 3).

Population genetics

Our first measure of genetic variation within populations is the estimation of the amount of within-population genetic variability. If hunted Greywing populations experience increased levels of gene flow as a result of increased immigration, it might be reasonable to expect that genetic variation among these populations might decrease. However, average heterozygosity of

the hunted populations is not lower than that of the unhunted populations, and is not significantly different from that of hunted populations of Greywing elsewhere (Grant & Little 1992; Chapter 2). This indicates that present levels of annual reduction in the populations by hunting (40-50% removal) does not affect the long-term effective population size of Greywing to any large extent. This confirms the conclusion of Grant & Little (1992; Chapter 2) that Stormberg subpopulations of Greywing act more or less as a single population extending over at least 1 500 km^2. Therefore, the relatively high electrophoretically-detectable genetic variability found in hunted populations of Greywing ($\underline{H}$ = 0,076) display the potential for these populations to buffer against deleterious effects of temporary, localized bottlenecks. Furthermore, the large effective population size might, like in the Willow Grouse (Lagopus lagopus lagopus) (Gyllensten 1985), mean that a reduction in 'local' effective population sizes would not necessarily cause a decrease in the amount of genetic variability. Although little is known about the effects of stochastic factors on changes in population size of Greywing, the similar proportions of genetic variation contained within populations to that found in Willow Grouse (0,95; Gyllensten 1985), and the low proportion due to difference between years compared to Willow Grouse (0,025; Gyllensten 1985) suggest that any temporal genetic variation in Greywing populations is less likely to be due to stochastic factors.

The $\underline{F}$-statistics for unhunted populations show general deficits of heterozygotes, similar to the findings of Grant & Little (1992; Chapter 2). This suggests that there are similar levels

of outbreeding in hunted and unhunted populations of Greywing.

The estimates of the number of migrants based upon F_{ST} between populations for the hunted and unhunted populations were similar. On average, 7-9 birds effectively migrated between populations each generation. This level of migration is high, considering the territorial behavior and average social unit (covey) size of eight individuals (Mentis & Bigalke 1980) of this species. However, these results are also similar to migration levels found by Grant & Little (1992; Chapter 2) for Greywing. The "private-allele" estimates of the number of migrants was, however, not similar for hunted and unhunted populations. The significantly fewer migrants among unhunted populations was anticipated, because temporary effects of hunting show a 'pulse' of immigration immediately after hunting, which was pronounced when hunting took place early in the hunting season. We suggest that this immigration rate is responsible for the greater movement into hunted populations in the short-term, but that overall natural levels of local extinction and re-colinization are sufficiently high to balance effects of genetic homogenization in the long-term.

Conclusions

We conclude that there is little between-population variation in the demography and genetics of hunted and unhunted Greywing Francolin populations, at present levels of hunting. Our explanation for this is three-fold: (i) Greywing populations on the Stormberg have inherently high effective population sizes, probably due to the high rates of migration, which effectively buffers them against the effects of temporary, local reductions

in population size. (ii) Hunting of this species using traditional methods (i.e. wingshooting over pointing dogs with shotguns during the non-breeding season) results in relatively random removal of individuals from the population, at least related to age, above one year, and sex. (iii) Present hunting strategies (i.e. attempting to remove half of the individuals per covey, and hunting over the same area once per season) apparently results in removal levels which, although stimulating local immigration, compensate natural mortality, and therefore no significant deviation from 'normal' rates of immigration are experienced by hunted populations.

Appendix 10.1. Allele frequencies for 17 polymorphic loci in Greywing Francolin collected from hunted and unhunted populations during 1990-1991 on the Stormberg Plateau, eastern Cape Province, South Africa.

		Locality													
		Unhunted populations						Hunted populations							
			L12		C4										
Locus	Allele	L13	1990	1991	1990	1991	C5	H25	H24	H21	H12	H11	H10	H8	H3
		n = 17	30	21	54	40	44	22	40	26	23	26	20	26	25
Aat-2	80	0	0,033	0	0	0,025	0,011	0,023	0	0	0	0	0	0	0
	- 20	0,324	0,150	0,119	0,278	0,162	0,227	0,409	0,250	0,193	0,239	0,231	0,200	0,077	0,320
	- 40	0	0	0	0	0	0	0	0,013	0	0	0	0	0	0
	-100	0,618	0,617	0,738	0,704	0,738	0,739	0,523	0,687	0,788	0,717	0,673	0,800	0,923	0,620
	-140	0,058	0,200	0,143	0,018	0,075	0,023	0,045	0,050	0,019	0,044	0,096	0	0	0,060
Ck-A	67	0,088	0,009	0,014	0	0	0	0	0	0	0	0	0	0	0
	100	0,912	1,000	1,000	0,991	0,986	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000
Ck-B	85	0	0	0	0,009	0,014	0	0	0	0	0	0	0,050	0	0
	100	1,000	1,000	1,000	0,991	0,986	1,000	1,000	1,000	1,000	1,000	1,000	0,950	1,000	1,000
Gpi	80	0	0	0	0	0	0,034	0	0	0,019	0	0	0	0	0
	-100	1,000	1,000	1,000	1,000	1,000	0,966	1,000	1,000	0,981	1,000	1,000	1,000	1,000	0,980
	-150	0	0	0	0	0	0	0	0	0	0	0	0	0	0,020
Idh-A	-100	0,971	1,000	0,952	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	0,975	1,000	1,000
	-120	0,029	0	0,048	0	0	0	0	0	0	0	0	0,025	0	0
Ldh-B	0	0	0	0	0	0	0	0	0	0,077	0,065	0	0	0	0
	100	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	0,923	0,935	1,000	1,000	1,000	1,000
Me	70	0	0	0	0,009	0,025	0	0	0	0	0	0	0	0	0
	100	1,000	1,000	1,000	0,991	0,975	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000
Mpi	80	0	0	0	0,009	0	0	0	0	0	0	0	0	0	0
	93	0	0	0	0	0	0,128	0	0	0	0	0	0	0	0
	100	1,000	0,933	0,975	0,880	0,913	0,802**	0,932	0,875	1,000	0,955	0,820	0,868	0,962	0,980
	107	0	0,067	0,025	0,111	0,087	0,070	0,068	0,125	0	0,045	0,180	0,132	0,038	0,020
Np	90	0,118	0,083	0,214	0,102	0,087	0,068	0,059	0,113*	0	0,109	0,038	0,025	0,019	0,060
	100	0,882	0,917	0,786	0,898	0,913	0,932	0,941	0,887	0,962	0,891	0,942	0,925	0,981	0,920
	105	0	0	0	0	0	0	0	0	0,038	0	0,020	0,050	0	0,020
Pep-A	100	0,971	1,000	0,952	0,917*	0,987	0,943	0,864	0,962	0,981	1,000	1,000	0,900	1,000	1,000
	108	0	0	0	0,019	0	0,023	0,136	0	0,019	0	0	0	0	0
	120	0,029	0	0,048	0,064	0,013	0,034	0	0,038	0	0	0	0,100	0	0
Pep-B	80	0,059	0,067	0,167	0,083	0,100	0,091	0,045	0,038	0,116	0,065	0,058	0,175	0,039	0,060
	100	0,853	0,933	0,833	0,880	0,887	0,875	0,932	0,875	0,865	0,848	0,711	0,725	0,942	0,920
	104	0,029	0	0	0	0	0	0	0	0	0	0	0	0	0
	120	0,059	0	0	0,037	0,013	0,034	0,023	0,087	0,019	0,087	0,212	0,075	0,019	0,020
	140	0	0	0	0	0	0	0	0	0	0	0,019	0,025	0	0

Appendix 10.1, continued

Pep-C	80	0,029	0	0,048	0,019	0,013	0,012	0,045	0,024	0,058	0	0,038	0	0,058	0,060
	85	0,088	0,017	0	0,028	0,013	0,011	0,045	0,063	0	0	0	0	0	0
	90	0,765	0,916	0,928	0,925	0,912	0,966	0,886	0,900	0,904	1,000	0,962	1,000	0,942	0,920
	100	0,118	0,067	0,024	0,028	0,062	0,011	0,024	0,013	0,038	0	0	0	0	0,020
Pep-D	60	0	0	0	0	0	0	0,023	0	0	0	0,038	0,025	0	0
	70	0,176	0,117	0	0,083	0,113	0,125	0,045	0,075	0,058	0,044	0,038	0,125	0,077	0,040
	100	0,676	0,750	0,786	0,778	0,637	0,830	0,773	0,750	0,846	0,913	0,674	0,850	0,788	0,780
	115	0,148	0,133	0,214	0,139	0,250	0,045	0,159	0,175	0,096	0,043	0,250	0	0,135	0,180
Pgd-1	70	0	0,017	0,048	0,194	0,213	0,250	0,068	0,125	0,058	0,196	0,231	0,175	0,019	0,120
	80	0	0,017	0	0,009	0,013	0	0,045	0	0	0	0	0	0,231	0
	100	1,000	0,916	0,928	0,685	0,700	0,705	0,773	0,700	0,827	0,717	0,692**	0,825	0,731	0,740
	115	0	0,050	0,024	0,093	0,075	0,045	0,091	0,162	0,115	0,087	0,077	0	0,019	0,100
	120	0	0	0	0,019	0	0	0,023	0	0	0	0	0	0	0,040
	140	0	0	0	0	0	0	0	0,013	0	0	0	0	0	0
Pgm-1	85	0,059	0,150	0,262	0,194	0,113	0,148	0,159	0,150	0,174	0,130	0,116	0,225	0,077	0,140
	100	0,941	0,833	0,738	0,778	0,887	0,818	0,750	0,837	0,769	0,826	0,769	0,700*	0,827	0,760
	115	0	0,017	0	0,028	0	0,034	0,068	0,013	0,019	0,044	0,115	0,025	0,096	0,080
	70	0	0	0	0	0	0	0,023	0	0,038	0	0	0,050	0	0,020
Pgm-2	60	0	0,050	0,048	0,065	0,013	0,011	0	0,038	0,038	0,022	0	0	0,038	0
	90	0	0	0	0	0	0	0	0	0,038	0	0	0	0	0
	100	1,000	0,950	0,952	0,935	0,987	0,989	1,000	0,962	0,924	0,956	0,865	1,000	0,962	1,000
	120	0	0	0	0	0	0	0	0	0	0,022	0,135	0	0	0
Sdh	10	0	0	0	0	0	0	0,023	0	0	0,087	0	0	0,019	0
	-100	1,000	1,000	1,000	1,000	1,000	1,000	0,977	1,000	1,000	0,913	1,000	1,000	0,981	1,000
F (average)		-0,091	0,010	0,129	0,092	0,006	0,068	-0,023	0,053	0,031	0,031	-0,047	-0,101	0,018	-0,079

Significant departures from Hardy-Weinberg proportions, *P<0,05, **P<0,01.

SYNTHESIS

Genetic distances between distant Greywing Francolin populations were discordant with the geographical arrangement of sampling (Chapter 1), probably indicating that this species acts as a panmictic megapopulation over its geographical range. Therefore, although geographical differences were found in timing of breeding (Chapter 3) and other regional differences in habitat and diet preferences are apparent (Chapter 6) which might require flexibility in management, the species can be regarded as one unit in the 'currency' of conservation biology.

Furthermore, Greywing have a higher degree of population stability than was suspected, large effective population sizes and the capacity to occupy suitable, but vacant, habitats. Although genetic differentiation is evident on a large geographical scale, large numbers of dispersing individuals produce outbred subpopulations on a fine geographical scale. Greywing therefore have a wealth of genetic variability that may buffer populations against habitat changes, and sufficient mobility to balance moderate removal by hunting (Chapter 2).

The major factors which influence the population dynamics of Greywing Francolin are habitat availability (especially moderately grazed grasslands) (Mentis & Bigalke 1981a; Mentis & Little 1992; Chapter 6), predation by small carnivores and crows (especially of hens and eggs during the incubation period) (Chapter 3) and the availability of arthropods which is linked to timing and amount of rainfall (especially during the fledging period) (Chapter 3). There appears to be no need for concern regarding potentially adverse effects resulting from the loss of

genetic variability (Chapter 2) or the prevalence of parasites (Chapters 7 & 8). Greywing populations are, in fact, among the most genetically variable phasianids studied to date, and examination of more than 3 000 shot birds revealed no adverse effects which were correlated with body mass or other measures of fitness, at present population levels.

Management strategies necessary for the sustainable utilization of this important gamebird are: maintenance of grasslands in a vigorous state (i.e. neither degraded nor moribund) preferably by moderate grazing, reduction of predators (particularly small carnivores and crows, before and during the incubation period), and cessation of grassland burning before 31 August.

For sustainable, economically viable hunting, I suggest that groups of between four and seven hunters should be offered at least between 50 and 65 Greywing per hunt, and that these populations be hunted only once per season with hunters removing no more than 50% of a covey. Furthermore, hunting should be done between 15 April and 31 July in the summer-rainfall region and between 1 April and 30 June in the winter-rainfall region. There are no significant life history differences between moderately hunted and unhunted populations, using this hunting strategy (Chapter 10). Present populations produce economically viable rough shooting in areas of medium to high abundance.

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