A STUDY OF THE ECOLOGY OF THE NAMAQUA SANDGROUSE AND OTHER ARID-ZONE BIRDS

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"Part of facing up to the realities and complexity of nature is admitting that any approach we take will be incomplete, imperfect, provisional, experimental. The important thing is to try."

Stephen Budiansky in *Nature's Keepers*

And here I try . . .

I dedicate this thesis to my mother

COLLEEN LLOYD

for her many sacrifices to ensure my first-class education,

and to

DEKKER and SIKKIE STADLER

whose hospitality and support kept me sane and made much of this study possible.

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ABSTRACT

This field study set out to identify the key ecological factors influencing the population dynamics of the Namaqua Sandgrouse *Pterocles namaqua*, through an investigation of diet and the nutritional demands during different stages of the annual cycle, the timing of breeding seasons and movements in relation to patterns of rainfall-dependent food availability, breeding success and the factors limiting productivity. In addition, the nesting habits and success of 11 coexisting arid-zone bird species were examined to test a variety of hypotheses regarding the relationship between nest-predation rate and nest site, nest density, predator-avoidance behaviour, stage of the nesting cycle and season, and degree of residency. Furthermore, the importance of rainfall as a breeding stimulus and its effects on clutch size were investigated for several species.

The Namaqua Sandgrouse is an obligate granivore at all times, feeding on the seeds of annual plants, primarily of the family Fabaceae. Even while breeding, energy is the first-limiting nutrient in the foods of adults. Growing chicks have a proportionally greater protein demand, and are more dependent than adults on protein-rich legume seeds to satisfy first-limiting amino acid requirements. The chick growth phase was identified as the most nutritionally demanding stage in the annual cycle. The breeding season was found to be unexpectedly variable, and not consistently correlated with periods of peak food availability. The peak nesting period ranges from January-May in northwestern Namibia; June-October in the Kalahari; September-December in the Nama Karoo - all late-summer (January-April) rainfall regions. The possible complicating influences of biannual breeding, moulting, adult nutritional reserves and seasonal variation in nest-predation pressure are discussed. The Namaqua Sandgrouse is largely nomadic within its range, but also undertakes an annual "east-west" partial migration within South Africa. This movement is largely between two late-summer rainfall regions, so is not directly linked to gradients in food availability. Nesting success ranged from 5.7% to 13.5% over four consecutive breeding seasons ($n = 278$ nests). Predation, primarily by small mammals, was responsible for 96% of nest losses. Estimates of annual recruitment in a core breeding area ranged from minima of 3-10% to maxima of 6-20% over three seasons. Possible reasons for this sustained low level of breeding success are explored. The implications of these findings to the management of the Namaqua Sandgrouse as a resource for sustainable wing-shooting are discussed.

Nesting success among other arid-zone species ranged from 3.5% to 75.4%, predation accounting for 94% of nest losses ($n = 588$). Predator-avoidance behaviour and nest site accounted for much of the variation in nesting success. Nest predation was inversely related to nest density, and decreased as the breeding season progressed from spring to midsummer. Daily egg-predation rates were higher than daily nestling-predation rates for seven of the nine altricial species studied. Among ground-nesters, territorial residents incurred significantly lower ($U_{4,6} = 24.0$, $P < 0.02$) daily nest-predation rates (3.41%, $n = 4$) than nomads (6.91%, $n = 6$), suggesting that residency enhances nest survival. Breeding activity was strongly correlated with rainfall in most species, but resident insectivores responded immediately to rainfall events as small as 6 mm while nomadic granivores exhibited a delayed response only to larger rainfall events (> 40 mm). Following large or cumulative rainfall events, over 50% of species studied showed evidence of an increase in clutch size, sometimes within a week. For example, average clutch size in the Spikeheeled Lark *Chersomanes albofasciata* ranged from 2.00 (± 0, $n = 13$) during three relatively dry seasons, to 2.83 (± 0.39, $n = 23$) following a 54 mm rain shower, to 3.30 (± 0.66, $n = 10$) and a maximum clutch size of five following 78 mm of follow-up rainfall.

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PLoyd

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CHAPTER ONE

GENERAL INTRODUCTION

The Namaqua Sandgrouse

Sandgrouse (Pteroclidae: 16 species) are medium sized (150-600 g) terrestrial granivores that are highly specialised for life in arid and semi-arid habitats within a largely Afro-Asian distribution. Superficially resembling pigeons, they are currently classified within their own order (Pterocliformes) and are considered to be more closely related to the shorebirds (Charadriiformes) than to the doves and pigeons (Columbiformes) (Maclean 1984, Sibley *et al.* 1988).

Research on sandgrouse has concentrated primarily on their physiological and behavioural adaptations to life in arid lands (e.g. Maclean 1976, Thomas 1984, Hinsley & Ferns 1994). It is only recently, as interest in the commercial exploitation of sandgrouse for sport shooting has increased, that studies have begun to investigate the demographics and movements of sandgrouse populations and the factors that determine the productivity and timing of breeding activity and movements (e.g. Malan *et al.* 1994, Little *et al.* 1996, Njoroge *et al.* 1997, Suárez *et al.* 1997, Tarboton & Blane unpublished).

A thorough understanding of the population dynamics and the key ecological factors that influence annual variations in population sizes is required before an effective strategy for the sustainable management of a species as an exploited resource can be developed. This thesis is the first detailed attempt to study the population dynamics of the Namaqua Sandgrouse *Pterocles namaqua*. This southern African endemic has a widespread distribution in the arid and semi-arid west and interior, generally in areas where the annual rainfall is less than 300 mm (Harrison *et al.* 1997). The high mobility and nomadic nature of this species meant that some demographic parameters, such as first-year juvenile and adult survival were not studied due to logistical difficulties and the perceived impossibility of completing the task within a limited time frame. In an effort to determine the nature of movements between regions, a population genetic study was conducted with the aim of examining the degree of regional population genetic differentiation through sequencing of the

D-loop region on the mitochondrial DNA genome. Unfortunately, this study proved unsuccessful, despite several months work, due to problems with primers and an apparently quirky D-loop region in sandgrouse.

Chapter 2 examines the basic breeding biology of the Namaqua Sandgrouse, building on the work of Maclean (1968), and providing a detailed analysis of nesting success and estimates of annual recruitment. Due to the very high levels of nest predation by small-mammal predators, Chapter 3 examines possible influences of investigator disturbance on nesting success, to ensure unbiased estimates of the latter parameter. In Chapter 4, the adaptiveness of nest-site selection and highly variable clutch pigmentation in the Namaqua Sandgrouse is examined. Furthermore, a random-walk model is developed to simulate the foraging behaviour of a typical nest predator to investigate to what extent nest predation may be incidental i.e. random. The daily activity pattern of a nonbreeding population of Namaqua Sandgrouse is detailed in Chapter 5, and compared to that of a breeding population. The results provide insights into the drinking behaviour and sociality of these birds, and are used in later time budget analyses. Chapter 6 describes the diet of Namaqua Sandgrouse in terms of seed species composition and nutritional content. Using estimates of the daily requirements for energy and limiting amino acids, I construct daily energy and limiting nutrient profiles for this species during different stages of the annual cycle. These are used to identify the period of most critical food demand. In Chapter 7, the timing of breeding seasons across the southern African distribution of the Namaqua Sandgrouse is related to rainfall patterns, food availability and food demands in an attempt to find a predictive correlation between rainfall/food availability and breeding. Alternative hypotheses to explain the unusual variability in the timing of breeding are then investigated. Finally, various issues relating to the sustainable hunting of this species are examined in Chapter 8, and a few practical recommendations for its management are offered.

Other arid-zone birds

In the truly arid zone of southern Africa, annual rainfall is both low (50-250 mm mean annual rainfall) and highly variable between years (Tyson 1986). In this unstable and unpredictable environment, the vegetation is often dominated by annuals. Annual plants allocate a major portion of productivity to reproductive output (Hirshfield & Tinkle 1975), and when and where environmental conditions are favourable, produce huge quantities of seeds (Brown *et al.* 1979). Due to the variability and patchiness of rainfall, abundant food supplies (green vegetation, seeds and insects) are produced patchily in space and time. These circumstances have encouraged the evolution of nomadism, particularly among granivorous birds, enabling them to track patches of high resource availability for as long as possible (Dean 1997).

Nest predation is the primary source of mortality early in a bird's life (Ricklefs 1969, Martin 1995), and has been found to vary with nest site (Osborne & Osborne 1980, Marzluff 1988, Martin 1993, Schieck & Hannon), nest density (Dunn 1977, Page *et al.* 1983, Hill 1984), season (Nolan 1963, Newton 1964, Roseberry & Klimstra 1970, Gottfried 1978) and stage of the nesting cycle (Skutch 1949, Perrins 1965, Redondo & Castro 1992, Haskell 1994). Chapter 9 explores nest-predation rates among a variety of arid-zone species in relation to nest site, nest density, predator-avoidance behaviour, stage of the nesting cycle and season, and degree of residency (nomad vs resident). I was particularly interested in comparing the nest-predation rates incurred by nomads to those of residents in a situation of high nest-predation risk. Nomads, with their more limited knowledge of predator activity within the nesting environs, were expected to incur higher nest-predation rates than the normally territorial residents. Chapter 10 investigates the influence of rainfall as a stimulus to breeding and the differences in response between residents (mostly insectivorous) and nomads (mostly granivorous). In the arid zone, where species have to make maximum use of erratic and unpredictable breeding opportunities that vary greatly in quality, flexibility in clutch size may be selected for. This hypothesis is evaluated by recording the clutch sizes of various species between wet and dry seasons and before and after significant rainfall events.

CHAPTER TWO

THE BREEDING BIOLOGY OF THE NAMAQUA SANDGROUSE

SUMMARY

The breeding biology of the Namaqua Sandgrouse *Pterocles namaqua* was studied and its nesting success determined through the observation of 278 nests over four consecutive breeding seasons at Droëgrond, Northern Cape Province, South Africa. The normal clutch of three eggs is laid over five days (± 48 hr laying interval). The incomplete clutch is left unattended overnight, but is attended during the heat of the day by the female on days when an egg is laid and by the male on alternate days. After clutch completion, the pair share incubation duties, the female flying to relieve the male 151 (± 21) min after sunrise and the male flying to relieve the female 105 (± 21) min before sunset. The incubation period is 21 days from clutch completion, and the three chicks normally hatch within 18 hours of each other. Nesting success ranged from 5.7% to 13.5% between seasons and averaged 8.2%. Predation, primarily by small mammals, was responsible for 96% of nest losses. Estimates of annual recruitment at Droëgrond ranged from minima of 3-10% to maxima of 6-20%, and are believed to be representative of a core area in the distribution of the Namaqua Sandgrouse in South Africa. These low estimates suggest that annual juvenile recruitment may be too low to maintain Namaqua Sandgrouse populations locally. Possible reasons for the sustained low level of breeding success are discussed.

INTRODUCTION

Many of the early insights into the breeding biology of sandgrouse were gained from observations on captive breeding birds. Meade-Waldo (1896), for example, was the first to describe the unique habit whereby sandgrouse convey water to their chicks: the male soaks his belly feathers with water before flying back to the chicks who then strip the water from his feathers with their bills. Although this behaviour was subsequently confirmed (e.g. Meade-Waldo 1921, St. Quintin 1905, Buxton 1923, Heim de Balsac 1936, Hoesch 1955), several authors remained sceptical (e.g. Archer & Godman 1937, Meinertzhagen 1964, Hüe & Etchécopar 1957, Schmidt-Nielsen 1964) until Cade and Maclean (1967) outlined the special adaptations of the belly feathers of male sandgrouse that allow efficient water absorption and transport. Marchant (1961), studying the Pintailed Sandgrouse *Pterocles alchata* and Spotted Sandgrouse *P. senegallus*, and Maclean (1968), studying the Namaqua Sandgrouse, provided the first detailed accounts of the breeding biology of sandgrouse in the wild and, apart from a recent study on the Yellowthroated Sandgrouse *P. gutturalis* (Tarboton & Blane unpublished), the only data on sandgrouse breeding success.

An analysis of the sustainability of hunting requires an understanding of the demography of the target species, and it is particularly important to obtain reasonable estimates of annual recruitment and mortality. The determination of annual adult mortality in a species as mobile and unpredictably nomadic as the Namaqua Sandgrouse would require a major and long-term, mark-recapture study. Such an undertaking did not fall within the scope of this thesis proposal. Instead, I concentrated on obtaining data on nesting success and annual recruitment, although estimation of the latter was hampered by an inability to be present at the study site throughout the extended breeding season of this species.

This chapter reports on observations and data gained from studying the Namaqua Sandgrouse over four breeding seasons. It adds to information on the breeding biology of this species reported by Maclean (1968), and provides the first detailed analysis of the breeding success of any sandgrouse species.

STUDY AREA AND METHODS

The study was conducted over four early-summer seasons (August-December 1993-1996) on the farm Droëgrond (29°07'S 20°16'E), encompassing an area of 10 000 ha of flat, arid rangeland in the Northern Cape Province, South Africa. Annual rainfall measured at a rain-gauge located centrally in the study site over the period 1958-1996 averaged 116.1 mm (range 20.5-494.2 mm; 71% coefficient of variation). Most rain falls in late summer, from December to April, when daily maximum temperatures average 36-38°C over the hottest month. The vegetation is Bushmanland Nama Karoo (Hoffmann 1996), and consists of mixed grassland (*Stipagrostis ciliata* and *S. obtusa*) and short shrubland (*Rhigozum trichotomum*, *Salsola tuberculata* and *Hermannia spinosa*) with a projected ground cover of 5-10%. Larger shrubs (*Lycium austrinum*) and stunted trees (*Boscia albitrunca* and *Parkinsonia africana*) are more widely scattered.

Nests were found randomly through the nesting period, either by flushing birds while cycling through the study area or, more usually, by following single birds (using binoculars while standing in an elevated position) flying to the nest to relieve their mates during the morning and afternoon nest-relief periods. Nest-relief times were recorded whenever nests were found in this manner. Relative nest densities were determined by: 1) the number of nests found per nest-relief observation period, and 2) the number of nests found per 100 km of cycling effort (measured with an odometer attached to the bicycle). Time-lapse cameras (one frame every 60 s) were set up at three nests to monitor sandgrouse behaviour during the egg laying period, and at several other nests to monitor incubation behaviour and possible predation.

Nests were marked and visited as detailed in Chapter 3. When a nesting attempt failed, the nest environs were examined to establish the cause of failure and, where possible, the identity of any nest predators. The Rhombic Eggeating Snake *Dasypeltis scabra*, which feeds exclusively on birds' eggs, was identified as the predator when crushed shells were found near the nest and/or when eggs disappeared one at a time. Small mammals were identified either by their tracks, or their habit of biting a chunk out the side of the egg. Larger mammals were identified by their tracks alone. No avian nest predators occurred at the study site. Clutch size was recorded only if it remained unchanged between visits, and therefore does not include nests lost to predation prior to the second visit or during the egg-laying period, or nests where definite evidence of Eggeating Snake predation was found.

Nesting success was determined using the method of Mayfield (1961, 1975), namely:

$$success = \left(1 - \frac{losses}{exposure}\right)^{np}$$

where *exposure* is the total number of active nest days, and *np* is the nesting period (laying period plus incubation period = 25 days for the Namaqua Sandgrouse). Statistical comparisons of daily mortality rates were effected by calculating the z statistic as the ratio of the difference between two mortality rates to its standard error (Johnson 1979).

The original nest records of Maclean (1968) from the Kalahari Gemsbok National Park, 300 km to the north of the study site, were reanalysed using the Mayfield method for comparison with the present study.

In order to estimate juvenile recruitment, regular waterhole counts were made of the number of belly-soaking males (as a proportion of the total drinking population) and juvenile males in the drinking population. In a study of a stable population of Yellowthroated Sandgrouse in the Thabazimbi region, North-west Province, Warwick Tarboton and Sheila Blane collected reliable counts of belly-soaking males and juveniles over a five-year period (1988-1992; Tarboton & Blane unpublished). Using these data, I combined the totals for each month and determined the average monthly frequencies (birds/(total monthly count)) of belly-soaking males and juveniles over the five years. These frequencies were then added to give totals for an average year. Hinsley and Hockey (1989) noted that a captive-bred juvenile Doublebanded Sandgrouse *P. bicinctus* had a dusty-looking version of female plumage at the age of three months. Assuming that juveniles appear at the waterhole for the first time when they are two months old (see under discussion), this observation suggests that juveniles may be distinguishable from adults in the field for only one additional month. On the other hand, Tarboton and Blane (unpublished) were able to distinguish juveniles for up to two months after the last belly-soaking males were noted. Using the assumption that juveniles were distinguishable from adults for between one month and two months after they first appeared at the waterhole, average annual recruitment in the Yellowthroated Sandgrouse was estimated as ranging between J and $J/2$ respectively, where J is the total of the monthly juvenile frequencies (juveniles/(total monthly count)) for the average year. In the scenario where juveniles are distinguishable for two months, they are assumed to be counted twice during the two month period, hence the $J/2$ recruitment estimate.

Estimates of annual Namaqua Sandgrouse recruitment were obtained by multiplying the annual Namaqua Sandgrouse belly-soaking male frequency totals with a constant (C and $C/2$) derived from the relationship between belly-soaking male (B) and juvenile (J) frequency totals in the Yellowthroated Sandgrouse:

$$C = J / B.$$

Although estimates of recruitment derived in this manner are imprecise, they do serve as a best estimate using the limited knowledge available, and provide a basis for comparing recruitment between species, localities and years. Drinking population and belly-soaking counts for Namaqua Sandgrouse from other localities across southern Africa (detailed in Chapter 7) were used to estimate recruitment at these localities.

RESULTS

Nest site and nest construction

Namaqua Sandgrouse generally site their nests in exposed situations, but within a local concentration of objects, most of them less than 15 cm high and concentrated within 30 cm of the nest centre (see Chapter 4). Nest to object orientation is random, indicating that the nest is sited close to objects neither for shade nor shelter from prevailing winds. The nest consists of a shallow (never more than 2 cm deep), roughly circular scrape. The pair appear to select the nest site and scratch out the scrape together. On the four occasions that nests were found before the first egg had been laid, the pair was disturbed at the nest. These nests were found between 10h55 and 11h45. An egg had been laid in three of the nests by the next day (see Appendix 2.1), but the fourth was abandoned. These observations suggest that the pair select the nest site after their morning drink, and probably lay the first egg during the course of the afternoon (see below).

The laying period

Two nests, each with one egg and the pair in attendance two days before the second egg was laid, were found at 14h45 and 15h00. The presence of the female suggests that the first egg had just been laid. Maclean (1968) noted that a female laid the first egg of a clutch at 12h20. Incubation is irregular while the clutch is incomplete (see Appendix 2.1). At three nests monitored with cameras over five days when an egg was laid, the females arrived at the nest midmorning (08h40-11h05), often accompanied by their male partners. The females then sat on the nest for between 50 min and 6.5 hours, and appear to be responsible for most "incubation" on egg-laying days. At nest #175, the pair arrived together at 11h05, the female sat on the nest until 11h58, whereafter the pair left together and the incomplete clutch was left exposed for the remainder of the day. At nest #123, the male remained with the female until 12h11, the female leaving the incomplete clutch at 16h01. At two nests where the pair arrived together on the day the female laid the third egg, the male left again within 10 min.

At 10 nests where 15 intervals between successive eggs in the clutch were monitored, an egg was laid every other day (i.e. closer to a 48-hour interval than the 24-hour interval suggested by Maclean (1968)). The interval between the laying of the first and third egg is therefore approximately four days. A 48-hour laying interval has been observed in Pintailed *P. bicinctus* (Marchant 1961, Frisch 1970), Doublebanded (Hinsley & Hockey 1989) and Pallas's Sandgrouse *Syrrhaptes paradoxus* (Grummt 1985).

On the alternate days that the female did not lay an egg (day 2 and 4 of the laying period), the male arrived during the normal morning nest-relief period (occasionally a little later), remaining until the early afternoon (14h28-15h23). The eggs were therefore left unattended for the early part of the morning, the latter part of the afternoon, overnight, and during overcast or rainy conditions.

The normal clutch size for the Namaqua Sandgrouse is three. The average for 224 nests was 2.88 (*s.d.* = 0.33). As the Eggeating Snake commonly takes only one sandgrouse egg at a time, several of the recorded two egg clutches may have originally had three eggs, but lost one to this snake.

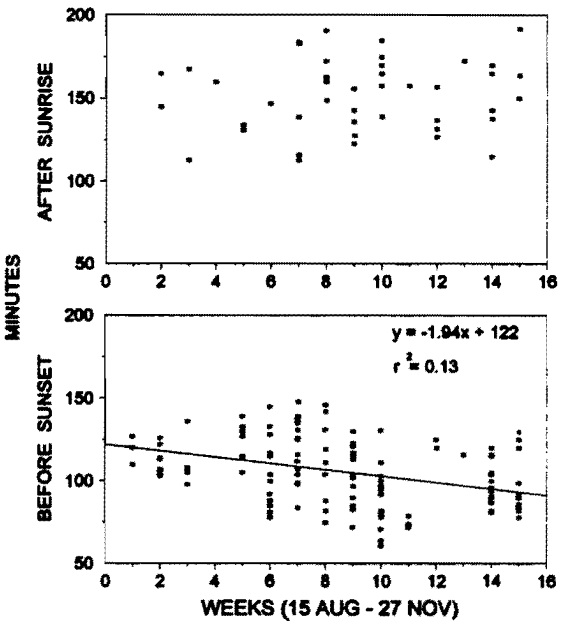

Figure 2.1. Morning and afternoon nest relief times of Namaqua Sandgrouse at Droëgrond recorded during the breeding seasons of 1993-1996.

Incubation

On clutch completion, incubation was continuous. The female incubated through the day, flying to relieve the male at the nest an average of 151 (*s.d.* = 21, *n* = 48) min after sunrise. The male returned in the afternoon to relieve the female 105 (*s.d.* = 21, *n* = 126) min before sunset. The female generally arrived at the nest later if it was overcast in the morning, and the male returned earlier if it became overcast in the early afternoon. This suggests that the birds use either the height of the sun or the amount of sunlight as a cue. Morning nest relief times did not vary through the breeding season ($r_{48} = 0.10$, n.s.), whereas afternoon nest relief times did ($r_{126} = 0.36$, $P < 0.001$). The afternoon nest relief tended to occur later as the season progressed from late winter to midsummer (Fig. 2.1).

In the morning, the female flew to the nest after drinking. After the morning relief, the male flew to drink, and thereafter to feeding sites for the rest of the day. The results of several afternoon waterhole counts suggest that incubating females may not usually fly to drink again after being relieved in the afternoon. On 28 September 1993, when the nesting season was already well under way at Droëgrond, 344 birds drank in the morning (five belly-soaking males), but only 28 drank in the afternoon (sex ratio 16♂ :12♀), of which three were single females that may have arrived to drink after incubating during a hot day. On 17 October 1993, 69 birds drank in the afternoon (sex ratio 42♂ :27♀), with seven possible single females. On 5 November 1993, 945 birds drank in the morning (66 belly-soaking males), 63 drinking in the afternoon (three belly-soaking males and sex ratio 37♂ :26♀), of which six were possibly single females. On 9 November 1994, 1022 Namaqua Sandgrouse drank at a waterhole in the Kalahari Gemsbok National Park in the morning (187 belly-soaking males and sex ratio 256♂ :159♀), and 80 drank in the afternoon (one belly-soaking male and sex ratio 32♂ :47♀) after a very hot day. The female-biased sex ratio of the latter afternoon count provides the strongest evidence that some females drink twice a day. Nonetheless, these birds are likely to be in the minority, judging by the small number that do drink in the afternoon.

At the only nest followed from laying to hatching, the incubation period (interval between the laying and hatching of the third egg) was 21.0 days. At another five nests found with a complete clutch of three eggs, three hatched after 21 days, and two after 20 days. These data support Maclean's (1968) estimation of a 21 day incubation period for this species.

Hatching

Hatching success among 173 eggs that survived to hatch was 94%. The eggs may take several days to hatch after the first cracks appear in the shell. However, at all 21 nests followed over the hatching period, the three chicks hatched out the shells within a 24-hour period (see Appendix 2.2). Hatching rarely, if ever, occurs at night. In all seven closely-monitored cases where one or two chicks hatched in the afternoon, the remaining two or one hatched the next morning. In some cases, the three chicks hatched through the course of the morning and early afternoon of the same day. Soon after hatching, the adult incubating at the time picked up the shells and carried them off to a distance of 10-20 m, where they were dropped. Hatched shells are therefore rarely found in close proximity to the nest. This is probably a predator-avoidance behaviour, for the shells usually have traces of blood in the membranes.

On the first morning of there being chicks in the nest, the male flew to the waterhole after being relieved by the female, and returned with saturated belly feathers to give the hatched chicks their first drink. At one nest under continual observation, one egg had not yet hatched by the time the male returned with water for the first two chicks. The third egg hatched a short while later, whereupon the male flew off again to soak his belly feathers. On his return, the first two chicks were again offered water, before the male crouched over the still weak third chick in the nest, so that it could drink.

After watering the chicks, the male appeared to remain with the female, particularly if all three chicks had hatched. The precocial chicks began to make exploratory movements outside the nest within a few hours of hatching. The adults usually led the chicks away from the nest within 12 hours of the last chick hatching (Appendix 2.2).

Nest predation and nesting success

Table 2.1. A summary of the total or partial nest losses of Namaqua Sandgrouse at Droëgrond, expressed as percentages taken by different predators, with sample size in brackets.

	Eggeating Snake	Other snake	Small mammal	Large mammal	Unidentified mammal	Unidentified predator	Sheep trampling	Abandoned	Total nests with losses
1993	43.5 (10)		13.0 (3)	8.7 (2)	30.4 (7)	4.3 (1)	4.3 (1)		23
1994	16.2 (22)	0.7 (1)	55.9 (76)	6.6 (9)	19.1 (26)	2.2 (3)	1.5 (2)	2.2 (3)	136
1995			33.3 (3)	11.1 (1)	22.2 (2)	33.3 (3)			9
1996	13.0 (3)		39.1 (9)		21.7 (5)	26.1 (6)		4.3 (1)	23
Combined	18.3 (35)	0.5 (1)	47.6 (91)	6.3 (12)	20.9 (40)	6.8 (13)	1.6 (3)	2.1 (4)	191
Combined*	19.6 (35)	0.6 (1)	70.8 (126)	9.6 (17)			1.7 (3)	2.2 (4)	178

*Percentages expressed by ignoring the "unidentified predator" category and distributing the "unidentified mammal" records proportionally among the "small mammal" and "large mammal" categories. This gives a better reflection of the relative importance of the various predator groups.

Predation accounted for 96% of all nest losses (Table 2.1). The nocturnal Eggeating Snake, a specialist egg predator, accounted for 43.5% of nest losses in 1993, but only 19.6% for the four seasons combined. While commonly taking only one or two eggs at a time, these snakes generally made repeated visits to nests at intervals of 1-8 days to consume the entire clutch. This suggests that the snakes are able to relocate nests with relative ease. Eggeating Snakes did not appear to discriminate between fresh eggs and long-incubated eggs; several nests with eggs about to hatch were also destroyed. In these latter situations, the snakes did not derive much nutrition from the eggs, being unable to extract the chick. It was surprising then that most Eggeating Snakes confronted with an older nest proceeded to crush all the eggs in the clutch. Another snake, the Cape Cobra *Naja nivea*, took only a single clutch, swallowing the eggs whole.

Mammalian predators accounted for 80.4% of the remaining nest losses, small mammals, mainly the diurnal Yellow Mongoose *Cynictis penicillata*, Cape Grey Mongoose *Galerella pulverulenta* and Suricate *Suricata suricatta*, and the nocturnal Striped Polecat *Ictonyx striatus*, taking nearly eight times as many nests as nocturnal larger mammals, which included Bateared Fox *Otocyon megalotis*, Cape Fox *Vulpes chama*, Aardwolf *Proteles cristatus* and Aardvark *Orycteropus afer*.

Nesting success (quantified as the proportion of nests at which 1-3 chicks hatched) ranged between 5.7% and 13.5%, averaging 8.2% over the four years studied (Table 2.2).

Table 2.2. Summary of nesting data for Namaqua Sandgrouse at Droëgrond and the Kalahari Gemsbok National Park (KGNP). Whole nest losses include losses due to predation and losses due to other causes (in brackets).

	Droëgrond					KGNP*
Year	1993	1994	1995	1996	Overall	1965-66
Rainfall (mm)	83	127	75	215		
No. nests	35	193	14	36	278	24
Exposure (days)	299	1369	100	212.5	1980.5	152.5
Nest losses	22(1)	129(5)	9(0)	22(1)	182(7)	7(2)
Daily predation rate ±SE (%)	7.36 ±1.51	9.42 ±0.79	9.00 ±2.86	10.35 ±2.09	9.19 ±0.65	4.59 ±1.81
Predation (%)	85.20	91.58	90.54	93.49	91.02	69.11
Success (%)	13.52	7.61	9.46	5.71	8.15	21.86

*The nest records of Maclean (1968) reanalysed using the Mayfield method.

1992 was an exceptionally dry year (20.5 mm), the largest single rain event being 6 mm. 1993 was relatively dry (83.0 mm), and showers of 29 mm in February and 13 mm in March were the only two rain events exceeding 10 mm. The 1993 breeding season (starting in September) therefore followed a severe two year drought. Moderate numbers of birds moved into the area to breed (Chapter 7), and nesting success (13.5%) was higher than over the following three years.

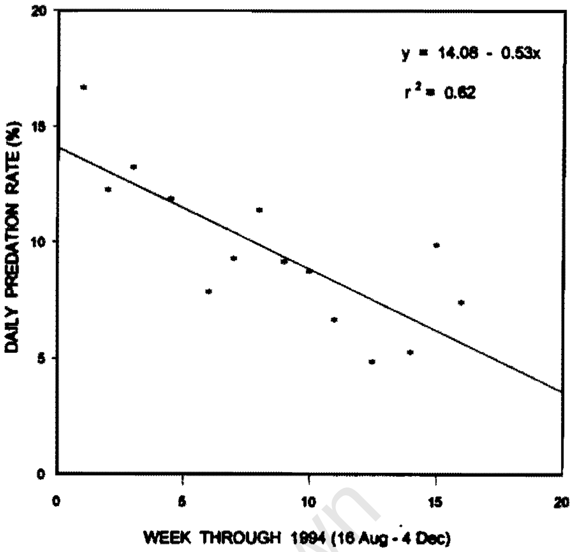

Figure 2.2. Daily predation rates on Namaqua Sandgrouse nests through the 1994 breeding season.

In 1994 (126.8 mm), 40.5 mm fell during several showers in early February. This, together with follow-up rains of 24.5 mm (4-7 March) and 11.5 mm (31 May), resulted in good ephemeral plant germination, growth and seed set (Chapter 7). Large numbers of Namaqua Sandgrouse moved nomadically into the area in April, to exploit superabundant seed-food supplies. The increased population size during the 1994 breeding season, which started in August, resulted in elevated nest densities (Table 2.3). As nest density increased as the season progressed from spring into summer (Table 2.3), predation rates decreased (Fig. 2.2).

1995 was another dry year (75.2 mm), with only a single event (21.6 mm on 20 November) exceeding 10 mm, and a small Namaqua Sandgrouse population present at the study site through the breeding season. Nest densities were therefore low, but nest-predation rates remained high. 1996 was a year of good rainfall (214.8 mm). The two most important events were soft, soaking rains of 53.5 mm (23-25 July) and 77.5 mm (7-8 November), which resulted in a huge influx of nomadic passerines. Both these birds and the local residents nested in large numbers through spring and summer, resulting in high overall nest densities. Although present in relatively large numbers, the nesting response of Namaqua Sandgrouse was subdued, and nest densities remained low for much of the season (Table 2.3). Nest-predation rates on this species were surprisingly high in 1996 (Table 2.2), given the abundance of alternative prey for potential sandgrouse nest predators.

Daily nest-predation rates on Namaqua Sandgrouse were not significantly different between years at Droëgrond ($z = 0.14\text{-}1.21$, all $P > 0.05$), but were significantly higher at Droëgrond than at the Kalahari Gemsbok National Park ($z = 2.53$, $P < 0.01$).

Table 2.3. Relative Namaqua Sandgrouse nest density at Droëgrond during the early summer breeding season in the years 1993 to 1996. Monthly nest densities (in the first and latter half of each month) were quantified as the average number of nests per nest-relief observation period (see methods). Included as an annual average is the relative nest density as the number of nests found per 100 km of cycling effort in each season.

Month & year	No. of obs. periods	Nests found	Nests/obs. period	Distance cycled (km)	Nests/ 100 km
Sep '93	-	-	-		
	4	1	0.25		
Oct '93	11	2	0.18		
	15	5	0.33		
Nov '93	14	6	0.43		
	12	6	0.50		
1993	56	20	0.36	1196	0.67
Aug '94	-	-	-		
	23	18	0.78		
Sep '94	-	-	-		
	20	31	1.55		
Oct '94	15	23	1.53		
	15	19	1.27		
Nov '94	-	-	-		
	9	9	1.00		
1994	72	100	1.39	1385	3.68
Sep '95	13	1	0.08		
	-	-	-		
Oct '95	6	2	0.33		
	-	-	-		
1995	19	3	0.16	-	-
1996				1798	0.72

Chick development and survival

The chicks are self feeding from the moment they hatch, and feed on the same seeds as adults (Chapter 6). At several nests under continual observation during the hatching period, the adults started to encourage the chicks to peck at and swallow items (presumably seeds). The adult pecked repeatedly at the ground in front of the chick, and seemed to pick up and drop items. Hinsley and Hockey (1989) noted similar behaviour in captive, breeding Doublebanded Sandgrouse, where the adult would repeatedly pick up and drop a seed in front of the chick until the chick picked it up and swallowed it. Without this encouragement to feed in their first few days of life, sandgrouse chicks have been known to die (Hinsley & Hockey 1989).

Day-old sandgrouse chicks were encountered more often than chicks of any other age. They were normally seen walking in the company of the adult pair, presumably from the exposed nesting habitat towards drainage line feeding sites with better cover. Thereafter the highly cryptic chicks were very rarely encountered. Despite several thousand kilometres of cycling and driving and months spent in the field through the breeding season, chicks older than a few days were encountered on only five occasions.

Juveniles appeared at the waterhole for the first time once they were almost fully grown and moulting into an adult-type plumage. It was only possible to identify juvenile males with any certainty (within the range of normal field observation), which differed from adult males by being slightly smaller in size and having a number of scaly-patterned feathers on the chest.

In the 1993-94 breeding season, no juveniles had made an appearance at the waterhole by 18 November 1993, despite nesting starting in September and males starting to belly-soak from the end of September (Appendix 2.3). Thus, juveniles do not appear at the waterhole before the age of two months. In 1994, Namaqua Sandgrouse started nesting in relatively large numbers by at least the middle of August. Despite the earlier start to nesting, and a considerably greater nesting density (due to a larger population) in the 1994 season compared with the 1993 season (Table 2.3), the total number of belly-soaking males was approximately the same by the start of December in each year (Appendix 2.3). On 3 December 1994, after four months of nesting activity, only four juvenile males were counted at the waterhole among a drinking population of a little over 9000. Due to the difficulty of identifying juveniles in a large drinking population, this is undoubtedly an undercount, but there were certainly no more than 15. Assuming a 1:1 sex ratio, this gives a total juvenile count of no more than 30. Three months later, in early March 1995, very few juvenile males were counted at the waterhole. In neither 1995 nor 1996 were more than ten juvenile male sandgrouse counted among the drinking population (Appendix 2.3).

Annual recruitment estimates for the Namaqua Sandgrouse varied substantially between localities and between seasons at the same locality (Table 2.4, Appendix 2.4).

Recruitment estimates ranged from minima of 3-33% (assuming juveniles are distinguishable for two months) to maxima of 5-66% (assuming juveniles are distinguishable for one month).

From a total of 16 definite family groups (the adult pair with juveniles) observed at waterholes in Bushmanland and the Kalahari during the period of the study, the average number of juveniles per family group was 1.69 and no family included three juveniles. Maclean (1968) similarly noted that it was rare to find more than two large young in a family group in the Kalahari Gemsbok National Park.

Table 2.4. Estimated annual sandgrouse recruitment from monthly adult:juvenile ratios in waterhole counts (Yellowthroated Sandgrouse = YTS; Tarboton & Blane unpublished) or from monthly belly-soaking frequencies (Namaqua Sandgrouse = NS; see methods) using the assumption that juveniles are distinguishable from adults for either one month (Recruitment 1) or two months (Recruitment 2). See Appendix 2.4 for details of monthly waterhole counts. KGNP = Kalahari Gemsbok National Park. See Figure 7.1 for a map of the listed localities.

	% Belly-soakers	Recruitment 1	Recruitment 2
YTS 1988-92 (average)	59	36	18
NS Droëgrond 1993-94	31[1]	19	10
NS Droëgrond 1994-95	9	6	3
NS Droëgrond 1995-96	16-33	10-20	5-10
NS Soetdoring 1994-95	17	10	5
NS Soetdoring 1995-96	13	8	4
NS KGNP 1995-96	108	66	33
NS Pioneer 1994-95	32	20	10
NS Chyandour 1994-95	42-83	25-51	13-25
NS Langberg 1994-95	9	5	3
NS Langberg 1995-96	33	20	10

[1] Assumes that the belly-soaking total recorded in Appendix 2.4 is representative of only half the 1993-94 breeding season.

DISCUSSION

Egg laying, incubation and hatching

By laying an egg every second day, Namaqua Sandgrouse reduce the daily nutritional demands on females during the egg-laying period. Because the male assists in protecting the eggs, the female is allowed more time to feed during this nutritionally demanding time. Maclean (1968) was of the opinion that incubation in the Namaqua Sandgrouse started with the first egg of the clutch, the male incubating at all times of the day, but my observations do not support this. The presence of a bird on incomplete clutches during only hot, sunny weather suggests that it is only there to protect the eggs from the heat of the sun. It was not determined whether the birds actually incubated the eggs during this time. Captive Doublebanded Sandgrouse sat on the eggs of incomplete clutches for much longer periods in hot weather, but were not thought to be incubating (Hinsley & Hockey 1989). J. F. Reynolds in Cramp *et al.* (1985) observed that in the Chestnutbellied Sandgrouse *P. exustus*, the incomplete clutch was covered by the male through the day, but after clutch completion, the female incubated during the day and the male at night. No mention was made of overnight incubation during the laying period. The incomplete clutch is left unattended overnight in both the Pintailed and Spotted Sandgrouse (Marchant 1961). Marchant (1961) noted that the incomplete clutch of both species was incubated by the female during daylight. As he did not observe nests for any length of time, and as the female was always closely attended by the male, one probably cannot be certain that the female was at the nest simply to lay an egg rather than to incubate as such. Doublebanded Sandgrouse in captivity began incubation with the laying of the last egg (Hinsley & Hockey 1989). The incomplete clutch is therefore allowed to cool down overnight, which would delay egg development until the clutch is complete. This behaviour is probably responsible for the observed synchronous hatching of sandgrouse chicks.

Maclean (1968) reported that the male Namaqua Sandgrouse returns to the vicinity of the nest after drinking, but I found no evidence of such behaviour. George (1969) recorded that the male Spotted Sandgrouse remains nearby while the female is incubating, giving warning calls at the approach of danger, but Marchant (1961) writes for both Spotted and Pintailed Sandgrouse that "once the female is on the eggs during full incubation I never saw the male approach the nest nor even suspected its presence within the range of ordinary observation". In the Doublebanded Courser *Rhinoptilus africanus*, the presence of the nonincubating mate in the nest vicinity (acting as a sentinel to warn the incubating bird of approaching danger) may substantially reduce predation risk (see Chapter 9). Were sandgrouse to engage in similar behaviour, they might reduce predation risk in a similar fashion. The differences in the reported behaviour of different sandgrouse species may depend on food availability in the nest surrounds. The Namaqua Sandgrouse studied here invariably nested some distance from areas of suitable food availability, which would explain why the birds incubated alone.

Maclean (1968) reports that, after being relieved at the nest in the afternoon, the female flies again to drink, but supplied no corroborating evidence. The small numbers of females counted drinking in the afternoon during the breeding season in this study suggest that incubating females do not often drink a second time. Despite being exposed to extreme temperatures while incubating in summer, female Namaqua Sandgrouse may not need to drink more than once a day due to their efficient thermoregulatory and osmoregulatory adaptations (Thomas & Maclean 1981; Thomas 1984). Incubating females have just over three hours of daylight in which to fly to and from the nest, to drink and to feed. Drinking more than once a day would, therefore, increase energy expended on flight and reduce the already limited time for feeding. The combination of these factors probably explains why incubating females do not generally drink twice a day.

Synchronous hatching of the chicks is advantageous for two reasons. Firstly, the exploratory movements of the precocial chicks around the exposed nest site could attract the attention of a passing predator. Secondly, because food availability around the nest site is generally scarce and the chicks are self feeding, they must usually walk some distance to the closest site of suitable food supply after hatching. Synchronous hatching therefore ensures that the first-hatching chick does not wait too long before feeding properly for the first time.

Nesting success

In 1993, Namaqua Sandgrouse at Droëgrond were nesting during drought conditions towards the end of an exceptionally dry two year period. Most bird species in the arid zone breed after rainfall (see Chapter 10). As one of the few species nesting at a time when food availability for potential nest predators was low, Namaqua Sandgrouse were expected to have suffered higher nest-predation rates than normal. Nest predation was, however, lower in 1993 than in the following three years. This can be largely attributed to much reduced predation by mammalian predators, whose populations may have been reduced by the drought. Suricate populations are known to crash during drought conditions (Clutton-Brock *et al.* in press). Predation by the Eggeating Snake, on the other hand, was at its highest level in the 1993 season. Snakes are generally more tolerant of food deprivation than are mammals, and may not have been as hard hit by the drought.

Although sandgrouse nest-predation rates did vary between years, the magnitude of this variability ($CV = 4\%$; Table 9.7) was relatively small when compared to the variance in annual rainfall ($CV = 51\%$) and changes in relative nest density (Table 2.3). However, because predation rates were so high, relatively small changes in nest predation resulted in appreciable changes in nesting success. For example, the 7% increase in nest predation between 1993 and 1994 resulted in a 44% reduction in nesting success. These predation rates are among the highest reported for any bird (Ricklefs 1969a, Martin 1993), and four consecutive years of data strongly suggest that they are sustained over the medium to long term.

Although they were the principal, and clearly very important, predators of Namaqua Sandgrouse nests, the small mammals in this region are primarily insectivorous (Smithers 1983, Cavallini & Nel 1995). Despite the high nutritional reward of finding a bird's nest, these mammals do not appear to specialise on birds' nests as food, even when nest density increases dramatically. The available evidence suggests that they locate the nests accidentally during their daily foraging movements in search of insect food (see Chapter 4). When insect food is less abundant, these animals probably have to travel greater distances while foraging, increasing the probability of finding birds' nests. This would seem the most likely explanation for the observed decrease in daily predation rates as the season progressed from late winter into summer during the 1994 breeding season (Fig. 2.2; see also Chapter 9).

Chick development and survival

Data on chick development were not collected in this study. Maclean (1968) estimated that at the age of three weeks, Namaqua Sandgrouse chicks were almost fully feathered, but unable to fly, and flew capably only at the age of approximately six weeks. Doublebanded Sandgrouse chicks can fly strongly at the age of four weeks though (Hinsley & Hockey 1989). Maclean's (1968) estimation that juveniles fly to the waterhole to drink for the first time at the age of approximately two months is supported by my observations showing that juveniles did not appear at the waterhole until at least two months after nests started hatching. Likewise, Tarboton & Blane (unpublished) found that juvenile Yellowthroated Sandgrouse appeared at the waterhole (nearly adult sized) approximately two months after males in the population started belly-soaking. A captive-bred juvenile female Doublebanded Sandgrouse had a pale, dusty-looking version of female plumage at three months and moulted into adult plumage at the age of 3-6 months (Hinsley & Hockey 1989).

At Droëgrond, estimates of annual recruitment varied substantially between seasons (Table 2.4). The smaller proportion of belly-soaking males in the 1994 season was a reflection of the reduced nest survival (due to higher nest predation) in that year. Sandgrouse are known to lay replacement clutches following nest predation, with laying intervals between successive clutches as short as four days in captive birds (Grummt 1985, Wilkinson & Manning 1986). Frisch (1970) reports that a captive Pintailed Sandgrouse began laying again one day and seven days after the death of the chicks of previous broods. Therefore, the very low estimate of recruitment (3-6%; Table 2.4) in the 1994-95 season, despite an extended breeding season and nesting success of 7.6% (Table 2.2), suggests that predation on the chicks after hatching, and before they reach independence, may be substantial.

Sex ratios

The male-biased sex ratio observed at Droëgrond (1.28:1; Appendix 2.3) is similar to the sex ratio in hunting bags at the Langberg for birds shot during both a breeding season (1.36:1, n = 375 birds) and a nonbreeding season (1.31:1, n = 437 birds). Tarboton and Blane (unpublished) similarly noted a male-biased sex ratio (1.35:1, n = 7307 birds) in the Yellowthroated Sandgrouse. This bias is not due to differential mortality on incubating birds, as no adult mortality on the nest was noted. Two possible explanatory hypotheses deserve further study; males may have a longer life expectancy than females, or the bias may be due to facultative manipulation of sex ratios. Shelley Hinsley (pers. comm.) observed a captive female Doublebanded Sandgrouse that left its first brood in the care of the male parent and laid a second clutch with another male. Should such behaviour occur in the wild, it could provide the selective basis for facultative sex ratio manipulation (Gowaty 1991).

Conservation concerns

The predation rates observed at Droëgrond are probably representative of the Bushmanland region (uniform in habitat and topography) as a whole, which is a core area for this species in South Africa, particularly during the breeding season (Harrison *et al.* 1997). The average nest-predation rate for Namaqua Sandgrouse at Droëgrond (91.0%) is considerably higher than the 53.9% recorded for a stable Yellowthroated Sandgrouse population (Tarboton & Blane unpublished). Furthermore, estimated annual recruitment for Namaqua Sandgrouse at Droëgrond and several other sites was generally less than half that estimated for Yellowthroated Sandgrouse (Table 2.4). The only exceptions were at Chyandour and the Kalahari Gemsbok National Park.

Nest failure rates greater than 70% have been implicated in population declines in shrubsteppe passerines on the Iberian Peninsula (Suárez *et al.* 1993, Yanes & Suárez 1995) and Neotropical migrants (Sherry & Holmes 1992, Böhning-Gaese *et al.* 1993, Donovan *et al.* 1995, Hoover *et al.* 1995). These declines are thought to be caused by unnaturally elevated nest-predation rates due, in turn, to either edge effect resulting from habitat fragmentation (Wilcove 1985, Sherry & Holmes 1992, Paxton 1994, Donovan *et al.* 1995, Hoover *et al.* 1995), or increasing densities of small, generalist predators following the anthropogenic exclusion of top predators (Eisenberg *et al.* 1979, Glanz 1982, Emmons 1984, Soulé *et al.* 1988).

Habitat fragmentation is not an issue at Droëgrond, and the high predation rates were not the result of abnormal events in a stochastic environment, as there was little interannual variation in predation intensity despite considerable variation in rainfall, and therefore the productivity of the environment (Tables 2.2 and 9.7). The study site at Droëgrond is, however, in a sheep farming region where top predators (Blackbacked Jackal *Canis mesomelas*, Caracal *Caracal caracal* and large raptors) have been subjected to intense control programmes that involve the use of poisons, traps and hunting. The Tawny Eagle *Aquila rapax*, an important predator on small mammals (Clutton-Brock *et al.* in press), has disappeared from the Bushmanland region within the last 100 years (Boshoff *et al.* 1983).

Daily nest-predation rates on Namaqua Sandgrouse were significantly lower in the Kalahari Gemsbok National Park, where an entirely natural complement of predators is present, than they were at Droëgrond. Although the high estimated annual recruitment at the Kalahari Gemsbok National Park during the 1995-96 season (33-66%) is due partly to the very extended breeding season, the high proportion of belly-soaking males within months (Appendix 2.4) supports the suggestion of a higher level of nesting success at this site. A case could, therefore, be made for mesopredator release (*sensu* Soulé *et al.* 1988) being responsible for the higher nest predation at Droëgrond. However, this argument is weakened by the finding that nest-predation rates did not differ significantly between these two sites when a variety of bird species is considered, although additional factors may have complicated this result (see Chapter 9).

A possible contributing factor to the high nest-predation rates at Droëgrond is the abundance of harvester termites (Hodotermitidae) in the Bushmanland region. The small mammals that are the principal nest predators are primarily insectivorous, and harvester termites are important dietary items. These subterranean insects emerge on the ground surface to forage for vegetable matter at irregular intervals, where they are easy prey for a variety of predators (Coaton 1958, Dean 1993). Animals can also scratch open frass mounds to expose worker termites. Not only are these termites very abundant in the Bushmanland Nama Karoo, but they are active year round (Dean 1993, pers. obs.). This rather predictable food supply in an otherwise unpredictable and highly variable environment may help to maintain relatively dense small mammal populations.

Without data on average annual adult survival, it is difficult to evaluate whether annual recruitment of 3-20% is sufficient to maintain populations over the long term. Annual adult mortality among charadriiforms, to which sandgrouse are most closely related, is commonly 20-40% (Boyd 1962, Brooke & Birkhead 1991, Gill 1995). This suggests that, if the relatively low productivity of the Namaqua Sandgrouse is sustained in the long term within the core Bushmanland region, a population decline is likely to result. Long-term records for a hunting estate in the Northern Cape show an apparent Namaqua Sandgrouse population decline between 1950 and 1992, but this may be an artefact of increased sandgrouse dispersion in response to an increased number of artificial watering points being constructed over this period (Little *et al.* 1996).

In summary, the present status of the Namaqua Sandgrouse in South Africa is uncertain. While its annual productivity, within the Bushmanland region at least, appears to be too low to maintain populations, there is no irrefutable evidence of a population decline. Future studies should determine a) annual adult survival, and b) more accurate and longer-term estimates of breeding success in various regions of the Namaqua Sandgrouse's distribution, particularly in areas where harvester termites are absent, and in hyperarid regions (such as the Namib desert) where conditions are unfavourable for small mammals. These studies should be coupled with an investigation of the degree of movement of breeding populations between these different regions, for such movement may mask poor reproductive output in certain regions.

Appendix 2.1. Summary of observations at Namaqua Sandgrouse nests during the egg-laying period.

Nest No.	Date	Time	Eggs	Comments
16	29 Oct	11h10	0	Pair at empty nest scrape.
	30 Oct	09h20	1	Bird on nest.
		16h50	1	No bird on nest.
	31 Oct	18h00	2	No bird on nest.
	01 Nov	07h15	2	No bird on nest. ♂ flew in at 08h04 to sit on eggs.
	02 Nov	17h40	3	♂ incubating
175	18 Oct	11h45	0	Pair at empty nest scrape.
	19 Oct	05h40	1	No bird on nest. Egg laid previous day.
		19h05	1	No bird on nest.
	20 Oct	05h25	1	No bird on nest. Camera set.
		±11h05		Pair arrive together - ♂ & ♀ move on and off nest.
		±11h18		♀ settles on nest.
		±11h58		♀ leaves nest, and pair leave together. No bird returns for rest of the day.
		19h25	2	
	21 Oct	06h18	2	No bird on nest. Camera set.
		±09h44		♂ arrives to sit on eggs.
		±15h23		♂ leaves nest.
		19h15	2	
	22 Oct	06h20	2	No bird on nest. Camera set.
		±08h47		Pair arrive together. ♂ on nest, then ♀ on nest.
		±08h54		♀ settles on nest & ♂ leaves.
		±16h30		♀ leaves nest.
		±17h18		♂ arrives to incubate.
		19h10	3	♂ on nest.
195	22 Oct	10h55	0	Pair at empty nest scrape.
	23 Oct	14h40	1	♂ on nest.
	24 Oct		0	Nest predation.
109	27 Sep	14h45	1	Pair on nest. Egg probably just laid.
	28 Sep	15h20	1	
	29 Sep	16h55	2	
	30 Sep	06h05	2	No bird on nest.
		19h07	2	No bird on nest.
	01 Oct	06h19	2	No bird on nest.
		18h37	3	
123	30 Sep	15h00	1	♀ on nest, ♂ nearby. Egg probably just laid.
	01 Oct	17h00	1	No bird on nest.
	02 Oct	06h32	1	No bird on nest. Camera set.
		±09h37		Pair arrive together. ♀ onto nest, ♂ remaining near nest, periodically approaching ♀ until ±12h11, when ♂ left.
		±16h01	2	♀ walks off nest & leaves.
		19h03	2	No bird on nest.
	03 Oct	06h16		No bird on nest. Camera set.
		±08h18		♂ arrives to sit on eggs.
		±15h00	2	♂ walks off nest, stands for 4 mins, then leaves.
		19h38	2	No bird on nest.
	04 Oct	06h38	3	No bird on nest.
		14h00		♀ incubating.

Appendix 2.1. *continued*

Nest No.	Date	Time	Eggs	Comments
28	17 Nov	08h30	1	♀ flew in alone to nest at 08h23.
	18 Nov	18h40	2	No bird on nest.
	19 Nov	15h55	1	♂ on nest. One egg lost to *Dasypeltis* predation.
	20 Nov	05h25	1	No bird on nest, egg cold.
		10h25		♀ sitting tight.
		17h35	2	♂ incubating, clutch complete.
141	05 Oct	14h55	1	Bird on nest.
	06 Oct	14h45	2	
	07 Oct	11h35	2	No bird on nest, due to rain overnight and during the morning.
	08 Oct	12h45	3	♀ incubating.
153	11 Oct	13h15	1	♂ on nest.
	12 Oct	06h00	1	No bird on nest. Camera set.
		±09h34		Pair arrive together, ♀ onto nest.
		±09h45		♀ still on nest, ♂ seen for the last time.
		±12h30		♀ still on nest. Camera stops.
		18h55	2	No bird on nest.
	13 Oct	06h29	2	No bird on nest. Camera set.
		±09h00		♂ arrives to sit on eggs.
		±14h28		♂ leaves.
		19h11	2	No bird on nest.
	14 Oct	06h12	2	No bird on nest. Camera set.
		±08h27		♂ arrives & sits on eggs.
		±08h42		♀ approaches nest & relieves ♂. ♂ remains near nest for 4 mins before leaving.
		±17h24		♀ leaves nest.
		±17h37		♂ arrives on nest.
		±18h04		♂ standing off nest for 3 mins, then no bird in view for 3 mins.
		±18h10		Several suricates eating the eggs. ♂ returns to check nest after they have left.
221	22 Nov	11h10	1	♂ on nest.
	23 Nov	16h40	2	
	24 Nov	16h30	2	
	27 Nov		0	Predation.
234	29 Nov	09h15	1	♀ on nest.
	30 Nov	13h55		♂ sitting tight.
	01 Dec		0	Predation.
121	29 Sep	15h15	2	♂ on nest.
	30 Sep	14h35	2	♂ on nest.
	01 Oct	17h15	2	♂ incubating, clutch complete.
226	23 Nov	13h30	2	♂ on nest.
	24 Nov	07h00	2	♂ on nest, ♀ nearby.
	28 Nov		0	Predation.
30	17 Nov	15h55	2	
	18 Nov	18h55	2	No bird on nest.
	19 Nov	15h35	3	♀ incubating.

Appendix 2.1. *continued*

Nest No.	Date	Time	Eggs	Comments
GM*	22 Nov	14h40	2	♀ sitting on eggs.
	23 Nov	06h40	2	No bird on nest - eggs cold.
		11h30	2	♂ sitting on eggs.
	25 Nov	12h30	3	♀ incubating.
85	21 Sep	14h30	2	♂ on nest.
	22 Sep	10h30	3	
107	27 Sep	09h45	2	Single bird flew in to nest at 09h11.
	28 Sep	11h10	3	♀ incubating.
165	15 Oct	09h25	2	♂ on nest.
	16 Oct	10h30	3	♀ incubating.
194	22 Oct	11h20	2	♂ on nest. Single bird flew in to nest at 08h28.
	23 Oct	14h20	3	♀ incubating.
225	23 Nov	09h20	2	♂ on nest. Single bird flew in to nest at 07h53.
	24 Nov	17h20	3	♀ incubating.
240	09 Sep	10h00	2	♀ on nest. Single bird flew in to nest at 09h28.
	10 Sep	18h10	3	
265	05 Nov	09h30	2	♀ on nest. Single bird flew in to nest at 08h40.
	09 Nov	15h00	3	♀ incubating.
103	26 Sep	08h45	2	No bird on nest overnight, or at this time.
		10h00	3	♀ incubating.

*Nest observed by Gordon Maclean (1968)

Appendix 2.2. Summary of observations at Namaqua Sandgrouse nests at the hatching stage.

Nest No.	Date	Time	Eggs	Comments
1	14 Oct	09h15	3	
	15 Oct	11h10	0	Chicks crouched separately 1-2 m from nest.
2	23 Oct	10h50	3	
		18h00	2	1 newly hatched chick in nest.
	24 Oct	06h00	2	
		07h00	1	2nd chick hatched.
		11h15	0	3rd chick hatched.
		15h45		3 chicks in nest.
	25 Oct	05h45		No sign of adults or chicks - left previous afternoon.
9	23 Oct	10h40	3	
	24 Oct	15h40	0	3 chicks in nest.
	25 Oct	06h00		♂ brooding chicks in nest. ♀ arrived to relieve ♂ at 07h40, the latter flying off to collect water.
25	25 Nov	16h00	2	1 freshly hatched chick - feathers still wet.
	26 Nov	05h30	1	2 chicks in nest - 2nd hatched previous afternoon.
		10h00	0	3rd chick hatched.
32	23 Nov	05h50	2	1 freshly hatched chick - feathers still wet.
		08h00	1	2nd chick hatched.
		10h15	0	3rd chick hatched.
46	18 Aug	16h50	3	
	19 Aug	14h30	0	3 chicks, none properly dry & one freshly hatched - all hatched today.
57	13 Sep	12h00	3	
		17h37	1	2 chicks in nest.
	14 Sep	15h00	0	No sign of birds - chicks have left nest.
99	15 Oct	06h30	3	
		18h20	2	1 chick in nest.
	16 Oct	06h00	2	
		08h25	0	2nd & 3rd chicks hatched together.
119	11 Oct	10h45	3	
		18h35	0	3 chicks in a scrape 20 m from nest.
175	22 Oct		3	3rd egg laid in late morning.
	11 Nov	18h35	3	
	12 Nov	09h50	1	2 chicks hatched this morning - neither properly dry.
		15h15	0	2 chicks dry, 3rd half dry.
180	19 Oct	18h20	2	1 freshly hatched chick.
	20 Oct	06h00	2	
		11h10	1	2nd chick hatched.
	21 Oct	16h40	0	No sign of birds - have left nest.
198	12 Nov	06h40	2	1 freshly hatched chick - feathers still wet.
		15h45	1	2nd chick not quite dry, 3rd egg about to hatch.
	13 Nov	15h45	0	No sign of birds - have left nest.
209	23 Nov	13h40	2	1 chick not dry, so recently hatched.
	24 Nov	05h20	1	2 chicks in nest.
		09h00	1	3rd egg about to hatch.
210	23 Nov	13h25	2	1 chick not dry, so recently hatched.
	24 Nov	07h00	1	2 chicks in nest.
		08h55	1	3rd egg hatching - the lid about to fall off.
216	23 Nov	14h20	3	
	24 Nov	19h00	0	3 chicks in a scrape 3 m from nest.

Appendix 2.3. Summary of Namaqua Sandgrouse population counts at Droëgrond from 1993 to 1996, including the number of belly-soaking males and juvenile males as an indicator of breeding activity and nesting success.

Date	Total population	Subtotal population	No. belly-soaking males	No. juvenile males	Sex ratio ♂ : ♀
21 Sep '93	323		1		
28 Sep '93	344		5		
11 Oct '93	480		8		42:27
22 Oct '93		40	5		26:13
28 Oct '93	889		67		
05 Nov '93	945		66		189:67
18 Nov '93	1048		105		180:90
02 May '94	8700		6		120:120
17 May '94	10800				
15 Jun '94	5000				
24 Jun '94	3002	2623	10		
13 Jul '94	5600				68:57
05 Aug '94	4100				
18 Aug '94	5872	2370	6		
21 Aug '94		3300	3		40:33
27 Aug '94	11052				
13 Sep '94	7150		13		
22 Sep '94		697	5		
28 Sep '94	7027				
05 Oct '94		886	11		103:89
15 Oct '94		410	5		
24 Oct '94		945	14		
12 Nov '94	6858	1237	35		244:198
21 Nov '94		680	29		105:66
24 Nov '94		604	26		69:54
29 Nov '94	8376				
03 Dec '94	9032		115	4	
10 Mar '95	8430	280	4	0	108:89
16 Mar '95		3600	20	2	64:63
08 Apr '95	1817	449	5	3	144:118
14 Apr '95	719	246	3	2	120:115
02 May '95	65		0	0	
05 Jun '95	48		0	0	
08 Sep'95	287		1	0	99:86
04 Oct '95	309	222	5	0	44:33
17 Oct '95	319		6	0	152:120
31 Oct '95	243		10	0	119:93
12 Nov '95		295	23	1	92:83
14 Nov '95		656	13	7	222:182
04 Dec '95	64		2	4	39:25
20 Jan '96	917		19	1	131:89
03 May '96	422	59	3	1	29:24
10 May '96	419	136	6	2	64:51
24 Sep '96	1269	661	0	0	289:256
30 Sep '96		2258	6		
16 Oct '96	2098	493	1	0	222:193
29 Nov '96		283	2	2	152:131
14 Dec '96		640	12	3	
					3276:2565
					1.28:1

Appendix 2.4. Counts of adults and the frequencies of belly-soaking males and juveniles (Yellowthroated Sandgrouse only) for the Yellowthroated Sandgrouse (1988-1992) and Namaqua Sandgrouse at various localities.

	Yellowthroated Sg.			Droëgrond '93-94		Droëgrond '94-95		Droëgrond '95-96		Droëgrond '96-97		Soetdoring '94-95		Soetdoring '95-96	
Month	Adults	% B-s.	% Juv.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.
1	275	0	0.36				0.08*					2086	0	495	0
2	243	0	0			5670	0.16					2730	0.37	665	0.60
3	286	0	0	667	0.90	7847	0.23	287	0.35	2919	0.21	812	3.57	1539	2.60
4	254	0	0	1409	5.68	2241	1.34	784	2.68	493	0.20	844	3.55		2.99*
5	679	0	0	1993	8.58	2521	3.57	951	3.79	283	0.71	650	0.92	974	3.39
6	829	3.14	0			9032	1.27	64	3.13	640	1.88	1749	1.32	924	1.84
7	1348	10.53	0.37				0.31*	917	2.07			2799	3.36	723	1.52
8	1042	10.56	1.82				0.31*					1432	2.23		
9	858	11.66	2.56			3880	0.62					1742	1.61		
10	981	17.13	13.05			695	1.15					674	0		
11	339	5.90	6.49	8700	0.07	65	0	195	4.62						
12	168	0	11.31	2623	0.38							396	0		
Totals		58.91	35.97		15.61		9.04		16.62				16.93		12.94

continued

	KGNP '95-96		KGNP '96-97		Pioneer '94-95		Chandour '94-95		Langberg '94-95		Langberg '95-96	
Month	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.	Adults	% B-s.
1			741	5.13	1498	1.07	245	0.41	398	0	710	0
2	849	2.47	825	5.70	748	3.34	214	0.93			3587	0.72
3	571	8.41				7.05*	268	0.75			925	7.35
4		13.35*			400	10.75	151	11.26				6.13*
5	1022	18.30			437	7.55	143	12.59	267	0.75	204	4.90
6	1433	11.58			519	2.50	209	15.79		1.44*	1144	0.96
7	915	8.63								1.44*	1007	3.87
8	735	10.88								1.44*		2.53*
9	944	11.55							47	2.13		2.53*
10	1054	11.29								1.15*		2.53*
11	460	5.43							580	0.17	5804	1.19
12	393	5.60							1412	0.35		0.59*
Totals		107.50				32.26		41.72		8.87		33.32

*Missing data points calculated as the average between the preceding and following counts.

CHAPTER THREE

INVESTIGATOR EFFECTS ON THE NESTING SUCCESS OF ARID-ZONE BIRDS

SUMMARY

This study examined whether regular researcher visits affected egg survival or nest predation for three ground-nesting bird species. Daily predation rates on Namaqua Sandgrouse *Pterocles namaqua* nests were not significantly different from those expected under conditions of a constant average predation rate, indicating daily visits had no cumulative effect on predation probabilities. Frequently visited finchlark nests suffered similar predation to infrequently visited nests, suggesting regular visits had no additive effects on nest survival. Nests of both Greybacked Finchlark *Eremopterix verticalis* and Blackeared Finchlark *E. australis* discovered at the egg stage did not produce significantly fewer young than nests discovered at the nestling stage, suggesting investigator disturbance had no effect on egg survival. These results from the southern hemisphere subtropics support the findings of limited north-temperate studies that mammalian nest predation does not increase after researcher disturbance.

INTRODUCTION

Nests of birds must usually be visited regularly by an investigator if breeding success is to be determined. The disturbance associated with regular nest visits may, however, affect the success of the sample of nests under observation (reviewed in Götmark 1992). Visiting a nest can influence breeding success in a number of ways: (1) birds that defend their nests against predators, either actively or passively, leave their nests vulnerable to predation when displaced (MacInnes and Misra 1972, Strang 1980, Westmoreland and Best 1985); (2) predators may be attracted to the vicinity of the nest by the presence of the investigator (Liversidge 1970, Veen 1977, Strang 1980, Götmark *et al.* 1990), by nest markers left as aids for future visits (Picozzi 1975, Hamas 1984, Reynolds 1985, Greenwood and Sargeant 1995), or by the distraction or alarm behaviours of the displaced birds (Hammond and Forward 1956); (3) predators may follow the observer's tracks or scent to a nest (Liversidge 1970, Bowen *et al.* 1976) or be repelled by these (MacIvor *et al.* 1990, Mayer-Gross *et al.* 1997), or be attracted by the scent of faeces deposited by a bird frightened off its nest (Clark and Wobeser 1997); (4) exposure of the eggs or nestlings to the elements when the parent is displaced may reduce their survival (White and Thurow 1985, Piatt *et al.* 1990); and (5) nest abandonment may be increased (Steenhof and Kochert 1982, Piatt *et al.* 1990).

In his review of the effects of investigator disturbance on nesting birds, Götmark (1992) noted that of 225 studies, only 6% emanated from regions of the world other than North America and Europe. Furthermore, where predators were identified, avian predators dominated in 40 studies and mammals in only 17. Götmark (1992) found little evidence of increased predation by mammals, despite widespread belief that mammalian predators pose a great threat to nests visited by researchers.

Nest predation is reported to be generally higher in tropical than in north temperate regions (Skutch 1949, Ricklefs 1969a), where mammals or snakes are the dominant predators. In the arid, subtropical ecosystem at Droëgrond, where small mammals were the principal nest predators, nest-predation rates were commonly 70-80% and as high as 96% between species (Chapters 2 & 9). Furthermore, hatching success was as low as 86%. These results, particularly the extreme predation levels, lead to concerns about the possible influence of investigator effects (c.f. Götmark 1992). This chapter examines investigator effects on egg survival and nest predation of three ground-nesting species, the Namaqua Sandgrouse, Greybacked Finchlark and Blackeared Finchlark, to ensure unbiased estimates of nesting success.

STUDY AREA AND METHODS

The study was conducted over four summer seasons (August-December 1993-1996) in an area of 10 000 ha on the farm Droëgrond. The characteristics of the study site are detailed in Chapter 2.

Nest predators were identified most accurately for the Namaqua Sandgrouse (Chapter 2), and are assumed to be similar for other ground-nesting species. The principal predators on Namaqua Sandgrouse nests were small mammals, including the Yellow Mongoose *Cynictis penicillata*, Cape Grey Mongoose *Galerella pulverulenta*, Striped Polecat *Ictonyx striatus* and

Suricate *Suricata suricatta* (71% of nest losses), a specialist egg predator, the Rhombic Eggeating Snake *Dasypeltis scabra* (20% of nest losses), and larger mammals, including the Bateared Fox *Otocyon megalotis*, Cape Fox *Vulpes chama*, Aardwolf *Proteles cristatus* and Antbear *Orycteropus afer* (9% of nest losses). Other snakes (all common to the study site) suspected of preying on nestlings of altricial species include the Cape Cobra *Naja nivea*, Namib Sand Snake *Psammophis leightoni*, Namib Tiger Snake *Telescopus beetzii* and Horned Adder *Bitis caudalis*. No avian nest predators occurred at the study site.

The Namaqua Sandgrouse lays a clutch of three eggs in a shallow scrape, usually fully exposed to the elements (Chapter 2). These cryptic birds generally sit tight on the nest during the approach of a predator (Maclean 1968, pers. obs.), relying on camouflage to avoid detection. The nest of both Greybacked and Blackeared Finchlark consists of a cup of dry grass and rootlets sunk into a neat scrape in the soil, with the lip level with the soil surface. Nests are sited against the base of a low grass tuft or herb, with a predominantly easterly to southerly aspect to gain some shade during the hottest times of the day. Clutch size ranges from 1-5 in the Greybacked Finchlark and from 1-4 in the Blackeared Finchlark, but is commonly 2-3 for both species (Maclean 1970a, Chapter 9).

Nests were marked as inconspicuously as possible, 10-20 m from the nest, with either a small folded square of white toilet paper spiked on a shrub (mimicking a common flower) or by placing one stone on top of another. An arrow drawn in the sand indicated the bearing of the nest from the marker. Nests were visited while cycling a mountain bike. This left a track in the sand, together with footprints near the nest when the observer stopped to check the nest contents. An effort was made to approach nests from a different direction on each visit. All nests were found randomly within the 10 000 ha study area. Namaqua Sandgrouse nests found over the four breeding seasons (1993-1996) were combined for analysis. Finchlark nests were located in the 1996 breeding season only.

Namaqua Sandgrouse nests were located at random through the 25 day nesting period (4 days laying and 21 days incubation), by following birds flying to the nest to relieve their mates, and monitored once a day thereafter. The incubating bird was either flushed or induced to walk off the nest; the contents being checked from a short distance using binoculars. When flushed, the bird flew up noisily, giving an alarm call, sometimes landing a short distance away to give a "broken-wing" distraction display. If the act of visiting a nest influences the probability of subsequent predation, repeated nest visits should magnify this effect due to the ever increasing number of tracks leading to the nest. If predators are attracted, predation rates would be expected to increase, and if they are repelled, would be expected to decrease over time.

Daily predation rates were determined using the method of Mayfield (1975) described in Chapter 2. Because the sample of active nests decreases with time, progressively longer time classes were used to maintain roughly equivalent exposure levels (216-335 nest days) between classes. The time classes used were: 1, 2, 3, 4-5, 6-7, 8-9, 10-12 and 13-25 days under observation. The standard error of each estimator was determined using the method of Johnson (1979).

Finchlark nests were located opportunistically by searching for flushing birds while cycling a mountain bike throughout the study area. These birds were used to test whether nesting success was different between nests visited frequently and infrequently. Nests were paired by species and clutch size in the order that they were found, thus randomising nest selection for each of the two groups, but controlling for possible clutch-size and interspecific differences in predation vulnerability. The frequently visited sample was revisited at least every second day. Because finchlark chicks may leave the nest from the age of seven days, nests in the infrequently visited group were visited every six days. Predation rates were lower on nestlings than on eggs (Chapter 9), but because nests were assigned randomly to the two groups, and always at an unknown stage in the incubation period, this difference was controlled for. The incubating bird was flushed to check the nest's contents on each visit.

To test whether observer disturbance affected the survival of finchlark eggs, the number of chicks fledging from nests discovered during incubation was compared with the number fledging from nests discovered at the nestling stage. Because the adults commonly removed eggs that failed to hatch, I could not determine the hatching success of nests found at the nestling stage.

RESULTS

From a total of 278 Namaqua Sandgrouse nests observed, 182 predation losses occurred over 1 987 nest days. The daily predation rate decreased from 11.5% after one day under observation, to 5.2% after 6-7 days, increasing to 9.6% thereafter (Fig. 3.1). The observed predation frequencies did not differ significantly from those expected under conditions of a constant average predation rate ($\chi^2_7 = 9.51$, $P > 0.05$).

Frequently visited finchlark nests did not incur significantly higher levels of predation than infrequently visited nests at either day 6 or day 12 of the observation period (Table 3.1). For both finchlark species, the mean number of chicks fledged from nests discovered during incubation compared with nests discovered during the nestling period were not significantly different (Table 3.2).

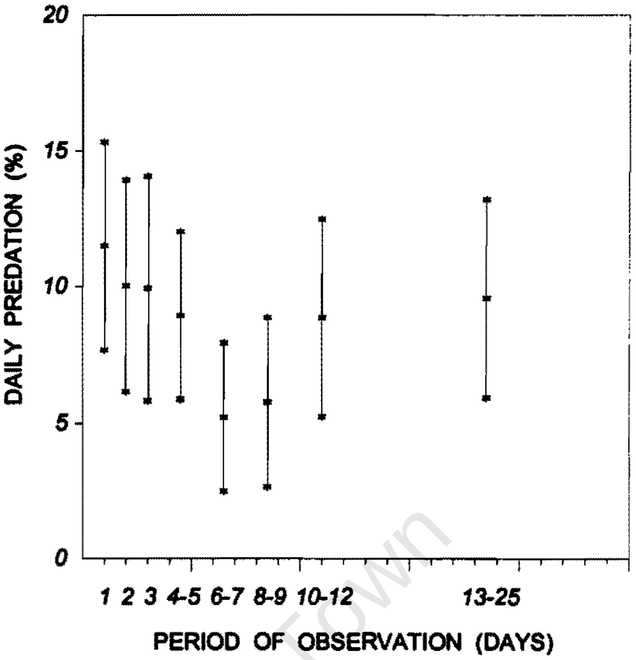

Figure 3.1. Daily predation rates on Namaqua Sandgrouse nests through the period of observation, with 95% confidence intervals (± 2 *S.E.*) indicated. The number of days under observation equals the number of prior visits to the nests. Nests located in four consecutive breeding seasons (1993-1996) at Droëgrond were combined in this analysis. Observed predation frequencies did not differ significantly from those expected under conditions of a constant average predation rate ($\chi^2_7 = 9.513$, $P > 0.05$).

Table 3.1. Number and fate of finchlark nests visited frequently (at least every second day) and infrequently (every 6 days) at day 6 and day 12 of the observation period, during the 1996 breeding season at Droëgrond.

	Frequently visited		Infrequently visited	
	Day 6[a]	Day 12[b]	Day 6	Day 12
Survived	51	33	55	29
Predation	31	41	27	42
Total	82	75	82	71

[a] $\chi^2_1 = 0.240$, $P > 0.05$ (with the Yates correction)

[b] $\chi^2_1 = 0.083$, $P > 0.05$ (with the Yates correction)

Table 3.2. Number of chicks fledging from nests discovered at the egg stage *versus* those discovered at the nestling stage for the Blackeared Finchlark *E. australis* and Greybacked Finchlark *E. verticalis*, during the 1996 breeding season at Droëgrond.

	E. australis		*E. verticalis*	
Stage found	Egg	Nestling	Egg	Nestling
Mean	2.10[a]	2.08[a]	2.36[b]	2.25[b]
s.d.	0.83	0.67	0.85	0.68
n	31	12	42	24

[a]Mann-Whitney $U_{12,31} = 179, P > 0.05$
[b]Mann-Whitney $U_{24,42} = 458.5, P > 0.05$

DISCUSSION

Namaqua Sandgrouse suffered consistently high clutch predation levels, from 85% to 93%, over four consecutive breeding seasons (Chapter 2). This led to concern that small mammal predators were locating nests by following the observer's tracks or scent to the vicinity of the nest, resulting in an unnaturally high predation rate. As there is no clear causal explanation for the roughly parabolic nature of the observed relationship between daily predation rate and the period of observation, which is equivalent to the number of nest visits (Fig. 3.1), it seems prudent to ascribe the observed pattern to sampling variability. There was certainly no increasing trend in predation probability, which would be expected if the predators were following the observer's tracks to the nest. This conclusion is supported by the lack of evidence of a difference in the levels of predation on frequently *versus* infrequently visited finchlark nests (Table 3.1). In his review, Götmark (1992) found no evidence for increased predation by mammals, despite a widely held belief that mammalian predators would pose a great threat to nests visited by researchers. In fact, in a study on plovers, MacIvor *et al.* (1990) found that foxes may avoid nest sites with human scent. Mayer-Gross *et al.* (1997) and Osborne and Osborne (1980) found evidence to suggest a similar effect. At Droëgrond, small mammal predators regularly fall victim to traps and poisons set for larger predators in this sheep-farming region. They could therefore be expected to avoid sites showing evidence of human activity. Only Liversidge (1970) has documented a case where a mammalian predator, in this case the Vervet Monkey *Cercopithecus pygerythrus*, first watched and then followed the researcher's route to plunder nests. These results from the southern hemisphere subtropics therefore support the findings of limited north temperate studies (see Götmark 1992) that mammalian nest predation does not increase in response to researcher disturbance.

In Blackeared and Greybacked Finchlark nests, 13% and 14% of all eggs failed to hatch (Chapter 9). To monitor the nests, the incubating bird was flushed, exposing the eggs to temperature extremes and the possibility of increased egg death. Although several studies in temperate regions have found evidence for such an effect (reviewed in Götmark 1992), this study showing that nests found during incubation did not produce fewer young than nests found at the nestling stage (Table 3.2), suggests that observer disturbance had no deleterious effect on finchlark egg survival.

CHAPTER FOUR

NEST-SITE SELECTION, EGG PIGMENTATION AND CLUTCH PREDATION IN THE NAMAQUA SANDGROUSE

SUMMARY

Nest survival can, among a variety of factors, depend on nest-site complexity and concealment, and clutch crypsis. Nest-site selection by Namaqua Sandgrouse *Pterocles namaqua* was strongly non-random. Nests were sited within a local concentration of objects, most of them less than 15 cm high and concentrated within 30 cm of the nest centre. Nest-object orientation was random, indicating that the nest was sited close to objects neither for shade nor shelter from prevailing winds. A discriminant function analysis, using nine different object type, height and distance category totals as variables, failed to discriminate nest fate (survival *versus* mammal predation), suggesting that variability in nest-site complexity and concealment was subject to neutral selection. A random-walk model simulating the foraging movements of a small-mammal predator raised the possibility that the high level of nest predation suffered by Namaqua Sandgrouse was largely incidental (i.e. random).

Namaqua Sandgrouse eggs are highly variable in appearance, but intra-clutch variability was found to be less than that between clutches of different individuals. Intra-clutch diversity in pigment cover, the number of wreathed eggs, the dominant pigment pattern, and the overall shade of the clutch (light/dark) did not affect clutch survival. However, clutches exhibiting diversity in background colour, pigment pattern or pigment intensity between eggs survived significantly better than clutches whose eggs were uniform for these variables, suggesting there is some selection for clutch crypsis through visual diversity.

INTRODUCTION

Clutch predation is a major cause of reproductive loss in birds (Ricklefs 1969a, Martin & Clobert 1996), and is considered to be a strong selective force in nest-site selection (Martin 1988, Schieck

& Hannon 1993). Certainly, a growing body of evidence shows that birds can identify nest sites with characteristics that reduce the risk of predation (Bekoff *et al.* 1987, Martin & Roper 1988, Marzluff 1988, Möller 1988, Kelly 1993). Among shrub and tree-nesting species, nest success is often greater for more concealed nests or those in sites with greater micro or macrohabitat complexity (Osborne & Osborne 1980, Martin & Roper 1988, Kelly 1993, Rivera-Milán 1996). A similar effect has been found for several ground-nesting species, mostly from well vegetated sites (Schrank 1972, Bowman & Harris 1980, Hill 1984a, Schieck & Hannon 1993, Gregg *et al.* 1994).

Ground-nesting birds in flat, sparsely vegetated habitats often site their nests beside objects or clumps of vegetation. Suggested advantages of this behaviour include protection from the weather, either as a wind-break (Tomkins 1944) or sun-shield (Maclean 1970a, With & Webb 1993), and concealment from predators through "disruptive effects" (Croze 1970, Graul 1975, Hockey 1982). Many species, particularly within the order Charadriiformes, possess cryptically-pigmented eggs, and Hockey (1982) suggested that within-clutch differences in egg markings should increase nest complexity and hence the crypsis of the clutch.

This chapter examines nest-microhabitat and egg-appearance variables in relation to clutch predation to test hypotheses concerning the adaptiveness of nest-site selection and clutch pigmentation in the Namaqua Sandgrouse, a species that incurred 85-93% nest predation over four consecutive breeding seasons, primarily by small-mammal predators (Chapter 2).

STUDY AREA AND METHODS

The study was conducted over the summer breeding season August-December 1994 on the farm Droëgrond. Study site characteristics are detailed in Chapter 2, and nests were monitored as described in Chapter 3.

Nest site

Once the nesting attempt had ended, the habitat (arid grassland, arid grassland with scattered shrub patches, arid shrubland, or rocky rise), presence of stones in the vicinity of the nest (none, pale stones only, dark stones only, or mixed pale and dark stones), and substratum surrounding the nest (fine sand, coarse sand, pebbles, or stones/rock) were noted. In addition, the height of and distance to all objects in each of four quadrants (north, east, south and west) within a 1 m radius of the nest centre were recorded. These measurements were repeated for a control point 2 m to the north of each nest. Objects were classified as solid (stones, dense grass tufts and shrubs) or sparse (spindly grass tufts and shrublets).

To test whether nests were sited to garner shade from the sun or protection from the prevailing winds, the numbers of objects around nests were compared for each of the four orientations. To test whether nest-site placement was random in relation to objects in the immediate vicinity, the object totals from five height classes (3-4 cm, 5-9 cm, 10-14 cm, 15-29 cm and ≥30 cm) were compared for each of two distance classes (0-29 cm and 30-100 cm) at nests, and between the nest sites and control points.

To investigate the adaptive importance of a concentration of objects around the nest to crypsis and concealment, discriminant function analysis (DFA) was run on the object totals of nine different object type (solid or sparse), height (3-9 cm or ≥10 cm) and distance (0-29 cm or 30-100 cm from the nest) variables. Solid objects were distinguished from sparse objects by their differing ability to conceal the nest site. A 10 cm height threshold was used since an incubating sandgrouse sat approximately this high. A 30 cm distance threshold was used since the greatest concentration of objects occurred within a 30 cm radius of the nest. Since crypsis and concealment were not likely to be effective against the Rhombic Eggeating Snake *Dasypeltis scabra*, nests lost to mammal predation were compared with those that survived to hatch, ignoring nests lost to snakes.

Predation frequencies were compared between nest habitat and microhabitat variable categories to determine whether predation was random at these levels.

Egg pigmentation

Using photographs of the eggs, together with the shells if their collection after depredation was possible, the background colour (1 or 2; cream or beige), pigment cover (from 50 point grid), pigment patterning (1-4 for speckled, speckled/spotted, spotted, and blotched respectively), pigment intensity (1 or 2; light or dark) and presence or absence of a pigment concentration into a wreath at one end of the egg were recorded for each egg.

To test the hypothesis that darker clutches survived better than lighter clutches (the substratum was invariably darker than the eggs), two variables were used in a DFA. The first was the average pigment cover for the clutch. The second was derived by summing the dominant background colour and the dominant pigment intensity within the clutch, which quantified the general shade of the eggs from pale to relatively dark on a scale of 2 to 4. To test the hypothesis that visual diversity within the clutch enhanced clutch crypsis, and hence clutch survival, two variables were used in a DFA. The first was diversity in pigment cover, calculated as the largest difference in pigment cover between eggs within the clutch. The second was the number of wreathed eggs within the clutch. Furthermore, the survival of clutches exhibiting within-clutch differences in background colour, pigment intensity or pigment pattern was compared to clutches showing uniformity for all three variables. All the above analyses considered 3-egg clutches only, comparing nests that hatched to those lost to mammal predation, and thus ignoring those lost to snakes.

Predator-simulation model

The prevailing predator avoidance behaviour of the Namaqua Sandgrouse is to sit tight on the nest during the approach of a predator, relying on its cryptic plumage to avoid visual detection (Maclean 1968, pers. obs.). The incubating bird generally flushes directly off the nest at a minimum distance of 2 m from a predator. The Yellow Mongoose *Cynictis penicillata* has a primarily insectivorous diet (Smithers 1983), but was one of the principal nest predators at the study site (Chapter 2).

A simple random walk model was developed to simulate the success of a Yellow Mongoose *Cynictis penicillata* in locating sandgrouse nests opportunistically during its daily movements by flushing the incubating birds. In habitat largely similar to that of the study site, the Yellow Mongoose had a mean home range size (minimum convex polygon) of 102 ha, moved (linear distance between successive locations recorded every 15 min) 3.2 km/day and had a density of 6-7 individuals/100 ha (Cavallini & Nel 1995). The model estimated the success of nest location by a single animal covering 3.2 km/day within a 100 ha area during a typical 25-day sandgrouse nesting period. The model area, in which 10 nests were randomly placed, was divided into 640 000 1.25 m x 1.25 m cells. The daily foraging route of a mongoose was simulated as a random walk, assuming that the mongoose moved predominantly in a forward direction ($p = 0.65$), had an equal probability of turning to either side ($p = 0.15$) and rarely ($p = 0.05$) backtracked on its path. These probabilities approximate the natural foraging behaviour of mongooses (Paulo Cavallini and Jan Nel, pers. comm.). Boundary conditions were defined such that if the mongoose reached the border of the model area, new co-ordinates were randomly assigned within the model area. The mongoose's daily starting point (den) was the centre of the model area. Nests were recorded as located if the nest cell midpoint fell within the path of the mongoose, assuming that the mongoose moved between cell midpoints and was capable of detecting all nests within a 1.77 m radius of itself (i.e. nests occupying any of the eight surrounding cells). Mean incidental nest predation was estimated as the mean proportion of nests found over a 25-day period, averaged over 100 simulations. A brief sensitivity analysis was conducted to test the sensitivity of model results to nest density, location path width and daily distance travelled by the mongoose. Furthermore, predator density was increased to estimate the number of predators necessary to simulate predation rates of the same magnitude as those observed in the field.

RESULTS

Nest site

There were no significant differences in the orientation of objects (north, east, south, west) of different height at different distances from the nest (Table 4.1). The object totals among height classes were significantly different between the nest site and the point 2 m to the north for both the 0-29 cm and 30-100 cm distance classes (Table 4.2). On average, the number of objects within a 1 m radius of the nest was nearly double that within 1 m of the control point 2 m to the north of the nest. Furthermore, compared to control points, nests had proportionally more objects within 30 cm

Table 4.1. Total objects in different distance classes in the four orientations within a 1 m radius of Namaqua Sandgrouse nests (n = 146). Chi-square tests testing whether the distribution of objects within height classes was random with respect to orientation around the nest were non-significant (all objects: χ^2_{15} = 18.55, *n.s.*; objects ≥ 15 cm high: χ^2_9 = 9.27, *n.s.*).

Distance Classes (cm)	Orientation			
	N	E	S	W
	All objects (≥ 3 cm high)			
0-9	46	43	50	45
10-14	61	61	50	70
15-19	40	39	37	38
20-29	70	69	80	68
30-49	113	127	115	110
50-100	374	469	440	450
Totals	704	808	772	781
	Objects ≥ 15 cm high			
0-9	9	13	10	11
10-14	8	9	5	6
15-29	16	8	18	8
30-100	48	49	52	46
Totals	81	79	85	71

of the nest than 30-100 cm distant (Table 4.2). These results indicate that Namaqua Sandgrouse chose to site their nests within a local concentration of objects, most of which were less than 15 cm high, but which were not orientated to provide shade from the sun (north to north-west during the hottest part of the day) or protection from the prevailing northerly and westerly winds.

The discriminant function analysis was unable to discriminate between successful and failed nests using the nine object type, height and distance categories (Table 4.3). There were also no significant relationships between nest fate and the nest-site variables of habitat, substratum, and presence of stones around the nest (Table

Table 4.2. Total objects (*n* = 146 sites) in height-distance classes, within a 1 m radius of Namaqua Sandgrouse nests, and a point 2 m to the north of each nest. The object totals among height classes were significantly different between the nest site and the point 2 m to the north for both the 0-29 cm (χ^2_4 = 18.34, $P < 0.01$) and 30-100 cm (χ^2_4 = 13.80, $P < 0.01$) distance classes.

Distance classes (cm)	Height classes (cm)					
	3-4	5-9	10-14	15-29	$30	Totals
			Nest site			
0-29[a]	26	35	12	82	40	867
30-100[b]	85	92	22	149	46	219
Totals	1115	1284	349	231	86	3065
Ratio a/b	0.3	0.3	0.5	0.55	0.8	0.3
			2m north			
0-29[c]	10	7	23	26		22
30-100[d]	60	57	11	68	34	1394
Totals	70	64	140	94	40	1622
Ratio c/d	0.1	0.1	0.2	0.38	0.1	0.1

Table 4.3. Results of the discriminant function analysis testing whether nests that survived to hatch and those that failed to mammal predation differed with respect to object totals within various object type, height and distance classes within a 1 m radius of the nest. No significant differences (at $P < 0.05$) were detected in the analysis of variance.

Object type, height and distance from nest	Hatched *n* = 31 Mean (*s.d.*)	Predation *n* = 87 Mean (*s.d.*)	Pooled *n* = 118 Mean (*s.d.*)	Range	*F* statistic
Solid: ht. <10 cm 0-29 cm dist.	3.42 (2.64)	3.99 (3.17)	3.84 (3.04)	0-14	0.80
Sparse: ht. <10 cm 0-29 cm dist.	0.26 (0.58)	0.37 (0.88)	0.34 (0.81)	0-6	0.42
Solid: ht. <10 cm 30-100 cm dist.	9.61 (7.84)	11.17 (8.02)	10.76 (7.98)	0-30	0.87
Sparse: ht. <10 cm 30-100 cm dist.	0.84 (1.32)	1.01 (2.96)	0.97 (2.63)	0-19	0.10
Solid: ht. $10 cm 0-29 cm dist.	0.45 (0.72)	0.30 (0.57)	0.34 (0.62)	0-2	1.41
Sparse: ht. $10 cm 0-29 cm dist.	1.19 (1.11)	1.01 (1.40)	1.06 (1.33)	0-6	0.43
Solid: ht. $10 cm 30-100 cm dist.	0.74 (1.41)	1.00 (1.95)	0.93 (1.82)	0-14	0.46
Sparse: ht. $10 cm 30-100 cm dist.	1.71 (1.74)	1.82 (3.82)	1.79 (3.41)	0-27	0.02
Total	18.23 (9.81)	21.40 (11.77)	20.57 (11.30)	3-62	1.81

4. 4).

Table 4.4. Observed predation frequencies among samples of nests from different habitats and microhabitats compared with frequencies expected if predation was random. Variable codes: habitat (1 = arid grassland; 2 = arid grassland with shrub patches; 3 = arid shrubland; 4 = rocky rise); stones in nest vicinity (1 = none; 2 = pale stones only; 3 = dark stones only; 4 = mixed pale and dark stones); substratum surrounding nest (1 = fine sand; 2 = coarse sand; 3 = pebbles; 4 = stones or rock). Chi-square *P* values given.

	Variable code				
Variable	1	2	3	4	*P*
Habitat	10 (10.68)	25 (19.22)	79 (83.99)	7 (7.12)	0.56
Stones in nest vicinity	31 (33.24)	51 (45.79)	9 (10.34)	22 (23.63)	0.75
Substratum	12 (11.82)	80 (81.24)	16 (14.03)	5 (5.91)	0.88

Egg pigmentation

Namaqua Sandgrouse eggs were remarkably variable in appearance (Fig. 4.1). Eggs that were sparsely pigmented with a light pigment over a cream background appeared pale, but those that were heavily and darkly pigmented on a darker beige background appeared brown. Pigment pattern varied from fine speckling throughout, to marble-sized blotching, with some eggs possessing a concentration of pigment into a wreath at one end of the egg (Fig. 4.1). Inter-clutch variation was generally greater than intra-clutch variation. A clutch tended to contain eggs of the same pigment pattern (Table 4.5), and wreathed eggs were non-randomly distributed among clutches; clutches containing 2 or 3 wreathed eggs occurred at a significantly higher frequency than expected (Table 4.6).

Table 4.5. The variability of egg pigment pattern within clutches, expressed as the number of clutches containing eggs exhibiting the different pigment pattern extremes (n = 168 clutches).

	Pigment pattern code		
Pigment pattern code	1	2	3
1 (speckled)	57		
2 (speckled/spotted)	27	50	
3 (spotted or blotched)	6	12	16

Table 4.6. The observed *versus* expected (if random) frequency distributions of wreathed (light or heavy pigment concentration at one end) eggs among 3-egg Namaqua Sandgrouse clutches (χ^2_2 = 45.90, P < 0.001).

No. of wreathed eggs in the clutch				
0	1	2	3	Total clutches
97 (108.43)	19 (25.29)	14 (5.90)	11 (1.38)	141 (141)

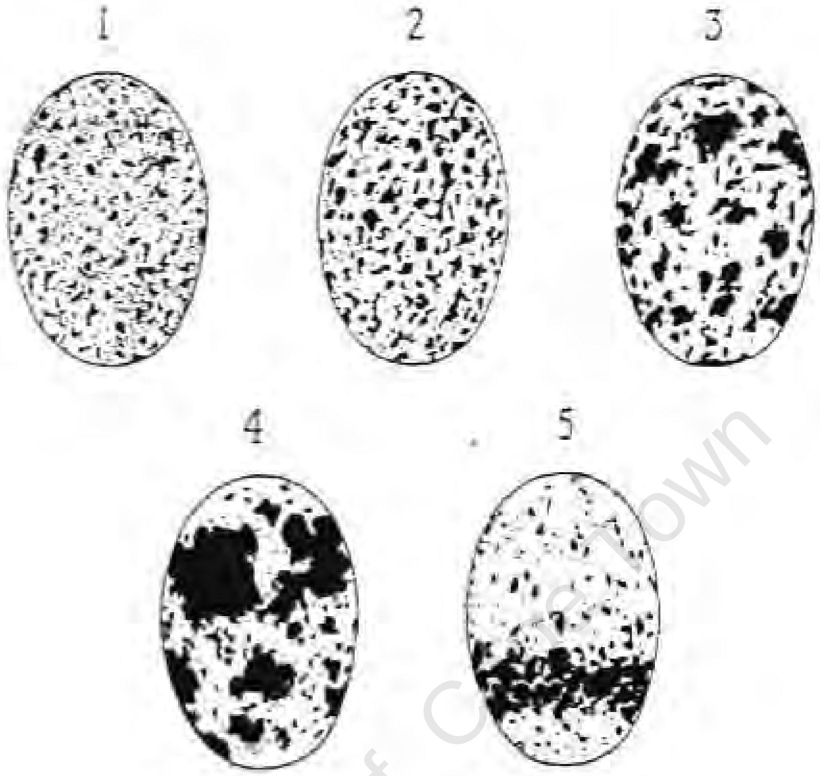

Figure 4.1. A sample of Namaqua Sandgrouse eggs, illustrating the range of variation in egg appearance encountered at Droegrond. 1 = speckled, 2 = speckled/spotted, 3 = spotted, 4 = blotched, 5 = wreathed.

The fate of nests was independent of clutch pigment pattern and substrate type (Table 4.7). The DFA was unable to discriminate successful from failed nests using clutch pigment cover and shade (light-dark) as variables (Table 4.8), suggesting that darker eggs survived no better than pale eggs on a predominantly dark background. While within-clutch variability in pigment cover and the number of wreathed eggs had no discernible effect on clutch fate, within-clutch diversity in background colour, pigment intensity or pigment pattern did appear to enhance clutch survival. Clutches exhibiting inter-egg differences in one or more of the latter three variables incurred significantly less predation than clutches whose eggs were uniform with respect to these variables (Table 4.9).

Table 4.7. Observed predation frequencies among Namaqua Sandgrouse clutches of different dominant egg patterns on different substrata compared with expected frequencies if predation was random (in brackets). Lumping the speckled/spotted and spotted, and pebbles and stones/rock categories to ensure minimum expected frequencies of 5, predation on clutches of different dominant egg pattern was independent of the substratum surrounding the nest ($\chi^2_3 = 0.64$, *n.s.*).

Substratum surrounding the nest	Dominant egg pattern of clutch			Total predation	Total hatched
	Speckled	Speckled/spotted	Spotted		
Fine sand	5 (4.71)	2 (4.04)	3 (1.25)	10	4
Coarse sand	36 (32.94)	29 (28.31)	5 (8.75)	70	30
Pebbles	4 (5.65)	8 (4.85)	0 (1.50)	12	3
Stones/rock	3 (1.88)	0 (1.62)	1 (0.50)	4	3
Total predation	48 (45.18)	39 (38.82)	9 (12)	96	
Total hatched	16	16	8		40

Table 4.8. Results of the discriminant function analyses testing whether nests that survived to hatch and those that failed to mammal predation differed for 1) clutch pigment cover and shade (light-dark) variables, or 2) intraclutch variability in pigment cover and the number of wreathed eggs. No significant differences (at $P < 0.05$) were detected in the analysis of variance.

Variable	Hatched $n = 34$ Mean (*s.d.*)	Predation $n = 80$ Mean (*s.d.*)	Pooled $n = 114$ Mean (*s.d.*)	Range	*F* statistic
Pigment cover	0.49 (0.11)	0.49 (0.12)	0.49 (0.12)	0.22-0.78	0.00
Clutch shade	3.18 (0.72)	3.09 (0.83)	3.12 (0.80)	2-4	0.37
Cover diversity	0.17 (0.10)	0.16 (0.08)	0.17 (0.09)	0.02-0.40	0.31
Wreathed eggs	0.74 (1.16)	0.60 (0.92)	0.64 (1.00)	0-3	0.44

Table 4.9. A 2x2 contingency table comparison of mammal predation frequencies between nests exhibiting inter-egg differences in background colour, pigment pattern or pigment intensity codes, and clutches uniform for these variables. Yates corrected $\chi^2_1 = 5.60$, $P < 0.02$.

	Diversity	Uniformity	Totals
Predation	18	80	98
Hatched	16	25	41
Totals	34	105	139

Predator-simulation model

The simulated mongoose located 22% of nests within its home range using a location radius of 1.77 m. The results of the sensitivity analysis are presented in Figure 4.2. The simulated relationship between the proportion of nests found and the number of predators increased in a non-linear fashion towards a maximum of 1, which can be described by an asymptotic exponential function $\alpha(1\text{-}e^{-\beta x})$ with upper limit $\alpha = 1$ (Fig. 4.3). An increase in the number of predators results in a less than proportional increase in predation because of the increased overlap in the search areas of the predators. Under the assumptions of the model, predator densities of 9-10 animals per 100 ha can account for predation rates of 88-92%.

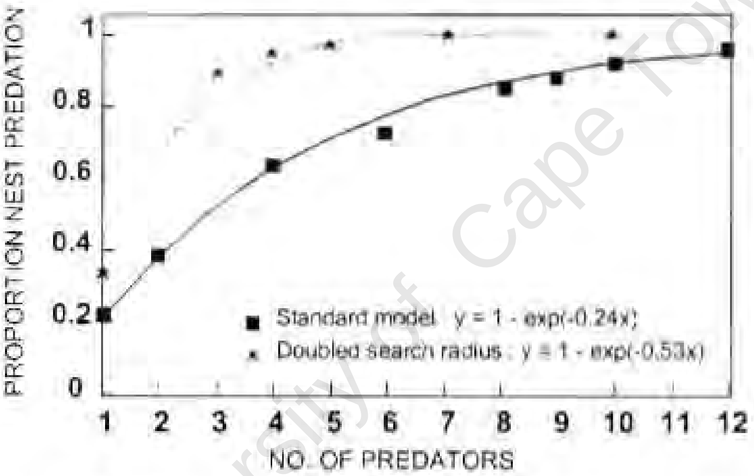

Figure 4.3. The simulated relationship between the proportion of nests found and the number of mongoose predators moving randomly in a 100 ha area over a 25-day period.

DISCUSSION

Nest site

Namaqua Sandgrouse sited their nests within a local concentration of low objects, but not in a manner to gain protection from the elements (Tables 4.1 & 4.2). This suggests that these objects might be important for the disruptive camouflage or concealment of the incubating bird in what was generally a rather exposed nest site. Despite considerable variation in the number of objects of different categories (which served as indices of both complexity and concealment) around the nest, the discriminant function analysis failed to discriminate nest fate using these variables (Table 4.3). Increased complexity and/or concealment therefore appeared to have no selective advantage in reducing nest predation among the nests sampled. Investigator-disturbance effects were ruled out by a parallel study which showed that predation probabilities were unaffected by the frequency of nest visits or the length of time nests were under observation (Chapter 3).

Nest predation may not be altogether random though. Most ground-nesting species in the arid regions of southern Africa site their nests at the base of small herbs, stones and grass tufts to get at least some shade during the hottest times of the day (Maclean 1970a, Chapter 9), when ground temperatures regularly exceed 45°C (Dixon & Louw 1978). However, few birds ever use a medium to large shrub for this purpose, despite the better provision of shade, probably because small-mammal predators frequent the vicinity of shrubs, either for shade or cover from aerial predators while out foraging (Clutton-Brock *et al.* in press). Furthermore, the strongly non-random choice of nest site by Namaqua Sandgrouse suggests there must be some selective advantage to be had.

Clutch pigmentation

Hockey (1982) found consistent differences in the patterns of pigmentation between eggs within African Black Oystercatcher *Haematopus moquini* clutches, but similar patterns between females. Namaqua Sandgrouse exhibited the opposite trend for differential pigmentation; differences were greater between females than within clutches (Tables 4.5 & 4.6). Such phenotypic variability may be maintained if the trait is under neutral selection or if it hinders the development of effective search images among visual predators that learn by experience (Tinbergen 1960, Owen & Whiteley 1986). The few Namaqua Sandgrouse clutches exhibiting diversity in background colour, pigment pattern or pigment intensity between eggs survived significantly better than clutches whose eggs were uniform for these variables (Table 4.9), suggesting there is some selection for clutch crypsis through increased nest complexity (Hockey 1982). It was surprising then that neither diversity in pigment cover within the clutch, nor the presence of wreaths disrupting the shape of the egg conferred a similar advantage (Table 4.8). Future experimental studies should test more rigorously the importance of the various clutch pigmentation variables to clutch crypsis and survival.

Predator-simulation model

Under the assumptions of the model, which are considered conservative, a single Yellow Mongoose could locate 22% of nests by flushing the incubating bird within a 1.77 m radius during its normal daily movements. Furthermore, a density of only 9-10 "mongoose units" per 100 ha is required to locate 90% of all sandgrouse nests on a purely incidental (random) basis (Fig. 4.2). Yellow Mongoose densities are probably higher than assumed in the model; reported densities vary from 2.9 individuals per 100 ha (P. Howard, 1994, unpublished PhD thesis, University of Pretoria) to 6-7 individuals per 100 ha (Cavallini & Nel 1995) in largely similar habitats. Although predator density estimates are not available, the study site supports healthy populations of a variety of other recorded nest predators, including the Cape Grey Mongoose *Galerella pulverulenta*, Striped Polecat *Ictonyx striatus*, Suricate *Suricata suricatta*, Bateared Fox *Otocyon megalotis*, Cape Fox *Vulpes chama*, Aardwolf *Proteles cristatus*, Aardvark *Orycteropus afer*, Cape Cobra *Naja nivea*, and the Rhombic Eggeating Snake (see Chapter 2), all of which are likely to have overlapping home ranges. In a North American study, Vickery *et al.* (1992) found that incidental nest predation by a single species, the Striped Skunk *Mephitis mephitis*, accounted for nest losses of 58% in grassland birds. It is, therefore, conceivable that nest-predation rates of roughly 90%, as recorded for Namaqua Sandgrouse (Chapter 5), are largely the result of incidental (i.e. random) nest predation by a spectrum of predators that commonly occur at the study site. The lack of a significant relationship between any of the nest-site variables and nest survival, supports such a hypothesis. Howlett and Stutchbury (1996), after finding a similar lack of a relationship between degree of nest concealment and survival in the Hooded Warbler *Wilsonia citrina* (50% nest predation), concluded that such an outcome is expected if nest predation is the result of nonspecialist predation that occurs by chance.

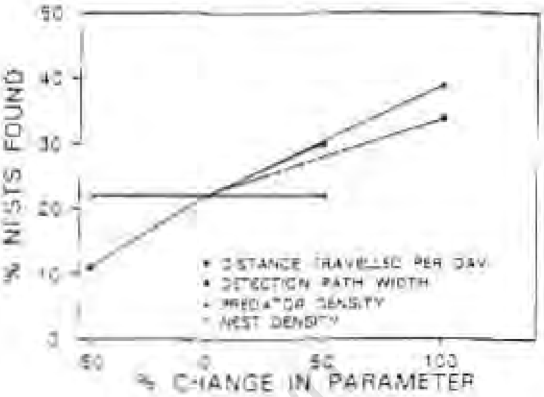

Figure 4.2 A brief sensitivity analysis of the predator-simulation model, showing how changes in each parameter affect the proportion of Namaqua Sandgrouse nests that are found.

CHAPTER FIVE

THE DAILY ACTIVITY PATTERN OF A NONBREEDING NAMAQUA SANDGROUSE POPULATION

SUMMARY

The daily activity pattern of a winter, nonbreeding Namaqua Sandgrouse *Pterocles namaqua* population with a superabundant food supply is described and compared with that of a summer, breeding population with a more limited food supply. The nonbreeding population moved *en masse* between a communal roost, a primary drinking point and two primary feeding sites each day. These birds spent approximately six hours feeding and 3 h 30 min engaged in activities not associated with feeding or breeding on the roosting site and around the watering site each day, but displayed no sign of breeding over a 5-month period. The breeding population spent approximately 12 hours a day on feeding sites, and spent little time drinking or on the roosts. These observations suggest that good food availability is not necessarily a proximate stimulus for breeding in this species.

INTRODUCTION

The Namaqua Sandgrouse is a medium sized (180 g) granivore specialised for life in the arid zone of southern Africa. Feeding almost exclusively (the chicks included) on the seeds of annual plants (Chapter 6), this species derives little preformed water from its diet, and must therefore drink regularly from normally widely dispersed sources of open water (Thomas 1984). One of the best documented features of sandgrouse behaviour is their well synchronised flights to water, where sometimes many thousands of birds may gather to drink together (Ward 1972). The question of how often individual birds fly to drink is still open to some speculation, however. Thomas and Maclean (1981) found that Namaqua Sandgrouse housed in an aviary in the Namib Desert, and exposed to summer conditions without water for three days suffered no ill effects. Although birds lost 3.4 g/100 g body mass per day on average, they made up 86 % of the lost mass at their first drink after dehydration. As the amount of water imbibed after the dehydration experiment was similar to that consumed during single drinking opportunities observed in the field, they concluded that Namaqua Sandgrouse individuals do not drink daily, but may last 3-5 days between drinks if not provoked to prolonged muscular activity in the interim. Little *et al.* (1993) made repeated observations over eight consecutive days of tagged birds appearing at three watering sites in an effort to determine drinking frequencies in the field. Their findings were somewhat inconclusive: some individuals drank on up to four consecutive days, but less than 50 % of tagged birds appeared on any single day. Because local population density estimates are based on the numbers of sandgrouse counted at waterholes (Thomas 1984, Little *et al.* 1993), it is important to determine drinking frequencies more accurately.

The timing of Namaqua Sandgrouse breeding seasons varies considerably across its southern African range (McLachlan 1985, Chapter 3). While other southern African sandgrouse species start breeding in early winter, when seed food availability peaks after the end of the late-summer rainy season (Skinner 1996, Harrison *et al.* 1997, Tarboton & Blane unpublished), some Namaqua Sandgrouse populations may start breeding up to five months after peak food availability, for reasons that are not particularly clear (Chapter 7).

This study examines the daily activity pattern of a local population of Namaqua Sandgrouse over a period of four months following a significant seed production event that resulted from good seasonal late-summer rains. My observations provide some new insights into the behaviour and drinking frequencies of nonbreeding Namaqua Sandgrouse, and demonstrate that this species does not necessarily breed when local food availability is maximal.

STUDY AREA AND METHODS

The study was conducted over the winter months April-August 1994 in an area between Prynnsberg farm (28°44'S 22°09'E) and the Orange River near Groblershoop, Northern Cape Province, South Africa. The vegetation at the study site consists of Shrubby Kalahari Dune Bushveld interspersed with raised areas of calcrete, sparsely vegetated with low shrubs of the

Karroid Kalahari Bushveld veld type (Low & Rebelo 1997). The area received good rains between January and March, which meant that annual plants grew well, and had set large quantities of seed by the end of April. The availability of legume seed (the chosen food of Namaqua Sandgrouse) at feeding sites was as high as 9.9 g/m^2 from April to August (Chapter 7). The seasonal influx of Namaqua Sandgrouse to the area occurred in March/April, most birds moving out again in August/September (Chapter 7).

The first two weeks of the study were spent observing the daily movements of sandgrouse and identifying their principal watering, roosting and feeding sites within the study area. Thereafter their daily activity pattern was quantified by counting the number of birds flying (within 5-min time periods) in different directions over vantage points along the principal flight lines between watering, roosting and feeding sites.

As a comparison, the activity pattern of a breeding population experiencing more limited food availability was quantified in a similar way on the farm Droëgrond (29°07'S 20°16'E) in the summer of 1994. Legume seed availability reached 4.5 g/m^2 at feeding sites on Droëgrond at this time (Chapter 7).

RESULTS

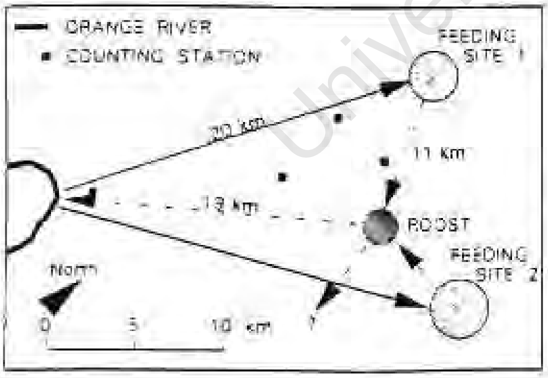

Figure 5.1 Map of the Prynnsberg study site, indicating the locations of the principal roosting, drinking and feeding sites, and points at which overflying sandgrouse were counted.

Between April and August, the Namaqua Sandgrouse at Prynnsberg exhibited a standard daily activity pattern. Eleven days of observations in June determined that the birds remained on their communal roosting site, on average, for the first 1 hr 45 min (see Figs 5.1 & 5.2). Thereafter there was a highly synchronised flight to the principal watering site on the banks of the Orange River, 19 km distant. Several morning watches conducted at points between the communal roost and feeding site 1 confirmed that very few birds left the roost before the synchronised flight to water. A number of birds flew from the roost to an unidentified watering point to the south, which accounts for the discrepancies between the roosting total and the total number of birds counted flying towards the Orange River drinking site (Fig. 5.2).

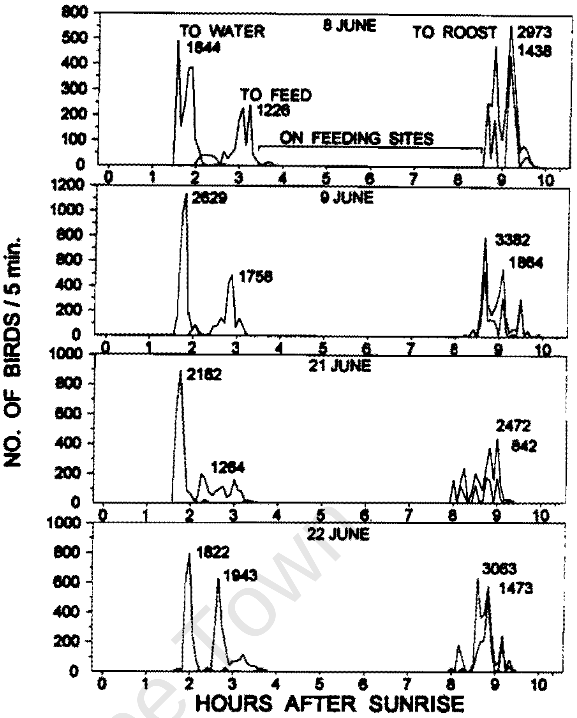

Figure 5.2. The daily movement pattern of a nonbreeding population of Namaqua Sandgrouse at Prynnsberg quantified as the number of birds flying past counting stations within 5-min intervals. Birds were counted leaving the roosting site (grey), arriving at feeding site 1 (black), and arriving at the roosting site. The roosting count is expressed as the total arriving from feeding sites 1 and 2 (grey), and the contribution from feeding site 1 (black). Sunrise at 07h20 and sunset at 17h40.

Counts from a vantage point near the latter drinking site established that most birds flew directly there (Fig. 5.3). Some flocks arriving up to 50 min later probably landed somewhere *en route*. The flocks did not drink immediately on arrival, but landed and waited for an average of 25 min before drinking. This staging behaviour is characteristic of a nonbreeding population (pers. obs.). The flocks generally waited until the first small flock ventured to the water's edge to drink. The sight of these birds taking off after drinking successfully normally precipitated a mass drinking response among the gathered birds. After drinking, the flocks flew directly to one of two main feeding sites, one to the northwest and the other to the northeast of the roost site. There the birds remained feeding until between one and two hours before sunset, whereupon they flew in waves back to the communal roosting site, arriving on average 1 h 20 min before sunset.

A notable characteristic of Namaqua Sandgrouse behaviour at Prynnsberg during the winter season of 1994 was the high degree of sociality they exhibited. The birds generally flew between localities in large flocks numbering up to several hundred, and the daily movements of the local population were well synchronised. This population spent an average of 6 h 05 min on the feeding sites and 3 h 30 min engaged in nonessential activities ("loafing") on the roost and around the drinking point each day. Namaqua Sandgrouse flying parallel with a moving vehicle were estimated to fly at a speed of 80 km/h. The time taken to cover the daily distance of 50 km (Fig. 5.1) was therefore estimated to be 45 min.

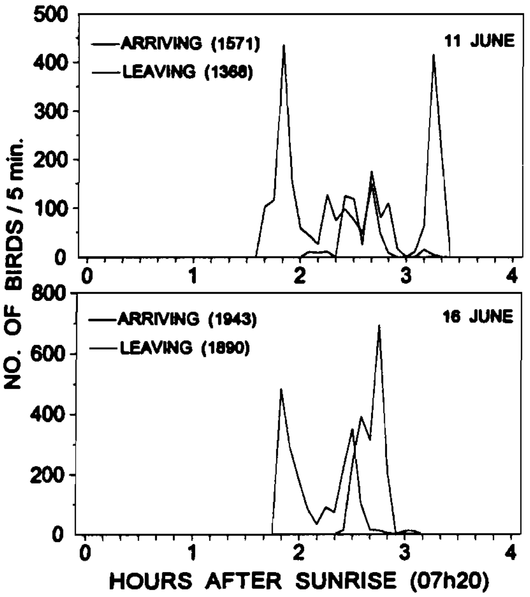

Figure 5.3. The arrival and departure (within 5-min intervals) of Namaqua Sandgrouse at the Orange River drinking site. Sunrise at 07h20.

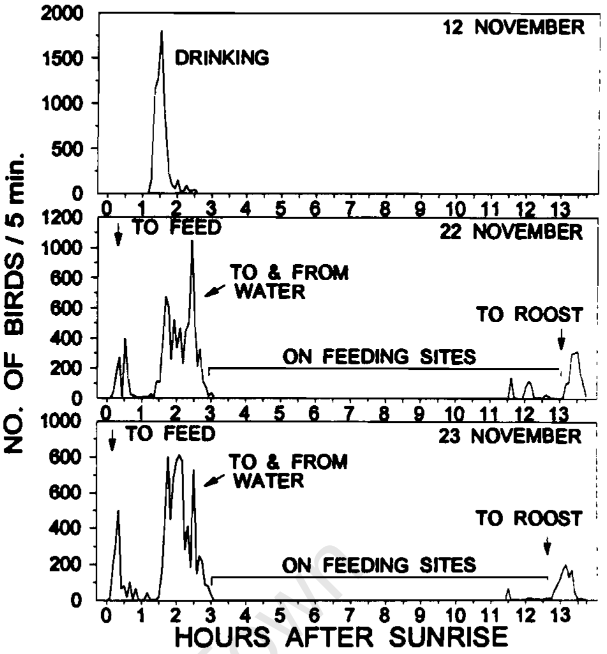

Figure 5.4. The daily movement pattern of a breeding population of Namaqua Sandgrouse at Droëgrond quantified as the number of birds counted within 5-min intervals either leaving the drinking site (12 November) or in the air over the primary feeding sites and nearby roosts (22-23 November). Sunrise at 05h30 and sunset at 19h15.

At Droëgrond, Namaqua Sandgrouse left their roosting sites approximately 20 min after sunrise to fly to feeding sites before the flight to drink (Fig. 5.4). Flocks arriving at the drinking site wasted little time staging, usually drinking within 10 min of their arrival. The return to the roosting sites in the late afternoon took place around 20 min before sunset. The breeding population therefore spent approximately 12 hours per day on the feeding sites, and less than an hour "loafing" on the roosting sites or around the watering point. The total daily flying time for breeding birds was estimated at 25 min. The total counts of birds flying to and from the roosts were lower than the counts of birds flying to and from the watering site because a) the roosts and feeding sites were widely dispersed and b) the counting station was sited on the flight path between the primary feeding area and the single watering point.

DISCUSSION

These observations show that during the period of the study at Prynnsberg, the local Namaqua Sandgrouse population flew to watering sites daily. In their study of a winter nonbreeding population, Little *et al.* (1993) noted that an appreciable proportion of the birds landing at waterholes did not in fact drink. In the present study, however, most birds arriving at the waterhole were observed to drink or at least attempt to drink. Winter daytime temperatures are the least water taxing for Namaqua Sandgrouse, particularly when not breeding. These birds appear physiologically capable of drinking only once every few days, even under summer conditions (Thomas & Maclean 1981), so it is unusual that they should expend a considerable amount of energy and expose themselves to heightened predation risk (Ward 1972, Ferns & Hinsley 1995) by flying to water each day. The reason for this behaviour may lie with their highly gregarious nature and their possible use of the watering site as an information centre (Ward 1972). In light of these observations, it seems prudent, when estimating local population densities from waterhole counts, to assume that the birds drink daily.

In comparison to the breeding population at Droëgrond, the nonbreeding population at Prynnsberg spent less time on the feeding sites (6 hrs *versus* 12 hrs) and more time "loafing" on the roost or around the watering site (3½ hrs *versus* less than 1 hr). Food availability at the latter sites was negligible (pers. obs.), so the birds were certainly not using the "loafing" time to feed. Seed-food densities were generally higher at Prynnsberg from April to August 1994 than they were at Droëgrond in November 1994 (Chapter 7), so it was surprising then that the Prynnsberg population showed no signs of breeding from April to August. The Namaqua Sandgrouse is certainly capable of breeding in winter (McLachlan 1985, Chapter 7). The breeding season for the few birds that remained at Prynnsberg through the summer months extended from September 1994 to January/February 1995, when food availability was considerably lower than it was through the preceding winter. These observations suggest that high food availability does not necessarily act as a proximate stimulus for breeding in the Namaqua Sandgrouse. This unusual response for an arid-adapted granivore (Wiens & Johnston 1977) is explored further in Chapter 7.

CHAPTER SIX

THE DIET AND NUTRITION OF THE NAMAQUA SANDGROUSE

SUMMARY

The diet of the Namaqua Sandgrouse is described, and best estimates of the daily seed intakes needed to meet limiting nutrient requirements during different stages of the annual cycle are determined. Namaqua Sandgrouse feed almost exclusively on seeds, and mainly on those of protein-rich legumes. The energy content (17-24 kJ/g) of selected seed species is less variable than protein (10-37%) and amino acid content. Energy is usually first limiting for adults, even females producing eggs. Essential amino acids appear to be more limiting than energy for growing chicks, suggesting that chicks may be more dependent on protein-rich legume seeds than are adults. The dietary requirements for limiting amino acids in a 19-day-old chick are similar to those of a female producing eggs, suggesting that chick development is the most nutritionally demanding stage in the annual cycle of Namaqua Sandgrouse.

INTRODUCTION

Sandgrouse (Pteroclidae) are highly specialised and successful inhabitants of the arid and semi-arid zones of Africa, the Middle East and Asia (Thomas 1984). The various species have a primarily granivorous diet, feeding mostly on the small, hard seeds of annual plants. Seeds are reported to be rich in energy and easily metabolised carbohydrates, but are deficient in other essential nutrients, particularly proteins and essential amino acids (Wiens & Johnston 1977). This has led to the assumption that large quantities of seeds are required to satisfy the energetic and nutritional needs of granivorous birds, particularly during periods of special nutrient demands. By feeding on the seeds of annual plants, which are produced superabundantly in arid regions following suitable rainfall, and adopting a nomadic lifestyle to track patches of high production, sandgrouse may be able to sustain high seed intake rates (Thomas 1984). In addition, they may feed selectively on seeds with a high energy and/or protein content (Dixon & Louw 1978, Thomas 1984).

For most birds, the physiological demands of reproduction are the most rigorous and critical within their annual cycle. Most species have therefore evolved the timing of breeding to coincide with the maximum availability of their species-specific food, particularly in strongly seasonal environments (Immelmann 1973). Three of the four species of southern African sandgrouse, namely Doublebanded Sandgrouse (*Pterocles bicinctus*), Burchell's Sandgrouse (*P. burchelli*) and Yellowthroated Sandgrouse (*P. gutturalis*) breed primarily through the dry winter months, from April to September, when seed-food availability is high following seasonal late-summer rains (Skinner 1996, Harrison *et al.* 1997, Tarboton & Blane unpublished). The Namaqua Sandgrouse (*P. namaqua*), on the other hand, does not necessarily breed when the food supply is maximal. This species has been observed to initiate breeding up to five months after seed production, the breeding season extending into the start of the rainy season when food availability can reach its lowest levels following seed germination (Chapter 7).

While there is a body of evidence detailing the diets of sandgrouse, no study has related the nutritional content of the seed species consumed to sandgrouse nutritional requirements during different stages of their annual cycle to identify potential bottlenecks. This study examines the diet of the Namaqua Sandgrouse and the nutritional content of its principal seed foods. Using published accounts of sandgrouse daily energy budgets (Hinsley 1992, Hinsley & Ferns 1994), and best estimates of the daily requirements for limiting nutrients, particularly essential amino acids, I construct daily energy and limiting nutrient requirement profiles for the Namaqua Sandgrouse.

METHODS

Diet

Crops were removed from 130 Namaqua Sandgrouse collected at irregular intervals over the period 1993-1995. The total contents of each crop were removed, air dried and individually separated into the fractions: grit, pebbles, different seed species, and other vegetable matter. Fractions were weighed to the nearest 0.01 g and the number of items counted. During the course of the study, seed and vegetative samples were collected from all flowering plants suspected of being consumed by Namaqua Sandgrouse and, once identified, served as a reference collection for the identification of seeds found in sandgrouse crops.

Seed nutritional content

The crude protein content of selected seed types was determined using the Kjeldahl procedure (A.O.A.C. 1975). The content of 16 amino acids in the selected seed types was determined using the method of McNab and Fisher (1984). The gross energy content of selected seed types was determined using an adiabatic bomb calorimeter (A.O.A.C. 1975). These analyses were performed by the technical staff of the Department of Animal Science and Poultry Science, University of Natal, Pietermaritzburg.

Digestion efficiencies

Amino acids: The efficiency of the digestive assimilation of 16 amino acids by Namaqua Sandgrouse was determined using the following experimental procedure. Wild-caught Namaqua Sandgrouse were housed in an aviary for one month with *ad libitum* access to water and lentil seed food. At the start of the experiment, four birds were moved to adjoining small wire cages (with no food but free access to water) from 09h00 on day 1. On day 2, each bird was fed 5 ml of a 50% (w/v) dextrose solution by means of a force-feeding tube that was long enough to reach the crop. This kept the birds in positive energy balance until force feeding of the test diet on day 3. Five grams of the test diet (lucerne seed) were fed at 09h00 on day 3 and trays placed under the cages to collect all excreta voided. The voided excreta were collected at 09h00 on day 5 and analysed for amino acid content as described above. The proportion of each amino acid assimilated by each bird was determined as:

$$\frac{A-B-C}{A}$$

where A is the amino acid content of the 5 ml lucerne seed fed to the birds, B is the amino acid content of the excreta, and C is an adjustment for the endogenous losses from the intestine. The birds were then given *ad libitum* access to water and their normal diet for a week before the experiment was repeated on the same four birds.

Gross energy: Hinsley (1992) calculated the digestive efficiency of gross energy in the

Doublebanded Sandgrouse to be 0.76. The same is assumed to hold true for the Namaqua Sandgrouse.

Time budgets

In June (10 h 20 min daylight), a nonbreeding Namaqua Sandgrouse population at Prynnsberg was observed to spend, on average, 3 h 05 mins on the roost in the early morning and late afternoon, 45 min flying, 25 min waiting around the waterhole and 6 h 05 min on feeding sites (Chapter 5).

The female Namaqua Sandgrouse relieves the male at the nest 2 h 30 mins (on average) after sunrise (n = 48), and the male returns to relieve the female 1 h 45 mins before sunset (n = 126) during summer (Chapter 2). During the nesting season, the female flies from the roost to feeding sites approximately 15 mins after sunrise, returning to the roost 10 min before sunset (Chapter 5). Both sexes were estimated to spend 25 mins per day flying, and 10 mins waiting around the waterhole when breeding at Droëgrond. There were 13 h 45 min daylight in November.

Daily energy expenditures

Hinsley (1992) and Hinsley and Ferns (1994) measured the resting metabolic rates (using open flow respirometry) of Doublebanded, Blackbellied (*P. orientalis*) and Pintailed Sandgrouse (*P. alchata*). They then determined the energy expenditures of breeding and nonbreeding birds using time budgets and estimates (based on previously published formulae or assumptions) of the relative energy costs of different activities. I estimated the daily energy budgets of breeding and nonbreeding Namaqua Sandgrouse in both winter (June) and summer (November) following the methods employed by Hinsley and Ferns (1994), after making several assumptions based on the findings of Hinsley (1992) and Hinsley and Ferns (1994).

The arid-adapted Doublebanded (mean adult mass = 189 g) and Pintailed Sandgrouse (mass = 290 g) were found to have daytime resting metabolic rates (RMRs) 46% and 38% less than the allometric prediction of Aschoff and Pohl (1970) (Hinsley 1992, Hinsley & Ferns 1994). Low RMRs appear to represent an adaptation to desert life among birds (Dawson & Bennett 1973, Dmi'el & Tel-Tzur 1985, Hinsley *et al.* 1993). The mean adult body mass of Namaqua Sandgrouse, which is significantly different between sexes (t_{843} = 10.18, $P < 0.001$), was 184.7 g for males (*s.d.* = 13.2, n = 548) and 174.8 g for females (*s.d.* = 13.9, n = 297; excluding females with well developed ovarian follicles [> 5 mm in diameter] or eggs in the oviduct) for birds collected at irregular intervals from 1991-1995. The Namaqua Sandgrouse is of equivalent body mass to the Doublebanded Sandgrouse, and the ranges of the two species overlap considerably in the arid regions of southern Africa (Harrison *et al.* 1997). The Namaqua Sandgrouse was therefore assumed to have RMRs 46% less than the allometric predictions of Ashoff and Pohl (1970):

Predicted active phase (daytime) RMR = $91W^{0.729}$ in kcal/day
Predicted resting phase (night time) RMR = $73.5W^{0.734}$ in kcal/day,

where W is weight in kg. Daytime RMRs are then 2.50 kJ/hr (3.75 mW/g) for males and 2.40 kJ/hr (3.81 mW/g) for females, while night time RMRs are 2.00 kJ/hr (3.01 mW/g) for males and 1.92 kJ/hr (3.05 mW/g) for females.

The costs of thermoregulation were determined as excess metabolic heat production (H_m in mW/g) below a lower critical temperature of 32.0°C using the regression equation:

$H_m = 9.65 - 0.187\ T_e$ (Hinsley 1992),

where T_e = operative temperature for a bird in direct sunlight at ground level. By comparing mean hourly air temperature from monthly means (for 1994) measured at Upington weather station (Fig. 6.1) to air, ground and operative temperatures recorded in Hinsley & Ferns (1994), a number of assumptions were made with regard to operative temperatures experienced by an incubating sandgrouse. Operative temperatures were assumed to exceed the assumed lower critical temperature (32°C) between 08h00 and 19h00 during

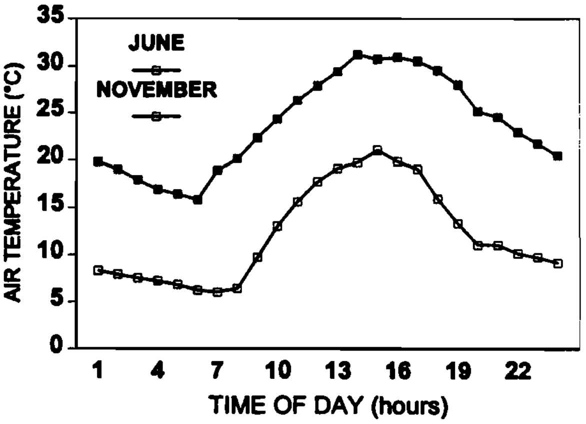

Figure 6.1. Average hourly air temperatures measured at Upington weather station for the months of November (summer) and June (winter) 1994.

November, and between 14h00 and 16h00 during June. Outside of these hours, operative temperature was assumed to equal ambient air temperature.

The cost of flying was calculated from equation 6 of Masman and Klaassen (1987) for the power output of flight:

$$e_f = 17.360 \cdot M^{1.031} \cdot b_w^{-4.236} \cdot S_w^{1.926}$$

where e_f is the energy expenditure of flight in watts, M is body mass (185 g and 175 g for males and females respectively), b_w is the wing span (47 cm and 45 cm) and S_w is the wing area (296 cm^2 and 270 cm^2). Wing measurements were taken from five adult males and five adult females. Energy expenditure of flight was 17.94 W (64.74 kJ/hr) and 17.06 W (61.57 kJ/hr), equivalent to 25.9 x RMR and 25.6 x RMR, for males and females respectively.

Hinsley and Ferns (1994) assigned a separate cost to each of daytime inactivity, foraging, preening, standing alert and walking. The average cost of all these activities considered together, for both male and female Pintailed Sandgrouse during both the nonbreeding season and while caring for chicks during the breeding season, was 1.5 x RMR. As I did not determine detailed time budgets for Namaqua Sandgrouse, I assumed that the costs of these activities (considered together) was 1.5 x RMR for both males and females while not breeding, and for males during the breeding season. Because females had limited time to feed during the incubation period, I assumed that they foraged continuously during daylight hours when not incubating or flying, the energetic cost of foraging being 2 x RMR (Ferns *et al.* 1979).

At operative temperatures above 32°C, the cost of incubation was assumed to be 1.3 x RMR (daytime), due to some movement on the nest by the incubating bird (Hinsley & Ferns 1994). At operative temperatures below 32°C, the cost of incubation was considered to be additive to RMR and was calculated using equation 5.53 of Kendeigh *et al.* (1977):

$$H_{inc} = n \cdot w \cdot h \cdot b \cdot \left(T_{egg} - T_{nest}\right) \cdot (1 - c)$$

where H_{inc} is the heat supplied to the eggs in kJ/h, n is the clutch size (3), w is the mean egg weight during incubation (10.1 g; Thomas & Maclean 1981), *h* is the specific heat capacity of eggs (0.003 kJ/g/°C; Ashkenazie & Safriel 1979 quoting D. W. Norton, unpubl. PhD thesis, University of Alaska), *b* is the cooling rate of the eggs (2.48°C/h/°C, predicted from egg weight; Kendeigh *et al.* 1977), T_{egg} is egg temperature (36°C; Caldwell & Cornwell 1975, Walsberg & Voss-Roberts 1983), T_{nest} is nest air temperature (31.9°C by day and 28.5°C at night; Caldwell & Cornwell 1975) and *c* is the fraction of the egg in contact with the brood patch (0.3). H_{inc} was then 1.18 kJ/hr at night and 0.65 kJ/hr during the day. The cost of incubation was then assumed to be H_{inc} + (1.3 x RMR) during daytime operative temperatures below 32°C, and H_{inc} + RMR at night.

Additional energy requirements for egg production

Whole-egg energy density of the eggs of precocial species averages 7.76 kJ/g (Walsberg 1983). Each 11.1 g Namaqua Sandgrouse egg (Thomas & Maclean 1981) is therefore assumed to contain 86.12 kJ energy. The digestive efficiency of gross energy was taken to be 0.76 (Hinsley 1992) and the efficiency of energy deposition as protein in eggs was taken to be 0.75 (Walsberg 1983). Dietary energy requirements then equate to 151.12 kJ per egg, or 453.35 kJ for a clutch of three. The length of the rapid follicular growth phase (T_{RG}) in the Namaqua Sandgrouse was calculated using the equation:

$$T_{RG} = 2.96 \cdot M_E^{0.278} \text{ (Walsberg 1983),}$$

where M_E = egg mass in grams (11.1 g for Namaqua Sandgrouse) and T_{RG} computes to 5.8 days. With a laying interval of two days and a clutch size of three eggs, the nutritional costs of producing a full clutch are therefore estimated to be spread over a total period of approximately 10 days in this species.

Amino acid requirements for daily maintenance and egg production

The dietary amino acid requirements for daily maintenance and egg production in the laying hen, as reported by McDonald and Morris (1985), are summarised in Table 6.1. For the purposes of this study, Namaqua Sandgrouse are assumed to have equivalent nutritional requirements per unit weight. The dietary amino acid requirements for individual amino acids (*AA* in mg) to produce a clutch of three Namaqua Sandgrouse eggs (11.1 g each) were calculated as:

$$AA_E = CR_E \times 11.1 \times 3$$

where CR_E is the coefficient of response (see Table 6.1) for the particular amino acid being considered. Unfortunately, sandgrouse diets were not analysed for the two essential amino acids cysteine and cystine. These two amino acids are particularly important for the synthesis of feathers, as they occur in high concentrations in keratin. It is not known whether seeds are deficient in cyst(e)ine, but these sulphur amino acids (SAAs) can also be synthesised from the other SAA, methionine. The daily requirement for methionine was therefore considered under two scenarios; a requirement to meet methionine needs alone, and a requirement to meet total SAA requirements. Again, these nutritional requirements are assumed to be spread over approximately 10 days.

Table 6.1. Dietary amino acid requirements (also referred to as the coefficients of response) for daily maintenance (mg amino acid per kg body weight per day) and egg production (mg amino acid per g egg output) in the laying hen (McDonald and Morris 1985), and the amino acid contents of body and feather proteins (g amino acid per kg protein) in the turkey *Meleagris gallopavo* (Emmans 1989). SAA = sulphur amino acids (methionine, cysteine and cystine).

Amino acid	Daily maintenance CR_M (mg/kg d)	Egg production CR_E (mg/g egg)	Body protein CR_{BP} (g/kg)	Feather protein CR_{FP} (g/kg)
Arginine	53	8.9	68	65
Histidine	16	3.3	26	8
Isoleucine	67	7.97	40	40
Leucine	32	12.5	71	70
Lysine	73	9.99	75	18
Phenylalanine	16	7.6	40	45
Threonine	32	6.9	42	44
Tryptophan	11	2.62	10	7
Valine	76	8.9	44	60
Methionine	31	4.77	25	6
Cysteine	49	3.53	11	70
SAA	80	8.3	36	76

Nutritional requirements for chick growth

A Gompertz growth model (Brown & Rothery 1993, pp 48-51) was fitted to growth (daily weight) data, kindly supplied by Shelley Hinsley, for six captive-reared (four hand reared together and two raised together by Doublebanded Sandgrouse surrogate parents) Pintailed Sandgrouse chicks. Assuming a similar growth rate for Namaqua Sandgrouse chicks (proportional to an average adult weight of 180 g), curves of growth (daily weight) and daily weight gain were plotted for a hypothetical Namaqua Sandgrouse chick. After calculating the instantaneous growth rates (*G* in grams), the daily body protein (*BP*) and feather protein (*FP*) gains for a 19 day (time t = 19) Namaqua Sandgrouse chick were determined using the expressions:

$BP_t = 0.18 \times G_t$ (Emmans 1989), and

$FP_t = BP_t^{1.21}$ (Emmans 1989).

The total dietary amino acid requirements of a 19-day-old chick were then determined as:

$$DR = AA_M + AA_{BP} + AA_{FP} = CR_M \cdot Wt_B + \frac{CR_{BP} \cdot Wt_{BP}}{c} + \frac{CR_{FP} \cdot Wt_{FP}}{c}$$

where AA_M is the amino acid required for maintenance, AA_{BP} is the amino acid required to produce body protein growth, AA_{FP} is the amino acid required to produce feather protein growth, *CR* are the coefficients of response (see Table 6.1) for maintenance, body protein growth and feather protein growth, and *c* is the efficiency of amino acid assimilation from the diet (0.8; Emmans 1989).

Daily seed intake

The daily intake (*DI* in grams) of the various seed types (considered alone) required to meet the daily dietary amino acid requirements (*DR* in grams) during different developmental stages was determined using the expression:

$$DI = \frac{DR}{SC/100}$$

where SC is the amino acid content of the particular seed type (from Table 6.5). The daily seed intake to meet daily dietary energy requirements was determined by dividing dietary requirements by the gross energy content of the particular seed type (from Table 6.5). The intake needed to meet the requirements for the first-limiting amino acid was then compared to the intake needed to meet energy requirements to determine which was more limiting.

RESULTS

Diet

Namaqua Sandgrouse consumed the seeds of a wide variety of plants (Table 6.2), all but two of the plant species being annuals. The two principal seed-plant families were the Fabaceae and Aizoaceae, comprising 57% and 20% of the diet (by weight) respectively. Leaves and fruits comprised <1% of the diet, and no animal remains were found in the crops of the 130 individuals collected. Small quantities of pebbles and grit were usually present in the diet. A single week-old chick collected in the late afternoon in the Langberg had a full crop of the same seeds that adult sandgrouse in the area were feeding on. Depending on the size of the seeds, a full crop contained between 3 000 and 40 000 seeds (Table 6.3). The crop seed contents of birds collected in the late afternoon (i.e. at the end of the day's feeding) averaged 8.24 g (Table 6.4), and the largest volume for a full crop of seeds was 23.5 ml (from a female).

Seed nutritional content and amino acid digestibilities

The nutritional content of selected seed species is summarized in Table 6.5. Legume species (family Fabaceae) generally had more than twice the amount of crude protein (31.7-37.4%) than non-legume species (9.8-18.6%). Gross energy content was less variable between seed species. Amino acid digestibilities ranged from 0.81 for asparagine to 0.99 for arginine, and averaged 0.97 for all amino acids considered together (Table 6.6).

Table 6.2. The total crop contents (seed item totals and weights) of 130 Namaqua Sandgrouse collected at various localities through the course of the study. See Figure 3.1 for map indicating positions of collecting sites.

Seed family	Seed species	Droëgrond (57)		Langberg (58)		Tontelbos (7)		Springbok (1)		Papkuil (6)		Graaf-Reinet (1)	
		# Items	Wt (g)	Items	Wt	Items	Wt	Items	Wt	Items	Wt	Items	Wt
Fabaceae	*Indigofera alternans*	271 720	162.23	2 541	1.97							20	0.01
	Lotononis spp.	13 091	5.71	329	0.35			3 689	3.55	5 292	3.51	2	0.02
374 996 (31%)	*Melolobium candicans*	868	10.71			1	0.01			1 091	3.35		
428.24 g (57%)	Unidentified sp. (98)	140	0.25	25	0.16								
	Requernia sphaerosperma			56 334	188.78								
	Tephrosia burchelli			2 720	15.68								
	Cassia italica			978	19.20								
	Acacia sp.			10	0.31								
	Unidentified sp. (108)					16 114	12.2						
	Medicago laciniata					13	0.03						
	Cullen obtusifolia					18	0.12						
Aizoaceae	*Limeum aethiopicum*			6 748	8.11			6	0.02				
	Limeum africanum	82 711	49.69			38	0.01						
402 892 (33%)	*Limeum arenicolum*	20 116	31.74	57	0.12								
155.31 g (20%)	*Limeum viscosum*			3 509	6.07								
	Gisekia pharnacioides	286 359	58.79	2 913	0.61								
	Trianthema triquetra	392	0.12	5	0.02								
	Hypertelis salsoloides			38	0.01								
Amaranthaceae	*Amaranthus* spp.	88 718	36.22	690	0.29								
Sterculiaceae	*Hermannia* spp.	328	0.35	842	0.62	1	<0.01	531	0.45	14	0.04		
Pedaliaceae	*Sesamum triphyllum*	2 025	2.59			1	<0.01						

Table 6.2. *continued*

Seed family	Seed species	Droëgrond (57)		Langberg (58)		Tontelbos (7)		Springbok (1)		Papkuil (6)		Graaf-Reinet (1)	
		# Items	Wt (g)	Items	Wt	Items	Wt	Items	Wt	Items	Wt	Items	Wt
Capparaceae	*Cleome* sp.	1 502	0.60										
Zygophyllaceae	*Tribulus* spp.	2 914	9.84			3	0.02			1 407	2.37		
Chenopodiaceae	*Chenopodium* sp.			172 746	51.83							1 100	0.33
Cyperaceae	Unidentified spp.	809	0.24	162 971	48.98								
Euphorbiaceae	*Chamaesyce inaequilatera*	122	0.06	173	0.06								
Lamiaceae	Unidentified sp.			200	0.29								
Acanthaceae	Unidentified sp.	1 991	2.61	98	0.24					6	0.04		
Poaceae	*Triticum* sp. Unidentified sp.			 7	 0.02	532	10.6 2						
Unidentified	Unidentified spp.	1 246	1.31	840	4.21	4	0.02						
Leaves/fruits		29	0.10	121	0.07	7	0.01			15	0.02		
Pebbles		78	0.83	600	10.98	70	1.39			16	0.27		
Grit			4.09		2.49				0.03		0.01		

Table 6.3. Full-crop contents (seed totals with weights in brackets) of selected Namaqua Sandgrouse adult individuals and a week-old chick, all collected in the late afternoon.

	Namaqua Sandgrouse individuals							
Seed sp.	1	2	3	4	5	6	7	Chick
Gisekia pharnacioides	40 456 (8.28g)					3 909 (0.80g)		
Cyperaceae unid. sp.		16 133 (4.84g)						21 (0.01g)
Chenopodium sp.			30 167 (9.05g)					
Amaranthus sp.				19 160 (7.76g)				
Indigofera alternans					17 967 (10.78g)			1 (0.01g)
Limeum africanum						15 467 (9.28g)		
Requernia sphaerosperma		1 849 (7.01g)					2 867 (12.17g)	409 (1.55g)
Tephrosia burchelli								22 (0.14g)
Limeum viscosum								20 (0.04g)
Other seeds	11 (0.01g)	21 (0.02g)	157 (0.55g)	844 (0.84g)	0	220 (0.14g)	25 (0.13g)	6 (0.06g)

Table 6.4. The average weights (g) of crop seed contents from Namaqua Sandgrouse adults collected in the late afternoon at either Droëgrond or the Langberg at different times of the year.

Locality	Date	Mean ± *s.d.*	*n*	Range
Droëgrond	23-11-1993	8.30 ± 0.91	3	7.27 - 8.98
Droëgrond	02-05-1994	6.26 ± 1.16	10	4.55 - 8.33
Langberg	12-05-1994	9.09 ± 1.19	13	7.01 - 10.88
Langberg	01-08-1994	7.60 ± 1.51	17	4.79 - 9.22
Droëgrond	15-08-1994	9.14 ± 3.27	6	4.05 - 12.32
Droëgrond	17-03-1995	9.36 ± 1.77	15	6.12 - 13.99
Langberg	22-03-1995	4.92 ± 1.88	6	3.15 - 7.88
Langberg	12-07-1995	10.40 ± 1.06	8	8.73 - 11.90
		8.24 ± 2.20	78	3.15 - 13.99

Table 6.5. Gross energy (GE), crude protein and amino acid content of selected Namaqua Sandgrouse seed food species.

Seed species	GE (kJ/g)	Protein (%)	Amino acid (%)																Recovery (%)
			Ala	Arg	Asp	Glu	Gly	His	Ile	Leu	Lys	Met	Phe	Pro	Ser	Thr	Tyr	Val	
R. sphaerosperma	21.09	37.37	1.65	3.67	4.52	7.92	1.79	1.23	1.61	3.23	2.33	0.39	2.02	2.01	1.76	1.23	0.73	1.96	95.92
Lucerne	19.69	31.71	1.39	3.10	3.64	5.85	1.88	0.99	1.42	2.41	2.65	0.43	1.50	1.61	1.41	1.20	1.01	1.67	95.01
T. burchelli	19.17	34.21	1.46	2.64	4.04	6.68	1.60	0.97	1.52	2.98	2.53	0.38	1.89	2.00	1.70	1.15	0.87	1.71	95.00
T. dregeana[1]	21.03	32.00																	
L. arenicolum	17.79	9.81	0.46	1.20	0.87	1.79	0.80	0.31	0.43	0.74	0.43	0.14	0.44	0.45	0.44	0.40	0.18	0.66	94.96
Cleome sp.	23.93	18.60	0.86	1.78	1.67	3.53	1.16	0.51	0.85	1.23	0.94	0.25	0.79	1.03	0.53	0.60	0.39	1.32	95.02
C. diandra[1]	21.18	16.00																	
C. luederitziana[1]	21.48	16.00																	
Cyperaceae unid. sp.	17.17	10.50	0.47	1.16	1.04	1.97	0.52	0.26	0.44	0.84	0.41	0.34	0.60	0.48	0.44	0.36	0.27	0.72	95.00
Gisekia/Chenopodium[2]	20.01	15.82	0.69	3.62	1.38	2.70	1.24	0.76	0.60	0.97	1.01	0.38	0.56	0.78	0.68	0.51	0.61	0.79	94.99

[1] From Dixon & Louw (1978)

[2] A 1:1 mix by volume of the two seed species

Table 6.6. The efficiency of amino acid assimilation (digestibility) in Namaqua Sandgrouse fed lucerne seed.

		Replicates							Mean
Amino acid	1/1*	1/2	1/3	1/4	2/1	2/2	2/3	2/4	all
Alanine	0.97	0.97	0.97	0.98	0.98	0.96	0.98	0.98	0.97
Arginine	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	0.99
Asparagine	0.82	0.76	0.78	0.81	0.87	0.68	0.86	0.86	0.81
Glutamine	0.99	0.98	0.98	0.99	0.99	0.98	0.99	0.99	0.99
Glycine	0.96	0.94	0.95	0.96	0.96	0.93	0.96	0.96	0.95
Histidine	0.99	0.98	0.98	0.98	0.99	0.97	0.99	0.94	0.98
Isoleucine	0.97	0.97	0.97	0.97	0.98	0.96	0.98	0.98	0.97
Leucine	0.98	0.97	0.98	0.98	0.98	0.97	0.98	0.98	0.98
Lysine	0.98	0.97	0.98	0.98	0.98	0.96	0.98	0.99	0.98
Methionine	0.97	0.96	0.96	0.97	0.98	0.95	0.98	0.98	0.97
Phenylalanine	0.98	0.97	0.98	0.98	0.98	0.97	0.98	0.98	0.98
Proline	0.98	0.98	0.98	0.98	0.99	0.97	0.99	0.99	0.98
Serine	0.98	0.97	0.97	0.98	0.98	0.96	0.98	0.98	0.98
Threonine	0.97	0.97	0.97	0.97	0.98	0.96	0.98	0.98	0.97
Tyrosine	0.98	0.97	0.98	0.98	0.99	0.96	0.99	0.98	0.98
Valine	0.98	0.97	0.97	0.98	0.98	0.96	0.98	0.98	0.98

*1/1 = Replication number / bird number.

Daily time and energy budgets

The estimated daily time and energy budgets of both breeding and nonbreeding Namaqua Sandgrouse are summarized in Table 6.7. During summer, energy budgets of nesting birds are 12% higher and 1% lower than non-nesting males and females respectively. During winter, the positive difference is 10% and 3% for males and females respectively. The cost of thermoregulation was nearly three times higher in winter than in summer. Due to the high costs of flying, daily energy budgets were sensitive to the length of time spent flying each day.

Table 6.7. Time and energy budgets of breeding and non-breeding Namaqua Sandgrouse at Droëgrond during summer and at Prynnsberg during winter.

	Summer				Winter			
	Breeding		Non-breeding		Non-breeding		Breeding	
Activity	Male	Female	Male	Female	Male	Female	Male	Female
Night inactivity	-	10h15min 19.73 kJ	10h15min 20.54 kJ	10h15min 19.73 kJ	13h40min 27.39 kJ	13h40min 26.31 kJ	-	13h40min 26.31 kJ
Night incubation	10h15min 32.68 kJ	-	-	-	-	-	13h40min 43.57 kJ	-
Day activity	9h50min 36.91 kJ	35min 2.10 kJ	13h20min 50.05 kJ	13h20min 48.08 kJ	9h35min 35.97 kJ	9h35min 34.56 kJ	5h20min 20.02 kJ	35min 2.10 kJ
Foraging		3h15min 15.63 kJ						2h55min 14.02 kJ
Day incubation	4h15min 15.61 kJ	9h30min 29.69 kJ	-	-	-	-	4h15min 16.58 kJ	6h05min 22.95
Thermoregulation	22.32 kJ	21.73 kJ	22.32 kJ	21.73 kJ	60.29 kJ	55.93 kJ	60.29 kJ	55.93 kJ
Flying	25min 26.97 kJ	25min 25.65 kJ	25min 26.97 kJ	25min 25.65 kJ	45min 48.55 kJ	45min 46.18 kJ	45min 48.55 kJ	45min 46.18 kJ
DEE	134.49 kJ	114.53 kJ	119.89 kJ	115.19 kJ	172.21 kJ	162.97 kJ	189.01 kJ	167.49 kJ

Table 6.8. The growth rates of Pintailed Sandgrouse chicks (P-tS), the Gompertz model fitted to the Pintailed Sandgrouse data and the estimated growth rates of Namaqua Sandgrouse chicks (NS).

Age (d)	Average P-tS weights (g)[1]	Gompertz model P-tS weights (g)	Gompertz model NS weights (g)	Instantaneous NS weight gain (g/d)	NS body protein weight gain (g/d)[2]	NS feather protein weight gain (g/d)[3]
1	13.80	8.75	5.43	1.18	0.213	0.038
3	18.60	13.12	8.15	1.55	0.279	0.053
6	29.15	21.95	13.63	2.12	0.382	0.078
8	35.30	29.34	18.21	2.48	0.447	0.094
10	44.40	37.82	23.45	2.80	0.504	0.109
12	60.55	47.23	29.32	3.06	0.551	0.122
14	66.25	57.37	35.62	3.25	0.586	0.131
16	70.80	68.02	42.23	3.38	0.608	0.137
17	77.03	73.46	45.60	3.41	0.614	0.139
18	84.25	78.94	49.01	3.43	0.617	0.139
19	85.58	84.44	52.42	3.43	0.618	0.140
20	90.70	89.93	55.83	3.42	0.615	0.139
21	94.93	95.39	59.22	3.92	0.611	0.138
22	99.98	100.80	62.58	3.35	0.604	0.136
23	97.50	106.14	65.89	3.30	0.595	0.133
24	109.33	111.39	69.15	3.24	0.584	0.130
26	115.68	121.56	75.47	3.10	0.558	0.123
28	129.55	131.22	81.46	2.93	0.527	0.115
30	137.73	140.31	87.11	2.74	0.493	0.106
31	143.23	144.62	89.78	2.64	0.475	0.102
36	154.50	163.79	101.68	2.14	0.386	0.079
42	180.50	181.69	112.80	1.59	0.287	0.055
53	214.00	202.74	125.84	0.85	0.154	0.026

[1] Measurements from six individuals

[2] Calculated as 0.18 x body weight gain (Emmans 1989)

[3] Calculated from: feather protein = (body protein)$^{1.21}$ (Emmans 1989)

Nutritional requirements for chick growth

The Gompertz growth model fitted to the Pintailed Sandgrouse growth data:

$$W_t = 224e^{-3.466e^{-0.0667t}}$$

(Table 6.8 & Fig. 6.2) accounted for 98.5% of the variance. For the growth curves fitted to the six individual chicks, mature weight (W_m) ranged between 162.7 g and 301.5 g, but averaged 224.4 g, and the rate of maturing (B, per day) ranged between 0.0393 and 0.0678, averaging 0.0667. Daily weight gain in a hypothetical Namaqua Sandgrouse chick peaks at 3.43 g at the age of approximately 19 days (Fig. 6.2).

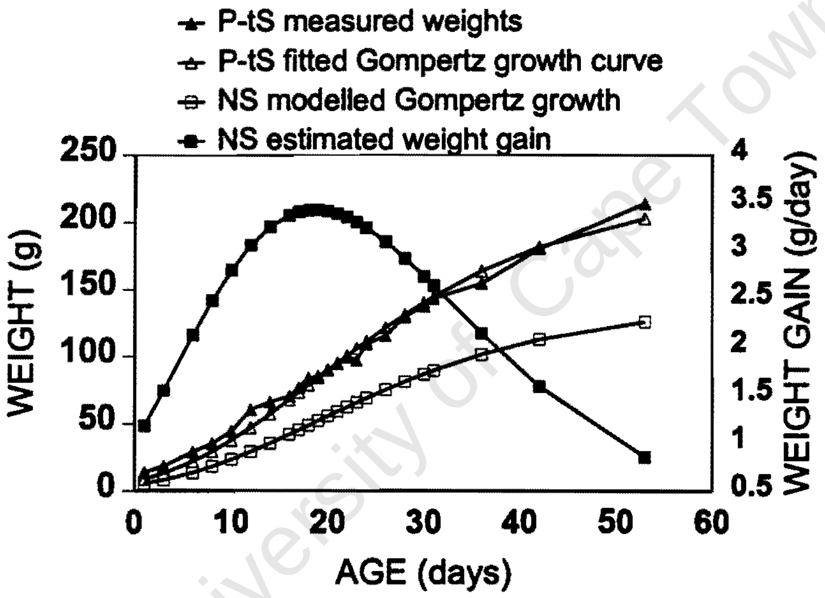

Figure 6.2. Observed and Gompertz-modelled growth curves for Pintailed (P-tS) and Namaqua Sandgrouse (NS) chicks. Weight measurements were averaged for six Pintailed Sandgrouse chicks.

Daily seed intake

Daily seed intakes needed to meet the estimated daily energy requirements of Namaqua Sandgrouse vary relatively little between seed species (Table 6.9), and range from 6.33-13.20 g/day for nonbreeding birds to 6.30-14.49 g/day for nesting birds to 8.19-15.49 g/day for females producing eggs.

For birds not producing eggs, dietary energy requirements are first limiting in all seed-food species, except in *Limeum arenicolum* if methionine must meet total SAA requirements (Table 6.10). In females producing eggs, the daily dietary requirement for either energy or methionine is first limiting, depending on whether the birds are breeding in winter or summer. Energy budgets were not determined for a developing chick, but an appraisal of seed intakes required to meet limiting amino acids (Table 6.10) suggests that amino acids may usually be more limiting than energy. Considering the scenario where methionine is not needed to compensate for cyst(e)ine deficiencies, threonine is first limiting in the seeds of *Requernia sphaerosperma, Tephrosia burchelli, Cleome* sp. and the *Gisekia pharnacioides/Chenopodium* sp. mix, while lysine is first limiting in *L. arenicolum* and the unidentified species of Cyperaceae. If methionine must compensate for total SAA needs, then it becomes the most seriously limiting nutrient for a developing chick.

Table 6.9. Daily seed intakes (grams) of different seed types (considered alone) required to meet daily energy requirements in male and female Namaqua Sandgrouse during summer and winter breeding and nonbreeding seasons, and during the 10 day egg production period (EP) in females. See Table 6.5 for full names of seed species.

Seed species	Summer non-br.	Winter non-br.	Summer breeding	Winter breeding	EP alone	Summer br. + EP	Winter br. + EP
			Males				
Requernia	7.48	10.74	8.40	11.79			
Tephrosia	8.23	11.82	9.23	12.98			
Limeum	8.87	12.74	9.95	13.98			
Cleome	6.59	9.47	7.39	10.39			
Cyperaceae	9.19	13.20	10.31	14.49			
Gis./Chen.	7.88	11.32	8.84	12.43			
			Females				
Requernia	7.19	10.17	7.14	10.45	2.15	9.29	12.60
Tephrosia	7.91	11.19	7.86	11.50	2.37	10.22	13.86
Limeum	8.52	12.06	8.47	12.39	2.55	11.02	14.94
Cleome	6.33	8.96	6.30	9.21	1.89	8.19	11.10
Cyperaceae	8.83	12.49	8.78	12.84	2.64	11.42	15.49
Gis./Chen.	7.58	10.72	7.53	11.01	2.27	9.80	13.28

Table 6.10. Daily seed intakes (grams) of different seed types (considered alone) required to meet daily amino acid requirements for maintenance and during the 10-day, egg-production period in female Namaqua Sandgrouse, and for maintenance and growth in a 19-day-old chick. SAA = methionine requirement to meet total sulphur amino acid (methionine, cysteine and cystine) needs on its own. First-limiting amino acid component in bold type. See Table 6.1 for full amino acid names and Table 6.5 for full names of seed species.

Seed species	Amino acids										
	Arg	His	Ile	Leu	Lys	Phe	Thr	Tyr	Val	Met	SAA
Daily maintenance requirements											
Requernia	0.25	0.23	0.73	0.17	0.55	0.14	0.45	0.26	0.68	**1.38**	(3.57)
Tephrosia	0.35	0.29	0.77	0.19	0.51	0.15	0.49	0.22	0.78	**1.45**	(3.73)
Limeum	0.77	0.92	2.74	0.76	2.94	0.64	1.42	1.09	2.02	**3.90**	(10.10)
Cleome	0.52	0.55	1.39	0.45	1.36	0.35	0.94	0.50	1.01	**2.14**	(5.51)
Cyperaceae	0.80	1.09	2.65	0.67	**3.11**	0.47	1.54	0.70	1.85	1.59	(4.09)
Gis./Chen.	0.26	0.37	**1.96**	0.58	1.26	0.50	1.10	0.32	1.68	1.41	(3.65)
Daily egg production requirements (alone)											
Requernia	0.81	0.89	1.65	1.29	1.43	1.26	1.86	1.19	1.52	**4.05**	(7.05)
Tephrosia	1.12	1.13	1.74	1.40	1.32	1.34	2.00	1.00	1.73	**4.24**	(7.37)
Limeum	2.47	3.59	6.20	5.64	7.67	5.78	5.82	4.93	4.51	**11.40**	(19.90)
Cleome	1.67	2.15	3.14	3.38	3.55	3.20	3.86	2.26	2.24	**6.25**	(10.90)
Cyperaceae	2.56	4.29	6.00	4.96	**8.09**	4.22	6.31	3.18	4.12	4.64	(8.08)
Gis./Chen.	0.82	1.46	4.43	4.30	3.29	**4.51**	**4.51**	1.44	3.75	4.14	(7.20)
Daily maintenance + egg production requirements											
Requernia	1.06	1.12	2.38	1.46	1.98	1.39	2.32	1.46	2.20	**5.44**	(10.60)
Tephrosia	1.48	1.42	2.51	1.59	1.82	1.49	2.49	1.22	2.51	**5.68**	(11.10)
Limeum	3.25	4.51	8.94	6.40	10.60	6.42	7.23	6.02	6.54	**15.33**	(30.00)
Cleome	2.19	2.70	4.53	3.84	4.91	3.55	4.79	2.76	3.25	**8.39**	(16.40)
Cyperaceae	3.36	5.39	8.66	5.63	**11.20**	4.68	7.85	3.89	5.96	6.23	(12.20)
Gis./Chen.	1.08	1.83	**6.39**	4.87	4.56	5.01	5.61	1.76	5.44	5.55	(10.80)
Daily maintenance and growth in a 19-day-old chick											
Requernia	1.82	1.75	2.37	2.08	2.63	1.92	**3.26**	1.23	2.29	1.39	(10.54)
Tephrosia	2.53	2.22	2.50	2.26	2.43	2.05	**3.50**	1.03	2.61	1.45	(11.02)
Limeum	5.56	7.03	8.90	9.10	**14.12**	8.86	10.18	5.07	6.8	3.91	(29.73)
Cleome	3.75	4.21	4.51	5.45	6.54	4.90	**6.75**	2.33	3.38	2.14	(16.27)
Cyperaceae	5.75	8.41	8.62	8.00	**14.91**	6.46	11.05	3.28	6.21	1.59	(12.08)
Gis./Chen.	1.84	2.85	6.36	6.93	6.07	6.91	**7.90**	1.48	5.66	1.41	(10.76)

DISCUSSION

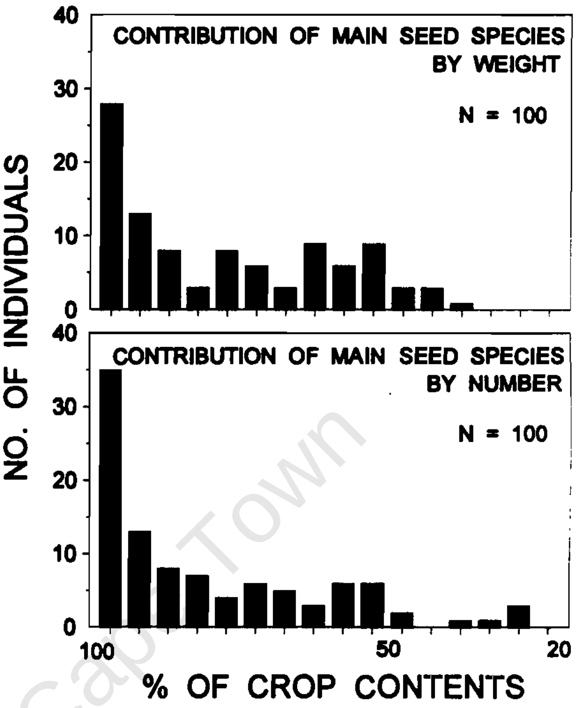

Figure 6.3. The frequencies and the proportional contribution of the dominant seed species in the crop by weight and item totals. The identity of the dominant seed species is variable between individuals. Only crop samples containing at least 1 g of seed were considered in the analysis.

From the dietary analysis, it can be concluded that Namaqua Sandgrouse feed almost exclusively on seeds, and mainly those of annual leguminous plants (Table 6.2). In most individuals sampled, the seeds of a single species comprised more than 50% (and commonly more than 95%) of crop seed contents by weight or item numbers (Fig. 6.3). This suggests that individuals are either highly selective in what they eat, or that they feed in localised patches where only the seeds of single species predominate. Soil sampling of the seed banks at localised sandgrouse feeding sites often found that single seed species predominated due to the patchiness of germination and growth in different plant species (see Chapter 3). The ability of the birds to feed selectively should not be discounted though, particularly in view of the differences in nutritional value of different seed species (see below). Furthermore, *L. arenicolum* and *L. viscosum* seeds often occurred at high densities at both the Langberg and Droëgrond, but were generally avoided unless other seeds were in short supply (Chapter 3, pers. obs.). *L. arenicolum* seed was the least nutritious of the species analysed (Table 6.5), in terms of both energy and limiting amino acid availability.

As expected, the protein-rich legume species were generally far richer in amino acids than non-legumes (Table 6.5). The only exception occurred with methionine, the *G. pharnacioides/Chenopodium* sp. mix and the unidentified species (Cyperaceae), all non-leguminous and not particularly rich in protein, being as equally rich in methionine as the legumes. Legume seeds are a dominant component of the diet in most sandgrouse species whose diet has been studied in any detail (Cramp *et al.* 1985, Johnsgard 1991). This has generally been ascribed to the higher protein content of these seeds relative to non-leguminous seeds, a conclusion which the results of this analysis provide more empirical support for.

The Namaqua Sandgrouse appears to digest the amino acids in its foods with the same or slightly greater efficiency (0.97 average; Table 6.6) than the chicken *Gallus gallus* (0.90 and higher; McDonald & Morris 1985).

The estimated Namaqua Sandgrouse energy budgets (Table 6.7) suggest that daily energy budgets in winter are greater than those in summer, due to the increased costs of heat generation for thermoregulation in the lower winter temperatures. Nesting increases energy expenditures by up to 13%. The daily seed intakes needed to meet even the increased energy demands of nesting are relatively small (6.30-14.49 g/day; Table 6.9). The average crop contents of birds collected in the late afternoon (8.24 g; Table 6.4) will be enough to meet much of these energy demands, and this ignores the quantity of seed emptied from the crop during the day's feeding. A bird will generally consume just sufficient of the limiting nutrient in its food in order to grow and/or reproduce at its potential (Emmans 1989). The real possibility that birds are consuming more than they need to balance the requirement for the most limiting nutrient suggests one of three things: 1) their basic requirements have been underestimated, 2) the birds are eating more to build up their nutrient stores, or 3) they are eating more in order to meet the requirements of a nutrient (such as a mineral) that has not been measured in this study. An underestimate of the amount of time spent flying, resulting in an underestimate of requirements, may account for much of the difference, but only more definitive studies will be able to resolve this issue. Estimated daily energy demands for females during the approximately 10 day egg production period increase by 21-30%, translating to an additional daily seed intake of 1.89-2.64 g (Table 6.9).

Comparing the estimated daily seed intakes required to meet the demands for the most limiting nutrients during the egg-laying period to the crop contents at the end of a day's feeding suggests that Namaqua Sandgrouse are easily able to satisfy these demands during periods of food abundance, but may be nutritionally challenged during periods of food scarcity. Only birds collected after widespread rainfall (Langberg on 22-03-1995; Table 6.4), when the food supply is expected to reach critically low levels (Wiens & Johnston 1977), had markedly lower crop contents. Without knowledge of crop-emptying times in sandgrouse, to estimate the quantity of seed that is collected but emptied from the crop during the day's feeding, it is difficult to evaluate to what extent the birds are able to satisfy their nutritional needs at such times.

The Gompertz growth model fitted the average Pintailed Sandgrouse growth data with reasonable accuracy, although the estimated age at maturity (224 g) was considerably lower than the 290 g average weight of adults. This latter result is probably due to the lack of continuous growth data after the age of 53 days. A day-old Namaqua Sandgrouse chick and an approximately 2-month-old female Namaqua Sandgrouse I collected weighed 7.0 g and 125 g respectively. These values correspond well with the weights estimated by the Gompertz model for Namaqua Sandgrouse at similar ages (Table 6.8).

In a 19-day-old Namaqua Sandgrouse chick, amino acids are almost certainly more limiting than energy in all the non-legume seed species analysed (Table 6.10). Energy may be first limiting in protein seeds, due to the high amino acid concentrations in these seeds, unless methionine is required to compensate for deficiencies in cyst(e)ine. Feathers contain unusually high concentrations of cyst(e)ine (Table 6.1), and the energetic efficiency of feather synthesis may be as low as 5-20% (Murphy & King 1992). Chicks grow feathers for a juvenile plumage during their first month, and then undergo a rapid moult into an adult type plumage between the ages of one and three months (Chapter 2). There is therefore a strong possibility that the dietary requirement for methionine will increase to compensate for deficiencies in cysteine during this period. These results suggest that growing sandgrouse chicks are more dependent on the protein-rich seeds of legume plants to provide them with their most limiting nutrients than are adult sandgrouse.

The dietary requirements for amino acids in a 19-day-old chick are similar to those of a female producing eggs (Table 6.10). However, a chick of this age is approximately one quarter of the weight of an adult female, and therefore unable to forage as much food as an adult. Chick development can therefore be regarded as probably the most nutritionally demanding stage in the annual cycle of Namaqua Sandgrouse. It is surprising, then, that Namaqua Sandgrouse in many regions of South Africa time the breeding season in such a way that the chicks are often present during times of lowest food availability (see Chapter 7). The implications of this conclusion to the timing of breeding are discussed further in Chapter 7.

CHAPTER SEVEN

POPULATION FLUCTUATIONS AND BREEDING ACTIVITY OF NAMAQUA SANDGROUSE IN RELATION TO RAINFALL AND FOOD AVAILABILITY

SUMMARY

In South Africa, the Namaqua Sandgrouse *Pterocles namaqua* exhibits a pattern of partial migration between two late summer rainfall regions, birds spending the summer months in the Nama Karoo and the winter months in the Kalahari. Across southern Africa, the breeding season for this species is unexpectedly variable, and not consistently correlated with periods of peak food availability. The peak nesting period ranges from January-May in northwestern Namibia, to June-October in the Kalahari, to September-December in the Nama Karoo, all late-summer rainfall regions. This suggests that some factor(s) other than proximate food availability is/are involved in determining the timing of movements and breeding in this species. The possible complicating influences of biannual breeding, moulting, adult nutritional reserves and seasonal variation in nest predation pressure are discussed.

INTRODUCTION

The Namaqua Sandgrouse is an obligate granivore, and even its chicks appear to feed solely on seeds from the day they hatch (Chapter 6). The advantage of a granivorous diet in an arid ecosystem is that annual plants produce superabundant quantities of seed in a predictable fashion following good rainfall (Brown *et al.* 1979). However, two drawbacks of such a diet are: 1) that the appropriate rainfall events are often patchily and unpredictably distributed in time and space, and 2) that most seeds remaining in the soil seed bank germinate following good rainfall, reducing food availability to critically low levels until the next seed crop is produced (Wiens & Johnston 1977). This particular suite of environmental features has favoured those granivorous birds that are capable of regional (nomadic) and/or seasonal (migratory) shifts in distribution and abundance in response to changing local food supplies (Wiens & Johnston 1977). A number of authorities recognise the Namaqua Sandgrouse to be nomadic through most of its range (e.g. Clancey 1979, Thomas 1984, Maclean 1993), although it is rare for this species to be totally absent from local areas at any time, except at the edges of its distribution (Harrison *et al.* 1997).

Clancey (1979) was the first to suggest that the southern populations of Namaqua Sandgrouse undertake migratory movements. He identified several specimens collected in northern Namibia and Botswana as belonging to what he designated as a southern race *P. n. furvus*. As these specimens were collected within the period April to August, when there is often movement of Namaqua Sandgrouse out of the southern and western parts of South Africa, he concluded that these birds were migrating north-south. In partial support of this hypothesis, Dean (1995) recorded Namaqua Sandgrouse in the southern Karoo only during the summer months of 1988/89, 1989/90 and 1990/91. Malan *et al.* (1994) provided more convincing evidence of an "east-west" partial migration by Namaqua Sandgrouse within South Africa, when they showed that reporting rates and population counts decreased in Namaqualand and the Nama Karoo (the "west") from April to July, at the time that they increased in the Kalahari (the "east"). This situation was reversed again between August and December. From these results they hypothesized that Namaqua Sandgrouse concentrate in the "west" from August to March, where they breed in the early summer months, and then migrate east and northeast for the period April to July. Malan *et al.* (1994) suggested further that these migratory movements enabled the birds to track the anticipated availability of seed between the predominantly summer rainfall region in the "east" and the predominantly winter rainfall region in the "west". This suggestion ties in neatly with the predicted movements of an opportunistic granivore, but ignores the reality that the Nama Karoo, the core region for Namaqua Sandgrouse in the "west", receives most of its rain at the same time (late summer) as the "eastern" region.

For most birds, the physiological demands of reproduction are the most rigorous and critical of any in their annual cycle. Most species have therefore evolved the timing of breeding to coincide with the maximum availability of their species-specific food, particularly in strongly seasonal environments (Immelmann 1971). Birds generally time the laying of the eggs to ensure that food is abundant for egg production and/or when the chicks hatch (Perrins 1970). Three of the four species of southern African sandgrouse, namely Doublebanded Sandgrouse *P. bicinctus*, Burchell's Sandgrouse *P. burchelli* and Yellowthroated Sandgrouse *P. gutturalis* breed primarily through the dry winter months, from April to September, when seed-food availability is high following the seasonal late-summer rains (Skinner 1996, Harrison *et al.* 1997, Tarboton & Blane unpublished). The Namaqua Sandgrouse is the only species whose range extends over both summer and winter rainfall regions. This species has been recorded nesting in every month of the year, although nesting is more pronounced over the period June to November (McLachlan 1985). No previous study of Namaqua Sandgrouse breeding seasons has, in a meaningful manner, related the timing of breeding of populations to proximate factors such as rainfall and the resultant increase in food availability.

This chapter presents the results of a study monitoring Namaqua Sandgrouse populations in both the "eastern" and "western" regions of their range in South Africa in relation to rainfall and food availability, in an attempt to elucidate the proximate factors controlling the timing of migratory movements and breeding seasons in this species.

METHODS

Three principal study sites were chosen to monitor population abundance and breeding activity in relation to rainfall and food availability: Droëgrond farm (29°07′S 20°16′E) in the Nama Karoo, and Prynnsberg farm (28°44′S 22°09′E) and Plaatjiesdam farm (28°42′S 22°35′E), located 42 km apart in the southern Kalahari (see Fig. 7.1). At the start of the study, an attempt was made to recruit volunteers to monitor Namaqua Sandgrouse populations at other sites across southern Africa. This initiative met

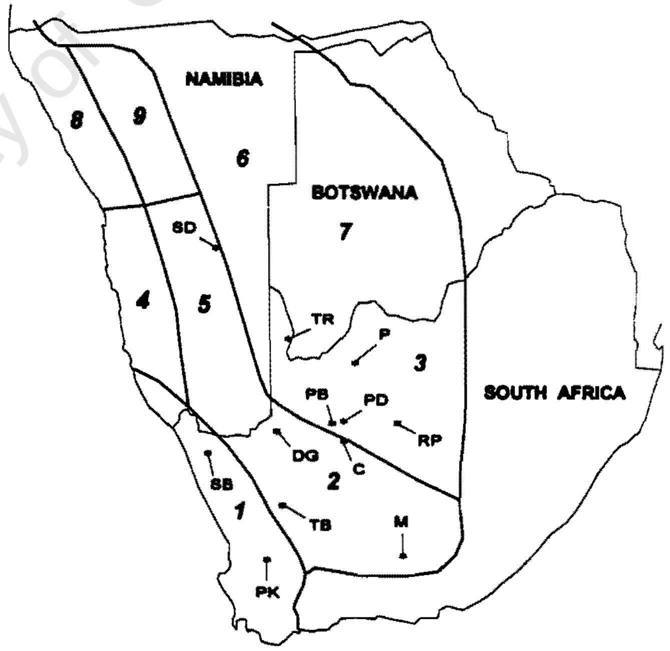

Figure 7.1. Regions within the southern African distribution of the Namaqua Sandgrouse and the locations of monitoring or collecting localities referred to in the text. Regions: 1) Namaqualand and southwestern Cape (winter rainfall); 2, 5) Nama Karoo; 3, 6, 7) Kalahari savanna; 4) southern Namib; 8) northern Namib; and 9) Etosha (2-9 all late summer rainfall). Monitoring localities: C= Chyandour farm; DG = Droëgrond farm; M = Melrose farm; P = Pioneer farm; PB = Prynnsberg farm; PD = Plaatjiesdam farm; PK = Papkuil farm; RP = Rooipoort; SB = Springbok; SD = Soetdoring farm; TB = Tontelbos farm; TR = Twee Rivieren.

with limited success, but sufficient data were gathered from five additional localities to justify their inclusion in this study. These localities were: Soetdoring farm (23°45'S 18°15'E), Twee Rivieren (26°25'S 20°30'E), Pioneer farm (27°15'S 22°45'E), Chyandour farm (29°20'S 22°32'E) and Melrose farm (32°15'S 24°30'E).

Population monitoring

Changes in the local abundance of Namaqua Sandgrouse were quantified by means of regular counts of birds gathering at either a permanent waterhole (Little *et al.* 1993) or favoured roosting site. At Droëgrond, watering points were limited, so the local population visiting an isolated and centrally located waterhole was counted during the morning drinking period. When drinking sites became more abundant after rainfall, counting was suspended until these natural, ephemeral sites dried up, or if only a few remained, the populations visiting each one were counted simultaneously to give a combined total. At Prynnsberg and Plaatjiesdam, suitable roosting sites were limited, and the birds exhibited a clear preference for a single roosting area at each of the two study sites. The local populations at these sites were therefore counted either when the birds flew from the roost to watering sites in the morning, or when they returned to the roost from their feeding sites in the late afternoon. Waterhole counts were conducted at the other sites in southern Africa monitored by volunteers.

Monitoring food availability

Rainfall at Droëgrond was measured from a rain gauge located centrally in the study site. Rainfall records were obtained from Vaalkop farm (28°42'S 22°25'E), situated almost midway between Prynnsberg and Plaatjiesdam farms, and assumed to be representative of the rainfall at the latter two sites. When rain showers resulted in the germination and growth of the annual plants on which Namaqua Sandgrouse feed, a number of actual or potential feeding sites were identified. Areas of approximately uniform food-plant distribution at these sites were selected and marked with wooden stakes driven into the ground. The soil-surface seed banks at these sites were monitored through regular sampling (described below). A record was kept of subsequent germination and seed-set events.

Namaqua Sandgrouse feed by walking slowly about and pecking up any seeds seen lying exposed on the soil surface. Although these birds do not scratch, sideways flicks of the beak while pecking can expose seeds hidden in the loose surface-sand layer. To sample food availability for Namaqua Sandgrouse, an 11 m x 1 m transect was laid out, and the two terminal and the single central 1 m^2 quadrats were demarcated. The loose surface layer of sand in each of the three quadrats was then systematically vacuumed using a *Safeway*™ car vacuum cleaner powered by a 12 V vehicle battery. The total sand sample from each quadrat was then separated into fractions of different particle size using a nested stack of metal sieves. The seeds (ignoring those seed species that appeared irregularly or with low abundance) separated into the following size fractions:

a) ≤2.18 mm >1.40 mm	*Requernia sphaerosperma* *Tephrosia burchelli* *Limeum arenicolum* *Limeum viscosum* *Tribulus zeyheri*
b) ≤1.40 mm > 0.71 mm:	*Indigofera alternans* *Limeum arenicolum* *Chenopodium* sp. Unidentified sp. 1 *Gisekia pharnacioides*
c) ≤0.71 mm > 0.36 mm:	*Gisekia pharnacioides*

The seeds of size a) above were separated from the soil and vegetable matter by hand. The soil sample fractions b) and c) above were individually poured into a container filled with a saturated solution of potassium carbonate ($K_2 CO_3$). The mixture was stirred vigorously and the fluid and suspended particles immediately decanted over a fine-mesh sieve. This procedure, which is reported as an effective and accurate method for extracting seeds from soil (Nelson & Chew 1977), was repeated four times for each sample. The plant material thus extracted was then rinsed in fresh water and air dried before the seeds were separated from the other matter with the aid of a 10x dissecting microscope, counted and weighed. Large samples were subsampled after determining the minimum size of subsample required to estimate the full sample seed content.

Breeding activity

All Namaqua Sandgrouse nesting records housed in the Avian Demography Unit, University of Cape Town and the National Museum of Namibia, together with additional published accounts, were summarised by month of nesting and region. The regions chosen are outlined in Figure 7.1.

Breeding activity was monitored in several ways. The gonads of any birds collected for other aspects of the study, or shot by local land owners or the clients of commercial wing-shooting operators, were measured to gauge their activity state. The volume (assuming a testis has an ellipsoid shape) of the largest testis of each individual was calculated using the following equation, which is derived from the formula for a volume of revolution:

$$Volume = \frac{\pi}{a + 0.5} b^{2a+1}$$

where $a = \frac{\ln(\frac{c}{2})}{\ln(\frac{b}{2})}$, b = testis length, c = testis width and the relationship $c = b^{a}$ is used to describe testis width as a function of testis length. The diameter of the largest ovarian follicle was measured in females. Field observations of behaviour, regular nest searching and waterhole counts of the number of belly-soaking males served as further indicators of breeding activity.

The presence of growing feathers (indicating moult) in the wing, tail and general body was noted for all collected birds to monitor the moult cycle of Namaqua Sandgrouse.

RESULTS

Rainfall and seed availability at Droëgrond

1992 was an exceptionally dry year (20.5 mm), the largest single rain event being 6 mm. There was almost certainly no germination of annual plants during this period of drought. 1993 was relatively dry (83.0 mm; Fig. 7.3), and showers of 29 mm in February and 13 mm in March were the only two rain events exceeding 10 mm. Annual plants, including *Indigofera* cf. *alternans* germinated in drainage lines that flowed after the February rains, but did not grow very large before drying out and setting seed through April. Seed availability was not sampled at this time, however.

In 1994, 11.5 mm fell on 31 January, and 13 mm and 16 mm on 4 and 6 of February respectively. These showers resulted in widespread annual plant germination. Follow-up rains totalling 24.5 mm (4-7 March) ensured good growth. The subsequent spell of warm, dry weather meant that the shorter-lived annuals such as *Gisekia pharnacioides*, *Limeum arenicolum* and *Amaranthus* sp. began to die off and set seed from April into May. When sites A, B and C were sampled in mid-May, most *G. pharnacioides* and *L. arenicolum* had senesced and the availability of their seed on the soil surface had reached a peak, with up to 18.60 g/m^2 of *G. pharnacioides* seed in high plant density patches, and up to 78.87 g/m^2 of *L. arenicolum* seed in places where harvester ants (*Messor* sp.) had piled the latter seed in heaps outside their colony entrances (Table 7.1, Fig. 7.2). Large numbers of Namaqua Sandgrouse were feeding at these sites, mainly on the tiny seeds of *G. pharnacioides*. *Indigofera* cf. *alternans* grew a deep tap root, was slower growing, and took longer to mature and set seed than did the other annuals. This plant species, which benefited from an additional shower of 11.5 mm on 31 May, set seed between June and September. By September, seed availability at sites A to C had decreased substantially. Namaqua Sandgrouse were no longer feeding at these sites, having moved to sites D to G to feed on the seeds of *I.* cf. *alternans* which were then abundantly available. *Indigofera* cf. *alternans* was not as abundant at site E as it was elsewhere, but this site was sampled as small groups of Namaqua Sandgrouse were nonetheless feeding there in September and December.

The only other significant rain event of 1994 was a localised shower of between 7 mm and 25 mm across the study site on 7 October. There was, however, surprisingly little annual plant germination in response to this rainfall, possibly because the rain did not fall fast enough to result in run-off into the drainage lines where most annual plants germinate and grow. By December, the availability of *I.* cf. *alternans* seed at site D had decreased markedly, as had the numbers of Namaqua Sandgrouse feeding there. Large flocks were still feeding on *I.* cf. *alternans* seed at site F in May 1995, when seed availability averaged 4.47 g/m^2, but had largely moved off this site by May, when seed availability had decreased to 0.37 g/m^2. Large flocks were still feeding at site G in May, where *I.* cf. *alternans* seed availability averaged 1.34 g/m^2, only weeks before most Namaqua Sandgrouse moved out of the region.

1995 was another dry year (75.2 mm). On 22 January, a sharp thunderstorm of 8.7-11.0 mm across the central to western portion of Droëgrond caused the main drainage lines to flow, after which annual plants germinated only in the drainage lines. The only seed-sampling site (incorporating sites A-G) that was affected was site E, where some *I.* cf. *alternans* germinated. On 11 March, a thundershower deposited only 3.5 mm in the central portion of

Droëgrond, but 13.5 mm in a localised patch 5 km to the west. The drainage lines in the latter area flowed again, causing additional annual plant germination and boosting the growth of plants that had germinated after the shower in January. Small follow-up showers totalling 19.0 mm in this western patch (but only 8.7 mm at the central rain gauge) fell over the period 23-28 March to boost growth. No further rain fell, and by May *G. pharnacioides* had died off and set seed at sites I and J, with seed availability as high as 32.90 g/m^2 in patches. *Indigofera* cf. *alternans* at site H was just starting to dry out and set seed at this time. Seed availability at site H peaked in June, but was still relatively high in September. The few Namaqua Sandgrouse that remained at Droëgrond through the winter, together with most of those that returned in the summer, concentrated their feeding in the patch incorporating sites H-J.

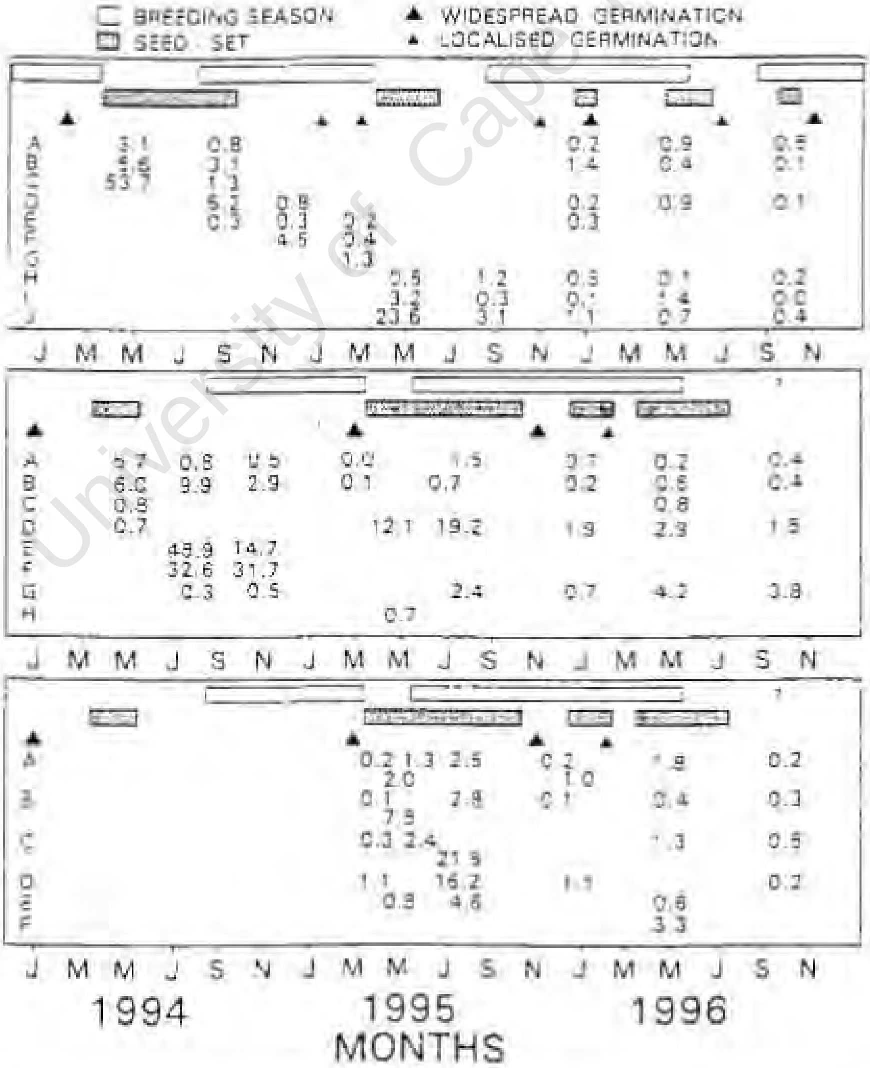

Figure 7.2. Average seed availability (g/m^2) for sampling sites (A-J) at Droëgrond (A), Prynnaberg (B) and Plaatjiesdam (C). See Tables 7.1-3 for detailed summaries of seed availability at each locality.

Table 7.1. Soil-surface seed availability (g/m^2) at sampling sites at Droëgrond, summarized as the mean and SD (in brackets) of three 1 m^2 samples.

Site	Seed Species	Sampling date								
		16 May 1994	12 Sep 1994	1 Dec 1994	31 Mar 1995	4 May 1995	5 Sep 1995	20 Jan 1996	10 May 1996	5 Oct 1996
A	*Gisekia pharnacioides*	3.12 (0.28)	0.77 (0.04)					0.24 (0.09)	0.15 (0.06)	0.08 (0.02)
	Limeum africanum								0.71 (0.47)	0.41 (0.05)
B	*Gisekia pharnacioides*	5.56 (0.91)	3.07 (1.04)					1.41 (1.25)	0.43 (0.21)	0.11 (0.03)
C	*Gisekia pharnacioides*	9.10 (8.92)	1.27 (1.21)							
	Limeum arenicolum	44.62 (30.57)								
D	*Indigofera* cf. *alternans*		4.86 (1.86)	0.77 (0.49)				0.24 (0.11)	0.70 (0.39)	0.12 (0.08)
	Limeum africanum		0.35 (0.60)	0.07 (0.12)					0.16 (0.15)	
E	*Indigofera* cf. *alternans*		0.32 (0.11)	0.29 (0.11)	0.18 (0.05)			0.27 (0.06)		
F	*Indigofera* cf. *alternans*			4.47 (2.08)	0.37 (0.20)					
G	*Indigofera* cf. *alternans*				1.34 (0.26)					
H	*Indigofera* cf. *alternans*					0.45 (0.09)	1.21 (0.62)	0.46 (0.12)	0.12 (0.05)	0.17 (0.09)
I	*Gisekia pharnacioides*					3.22 (1.73)	0.32 (0.26)	0.05 (0.06)	1.37 (0.64)	0.01 (0.01)
J	*Gisekia pharnacioides*					23.63 (16.20)	3.11 (0.40)	1.10 (0.41)	0.71 (0.42)	0.35 (0.19)

Table 7.2. Soil-surface seed availability (g/m^2) at sampling sites at Prynnsberg, summarized as the mean and SD (in brackets) of three 1 m^2 samples.

Site	Seed species	Sampling date										
		11 May 1994	11 Aug 1994	25 Nov 1994	21 Mar 1995	17 Apr 1995	10 May 1995	10 July 1995	28 Aug 1995	17 Jan 1996	6 May 1996	8 Oct 1996
A	*Requernia sphaerosperma*	5.66 (4.76)	0.84 (0.42)	0.46 (0.33)	0.02 (0.01)	0 (0)			1.52 (0.25)	0.70 (0.17)	0.22 (0.04)	0.41 (0.06)
B	*Tephrosia burchelli*	5.61 (1.83)	9.86 (5.20)	2.92 (1.46)	0.14 (0.06)	0 (0)		0.62 (0.13)		0.15 (0.08)	0.53 (0.43)	0.35 (0.19)
	Requernia sphaerosperma	0.43 (0.21)	0.05 (0.04)	0.02 (0.02)	0.01 (0.01)	0 (0)		0.07 (0.03)		0.04 (0.02)	0.06 (0.04)	0.03 (0.03)
C	*Indigofera alternans*	0.82 (0.26)									0.81 (0.09)	
D	*Limeum arenicolum*	0.56 (0.39)					11.93 (3.45)		16.12 (4.69)	1.84 (1.29)	1.92 (1.20)	1.48 (0.15)
	Requernia sphaerosperma	0.09 (0.15)					0.01 (0.01)		0.20 (0.33)	0.02 (0.03)	0.16 (0.09)	
	Limeum viscosum						0.16 (0.19)		2.90 (1.11)	0.06 (0.08)	0.02 (0.04)	
	Unidentified sp. 1										0.78 (1.29)	
E	*Chenopodium* sp.		48.93 (26.37)	14.70 (3.95)								
F	*Chenopodium* sp.		32.63 (16.47)	31.71 (10.23)								
G	*Requernia sphaerosperma*		0.30 (0.10)	0.46 (0.17)				0.40 (0.17)	2.41 (0.64)	0.72 (0.39)	2.49 (0.04)	2.10 (1.07)
	Tephrosia burchelli		0.02 (0.02)	0.01 (0.01)							0.05 (0.08)	0.09 (0.16)
	Limeum viscosum										0.53 (0.87)	1.63 (0.81)
	Indigofera alternans										1.14 (0.12)	
H	*Requernia sphaerosperma*						0.69 (0.22)					

and F respectively. By November, seed availability had decreased further, as seeds settled beneath the loose surface layer of the sandy soil over time, but was still high at some sites (e.g. B, E and F).

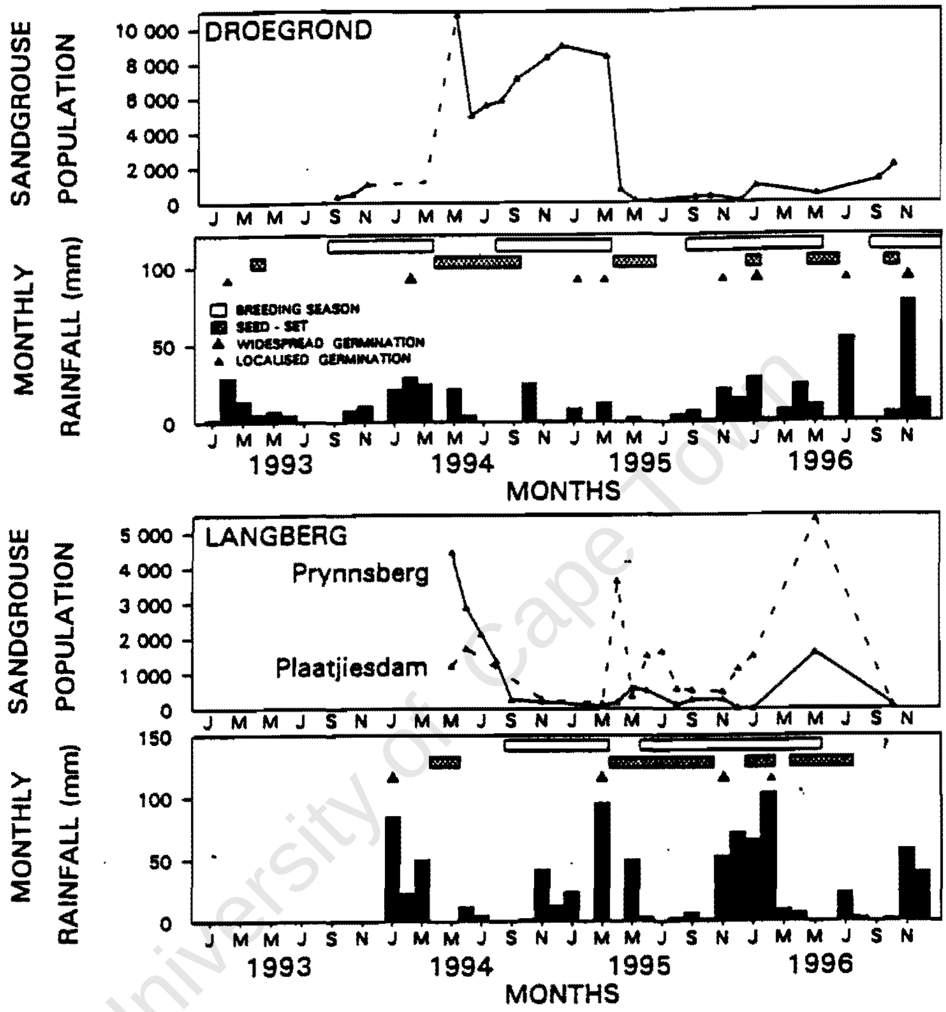

Figure 7.3. Namaqua Sandgrouse population fluctuations and breeding seasons in relation to monthly rainfall and seed-germination and seed-set events at Droëgrond farm and the Langberg (Prynnsberg and Plaatjiesdam farms).

Rainfall in early March 1995 resulted in limited germination of annuals, which meant there were still some seeds available on the soil surface. Heavier rains towards the end of March resulted in widespread germination of annuals, reducing seed availability to near zero. In mid-April at Plaatjiesdam, *L. viscosum* (e.g. site D) was setting abundant seed, while *R. sphaerosperma* (e.g. site A) and *L. arenicolum* (e.g. site B) were starting to set seed (Table 7.3). A month later, *L. arenicolum* and *L. viscosum* had finished setting seed, but *R. sphaerosperma* continued growing and throwing seed right through winter.

Table 7.3. Soil-surface seed availability (g/m^2) at sampling sites at Plaatjiesdam, summarized as the mean and SD (in brackets) of three 1 m^2 samples.

Site	Seed species	Sampling date							
		18 Apr 1995	17 May 1995	18 June 1995	4 Aug 1995	18 Dec 1995	16 Jan 1996	6 May 1996	10 Oct 1996
A	*Requernia sphaerosperma*	0.03 (0.01)	0.85 (0.41)	1.24 (0.12)	1.57 (0.62)	0.22 (0.03)	0.84 (0.16)	0.17 (0.01)	0.12 (0.01)
	Limeum viscosum	0.15 (0.16)	1.15 (1.37)	0.07 (0.02)	0.97 (0.58)	0.01 (0.02)	0.17 (0.15)	1.63 (1.24)	0.08 (0.01)
B	*Limeum arenicolum*	0.09 (0.07)	7.28 (4.41)		2.41 (2.79)	0.08 (0.06)		0.32 (0.20)	0.28 (0.08)
	Tribulus zehyeri	0 (0)	0.19 (0.27)		0.36 (0.32)	0.02 (0.02)		0.07 (0.03)	0.03 (0.04)
C	*Limeum viscosum*	0.23 (0.18)		1.88 (1.24)	8.14 (0.01)			1.12 (0.06)	0.14 (0.01)
	Limeum arenicolum	0.04 (0.02)		0.49 (0.30)	12.95 (10.38)			0.09 (0.06)	0.21 (0.20)
	Requernia sphaerosperma	0 (0)		0.02 (0.04)	0.37 (0.18)			0.12 (0.07)	0.11 (0.02)
D	*Limeum viscosum*	1.06 (0.21)					0.08 (0.02)		0.15 (0.01)
	Requernia sphaerosperma	0.02 (0.02)					1.06 (0.11)		0.08 (0.04)
E	*Requernia sphaerosperma*		0.59 (0.06)		4.45 (1.27)		1.33 (0.15)	0.29 (0.05)	
	Limeum viscosum		0.20 (0.17)		0.19 (0.12)		0.02 (0.02)	0.29 (0.06)	
F	*Indigofera alternans*							3.31 (0.22)	

At Prynnsberg, *R. sphaerosperma, T. burchelli* and *I. alternans* plants were still small and growing (and therefore not setting seed) over large areas in May, which meant there was little seed available at sites A-C and G. In localised patches, *R. sphaerosperma* (e.g. site K) and *T. burchelli* (not sampled) plants had grown larger, and were setting reasonable quantities of seed. The few Namaqua Sandgrouse in the area at this time concentrated their foraging in such patches. Furthermore, *L. arenicolum* plants at site D had grown well, and were setting large amounts of seed at this time, although no Namaqua Sandgrouse were attracted to this site at any time through the ensuing months. By July, *R. sphaerosperma* and *T. burchelli* plants at sites B, C and G had started to throw small quantities of seed, but the plants were still small and growing. *Limeum arenicolum* at site D had died back completely by July, with seed carpeting the soil surface. At the beginning of November, the situation was little altered, with *R. sphaerosperma* plants still growing slowly, and continuously setting small quantities of seed.

Moderate rainfall through November and December 1995 resulted in good germination of all annuals (reducing seed availability to low levels) and continued growth of *R. sphaerosperma* plants still alive from the previous season. Virtually no rain fell over the ensuing month, precipitating arrested development in most annuals, and some seed set. Good rains between February and May 1996, mostly in March, boosted plant growth again, although later seed production remained relatively low for most species. This was possibly due to a combination of high temperatures and the lack of follow-up rains after February. An exception was *I. alternans*, which carpeted the ground in some areas and had set copious amounts of seed by early May (e.g. Plaatjiesdam site F). Surprisingly, no Namaqua Sandgrouse frequented these *I. alternans*-rich sites at this time. Between May and October, no rain of any significance was recorded. This meant that *R. sphaerosperma* would have started dying back and setting copious quantities of seed from June. Seed availability at most sites was reduced to moderate to low levels by October.

Population fluctuations and breeding activity

Gonad size. Gonad size in both male and female Namaqua Sandgrouse served as a reliable indicator of breeding activity (Fig. 7.4, Table 7.4). In a nonbreeding population, mean testis length and volume for a sample of males were as low as 4.3 mm and 15 mm^3 respectively. In a breeding population, character means ranged from 6.2-7.9 mm and 39-56 mm^3 respectively.

In reproductively inactive females, all ovarian follicles were a transparent white colour, with diameters measuring 1.0-2.5 mm.

In preparation for reproductive activity, several follicles increased above 2.5 mm in diameter, and turned a pale yellow colour. During egg development, only three follicles ever enlarged over 4.0 mm in diameter. Table 7.5 illustrates the range in follicle sizes during egg development and immediately after laying. Follicles enlarged to around 20.5 mm in diameter before releasing the egg into the now swollen oviduct. Females that had completed egg laying could still be identified for several days after laying by their swollen oviduct and the presence of three flaccid sacs (empty follicles) in the ovary. The gradual increase in mean testis length of males at the Langberg between May and August 1994, while the females remained largely inactive (Table 7.4), suggests that males become reproductively active before females.

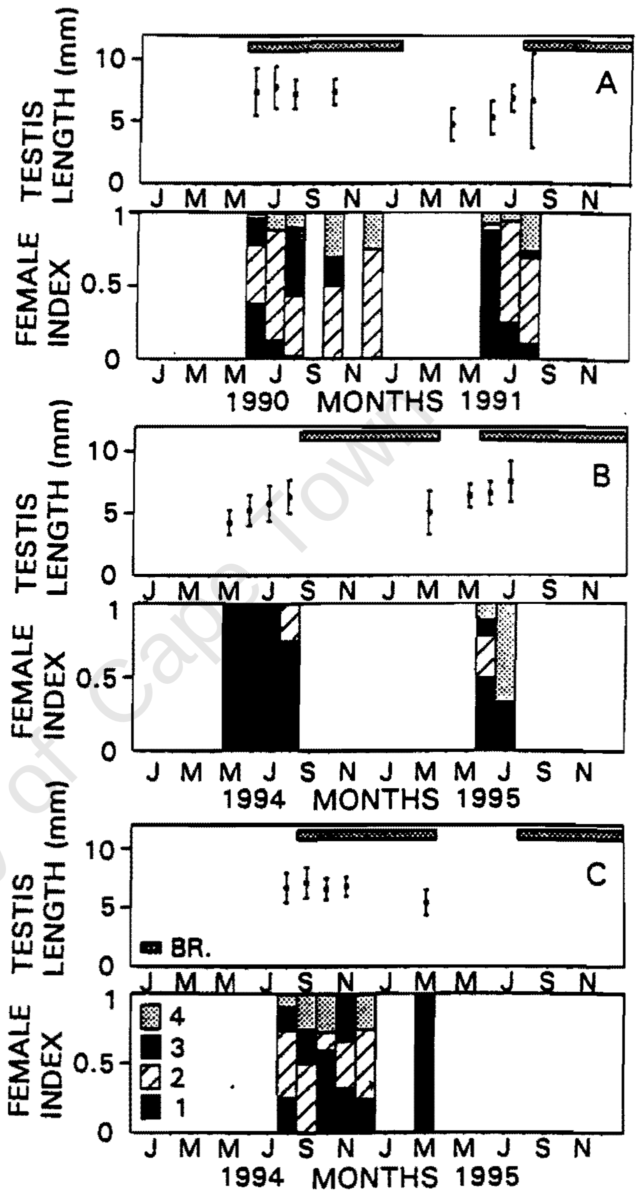

Figure 7.4. Namaqua sandgrouse gonad activity states in relation to breeding seasons at Rooipoort (A), the Langberg (B) and Droëgrond farm (C). Testis activity illustrated as mean testis length ±s.d. for samples of males. Female reproductive activity illustrated as the proportion of samples of females with ovaries exhibiting one of four activity states: 1) = inactive, largest follicle ≤ 2.5 mm diameter, 2) = active, largest follicle 2.6-5.0 mm, 3) = eggs developing, largest follicle >5.0 mm, and 4) = egg in oviduct or recently laid.

Table 7.4. Namaqua Sandgrouse reproductive activity summarised as mean testis length and volume, and female reproductive index frequencies where: 1) = inactive, largest follicle ≤ 2.5 mm diameter; 2) = active, largest follicle 2.6-5.0 mm; 3) = eggs developing, largest follicle >5.0 mm; and 4) = egg in oviduct or recently laid.

Locality	Month & year	Mean testis length (mm) ±*s.d.* (*n*)	Mean testis volume (mm^3)±*s.d.*	Female reproductive index				
				1	2	3	4	*n*
Rooipoort	Jun '90	7.5±1.9 (132)		38	40	18	3	(99)
	Jul '90	7.9±1.7 (12)	56±15	1	6	0	1	(8)
	Aug '90	7.3±1.2 (62)	48±17	1	20	23	5	(49)
	Oct '90	7.5±1.0 (10)	50±13	0	5	2	3	(10)
	Dec '90	7.2±1.3 (10)	52±20	0	3	0	1	(4)
	Apr '91	4.7±1.3 (5)	19±10					
	Jun 91	5.3±1.4 (33)	24±13	21	1	0	2	(24)
	Jul '91	6.9±1.1 (68)	38±13	8	22	0	2	(32)
	Aug '91	6.7±3.8 (37)	42±39	9	47	4	21	(81)
	Jun '95	6.6±0.8 (10)	39±13	1	8	0	1	(10)
Langberg	May '94	4.3±1.0 (24)		23	0	0	0	(23)
	Jun '94	5.3±1.2 (15)		21	0	0	0	(21)
	Jul '94	5.8±1.4 (16)		18	0	0	0	(18)
	Aug '94	6.4±1.3 (7)	32±17	6	2	0	0	(8)
	Mar '95	5.0±1.8 (5)	24±24					
	May '95	6.3±0.9 (9)	34±9					
	Jun '95	6.6±0.9 (21)	39±12	18	10	4	4	(28)
	Jul '95	7.5±1.6 (6)	53±20	0	0	2	4	(6)
Droëgrond	Aug '94	6.7±1.3 (23)	36±12	6	11	4	2	(23)
	Sep '94	7.2±1.3 (13)	44±15	0	4	2	2	(8)
	Oct '94	6.6±0.9 (13)	38±12	9	2	0	4	(15)
	Nov '94	6.8±0.8 (6)	45±14	3	3	3	0	(9)
	Dec '94	6.4±1.3 (4)	39±15	1	2	0	1	(4)
	May '95	5.4±1.1 (9)	24±11	10	0	0	0	(10)
G-Reinet	Nov '94	8.4±4.5 (4)	63±12	2	3	1	0	(6)
Tontelbos	Nov '94	6.7±1.2 (9)	43±18	1	1	1	0	(3)
Papkuil	Nov '94	6.3±0.6 (3)	39±10	0	1	2	4	(7)
Springbok	Nov '94	7.1±1.3 (7)	42±15	1	0	0	1	(2)
Soetdoring	Dec '94	6.2±1.2 (9)	39±25	0	3	0	0	(3)
Molopo R.	May '95	4.4±0.5 (6)	15±5	1	2	0	0	(3)

Table 7.5. The diameters (mm) of the three developing ovarian follicles measured from Namaqua Sandgrouse females collected at different stages during egg development and laying. E = egg in oviduct, L = egg laid.

Bird no.	1st follicle	2nd follicle	3rd follicle	Remaining follicle
1	7.5	4.0	4.0	
2	12.0	5.0	5.0	
3	19.0	14.5	8.0	
4	20.0	15.0	9.0	
5	E	8.0	5.0	
6	E	18.0	11.5	
7	E	18.0	11.0	
8	E	20.5	14.0	
9	L	?	7.0	
10	L	13.5	7.5	
11	L	E	7.0	
12	L	E	18.5	
13	L	E	20.0	
14	L	L	E	3.5
15	L	L	E	3.5
16	L	L	E	3.5
17	L	L	E	4.0
18	L	L	E	4.0
19	L	L	E	4.0

Droëgrond. During the drought year of 1993, Namaqua Sandgrouse numbers at Droëgrond increased substantially between September and November (Fig. 7.3). The increase in the counts of bellysoaking males in October indicates that nesting only started in September, continuing until at least December. After appreciable rains in February and March resulted in good ephemeral plant growth, large numbers of Namaqua Sandgrouse moved into the area through April and May to exploit superabundant seed reserves. Although food availability remained at equivalent levels until at least September, the substantial drop in numbers through the midwinter months suggests that many of the birds that arrived in April-May were on passage to the "east".

The gonads of both males and females were active from August until at least December (Fig. 7.4, Table 7.4). The 1994 nesting season started in August, continuing until at least the end of December. By March 1995, Namaqua Sandgrouse were still present in undiminished numbers (Fig. 7.3), but the birds appeared to be sexually inactive. Average testis length and volume were reduced, and no females sampled had active follicles in their ovaries (Fig. 7.4). There was no evidence of nesting, but an appreciable number of males were still belly-soaking for their chicks, suggesting that the nesting season ended in January-February. Despite patchy rains producing a patchily abundant food supply, Namaqua Sandgrouse numbers decreased dramatically through late March and April, few birds remaining by early May. The local population remained small through winter, increasing slightly through September, when the few birds in the area also began nesting. After a rain shower in November caused ephemeral plant germination, birds appeared to leave the study site, with few birds recorded in December. These plants had started setting seed in January 1996, resulting in an increase in Namaqua Sandgrouse numbers. Modest numbers were still present in May, and the count of belly-soaking males suggests that Namaqua Sandgrouse were nesting until at least March. The local population increased again through September and October, although few birds started nesting at this time. The unseasonal July rains may have delayed nesting. Nesting activity appeared to increase only in December, shortly before the study was terminated.

Prynnsberg and Plaatjiesdam. In May 1994, relatively large numbers of Namaqua Sandgrouse were present at both Prynnsberg and Plaatjiesdam, feeding on abundant seed supplies following good, but patchy, midsummer rains (Figs 7.2 & 7.3). Large numbers of Namaqua Sandgrouse remained in this region through winter. Despite an abundant availability of food (Table 7.2), these populations showed no sign of breeding activity until August (Fig. 7.4), when most birds left the region. Namaqua Sandgrouse numbers remained low through summer, increasing again as expected in April-May 1995 for the winter months. In 1995, nesting began in June and continued until at least March 1996, as there were still a number of males belly-soaking in May. Numbers at both sites dropped predictably in early summer, but recovered somewhat at Plaatjiesdam during December and January 1996. Large numbers had moved into the region again by May, to overwinter, but had moved out again by October. The timing and extent of breeding in the latter part of 1996 were not determined.

Other localities. In 1990 and 1991, Namaqua Sandgrouse at Rooipoort exhibited patterns of population fluctuations and breeding activity similar to those observed at Prynnsberg and Plaatjiesdam. Local numbers increased substantially in May, many birds moving out again through August (Malan *et al.* 1994). In 1990, Namaqua Sandgrouse gonads were active by June (Fig. 7.4), and birds nested from June until at least December. In April 1991, the testes of most males were much reduced, but increased in size through June to become fully active by July. Some females began to lay in July, and a large proportion of those sampled in August were at the laying stage.

At Pioneer farm, Namaqua Sandgrouse numbers fluctuated rather erratically, but were generally more abundant during winter (Table 7.6). In 1994, nesting started in July and continued until at least December. In 1995, the birds must have started nesting by June at the latest, since large numbers of males were already belly-soaking in July. In the Kalahari Gemsbok National Park nesting had started by July 1995, since appreciable numbers of males were belly-soaking in August (Table 7.6). The proportion of belly-soaking males peaked in November-December, but nesting continued until at least August 1996, when counting at this site was terminated.

The local Namaqua Sandgrouse population at Chyandour farm displayed no dramatic population fluctuations in the latter half of 1994, but did increase between June and December (Table 7.6). Birds started nesting in September, with a large proportion of males belly-soaking by December. Namaqua Sandgrouse at Melrose farm exhibited similar dynamics, the highest numbers recorded in November 1994, and nesting starting around September.

Namaqua Sandgrouse at Soetdoring farm exhibited a similar pattern of population fluctuations and breeding to those at Droëgrond, with generally larger populations during the summer months than the winter months (Table 7.6). In 1994, following appreciable late summer rains, Namaqua Sandgrouse at Soetdoring nested from August to January-February 1995, the 1995-96 season starting again in August 1995, despite only 15 mm of rain during the summer rainy season.

Most of the Namaqua Sandgrouse collected at Melrose farm, Tontelbos farm, Papkuil farm, Springbok, and Soetdoring farm in November or December 1994 had enlarged gonads, signalling that local populations at all these localities were breeding at the time of sampling (Table 7.4).

Table 7.6. Namaqua Sandgrouse population counts (Pop.) and breeding activity, quantified by counts of belly-soaking males (B-s.), at various monitoring localities in the years 1994-1996.

	Soetdoring		Twee Rivieren		Pioneer		Chyandour		Melrose	
Month	Pop.	B-s.	Pop.	B-s.	Pop.	B-s.	Pop.	B-s.	Pop.	B-s.
Jan '94										
Feb										
Mar										
Apr										
May										
Jun	419	(0)			937	(0)	41	(?)		
Jul	1246	(0)			192	(1)	94	(0)	72	(0)
Aug	815	(0)			387	(11)	124	(2)	39	(0)
Sep	812	(29)					108	(2)	59	(2)
Oct	844	(30)			84	(13)	151	(17)	73	(2)
Nov	650	(6)			180	(13)	143	(18)	131	(5)
Dec	1749	(23)			519	(13)	209	(33)		
Jan '95	870	(21)								
Feb	1432	(32)								
Mar	1742	(28)								
Apr	319	(1)								
May	325	(1)								
Jun	396	(0)								
Jul	495	(0)			2566	(96)				
Aug	665	(4)	849	(21)	851	(42)				
Sep	1539	(40)	571	(48)						
Oct										
Nov	974	(33)	1022	(187)						
Dec	924	(17)	874	(121)						
Jan '96	723	(11)	915	(79)						
Feb			735	(80)						
Mar			944	(109)						
Apr			1054	(119)						
May			460	(25)						
Jun			393	(22)						
Jul			741	(38)						
Aug			825	(47)						
Sep										
Oct										
Nov										
Dec										

Nest records. Nest records from the winter rainfall region of Namaqualand and the south-western Cape (region 1, Fig. 7.1) indicate that Namaqua Sandgrouse populations there breed through the summer months, nesting from September to February (Table 7.7). This breeding season coincides with the period of peak food availability in these regions. Nest records from the summer rainfall Nama Karoo (regions 2 and 5) suggest peak nesting from August to October (Table 7.7). This is in general agreement with my own observations at Droëgrond, although the nest records fail to indicate that November and December are also important months for nesting. The nest records from the Kalahari in South Africa (region 3, Fig. 7.1) confirm the earlier observations of a nesting season that may start in June and extend to January. The Namibian nest records from the northern and southern Namib (regions 4 and 8, Fig. 7.1) show that nesting can take place here at any time of the year. Most nests were, however, recorded within the period January-July, suggesting that nesting may take place in response to the late summer rains that these regions experience.

Table 7.7. Namaqua Sandgrouse nest records summarized by approximate month of laying and region within southern Africa. Regions: 1) Namaqualand and southwestern Cape (winter rainfall); 2, 5) Nama Karoo; 3) Kalahari savanna; 4) southern Namib; 8) northern Namib (2-8 all late summer rainfall).

	Month of the year												
Region	J	F	M	A	M	J	J	A	S	O	N	D	Tot
1	5	5							6	7	11	7	41
2	1	1		1		2	2	6	13	14	2	1	43
5	1		1	1		1	2	3			1	1	11
3						4	11	2	3	3	1		24
3*	3		1			4	5	7	4	3	4	3	34
4	4	1	3	5	3	7	11	4	2	2	1	2	45
8	9	4	4	6	16	3				6	7	2	57

*Nest records of Maclean (1968) from the Kalahari Gemsbok National Park.

Moult

At most localities sampled during the course of the study, there were always some Namaqua Sandgrouse moulting at any time of the year (Fig. 7.5, Table 7.8). The proportion of the population undergoing at least some moult was highest in the late summer and early winter months (March to July), when more than 50% of the local population was usually moulting.

During the nesting season from August to November, the percentage moulting decreased to 10-40%. Of a total of 224 birds not undergoing active primary wing-feather moult, 74% carried both old and new primaries in the wing. This suggests that either primary wing-feather moult occurs slowly but continuously through the year, or that primary moult can be interrupted for part of the year, particularly while birds are breeding. Individuals moulting during the breeding season could not be distinguished as nonbreeding birds however, since breeding birds were equally likely to be moulting. Of a total of 36 females either developing (follicles greater than 5.0 mm in diameter) or laying eggs, 44% were undergoing some moult.

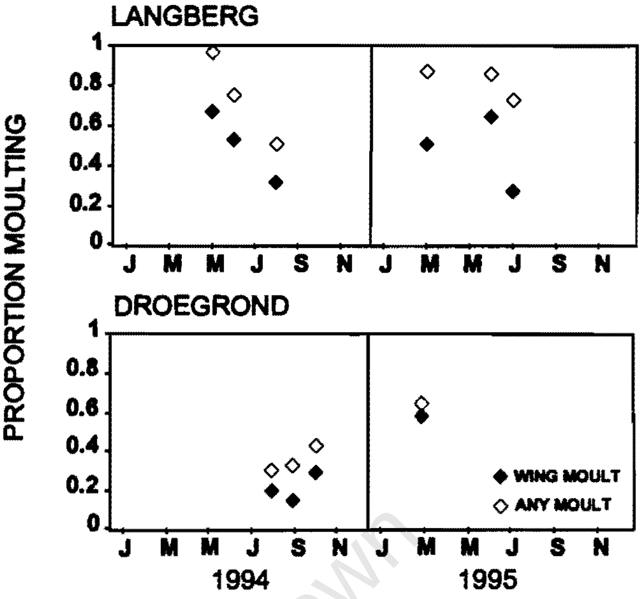

Figure 7.5. The proportion of Namaqua Sandgrouse undergoing primary wing moult and any moult (primary wing, secondary wing, body or tail moult) in relation to breeding seasons at Droëgrond farm and the Langberg.

Table 7.8. A summary of the percentage of birds undergoing primary wing-feather moult, secondary wing-feather moult, tail moult, and/or general body moult at various localities and at various times of the year.

Date	Locality	Primary moult	Secondary moult	Tail moult	Body moult	Any moult	Sample *n*
May '94	Langberg	67	33	41	96	97	(90)
Jun '94	Langberg	53	18	28	61	75	(57)
Aug '94	Langberg	31	0	0	44	50	(16)
Aug '94	Droëgrond	20	8	10	28	30	(40)
Sep '94	Droëgrond	14	0	10	29	33	(21)
Oct '94	Droëgrond	29	20	31	40	43	(35)
Oct '94	Tontelbos	31	23	23	23	38	(13)
Nov '94	Papkuil	20	0	20	10	30	(10)
Nov '94	Springbok	0	0	0	10	10	(10)
Mar '95	Droëgrond	59	12	24	59	65	(17)
Mar '95	Langberg	50	13	50	75	88	(8)
May '95	Molopo R.	0	0	0	0	0	(7)
Jun '95	Langberg	65	49	61	82	86	(51)
Jul '95	Langberg	27	20	53	20	73	(15)

DISCUSSION

Population fluctuations

The results of the population monitoring confirm the findings of Malan *et al.* (1994) that Namaqua Sandgrouse exhibit an "east-west" pattern of partial migration within South Africa. At Prynnsberg and Plaatjiesdam in the "east", local Namaqua Sandgrouse populations increased in April-May for the winter months, and decreased in August-September as expected. The influx of Namaqua Sandgrouse into this region in April-May coincides with the period of peak food availability after the late-summer rains. However, food may still be abundantly available at the time birds migrate out again in spring, as was the case at Prynnsberg in 1994. At Droëgrond, in the "west", Namaqua Sandgrouse numbers increased in spring (September-October) and decreased in autumn (April-May) as expected. The relative abundance each year depended on the quantity of ephemeral plant seed produced in the district as a whole after the late summer rainy season.

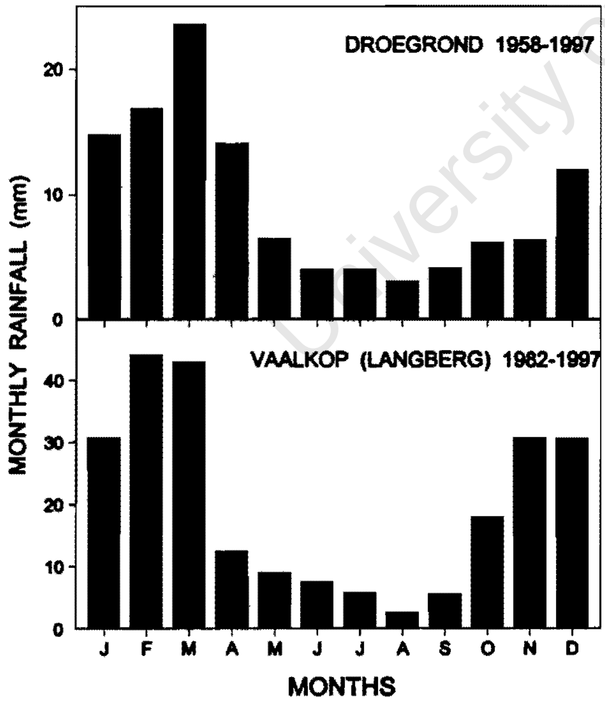

Figure 7.6. Mean monthly rainfall at Droëgrond farm and Vaalkop farm (Langberg).

Since Droëgrond falls within the late-summer rainfall region (Fig. 7.6), food availability generally peaks in April-May, although *I.* cf. *alternans* may continue to set seed until September in some years. The migratory exodus of Namaqua Sandgrouse at this time is therefore not in response to declining food availability. Furthermore, the spring influx often occurs months after peak seed set. In 1993 and 1995 for example, the spring influx occurred five months after ephemeral plants finished setting seed. During summer, birds also face a higher probability of suddenly encountering food shortages when most seeds germinate after good rains. It is only in the winter rainfall regions of Namaqualand and the southwestern Cape (region 1, Fig. 7.1) that

Namaqua Sandgrouse migrate in when food availability reaches a peak, and migrate out again before the winter rains reduce food availability to critically low levels. However, these winter rainfall regions do not support large populations of Namaqua Sandgrouse, and it is the summer rainfall areas of the Karoo that support the bulk of the Namaqua Sandgrouse populations in summer (Harrison *et al.* 1997, pers. obs.). Malan *et al.* (1994) are therefore incorrect in their assertion that the "east-west" partial migration occurs largely between winter and summer rainfall regions. There is, however, no straightforward hypothesis to explain why Namaqua Sandgrouse should be migrating between two late summer rainfall regions in South Africa.

Breeding seasons

The timing of breeding seasons for Namaqua Sandgrouse populations in different regions is unexpectedly variable, and not consistently correlated with periods of peak food availability. In the late summer rainfall areas, where other sandgrouse species exhibit an April-September breeding season during the period of peak food availability (Skinner 1996, Harrison *et al.* 1997, Tarboton & Blane unpublished), the breeding season for Namaqua Sandgrouse varies from January-July (in the northern Namib and Damaraland) to September-March (in the Nama Karoo).

Dixon and Louw (1978), studying the thermal behaviour of Namaqua Sandgrouse nests in the Namib, found that when the soil surface temperature at one nest exceeded 50°C, the incubating bird was unable to prevent the nest temperature from exceeding 45°C and killing the embryos. This observation led them to believe that Namaqua Sandgrouse in this region nest mainly in the winter months to avoid excessively high summer temperatures. Nonetheless, throughout the Nama Karoo and Kalahari, where temperatures are no less extreme, Namaqua Sandgrouse often nest through January, the hottest month of the year. Following two days in December, when ambient air temperatures reached 43°C, several nests under observation at Droëgrond hatched successfully. Midday temperatures of 48°C in the shade and soil temperatures of 68°C have been recorded near incubating Spotted Sandgrouse *P. senegallus* (George 1970), and Crowned Sandgrouse *P. coronatus* have been observed incubating at air temperatures of 41-51°C with no apparent ill effects (Johnsgard 1991). These observations suggest that the Namaqua Sandgrouse is capable of coping with extreme temperatures and nesting successfully through midsummer.

In the Nama Karoo, the nesting season commonly starts five months after food becomes generally abundant, and therefore at a time when the food supply is diminishing. A puzzling feature of this breeding season is that this region receives most of its rainfall as thundershowers between December and April. Namaqua Sandgrouse will therefore often have young, flightless chicks, the most nutritionally demanding stage of the annual cycle (Chapter 6), during the period of lowest food availability.

Possible hypotheses to explain these unusual breeding seasons include the following:

1) *Namaqua Sandgrouse breed twice in the year.* The Namaqua Sandgrouse is an opportunistic granivore, so one might predict that birds arriving in the "east" of South Africa from breeding grounds in the "west" would exploit the superabundant food supplies and breed a second time in the year. If so, one would expect them to start breeding soon after their arrival in April, when food is often at its most abundant, so that the chicks would be fully grown and independent by August, in time for the return migration to the "west". However, in years when a population-wide breeding response does occur in winter, nesting starts only in June. As a result, the chicks reach independence by September, at the earliest. The migratory exodus of birds in August must therefore exclude those that nested successfully (whose chicks would still be too young to migrate), and those still nesting. It is these birds that may remain in the "east" through the summer months, while those that leave on migration start nesting soon after arriving in the "western" regions. It appears unlikely then that Namaqua Sandgrouse will raise a brood in the "west" and another in the "east" within a single year, particularly given that high levels of nest predation (Chapter 2) are likely to necessitate repeat laying before a brood is raised successfully.

In Namibia, the main breeding seasons in the east (e.g. Soetdoring: August-March) and the west (Namib: April-September) are sufficiently spaced to allow for birds to breed twice in the year, should Namaqua Sandgrouse migrate between these two regions. Unfortunately, no data exist on the movements of Namaqua Sandgrouse within Namibia, although Clancey (1979) was of the opinion that populations from the southern Karoo migrate as far as northern Namibia, and that northern populations are largely resident.

2) *Moulting precludes an early start to breeding.* Moulting draws significantly on protein and energy reserves to synthesize new feathers and to offset the effects of poorer insulation and flight efficiency. The high energetic and nutritional demands of breeding and moult therefore usually

preclude simultaneous timing (Payne 1972). Namaqua Sandgrouse displayed a preference for moulting in late summer and the first half of winter (Table 7.8), when most populations were not breeding. Food availability over this period usually ranges from initially being at its most scarce (when the late summer rains induce most seeds to germinate), to being at its most abundant (when plants shed seed after growing to maturity) during the annual cycle. It could be argued that the period of peak moult is timed to coincide with the period of peak food availability, and that the annual moult therefore delays the start of the breeding season in Namaqua Sandgrouse by several months. Keratin synthesis requires particularly high proportions of the sulphur-containing amino acids methionine, cystine and cysteine (Murphy & King 1992), which may be limiting in a seed-only diet (Wiens & Johnston 1977). Without detailed data on the nutritional demands of breeding *versus* moult in Namaqua Sandgrouse, it is difficult to evaluate such an hypothesis. However, a body of circumstantial evidence argues against the nutritional demands of moult being higher or more critical than those of reproduction. Firstly, Namaqua Sandgrouse feed on a relatively protein-rich diet, where energy may be more usually first limiting than protein or amino acids (Chapter 6). Secondly, Namaqua Sandgrouse do not exhibit a well defined moulting period, a sizeable proportion of the population undergoing some moult at any time of the year. This means that birds are often moulting during the breeding season. In fact, during the breeding season, females producing eggs (probably the most energetically demanding stage of breeding in a precocial species) were just as likely to be moulting as those not producing eggs. In their study of Namaqua Sandgrouse in Namibia, Dixon and Louw (1978) found no evidence of a distinct moulting season, and also noted that sexually active birds showed signs of moult. These observations suggest that the moult may be a rather gradual process in this species, serving to spread the nutritional costs of the moult over a longer period of time, and thus lowering the daily requirements. In other sandgrouse species for which sufficient data exist, there is a complete post-breeding moult. This moulting period starts within a month or two of the start of nesting, and typically takes six months to complete (Cramp *et al.* 1985). Finally, the fact that most South African sandgrouse populations time the breeding season in such a manner that juveniles moult into their adult plumage (at an age of approximately two months) at the time of greatest food shortage, suggests that the nutritional demands of moult are not disproportionately high.

3) *Adults require several months to build up nutritional reserves for breeding.* After appreciable rains, most ephemeral plant seeds germinate. This results in a period of food scarcity for sandgrouse that lasts until the plants begin to set seed, whereafter food becomes superabundant. It could be argued that, following the period of food scarcity, sandgrouse require several months to build up their nutritional reserves again before breeding can commence. However, the weights of adult male Namaqua Sandgrouse remained relatively constant through the year at various localities (Fig. 7.7), failing to support the hypothesis. Furthermore, the results of Chapter 6 suggest that Namaqua Sandgrouse are able to forage successfully during periods of even relatively low food availability, and should be able to rapidly replenish nutritional reserves when food becomes superabundant.

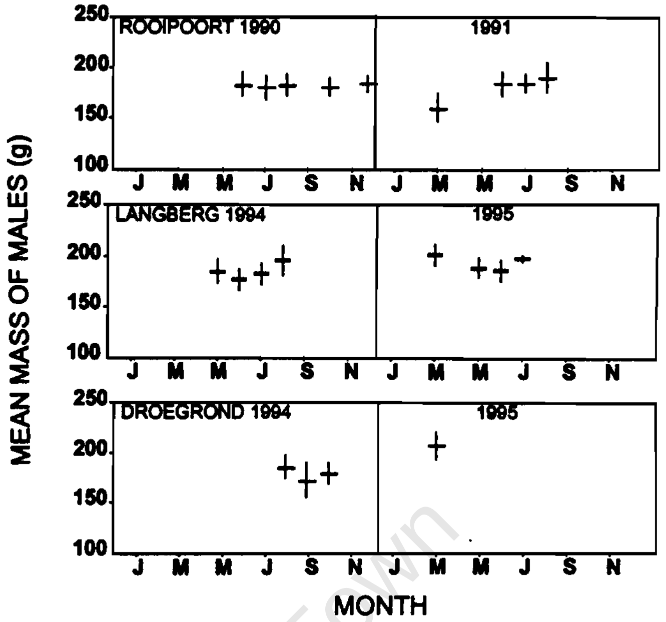

Figure 7.7. Mean sample weights of adult male Namaqua Sandgrouse (± *s.d.*) at different times of the year at Rooipoort farm, Droëgrond farm and the Langberg.

4) *The timing of breeding is influenced by seasonal variation in nest predation pressure.* Nest predation is the most important limiting factor on Namaqua Sandgrouse populations, and small reductions in nest predation can lead to appreciable increases in breeding success (Chapter 2). At Droëgrond, daily predation rates on the nests of Namaqua Sandgrouse and other bird species declined significantly between late winter and midsummer (Fig. 7.8). The small mammals that are the principal nest predators are primarily insectivorous (Smithers 1983). The seasonal differences in predation may relate to differences in insect food availability between winter and summer, with higher nest predation in winter a consequence of lower insect food availability (Chapter 9). If the probability of predation is substantially higher through the winter months than the summer months, Namaqua Sandgrouse may delay the start of breeding until the end of winter. This hypothesis might explain the timing of breeding in the Karoo, but does not explain the earlier start to breeding in the Kalahari and parts of Namibia, unless these regions experience

lower nest predation rates which then obviates the need to avoid winter breeding.

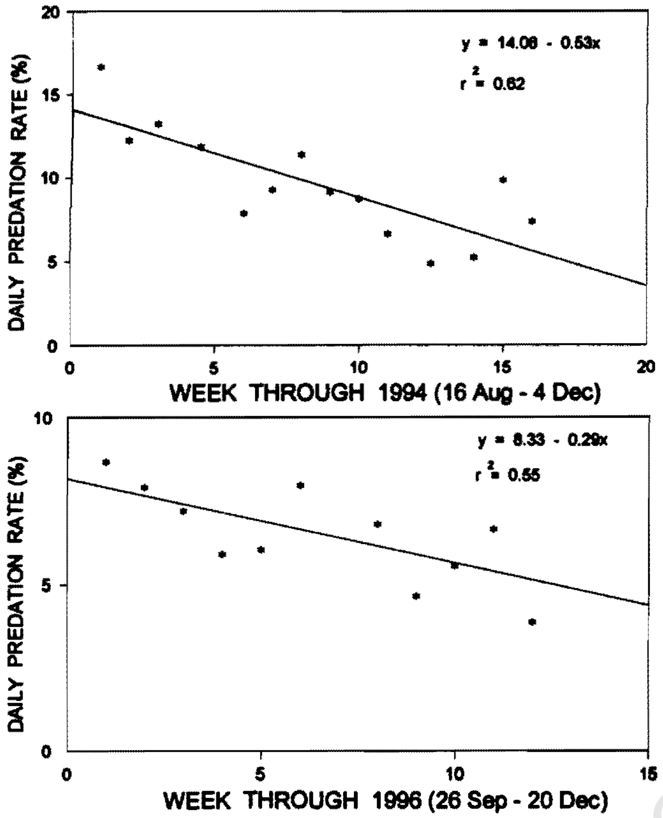

Figure 7.8. Seasonal changes in the daily nest predation rate on a) Namaqua Sandgrouse at Droëgrond farm in 1994 (see Chapter 2), and b) a variety of bird species at Droëgrond farm in 1996 (see Chapter 9).

The relationship between food availability, nomadism, migration, nest predation and the timing of breeding in the Namaqua Sandgrouse across its southern African distribution is clearly a complex one. This investigation of food availability as a proximate factor determining the timing of these events is unable to provide a simple explanatory framework for the observed patterns, particularly within South Africa. Future studies should aim to establish the movement and breeding patterns of Namaqua Sandgrouse and the differences in nest predation pressure between regions within southern Africa as a whole.

CHAPTER SEVEN

POPULATION FLUCTUATIONS AND BREEDING ACTIVITY OF NAMAQUA SANDGROUSE IN RELATION TO RAINFALL AND FOOD AVAILABILITY

SUMMARY

In South Africa, the Namaqua Sandgrouse *Pterocles namaqua* exhibits a pattern of partial migration between two late summer rainfall regions, birds spending the summer months in the Nama Karoo and the winter months in the Kalahari. Across southern Africa, the breeding season for this species is unexpectedly variable, and not consistently correlated with periods of peak food availability. The peak nesting period ranges from January-May in northwestern Namibia, to June-October in the Kalahari, to September-December in the Nama Karoo, all late-summer rainfall regions. This suggests that some factor(s) other than proximate food availability is/are involved in determining the timing of movements and breeding in this species. The possible complicating influences of biannual breeding, moulting, adult nutritional reserves and seasonal variation in nest predation pressure are discussed.

INTRODUCTION

The Namaqua Sandgrouse is an obligate granivore, and even its chicks appear to feed solely on seeds from the day they hatch (Chapter 6). The advantage of a granivorous diet in an arid ecosystem is that annual plants produce superabundant quantities of seed in a predictable fashion following good rainfall (Brown *et al.* 1979). However, two drawbacks of such a diet are: 1) that the appropriate rainfall events are often patchily and unpredictably distributed in time and space, and 2) that most seeds remaining in the soil seed bank germinate following good rainfall, reducing food availability to critically low levels until the next seed crop is produced (Wiens & Johnston 1977). This particular suite of environmental features has favoured those granivorous demand for this type of hunting expand in tandem with the predicted growth of the wider tourism industry. In this chapter, I examine issues relating to the sustainable shooting of the Namaqua Sandgrouse *Pterocles namaqua* and offer a number of practical recommendations for the management of this species as a gamebird.

DISCUSSION

The susceptibility of the Namaqua Sandgrouse to over-exploitation

Due to their dependence on usually limited watering sites in arid environments, sandgrouse are extremely susceptible to over-exploitation. In few exploited animals does the entire local population gather together at a predictable time each day and at a fixed and predictable site. Furthermore, sandgrouse may gather in spectacular numbers. Up to 50 000 Pintailed Sandgrouse *P. alchata* have been noted at waterholes in Turkey, Morocco and Algeria (George 1970, Johnsgard 1991), and I have counted in excess of 15 000 Namaqua Sandgrouse gathering at an isolated waterhole in the Kalahari. Such concentrations are the result of nomadic influxes into localised areas following patchy rains, and will give a false impression of the general abundance of the birds to observers with little knowledge of sandgrouse population movements. Should these large concentrations be exploited, it can have serious repercussions on the future abundance of sandgrouse within the wider region in which they move nomadically. Large concentrations of Burchell's Sandgrouse *P. burchelli* congregating at isolated waterholes in the Kalahari region of Botswana were subjected to winter-season hunting in the recent past, a practice that may still continue. Hunting bags often exceeded 100 per hunter (various hunters pers. comm.). This hunting pressure on breeding populations has apparently led to regional population declines of this species (Ken Oake pers. comm.).

Breeding seasons and shooting seasons

Hunting Namaqua Sandgrouse during their breeding season is particularly detrimental due to the length of the period (approximately three months) during which a breeding attempt is sensitive to the loss of one or both members of a breeding pair. Firstly, because the pair share incubation, the death of either partner during the 25 day nesting period will terminate the nesting attempt. Secondly, because the young are dependent on the male parent for their drinking water for a period of approximately two months, they are likely to die should the male parent be killed during this time.

A further problem is the variability of the breeding seasons of the Namaqua Sandgrouse, not only between regions, but between years within regions (Chapter 7). As a result, the breeding seasons of Namaqua Sandgrouse in the Northern Cape Province (South Africa) partially overlap the current shooting season (1 April to 15 July) in years when there is an early start to breeding (June-July). In South Africa, the only month in which Namaqua Sandgrouse rarely nest or still have dependent young is May. In Namibia, the situation is even more complex, as Namaqua Sandgrouse in different regions experiencing similar rainfall regimes exhibit very different breeding seasons. The net result is that the current shooting season for the whole of Namibia (1 September to 31 November, which may be modified on a regional basis in the future) falls within the largely nonbreeding season of birds inhabiting the northwest Namib, but broadly overlaps the breeding season of birds inhabiting the southeastern portion of the country (Rob Simmons pers. comm.). The problem is exacerbated by our incomplete knowledge of the breeding seasons in different regions across southern Africa, and the lack of a predictive understanding of the factors that determine the timing of breeding in the Namaqua Sandgrouse (see Chapter 7).

What is a sustainable offtake for the Namaqua Sandgrouse?

The answer to the question of what constitutes a sustainable offtake for the Namaqua Sandgrouse will depend on which definition of sustainability is adopted. The classical definition holds that a sustainable offtake is a level of offtake that does not exceed the capacity of the population to replenish itself (McCullough 1996). Using this definition, one might, based on the results reported in Chapter 2, conclude that there is no sustainable offtake level for Namaqua Sandgrouse, as recruitment may be too low to maintain populations over extensive areas. Only long-term monitoring studies will be able to resolve this issue more satisfactorily.

From a theoretical point of view, a sustainable offtake is reliant on natural density dependent factors that largely compensate for the offtake (Sinclair & Pech 1996, Callaghan *et al.* 1997). In other words, a sustainable hunting offtake removes the proportion of the population that would have died naturally due to density dependent factors (the 'doomed surplus') and/or stimulates breeding to replace the birds removed in the offtake. There is no evidence of density dependent mortality and/or natality in the Namaqua Sandgrouse. On the breeding grounds, nest predation did not increase as nesting density increased and, in fact, the opposite appeared to hold true (see Chapter 2). During periods of widespread drought, food limitation might result in density-dependent mortality, although such mortality could result more from chance events such as the failure of birds to find a very patchily distributed resource. Furthermore, the Namaqua Sandgrouse is a central-place forager in which the central place, the waterhole, may also be used as an information centre (Ward 1972). Their ability to find widely dispersed and cryptic food patches of high quality may therefore increase as the local population size sampling the area around the waterhole increases. Spinks and Plagányi (unpublished) used a simulation model to explore to what extent differences in resource distribution between arid and mesic areas affected the foraging success of a mole-rat species. In mesic areas (where mole-rats are naturally solitary and food is relatively evenly spread), individuals gained greater foraging returns by foraging alone. In arid areas (where mole-rats are naturally colonial and food is patchily distributed), increased group size with co-operative foraging did not increase energetic benefits, but diluted foraging costs and reduced the risks of unproductive foraging. They therefore found that group foraging represented an evolutionarily stable adaptation to foraging and survival in arid areas with patchy food resources.

In highly stochastic environments where plant-herbivore dynamics do not reach or closely approach equilibrium levels, the concept of a carrying capacity implicit in maximum sustainable yield models (Caughley 1976), is viewed more as a mathematical abstraction than from the perspective of sustainable utilisation (Macnab 1985, McLeod 1997). The amplitude of population fluctuations is determined by both the strength of density dependence and the size of density independent mortalities (Sinclair & Pech 1996). If density independent mortalities are high (e.g. high reproductive failure in Namaqua Sandgrouse), and if environmental conditions fluctuate markedly (as they do in arid zones), density dependent mortality may be relatively unimportant. The Budgerigar *Melopsittacus undulatus*, an abundant, nomadic granivore inhabiting arid and semi-arid regions of Australia, is thought to incur greater density independent mortality due to its unpredictable environment (Ford 1989, p. 175). Since density dependence is a central assumption of most sustainable offtake models, further research is required to determine the relative importance of density dependent and density independent factors to the population dynamics of the Namaqua Sandgrouse.

Martin (1997) adopted a rather different approach to the definition of sustainability, viewing the ultimate criterion of sustainability as the persistence of the species. In other words, as long as a species' populations are not reduced to the level that extinction is a real threat, then use can be regarded as sustainable. The attraction of sandgrouse to sport-hunters is, to a large extent, dependent on the numbers of birds that congregate at a waterhole (Malan *et al.* 1993), i.e. it is density-dependent. The corollary is that, should hunting lead to substantial reductions in populations, the species would approach commercial extinction well before it reached biological extinction.

The highly nomadic and migratory nature of the Namaqua Sandgrouse ensures that its southern populations range widely within South Africa at least, and probably into neighbouring Namibia and Botswana as well. This species can therefore be regarded as a commonly owned resource. History dictates that few, if any, commonly owned resources are managed in a sustainable fashion (Levin 1993, Ludwig *et al.* 1993), a phenomenon that has come to be known as the 'tragedy of the commons' (Hardin 1968). Martin (1997) states that tenure is the most important issue affecting sustainability of resource use, and that the avoidance of an open access situation is crucial. Over-exploitation leading to commercial extinction and the later slow recovery of populations when their exploitation is suspended is the usual sequence of events in open access fishing resources. The probability of the Namaqua Sandgrouse resource following this route will depend both on the future market demand for sandgrouse wing-shooting and the ability of conservation agencies and the hunting fraternity to enforce or adhere to management regulations and scientifically determined (as opposed to politically determined) quotas. The very nature of the arid environment, the widespread distribution of the Namaqua Sandgrouse and its extensive nomadism suggest that this species is likely to be resilient to over-exploitation. However, its low reproductive output, and the possibility that natural mortality and natality rates may be largely density independent, would ensure that population recoveries following over-exploitation would be slow.

Practical management recommendations

Management actions that can be taken to reduce the impact of hunting on populations include the following:

1. Avoid hunting through the breeding season as far as possible. The very extended breeding season in some years, together with the variability and unpredictability in the timing of breeding, confounds this management option. Hunting towards the end of the breeding season will be more detrimental than hunting at the start of the breeding season. Birds whose nesting attempts are terminated through the loss of the mate early in the season may find another mate and re-nest. If males are killed when a relatively high proportion of them are attending dependent young, these young will die, and no new nesting will be attempted towards the end of the season.

2. Avoid excessive disturbance to the drinking habits of the birds by ensuring that an alternative, undisturbed watering point is available within easy flying distance (within 10 km) of the waterhole being shot. Alternative waterholes should also be used as a management tool to control the numbers visiting any one waterhole (see below).

3. Avoid shooting at a waterhole attracting a drinking population that exceeds 800 birds. Although hunter satisfaction is positively correlated with the number of birds attending a waterhole, so too is the bag per hunter (Malan *et al.* 1993). Malan *et al.* (1993) found that a drinking population of at least 300 is required to satisfy hunter expectations. They also noted that the average bag per hunter exceeded 10 (the legal bag limit in the Northern Cape Province of South Africa) if the drinking population exceeded about 800 birds.

4. Use a number of waterholes as a mechanism for managing the numbers attending individual waterholes. Isolated waterholes often attract larger drinking populations, since they service larger areas. To ensure that drinking populations do not exceed 800, additional waterholes should be constructed to disperse the birds in years when there is a large nomadic influx. Such waterholes could be selectively closed down in years when there are fewer birds present in the area.

5. Site the shooting butts at least 100 m from the waterhole. Namaqua Sandgrouse often approach a waterhole from a considerable height, swooping lower as they get within 100-200 m of the water, and slowing down before they land. Having the butts 100 m from the

water is therefore a compromise between flight speed and accessibility to the guns. If the butts are too close to the water, the birds are easier to shoot, and if the butts are too far from the water, the birds are out of range.

6. Avoid shooting a local population (each waterhole) more than once. Malan *et al.* (1993) noted that the mean offtake per watering site increased from 13% for one hunt per site to 31% for two hunts per site and 49% for three hunts per site per season. Given the apparently low reproductive output of Namaqua Sandgrouse, hunting pressure should be kept to a minimum, and a restriction on the number of hunts per site is one method of addressing this. However, given the highly nomadic nature of this species, a total hunting quota would be a more practical method of controlling access, should the ability to enforce rights of access exist.

An important long-term management goal should be the development of an effective research and monitoring programme that aims to determine: 1) the breeding success of Namaqua Sandgrouse in different regions across its southern African distribution over a number of years, 2) the mean annual survival of first-year and adult birds, 3) a more thorough understanding of the breeding seasons of Namaqua Sandgrouse in different regions, and 4) the nature and extent of movement between regions.

CHAPTER NINE

THE INFLUENCE OF NESTING HABITS AND THE NOMADISM/RESIDENCY DICHOTOMY ON NEST PREDATION IN ARID-ZONE BIRDS

SUMMARY

The nesting habits and success of 11 co-existing species were examined in an arid, sub-tropical habitat in South Africa. Nesting success ranged from 3.5% to 75.4% between species, predation by mammals and snakes accounting for 94% of nest losses (n = 588). Predator-avoidance behaviour and nest site accounted for much of the variation in nesting success. The Doublebanded Courser and Namaqua Sandgrouse nested in similar situations. However, whereas the former ran rapidly off the nest when a predator approached, the latter sat tight. Nesting success for the Doublebanded Courser was 75.4% (n = 12), but only 8.2% (n = 278) for the Namaqua Sandgrouse. Nest predation was inversely related to nest density, and decreased as the breeding season progressed from spring to midsummer. Daily egg-predation rates were higher than daily nestling predation rates for seven of the nine altricial species, contrary to the widely held view that increased activity at the nest during the nestling period increases predation risk. Nest-predation rates of resident ground-nesters were similar to those of both resident and ranging shrub-nesters, and only the nomadic ground-nesters suffered significantly higher daily nest-predation rates than shrub-nesters. Among ground-nesters, territorial residents suffered significantly lower daily nest-predation rates than nomads, suggesting that residency enhances nest survival.

INTRODUCTION

The influence of nest predation on the evolution of avian reproductive strategies depends on the degree to which predation influences reproductive success and the extent to which the probability of predation can be reduced (Martin 1992). Studies across a variety of habitats and locations have established that nest predation is a primary and severe cause of breeding failure for many birds (Ricklefs 1969a, Martin & Clobert 1996). Predation rates vary with nest-site characteristics (Osborne & Osborne 1980, Marzluff 1988, Martin 1993, Schieck & Hannon 1993 and references therein), nest density (Dunn 1977, Page *et al.* 1983, Hill 1984b), predator abundance and behaviour (Dunn 1977, Summers & Underhill 1987, Goodrich & Buskirk 1995), and parental behaviour (Montgomerie & Weatherhead 1988).

Predation has been implicated as an important cause of the over-dispersion of birds' nests in situations where predators engage in "area-restricted searching" around prey items they find (Tinbergen *et al.* 1967, Croze 1970). Studies using artificial nests have shown that predation increases as the density and/or degree of clumping of nests increases (Tinbergen *et al.* 1967, Page *et al.* 1983, Sugden & Beyersbergen 1986, Picman 1988). Reduced dispersion or increased density of nests under natural conditions has variously been found to have no influence on predation rates (Erikstad *et al.* 1982, Boag *et al.* 1984, Watson *et al.* 1984, Andren 1991, Schieck & Hannon 1993), or to increase predation (Krebs 1971, Dunn 1977, Best 1978, Hill 1984b).

Research on the modification of predation risk by parental behaviour has focused on nest-defence behaviours, such as distraction displays and attack (see reviews by Montgomerie & Weatherhead 1988 and Martin 1992), with little attention to predator-avoidance behaviours. Nest predation has also been linked to variation in a number of life-history traits, including clutch size, fecundity and the length of the nestling period (Slagsvold 1982, Martin 1995, Martin & Clobert 1996, Julliard *et al.* 1997). A strategy that has received little attention in relation to nest predation is that of residency *versus* migration or nomadism. The suggestion that migrants or nomads might benefit from a predator swamping effect (e.g. Welty 1982, p. 553), is not well supported (e.g. Summers & Underhill 1987).

Skutch (1949) speculated that the presence of young in the nest and increased activity of the parents during the nestling period may attract the attention of predators, leading to increased predation risk during the nestling stage than during the incubation stage. Although there is some empirical evidence of a predation cost associated with chick begging (Perrins 1965, Redondo & Arias de Reyna 1988, Redondo & Castro 1992, Haskell 1994) or adult movements to and from nests (Erikstad *et al.* 1982), most studies have documented lower predation rates during the nestling period than during the incubation period (Nice 1957, Ricklefs 1969a, Roseberry & Klimstra 1970, Cresswell 1997).

This chapter examines nest-predation rates among species in relation to nest site, nest density, predator-avoidance behaviour, stage of the nesting cycle and season, and degree of residency. The data are used to test the following hypotheses: 1) ground-nesting species incur higher nest-predation rates than shrub nesters, 2) territorial residents incur lower nest-predation rates than nomadic or non-territorial residents that undertake wide-ranging movements, 3) differences in predator-avoidance behaviour can have an appreciable influence on nest-predation risk, 4) nest-predation rates are lower during the incubation period than during the nestling period, and 5) nest-predation rates increase as nest density increases.

METHODS

The study was conducted over four early-summer seasons (August-December 1993-1996) in an area of 10 000 ha on the farm Droëgrond. Study site attributes are detailed in Chapter 2.

Data collection

Nests were found randomly through the nesting period, either by flushing birds while cycling through the study area or, in the case of Namaqua Sandgrouse (see Appendix 9.1 for scientific names), by following birds flying to the nest to relieve their mates. Nests were marked and visited at intervals of 1-6 days, as described in Chapter 3. Depredation was assumed when eggs or nestlings (too young to fledge) disappeared. Mammal predation on shrub-nesting species was assumed when damage to the nests occurred, and snakes were assumed to be the culprits when no evidence of disturbance was found. No avian nest predators occur at the study site.

For ground-nesting species, the following characteristics were recorded for each nest site for a random sample of each species: a) a subjective estimate of nest camouflage evaluated as the degree to which the rim of the nest matched its immediate surroundings (1 = poor, 2 = fair, 3 = good, 4 = excellent), b) the proportion of the nest edge concealed by objects greater than the height of the incubating bird (0, 1-25%, 26-50%, 51-75%, or 76-

100%), c) the dominant substratum around the nest (1 = sand alone, 2 = sand with pebbles or scattered stones, or pebbles alone, 3 = pebbles with scattered stones, 4 = stones/rocks with pebbles), and d) the number of objects >3 cm high within a 1 m radius of the nest. The substratum codes served as an index of complexity of the nest environment. The object totals served as an index of both complexity and cover around the nest.

Clutch size was recorded only if it remained unchanged between visits, and therefore does not include nests lost to predation prior to the second visit, or nests found at the nestling stage. Rainfall was measured at a rain gauge located centrally in the study site. Daily average temperatures were obtained from the weather station at Upington, 120 km to the northeast of the study site, but which experiences similar weather conditions.

Calculations

Nesting success was determined using the method of Mayfield (1975):

$$success = \left(1 - \frac{losses}{exposure}\right)^{np}$$

where *exposure* is the total number of active nest days, and *np* is the period in the nesting cycle being considered. Overall nesting success (at least one precocial chick hatching or one altricial nestling fledging) was calculated as the product of success during the laying and incubation periods combined, and the nestling period. The variance of Mayfield's estimator was derived from the expression:

$$\frac{(exposure - losses) \times losses}{(exposure)^3}$$

developed by Johnson (1979). Statistical comparisons of daily mortality rates were effected by calculating the z statistic as the ratio of the difference between two mortality rates to its standard error (Johnson 1979).

The original nest records of Maclean (1967, 1968, 1970a, b) from the Kalahari, 300 km to the north of the study site, were reanalysed using the Mayfield method for comparison with the present study. These records were not complete enough to determine separate incubation and nestling stage predation rates, so only daily nest-predation rates were calculated.

When determining the length of the incubation or nestling periods, the laying of the last egg or fledging of the last chick was assumed to have occurred midway between two visits no more than two days apart. While the calculated periods for individual nests are therefore subject to some error, the species' average is reasonably accurate.

The observer's ability to find nests with eggs *versus* nests with nestlings was evaluated by comparing observed to expected nestling finds. Expected nestling finds were determined by assuming nests found with eggs were found halfway through the incubation period, Mayfield's (1975) assumption, and then calculating nest survival through half the incubation period and half the nestling period at the observed daily predation rates.

Relative nest density was determined as the number of new nests (corrected for observer bias) found per km cycled. Observer bias resulted from nests with nestlings being more difficult to find than nests with eggs. This bias was corrected using the formula:

New *nestl.* = Observed *nestl.* x (Expected *nestl.* / Observed *nestl.*),

where *nestl.* = nestling finds.

RESULTS

Nest site

The nest-site characteristics of the various species studied at Droëgrond are summarised in Tables 9.1 and 9.2. Several species sited their nests on the southern to eastern side of small plants to gain some shade during the heat of the day. Larklike Buntings nested in more concealed situations than the other species; there were more objects within 1 m of the nest and a greater proportion of the nest edge was concealed (Table 9.2). This species' nests were, however, among the easiest to locate, being predictably sited in rocky habitat and along road verges. Furthermore, the substantial rim of twigs of most nests did not often match the general substratum of sand, pebbles and stones.

Predator-avoidance strategy

Observations and categorisation of predator-avoidance strategies were based largely on the birds' reactions to the approach of a human observer. The Doublebanded Courser ran rapidly off the nest 30-100 m in advance of an observer, and it was rare for the observer to pinpoint the location of the nest from the movement of the bird even during a rapid approach on a bicycle. The non-incubating member of the pair usually remained in the vicinity of the nest, acting as both a sentinel and decoy. Namaqua Sandgrouse either walked off the nest in a skulking fashion in advance, or sat motionless, flushing directly off the nest at close range (3-5 m). Limited observations suggest it adopts the latter strategy when approached by other predatory mammals (Maclean 1968, pers. obs.). The remaining ground-nesters either ran, in the case of Spikeheeled Lark, or flew off the nest when approached. On cool days, most species left the nest once the observer was within 10-50 m, but on hot days they were more reluctant to leave.

Nest predators

Predation accounted for 93.9% of all complete nest losses (n = 588 failed nests), excluding the losses due to the rains of 7-8 November 1996, which are considered separately below. The identity of nest predators was determined most accurately for Namaqua Sandgrouse (Table 2.1). Mammalian predators accounted for 80.4% of nest losses, with small mammals, mainly the diurnal Yellow Mongoose, Cape Grey Mongoose and Suricate, and the nocturnal Striped Polecat, taking nearly eight times as many nests as nocturnal larger mammals, which included Bateared Fox, Cape Fox, Aardwolf and Aardvark. Egg predators are assumed to be similar for the other ground-nesters, but snakes might take an appreciable proportion of the nestlings of altricial species (see below).

There was evidence of mammal predation in only 7% of predation losses among shrub-nesting species. The blue egg-shells of the Chat Flycatcher were easier to locate than those of the other species, and of 10 nests with eggs lost to predation, definite evidence of Rhombic Eggeating Snake predation was found at seven of them, two others probably suffering a similar fate. The eggs of other shrub-nesters usually disappeared without disturbance to the nest. I therefore view this specialist snake as the principal egg predator of shrub-nesting species. The disappearance of chicks from nests in the absence of disturbance signs for even the closed-nesting species, suggests that snakes (which could include Cape Cobra, Horned Adder, Namib Tiger Snake and Namib Sand Snake) were important predators of nestlings.

Table 9.1. Nesting strategies compared among species at Droëgrond. Average incubation, nestling and nesting (includes laying, incubation and nestling) periods were calculated to the nearest half-day.

Species	Nest site and nest type	Predator avoidance strategy	Mean clutch size ±*s.d.* range (*n*)	Mean incubation period (*n*)	Mean nestling period (*n*)	Mean nesting period
Doublebanded Courser	ground - no nest exposed in open terrain	run early	1 ± 0 (12)	28.0 (1)	-	28.0
Namaqua Sandgrouse	ground – shallow scrape exposed in open terrain	sit tight	2.88 ± 0.33 2-3 (224)	21.0 (2)	-	25.0
Spikeheeled Lark	ground – sunken cup S-E of small plant	sit, run	2.70 ± 0.66 2-4 (46)	13.0 (4)	11.0 (2)	25.5
Sclater's Lark	ground – sunken cup exposed in bare patch	sit, fly	1 ± 0 (34)	11.0[a]	11.5 (9)	22.5
Greybacked Finchlark	ground – sunken cup S-E of small plant	sit, fly	2.72 ± 0.62 1-5 (245)	10.0 (12)	8.5 (20)	20.0
Blackeared Finchlark	ground – sunken cup S-E of small plant	sit, fly	2.67 ± 0.51 1-4 (113)	10.5 (11)	9.0 (21)	21.0
Tractrac Chat	ground – sunken cup S-E of small plant	sit, fly early	3 ± 0 (6)	14.0[b]	16.0[b]	32.0
Larklike Bunting	ground - sunken cup S-E of object, concealed	sit, fly late	3.26 ± 0.69 2-5 (23)	12.5[b]	12.5[b]	27.5
Rufouseared Warbler	shrub - closed oval mean ht 0.6m (0.1-1.5m)	sit, fly	4.67 ± 1.00 4-7 (9)	11.5[b]	12.0[b]	27.0
Chat Flycatcher	shrub - open cup mean ht 1.0m (0.5-1.8m)	sit, fly	3 ± 0 (15)	14.0[b]	12.0[b]	28.0
Cape Sparrow	shrub - closed ball mean ht 1.9m (1.5-2.5m)	sit, fly	4.38 ± 1.15 2-7 (16)	13.0[b]	19.0[b]	35.5

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[a] Calculated as twice the mean incubation before hatching for nests found randomly through the incubation period ($n = 20$)

[b] From Maclean (1993)

Table 9.2. Nest-site characteristics of ground-nesting species at Droëgrond, summarised as the percentage of nests within each substratum, camouflage and concealment category, with the number of objects within a 1 m radius of the nest and the distance to the closest shrub >50 cm high. Substratum codes: 1 = sand alone, 2 = sand with pebbles or scattered stones, or pebbles alone, 3 = pebbles with scattered stones, 4 = stones/rock with pebbles. Camouflage codes (the degree to which the rim of the nest matched its immediate surroundings): 1 = poor, 2 = fair, 3 = good, 4 = excellent. Concealment is given as the proportion of the nest edge concealed by objects greater than the height of the incubating bird.

Species (*n* nests)	Substratum				Camouflage				Concealment (%)					Objects
	1	2	3	4	1	2	3	4	0	1-25	26-50	51-75	76-100	Mean ± *s.d.*
Doublebanded Courser (5)	0	80	20	0					100	0	0	0	0	2 ± 2
Namaqua Sandgrouse (20)	30	10	50	10					35	50	15	0	0	19 ± 13
Spikeheeled Lark (30)	50	33	17	0	7	13	50	30	0	77	17	7	0	10 ± 8
Sclater's Lark (10)	0	40	60	0	0	10	0	90	90	10	0	0	0	5 ± 3
Blackeared Finchlark (105)	41	37	22	0	1	7	37	55	0	83	16	1	0	13 ± 10
Greybacked Finchlark (242)	33	42	22	3	0	5	31	64	0	86	13	1	0	14 ± 14
Larklike Bunting (29)	33	3	40	23	60	13	13	13	0	0	50	41	9	32 ± 17

Table 9.3. Nest predation and success variables (Mayfield 1975, Johnson 1979) compared among species at Droëgrond. Nestling deaths from the rains of 7-8 November were excluded from the nest success calculations.

Species	Hatch rate % (*n* eggs)	Daily egg predation ±*SE* (%)	Daily chick predation ±*SE* (%)	Egg vs nestling predation *z*	*P* value	Nest predation (%)	Nest success (95% conf. intervals)	Young produced ±*s.d.* (*n*)	Productivity per nesting attempt
Doublebanded Courser		0.50 ± 0.50	-			13.13	75.42 (50.46-100)	1	0.75
Namaqua Sandgrouse	94 (173)	9.19 ± 0.65	-			91.02	8.15 (5.64-11.71)	2.76 ± 0.50 (59)	0.23
Spikeheeled Lark	92 (63)	6.63 ± 1.23	3.89 ± 1.44	1.447	0.075	78.16	22.13 (10.57-32.78)	2.55 ± 0.69 (11)	0.56
Sclater's Lark	80 (25)	8.72 ± 1.96	2.19 ± 1.08	2.910	0.002	73.02	19.82 (8.51-33.64)	1	0.20
Greybacked Finchlark	86 (365)	7.23 ± 0.63	5.79 ± 0.74	1.485	0.069	75.04	23.38 (17.32-27.43)	2.31 ± 0.79 (71)	0.54
Blackeared Finchlark	87 (182)	6.38 ± 0.87	3.34 ± 0.73	2.668	0.004	66.39	31.44 (20.74-38.10)	2.17 ± 0.70 (41)	0.68
Tractrac Chat		3.20 ± 2.23	5.04 ± 2.84	0.511	0.305	73.79	25.97 (4.56-53.33)	3 ± 0 (4)	0.78
Larklike Bunting	85 (41)	11.93 ± 2.44	9.04 ± 3.05	0.740	0.230	95.90	3.53 (0.58-8.11)	2.33 ± 1.15 (3)	0.08
Rufouseared Warbler		1.56 ± 1.10	4.65 ± 2.62	1.087	0.140	50.86	44.59 (16.13-62.04)	3.75 ± 0.96 (4)	1.67
Chat Flycatcher	93 (29)	6.86 ± 2.50	1.57 ± 0.99	2.026	0.022	65.40	24.81 (7.60-57.53)	1.91 ± 0.83 (11)	0.47
Cape Sparrow		6.04 ± 1.95	3.06 ± 1.35	1.258	0.106	80.35	19.83 (5.76-38.81)	3.00 ± 1.31 (8)	0.59

Nest-predation rates

With the exception of Tractrac Chat and Rufouseared Warbler, daily nestling predation rates were lower than daily egg-predation rates within species (Table 9.3). This difference was statistically significant for Sclater's Lark, Blackeared Finchlark and Chat Flycatcher. A similar difference was observed in the nest finding ability of the observer; with the exception of the Tractrac Chat, fewer nests than expected were found at the nestling stage compared to the egg stage (Table 9.4).

Table 9.4. Assessment of observer ability to find nests with eggs *versus* nests with nestlings. Expected nestling finds were determined by assuming that nests with eggs were found halfway through the incubation period, Mayfield's (1975) assumption, and then calculating nest survival through half the incubation period and half the nestling period at the observed daily predation rates.

Species	Nests found with eggs	Nests found with nestlings	Expected nestling finds
Spikeheeled Lark	49	0	24.0
Sclater's Lark	42	4	22.4
Greybacked Finchlark	301	52	154.6
Blackeared Finchlark	132	23	76.3
Tractrac Chat	7	4*	3.6
Larklike Bunting	23	1	4.9
Rufouseared Warbler	11	2*	7.3
Chat Flycatcher	17	8*	8.8

* Most nests found by following adults carrying food

Daily nest-predation rates at Droëgrond were not significantly different from those on the same species in the Kalahari Gemsbok National Park (Wilcoxon paired-sample test: $T_{(2),9} = 20.0$, n.s.; see Table 9.5). Among ground-nesting species, daily nest-predation rates were significantly higher on nomads than on territorial residents (Mann-Whitney *U*-test: $U_{(1),4,6} = 24.0$, $P < 0.02$).

There were no true nomads among the shrub-nesting species, but a distinction was made between species occupying territories, and non-territorial species that undertake irregular local movements (ranging species). Daily predation rates were not significantly higher on ranging shrub-nesters than on territorial shrub-nesters ($U_{(1),5,6} = 20.0$, n.s.). Daily nest-predation rates on territorial, resident ground-nesters were equivalent to those on ranging shrub-nesters (Table 9.5), but higher than on territorial, resident shrub-nesters, although not significantly so ($U_{(1),4,6} = 7.0$, n.s.).

Table 9.5. Daily nest-predation rates compared among species, nest sites and degrees of residency. D = Droëgrond, K = Kalahari Gemsbok National Park, G-n. = ground nesting, S-n. = shrub nesting. Where daily nest-predation rates on a species were calculated separately for the two sites, the mean is given on the third line.

Species	Nests	Nest days	Daily nest-predation rates ± *SE* (%)			
			Resident G-n.	Nomadic G-n.	Resident S-n.	Ranging S-n.
Doublebanded Courser	12	^{D}199.5	(0.50 ± 0.50)			
	45	^{K}475.0	(0.84 ± 0.42)			
			0.67			
Fawncoloured Lark	12	^{K}106.0	3.77 ± 1.85			
Spikeheeled Lark	55	^{D}587.0	(5.79 ± 0.96)			
	28	^{K}250.5	(4.39 ± 1.29)			
			5.09			
Tractrac Chat	12	^{D}122.0	4.10 ± 1.79			
Sclater's Lark	46	^{D}389.0		5.66 ± 1.17		
Namaqua Sandgrouse	278	^{D}1980.5		(9.19 ± 0.65)		
	24	^{K}152.5		(4.59± 1.81)		
				6.89		
Pinkbilled Lark	42	^{K}326.0		6.44 ± 1.36		
Greybacked Finchlark	368	^{D}2700.0		(6.70 ± 0.48)		
	129	^{K}736.5		(8.96 ± 1.05)		
				7.83		
Blackeared Finchlark	159	^{D}1383.5		(5.06 ± 0.59)		
	47	^{K}334.0		(6.89 ± 1.39)		
				5.98		
Larklike Bunting	35	^{D}264.5		(10.98 ± 1.92)		
	33	^{K}297.5		(6.39 ± 1.42)		
				8.69		
Rufouseared Warbler	13	^{D}192.5			(2.60 ± 1.15)	
	21	^{K}251.0			(4.38 ± 1.29)	
					3.49	
Chat Flycatcher	26	^{D}242.0			(3.69 ± 1.22)	
	22	^{K}173.5			(4.03 ± 1.49)	
					3.86	

Table 9.5. *continued.*

Species	Nests	Nest days	Daily nest predation rates ± *SE* (%)			
			Resident G-n.	Nomadic G-n.	Resident S-n.	Ranging S-n.
Fiscal Shrike +	9	^{K}183.0			2.73 ± 1.21	
Forktailed Drongo	2					
Chestnutvented Titbabbler	12	^{K}110.5			0.91 ± 0.90	
Blackchested Prinia	20	^{K}206.0			1.46 ± 0.83	
Cape Penduline Tit +	7	$^{D+K}$173.5			1.15 ± 0.81	
Yellowbellied Eremomela	7					
Scalyfeathered Finch	30	$^{D+K}$419.0				2.15 ± 0.71
Cape Turtle Dove	9	^{K}66.0				3.03 ± 2.11
Yellow Canary	17	$^{D+K}$125.5				3.19 ± 1.57
Cape Sparrow	27	^{D}312.5				(4.48 ± 1.17)
	27	^{K}257.5				(8.54 ± 1.74)
						6.51
Namaqua Dove	20	^{K}226.0				2.65 ± 1.07
Means			3.41 ± 1.38	6.91 ± 1.07	2.27 ± 1.12	3.51 ± 1.31

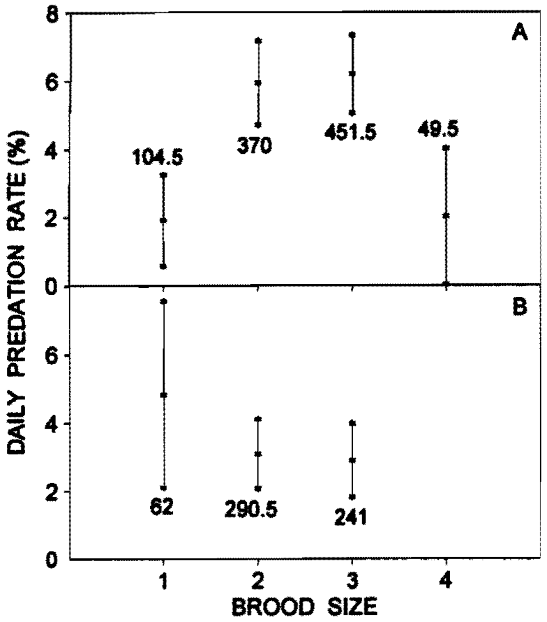

Figure 9.1. Daily predation rates (± 1*SE*) on broods of Grey-backed Finchlark (A) and Black-eared Finchlark (B) during the 1996 breeding season at Droëgrond. Exposure (nest days) is indicated above or below the error bars.

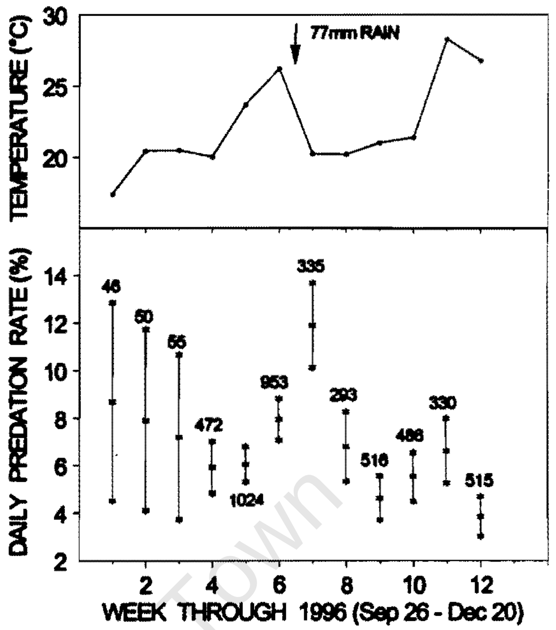

Figure 9.2. Daily predation rates for all species combined (± 1*SE*) and mean daily temperature during weeks 1-12 (September 26 to December 20) through the 1996 breeding season at Droëgrond. Exposure (nest days) is indicated above or below the error bars.

Daily predation rates on broods of one and four Greybacked Finchlark nestlings were similar and significantly lower than those on broods of two and three (Table 9.6, Fig. 9.1). Daily predation rates on Blackeared Finchlark nestlings were little altered with increasing brood size.

Table 9.6. Summary statistics (*z* values) of comparisons between daily predation rates of finchlark broods of different size, using the method of Johnson (1979). Grey-backed Finchlark statistics in the upper right, and those of Black-eared Finchlark in the lower left.

Brood size	Brood size			
	1	2	3	4
1		2.217*	2.441**	0.044
2	0.598		0.153	1.672*
3	0.660	0.130		1.819*

* $P < 0.05$
** $P < 0.01$

Excluding the week following substantial rain on 7-8 November as an outlier (week 7, Fig. 9.2), daily predation rates on all species combined decreased through the 1996 season. This relationship is described by the regression equation: $y = -0.29x + 8.33$ ($r_9 = 0.74$, $P < 0.01$). Nest density increased to an initial peak in weeks 4-5, then decreased until the rain event in week 7 stimulated a second flush of nesting, whereafter nest density

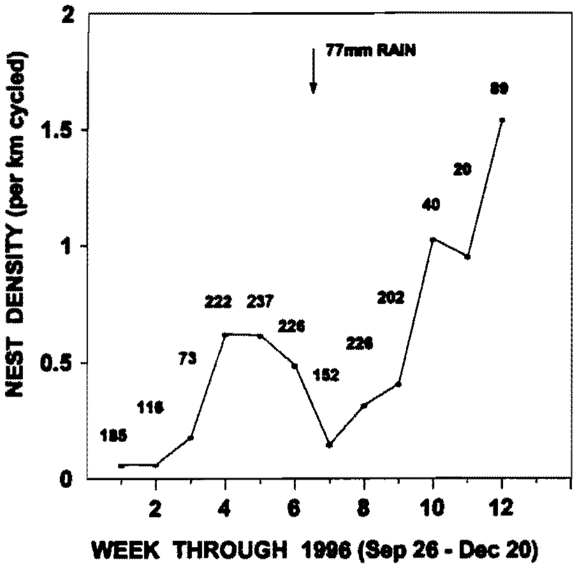

Figure 9.3. Nest density, measured as the number of new nests found per km cycled and corrected for observer bias, through the 1996 breeding season at Droëgrond. The distance cycled each week is indicated above the relevant data points.

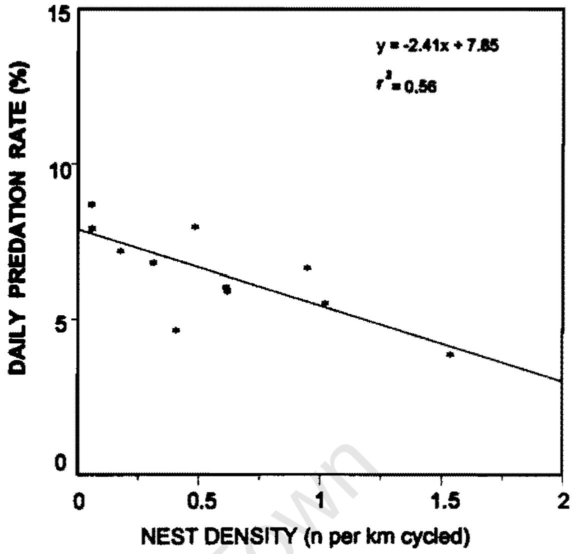

Figure 9.4. The relationship between nest density and daily predation rate (for all species combined) through the 1996 breeding season at Droëgrond (week 7 excluded). Regression $F_9 = 11.53$, $P < 0.01$.

increased steadily until the end of the study (Fig. 9.3). Combined daily predation rates were inversely related to nest density (Fig. 9.4). The coefficient of inter-annual variation in nest predation was low (3.9-15.1% within species) in comparison with variation in rainfall over the study period (51.3%: Table 9.7).

Table 9.7. Annual rainfall, with percent nest predation (1st line) and success (2nd line; exposure in nest days in brackets), and their coefficients of variation (*CV*) for species with sufficient data spanning more than one year at Droëgrond.

	1993	1994	1995	1996	*CV* (%)
Rainfall (mm)	83.0	126.8	75.2	214.8	51.3
Namaqua Sandgrouse	85.20	91.58	90.54	93.49	3.94
	13.52	7.61	9.46	5.71	36.75
	(299.0)	(1369.0)	(100.0)	(212.5)	
Spikeheeled Lark		74.69		79.99	4.85
		21.97		18.67	11.48
		(187.0)		(400.0)	
Sclater's Lark	60.84	80.96		79.11	15.10
	22.50	11.58		20.89	32.17
	(171.5)	(98.5)		(119.0)	

Other mortality

Following soaking rains on 7-8 November 1996 (77 mm in 48 hours), 58.8% and 42.9% of all nestlings (*n* = 102 and 49 respectively) of Greybacked and Blackeared Finchlarks died. This is much higher mortality than nestling mortality from other causes, respectively 6.9% (*n* = 101 hatchlings) and 8.7% (*n* = 69 hatchlings) for these two species. Of 14 finchlark nests with eggs at the time of the November rains, three were flooded and 11 survived, although four of the latter were later abandoned.

DISCUSSION

Nest site and degree of residency

Predation has been reported as greater on ground-nesting species than on open nest, above-ground-nesting species in shrub and grassland habitats, but lower in forest habitats (Martin 1993). My results indicate that it can be important to consider the degree of residency before generalising to such an extent. Nest-predation rates of resident ground-nesters were similar to those of both resident and ranging shrub-nesters, and only the nomadic ground-nesters suffered significantly higher daily nest-predation rates than shrub-nesters (Table 9.5). Sample sizes were small, however, and it would be useful to pursue more rigorously the hypothesis that long-term residency (which could be equated with experience of predator activity in the nest environs) enhances nest survival. Studies on Neotropical migrants suggest some (but as yet unrecognised) support for this hypothesis. Robbins *et al.* (1989), who studied trends in the populations of birds breeding in North America, found that populations of long-distance migrants had declined significantly between 1978 and 1987, whereas populations of short-distance migrants and residents increased during the same period (but see Böhning-Gaese *et al.* 1993). The population declines of these Neotropical migrants have been linked to elevated nest predation (Wilcove 1985, Böhning-Gaese *et al.* 1993, Paxton 1994, Donovan *et al.* 1995, Hoover *et al.* 1995).

Predator-avoidance behaviour

The potential adaptive significance of predator-avoidance behaviours is best illustrated by comparing the strategies of Doublebanded Courser and Namaqua Sandgrouse, two precocial species of equivalent body size with very similar nesting sites. Both species nested in exposed situations, but to subtly different degrees which probably relate to their contrasting predator-avoidance behaviours. The Namaqua Sandgrouse sited its nest adjacent to several low objects, presumably to interrupt the outline of a bird crouching on the nest (Chapter 2; see also Table 9.2). The Doublebanded Courser preferred even greater exposure (see Table 9.2), possibly to increase its field of view for the early detection of an approaching predator, and thus enhance the effectiveness of its strategy of abandoning the nest. Maclean (1967) noted that all Doublebanded Courser nests were sited for clear, all-round horizontal visibility. The incubating courser was assisted by its mate, which usually remained in the general vicinity of the nest, and acted as a sentinel (Maclean 1967, pers. obs.). Nest-predation rates differed markedly between these two species (Table 9.5), and are probably largely due to the different predator-avoidance behaviours they employ.

Using a predator-simulation model, I suggested (Chapter 4) that it was possible for the high levels of predation experienced by Namaqua Sandgrouse to be largely incidental in nature, if predators use the close-range flushing of the incubating bird as a cue for nest location. It follows that if the incubating bird is able to leave the nest undetected, the predator's nest-detection path width would be narrowed severely, since it could no longer rely on the flushing bird as a cue, and would have to rely on visual and/or olfactory cues from the eggs alone. This probably explains the lower predation levels the Doublebanded Courser experienced, although the potentially greater crypsis of a single egg (Croze 1970) could be a contributing factor.

Of the remaining ground-nesting species, only the Tractrac Chat and Larklike Bunting experienced markedly different daily egg-predation rates (3.2% and 11.9% respectively; Table 9.3). Once again, this difference may have been due to the behaviour of the incubating birds; the Tractrac Chat left the nest earlier, and the Larklike Bunting later, than most species. The delayed reaction of the latter could have been due to its habit of nesting in denser and more concealed situations. The higher predation rates it incurred may, however, be compounded by the relatively poor nest crypsis and/or its more predictable nesting locations.

Egg and nestling predation

Despite the increased activity at nests with nestlings, daily predation rates on nestlings were generally lower than those on eggs of the altricial species. Adults spend less time brooding nestlings than they do incubating eggs, and this could lead to a lower probability of a predator flushing an adult from the nest, and using this behaviour as a cue for nest location. Bowen and Simon (1990) noted that no nocturnal mammal predation on Greater Prairie Chicken *Tympanuchus cupido* nests occurred during egg laying, when females were away from nests, but appreciable predation occurred during incubation, when the females were on the nest all night. I located nests primarily by flushing birds on the nest while cycling through the study site, and consequently found far fewer nests at the nestling stage than at the egg stage (Table 9.4). If predators use similar cues, this could explain the lower predation rates on nestlings, and add further support to the idea that the absence of adults from the nest can substantially reduce predation risk. However, because the predators on altricial species were not properly identified, the possibility that the differences in predation rate between nesting stages is due to changes in the relative importance of different nest predators cannot be discounted. The Rhombic Eggeating Snake, for example, can be an important egg predator, but it does not take nestlings.

If increased activity at nests with nestlings does attract predators (Skutch 1949, Martin 1992), then predation risk should increase with brood size. Although I do not provide a rigorous test of this hypothesis, I failed to detect such a relationship among finchlarks (Fig. 9.1). The differences in daily predation rates among Greybacked Finchlark broods of different size (Table 9.6) are difficult to account for, but might be an artefact of variability in clutch size and predation rate, clutch size increasing (see Chapter 10) and predation rate decreasing (Fig. 9.2) through the breeding season. Smith and Andersen (1982) found no difference in the survival rates for Darkeyed Junco *Junco hyemalis* broods of different sizes. Cresswell (1997) found a significant decrease in predation rate between the first and second half of the nestling stage among Blackbirds *Turdus merula*, suggesting that increased noise from nests during the nestling stage did not increase the probability of nest predation.

Nest density

Predation rates at Droëgrond exhibited an inverse relationship with nest density (Fig. 9.4), but nest density *per se* is probably not the primary factor determining this relationship. Predation rates also decreased as the season progressed from spring to midsummer (Figs 2.2 & 9.2). A similar decrease in predation through the breeding season has been noted in several other studies, and attributed to changes in the behaviour, diet, density or species of predators (Nolan 1963, Newton 1964, Roseberry & Klimstra 1970, Gottfried 1978). The most plausible explanation for decreasing predation rates through the season at Droëgrond is an increasing availability of alternative food. The only specialist nest predator was the Rhombic Eggeating Snake, and snakes do not appear to respond to nests as prey in a density-dependent manner (Best 1978, Gottfried 1978, Gottfried & Thompson 1978). Although the recorded mammalian predators are generalists, if not opportunists, the bulk of their respective diets consists of arthropods (Smithers 1983). Arthropod abundance was not measured in this study, but is known to increase in summer and after appreciable rainfall in seasonal and arid environments (Louw & Seely 1982). If nest predation by these generalist predators is largely incidental (e.g. Vickery *et al.* 1992, Howlett & Stutchbury 1996, Chapter 4), then predation rates are expected to decrease as general food abundance increases.

This study, recording some of the highest nest predation and lowest nesting success figures reported to date, highlights the potential of nest predation to act as a selective force influencing the evolution of avian life-history traits. Intense nest predation selects for shorter incubation and nestling periods, to reduce the length of time the nest is exposed to predation (Ricklefs 1969b, Case 1978, Bosque & Bosque 1995). The Greybacked Finchlark, with an incubation period of 10.0 days and a nestling period of just 8.5 days (Table 9.1), has one of the shortest nesting periods of any bird (Gill 1995). At the time the chicks leave the nest, they are fully feathered, but not yet able to fly. Presumably predation risk is reduced by leaving the nest before fledging. An incubation period of 9-10 days is probably close to the physiological lower limit possible for birds; both chicks in a Blackeared Finchlark clutch that hatched 8.0 days (to the nearest half-day) after the second egg was laid died within a day of hatching (pers. obs.).

Nest failure rates greater than 70% have been implicated in population declines in shrubsteppe passerines on the Iberian Peninsula (Suárez *et al.* 1993, Yanes & Suárez 1995) and Neotropical migrants (Böhning-Gaese *et al.* 1993, Donovan *et al.* 1995, Hoover *et al.* 1995). At Droëgrond, nest-predation rates were invariably greater than 70% (Table 9.3).

These high predation rates were not the result of abnormal events in a stochastic environment, as there was little inter-annual variation in predation intensity despite considerable variation in rainfall (Table 9.7). In Chapter 2, I suggested that the high predation rates experienced at Droëgrond might be a consequence of meso-predator release following predator control programmes in this sheep farming region. This hypothesis is, however, weakened by the finding that nest-predation rates at Droëgrond were not significantly different from those on the same species in the Kalahari Gemsbok National Park, where an entirely natural complement of predators is present. The high nest-predation rates incurred by the Pinkbilled Lark, Greybacked Finchlark, Blackeared Finchlark and Larklike Bunting in the Kalahari Gemsbok National Park during Maclean's (1970a) study may, however, have been exacerbated by unusually high nest densities among these species. Maclean (1970a) noted that "so many moved into the area that the calcrete (a habitat of restricted area) could not accommodate them all". Furthermore, many of the Cape Sparrow nests that were lost to predation in Maclean's study were sited within the same tree in a semi-colonial fashion, and were probably destroyed together during a single visit by a Cape Cobra. Further studies are required to evaluate more rigorously the possibility of significantly different nest survival between sheep-farming areas that experience intense predator control programmes and protected areas with natural predator complements.

Based on the results of other studies (cited above), the exceptionally low nesting success of species such as Namaqua Sandgrouse, Sclater's Lark and Larklike Bunting (Table 9.3) at Droëgrond could be expected to be linked to population declines. However, there is no evidence of such a population decline, local or regional, for any species included in this study. Clearly, we have some way to go before we reach an acceptable understanding of the population dynamics of nomadic birds in arid, stochastic environments. I hope this study will stimulate both interest in this group and further studies on the adaptive value of predator-avoidance behaviour among nesting birds.

Appendix 9.1. Common and scientific names of birds, mammals and snakes mentioned in this study.

Birds
Doublebanded Courser *Rhinoptilus africanus*
Namaqua Sandgrouse *Pterocles namaqua*
Cape Turtle Dove *Streptopelia capicola*
Namaqua Dove *Oena capensis*
Spikeheeled Lark *Chersomanes albofasciata*
Fawncoloured Lark *Mirafra africanoides*
Pinkbilled Lark *Spizocorys conirostris*
Sclater's Lark *Spizocorys sclateri*
Greybacked Finchlark *Eremopterix verticalis*
Blackeared Finchlark *Eremopterix australis*
Forktailed Drongo *Dicrurus adsimilis*
Tractrac Chat *Cercomela tractrac*
Yellowbellied Eremomela *Eremomela scotops*
Cape Penduline Tit *Anthoscopus minutus*
Chestnutvented Titbabbler *Parisoma subcaeruleum*
Rufouseared Warbler *Malcorus pectoralis*
Blackchested Prinia *Prinia flavicans*
Chat Flycatcher *Melaenornis infuscatus*
Fiscal Shrike *Lanius collaris*
Cape Sparrow *Passer melanurus*
Scalyfeathered Finch *Sporopipes squamifrons*
Yellow Canary *Serinus flaviventris*
Larklike Bunting *Emberiza impetuani*

Mammals
Aardwolf *Proteles cristatus*
Caracal *Caracal caracal*
Bateared Fox *Otocyon megalotis*
Cape Fox *Vulpes chama*
Blackbacked Jackal *Canis mesomelas*
Striped Polecat *Ictonyx striatus*
Yellow Mongoose *Cynictis penicillata*
Cape Grey Mongoose *Galerella pulverulenta*
Suricate *Suricata suricatta*
Aardvark *Orycteropus afer*

Snakes
Namib Sand Snake *Psammophis leightoni*
Rhombic Eggeating Snake *Dasypeltis scabra*
Namib Tiger Snake *Telescopus beetzii*
Cape Cobra *Naja nivea*
Horned Adder *Bitis caudalis*

CHAPTER TEN

RAINFALL AS A BREEDING STIMULUS AND CLUTCH SIZE DETERMINANT IN SOUTH AFRICAN ARID-ZONE BIRDS

SUMMARY

Breeding activity and clutch sizes in a variety of arid-zone bird species were monitored in relation to rainfall over four consecutive spring-summer seasons at a site in the Northern Cape Province, South Africa. With the exception of Sclater's Lark *Spizocorys sclateri*, breeding activity of birds in the Nama Karoo increased markedly after appreciable rainfall. Some resident insectivores did breed in the absence of rainfall, even under drought conditions, but also responded rapidly to small rain showers. Nomadic granivores required more substantial rainfall to stimulate what was usually a synchronised, population-wide breeding response. The timing and length of the breeding season were dependent on the integrated effect that rainfall and temperature had on the growing season of the vegetation. Over 50% of species studied showed evidence of an increase in clutch size following large rainfall events. Greybacked Finchlark *Eremopterix verticalis* began laying larger clutches within one week of a rainfall stimulus, illustrating how rapid this response can be.

INTRODUCTION

External factors that proximally determine clutch size in birds include food, climatic variables, day-length, population density and predation pressure (Klomp 1970, Boag & Grant 1984, Young 1994, Juillard *et al.* 1997). In the arid to semi-arid sub-tropics, where rainfall is often erratic and unpredictable, it is rainfall, through its influence on food availability, that is the key proximal determinant of both clutch size and the timing of breeding in many species (Marchant 1960, Immelmann 1973, Boag & Grant 1984 and references therein). In southern Africa, the importance of rainfall to the timing of breeding seasons has been well established (see reviews by Maclean 1970b, Immelmann 1973), but its effect on clutch size has not been adequately documented. Although Maclean (1974a) noted several species whose clutch size increased after good rainfall, he concluded that clutch size in most southern African arid-zone birds is fixed and small. He suggested further that the small, fixed clutch is a response to high predation risk, a factor that is now recognised as important in driving the evolution of clutch size (Slagsvold 1982, Martin 1995, Juillard *et al.* 1997).

This chapter reports on a study of the breeding activity of arid-zone birds in the Northern Cape Province of South Africa, and shows that clutch size in many species is more closely tied to rainfall than previously thought.

STUDY AREA AND METHODS

The study was conducted over four early-summer seasons (August-December 1993-1996) in an area of 10 000 ha on the farm Droëgrond. Study site characteristics are detailed in Chapter 2. Nests were found by flushing birds while cycling randomly through the study area daily. Clutch size was recorded only if it remained unchanged between visits, and therefore does not include nests lost to predation in the interval before the second visit, or nests found at the nestling stage. Daily rainfall was measured at a rain gauge located centrally in the study site. Relative nest density was determined as the number of new nests (corrected for observer bias) found per km cycled. Observer bias resulted from nests at the nestling stage being more difficult to find than nests at the egg stage. This bias was corrected by multiplying new nestling finds by 3.31 and 2.97 for Blackeared Finchlark *Eremopterix australis* and Greybacked Finchlark respectively (see Chapter 9).

RESULTS

Rainfall

1992 was an exceptionally dry year (20.5 mm), the largest single rain event being 6 mm. 1993 was relatively dry (83.0 mm; Fig. 10.1), and showers of 29 mm in February and 13 mm in March were the only two rain events exceeding 10 mm. In 1994 (126.8 mm) 11.5 mm fell on 31 January, and 13 mm and 16 mm on 4 and 6 February respectively. This, together with follow-up rains of 24.5 mm (4-7 March) and 11.5 mm (31 May), resulted in good ephemeral plant germination, growth and seed set (see Chapter 7).

The only other significant rain event of 1994 was a shower of 25 mm on 7 October. 1995 was another dry year (75.2 mm) with only a single event (21.6 mm on 20 November) exceeding 10 mm. 1996 was a year of good rainfall (214.8 mm). The two most important events were soft, soaking rains of 53.5 mm (23-25 July) and 77.5 mm (7-8 November), which were the result of cyclonic cold fronts, as opposed to the convective thunder-storms that are the source of most of this region's rainfall. Cold winter weather following the July rains retarded plant growth. *Rhigozum trichotomum* only began flowering towards the end of September, and the grasses *Stipagrostis ciliata* and *S. obtusa* only started to set seed in the second week of October. This two month lag period in flowering response was considerably longer than the two week lag (normal after summer rain) after the November rains.

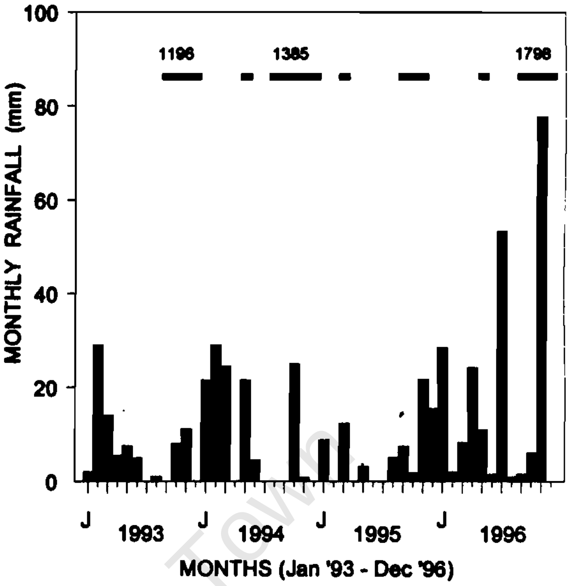

Figure 10.1. Monthly rainfall at Droëgrond over the study period. The bars at the top indicate months when the observer was present at the study site, the total distance cycled indicated where applicable.

Nesting activity

Despite the drought conditions that prevailed during the 1993 season (September to December), Sclater's Lark (a local nomad) was present, and breeding at the highest recorded density at the study site (see also Table 10.1). This breeding activity, from mid-September to mid-November, was therefore not in response to rainfall. This species was less common over the following three years, even after the good rains of 1996, but was always found breeding in the early-summer season.

Doublebanded Courser *Rhinoptilus africanus*, Spikeheeled Lark *Chersomanes albofasciata*, Tractrac Chat *Cercomela tractrac*, Chat Flycatcher *Melaenornis infuscatus* and Rufouseared Warbler *Malcorus pectoralis* were resident at the study site, and all exhibited some nesting activity in each early-summer season (Table 10.1). The nesting activity of these species increased markedly in the 1996 season, following the good July and November rains. The locally nomadic Cape Sparrow *Passer melanurus* was present at Droëgrond throughout the study period, but was only found nesting in the 1996 season. The eggs in five of the eight Spikeheeled Lark nests found in 1993 were laid within a week of a 6 mm rain shower, suggesting that this species can respond quickly to even small rainfall events during drought conditions.

Table 10.1. Nesting activity of various species at Droëgrond, expressed as the number of nests found per 100 km cycling effort (no. of nests indicated in brackets).

	Season		
	Sep-Dec 1993	Aug-Nov 1994	Sep-Dec 1996
Sampling effort (km cycled)	1196	1385	1798
Doublebanded Courser	0.167 (2)	0.072 (1)	0.667 (12)
Sclater's Lark	1.756 (21)	0.722 (10)	0.723 (13)
Spikeheeled Lark	0.669 (8)	0.144 (2)	2.113 (38)
Blackeared Finchlark	0	0	8.398 (151)
Greybacked Finchlark	0	0	20.467 (368)
Tractrac Chat	0.334 (4)	0.144 (2)	0.278 (5)
Chat Flycatcher		0.217 (3)	1.335 (24)
Rufouseared Warbler	0.084 (1)		0.612 (11)
Cape Sparrow			1.502 (27)
Larklike Bunting	0	0	1.947 (35)

The truly nomadic Blackeared Finchlark, Greybacked Finchlark, Stark's Lark *Alauda starki* and Larklike Bunting *Emberiza impetuani* were generally absent or uncommon visitors, with two exceptions. After 40.5 mm from thunder-showers over a few days in February 1994, and later follow-up rains, these nomadic species moved into the area in March-April, but little or no breeding took place. Most had left the area again by August 1994. When I arrived at Droëgrond on 17 September 1996, large numbers of the two finchlark species and lesser numbers of Stark's Lark and Larklike Bunting had already occupied the area following the good July rains. These birds had paired off and were displaying. Among the nomads, Blackeared Finchlark was the first to begin nesting, starting in the second week of October. Greybacked Finchlark and Larklike Bunting followed a week later. Despite being present and displaying in relatively large numbers from September, the first Stark's Lark nest was only found on 16 December, shortly before the study ended.

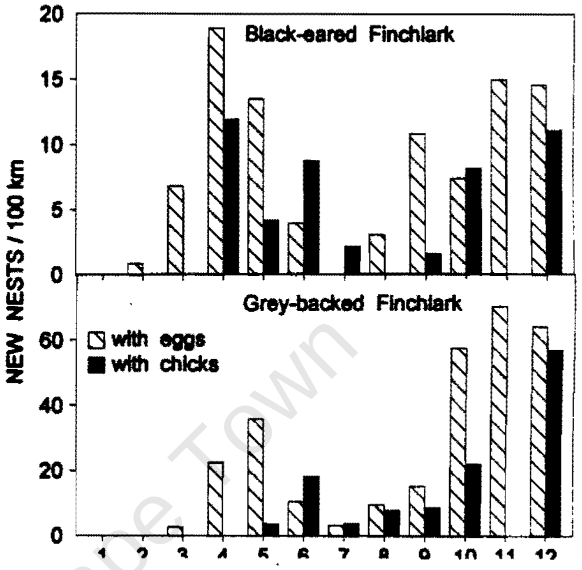

Figure 10.2. Finchlark breeding activity through the 1996 season, indicated as the number of new nests found each week with either eggs or chicks (corrected for observer bias) per 100 km of cycling effort. Rainfall of 77.5 mm fell at the start of week 7.

Egg laying in both finchlark species peaked approximately three weeks after the start of nesting in the 1996 season, and had largely ceased by the first week of November (week 6: Fig. 10.2). By 6 November, only 14% of both Blackeared Finchlark and Greybacked Finchlark nests under observation (*n* = 25 and 70 respectively) were still at the incubation stage. This marked decrease in nesting among the finchlarks corresponded with a noticeable drying out of the vegetation at Droëgrond by the end of October. Within days of the rains of 7-8 November, both species had begun nest-building again, the first eggs being laid one week after the rains ended (week 8: Fig. 10.2). This second bout of breeding was more prolonged than the first, and there was no sign of a decrease in egg laying by either species by the time the study was terminated on 20 December. Much of the vegetation was still green at this time.

Clutch size

Species that maintained a fixed clutch size regardless of rainfall (and presumably, therefore, variation in food supply), included Doublebanded Courser, Namaqua Sandgrouse *Pterocles namaqua* (Chapter 2), Sclater's Lark, Tractrac Chat and Chat Flycatcher (Table 10.2). In the early summer seasons of 1993-1995, which were all relatively dry, clutch size for Spikeheeled Lark was two (Table 10.2, Fig. 10.3). In 1996, the modal clutch size was three, and the mean increased from 2.83 after the July rains to 3.30 after the 77.5 mm of rain in

November: clutches of four and five eggs only appeared after the November rains. The clutch size differences between the three periods (1993-1995, 20 September - 6 November 1996, and 7 November - 18 December 1996) were significant (Kruskal-Wallis ANOVA by ranks: $H_{10,13,23} = 26.94$, $P < 0.001$). Both Blackeared Finchlark and Greybacked Finchlark showed similar increases in clutch size after the November rains of 1996 (Table 10.2, Fig. 10.3). The clutch size differences between the periods before and after the November rains were significant for both species (Mann-Whitney *U*-tests: $U_{(2),44,69} = 910$ for Black-eared Finchlark, $U_{(2),118,125} = 3166$ for Greybacked Finchlark, both $P < 0.001$). Sufficient data to illustrate the speed of this response exist only for Greybacked Finchlark, which began laying larger clutches as soon as laying resumed one week after the rain stimulus (Fig. 10.4). Clutch size in the other three species listed in Table 10.2 also increased in response to good rainfall, but there were insufficient data to test for significance.

Table 10.2. Mean clutch size ± *s.d.*, sample size (in brackets) and range in clutch size during different periods of breeding for various species at Droëgrond.

Species	1993-1995 (Aug-Dec)	1996 (Sep-Nov 6)	1996 (Nov 7-Dec)	Overall
Spikeheeled Lark	2 ±0 (13) 2	2.83 ±0.39 (23) 2-3	3.30 ±0.78 (10) 2-5	2.70 ±0.66 (46) 2-5
Greybacked Finchlark		2.37 ±0.57 (121) 1-4	3.07 ±0.46 (124) 1-5	2.72 ±0.62 (245) 1-5
Blackeared Finchlark		2.51 ±0.53 (69) 1-3	2.93 ±0.33 (44) 2-4	2.67 ±0.51 (113) 1-4
Rufouseared Warbler		4 ±0 (4) 4	5.20 ±1.10 (5) 4-7	4.67 ±1.00 (9) 4-7
Cape Sparrow		4.08 ±0.86 (13) 2-5	5.67 ±1.53 (3) 4-7	4.38 ±1.15 (16) 2-7
Larklike Bunting		3.17 ±0.51 (18) 2-4	3.60 ±1.14 (5) 2-5	3.26 ±0.69 (23) 2-5
Doublebanded Courser				1 ±0 (12) 1
Sclater's Lark	1 ±0 (25) 1	1 ±0 (5) 1	1 ±0 (4) 1	1 ±0 (34) 1
Tractrac Chat				3 ±0 (6) 3
Chat Flycatcher		3 ±0 (8) 3	3 ±0 (7) 3	3 ±0 (15) 3

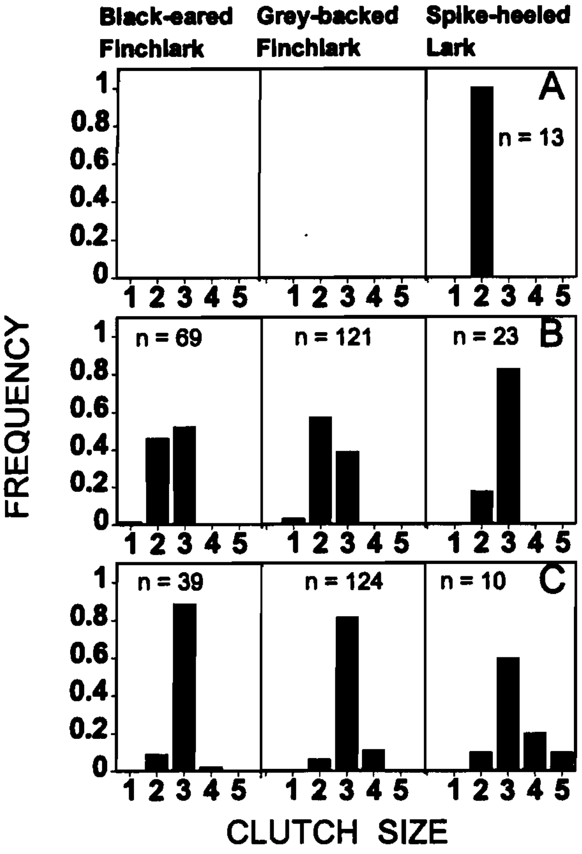

Figure 10.3. Frequencies of clutches of different size in Black-eared Finchlark, Grey-backed Finchlark and Spike-heeled Lark during three different periods of breeding activity. A = 1993-1995, B = 20 September to 6 November 1996, C = 7 November to 18 December 1996.

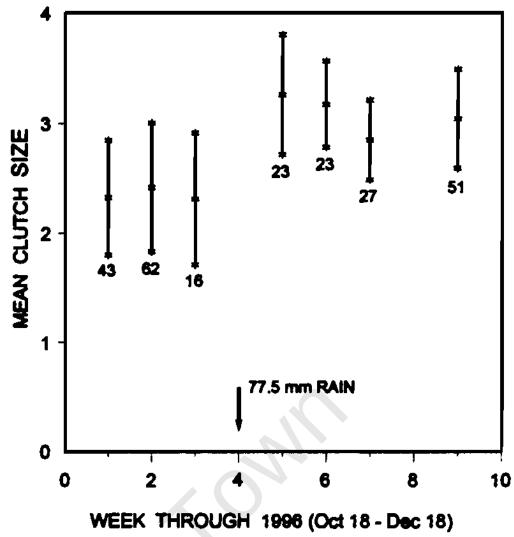

Figure 10.4. Mean clutch size (± *s.d.*) of Grey-backed Finchlark during weekly intervals through the 1996 breeding season. The sample number of nests is indicated below the corresponding bars.

DISCUSSION

Nesting activity

There is no obvious relationship between rainfall and nesting activity by Sclater's Lark. Nesting was recorded during each early summer season, and nest densities were highest during the severe drought of 1993 (Table 10.1). The principal food items of adult Sclater's Larks at Droëgrond are the relatively large seeds of *Enneapogon desvauxii* that are produced singly and are tightly enclosed at the bases of the leaf sheaths. The seeds are well protected from granivores, and only Sclater's and Stark's Larks appeared capable of extracting them. Average seed density, measured seven months after seed set in suitable habitat, was 454 seeds/m^2 (*s.d.* = 107, *n* = ten 1 m^2 quadrats sampled at 10 m intervals on a 100 m transect).

This source of food is therefore readily available even during extended droughts. However, the nestling is fed on insects, which are predictably abundant only after appreciable rainfall.

Several resident species (all insectivores) bred in drought conditions (Table 10.1). This suggests that arthropod availability increased sufficiently in spring and early summer, even in the absence of rain, to allow breeding by some individuals. By contrast, appreciable rainfall stimulated a population-wide breeding response. The breeding activity of Darwin's finches is closely correlated with rainfall: small events stimulate breeding in only a few individuals, and 15-20 mm is needed to induce a response in the population as a whole (Grant & Grant 1989, p 70). Maclean (1970b), in a study of birds breeding in the Kalahari, concluded that a rain event of over 25 mm was necessary to initiate breeding by opportunist species. My results from the Nama Karoo suggest that rainfall is not an absolute requirement for breeding by resident insectivores, and that certain species do respond to rain events as small as 6 mm. The spring breeding response is likely to be greater in years when the late summer rains of the previous season are substantial (Maclean 1974b).

The nomadic granivores (the finchlarks, Stark's Lark and Larklike Bunting) require more substantial rainfall to stimulate breeding. The 40.5 mm over several days in February 1994 led to a nomadic influx, but no breeding. Only the cold frontal rain events of 53.5 mm and 77.5 mm in 1996 stimulated breeding. It is not only the quantity of rain that is important, but also the nature of the rainfall. The soil in the Nama Karoo is generally hard, and if rain falls as a short thunder-shower, much of the water is lost as run-off. Such rainfall appears to be less effective than soft, soaking rain lasting several days. The two month delay between the start of breeding in the finchlarks and in Stark's Lark (also an opportunistic nomad) is unusual, and suggests that factors other than rainfall are involved. Maclean (1970b) noted a similar delayed breeding response by Stark's Lark in the Kalahari.

Breeding by finchlarks is highly synchronised, and the timing and length of the breeding season are dependent on both rainfall and temperature (Maclean 1970b, this study). Cold weather after rainfall delays the onset of breeding by as much as two months, presumably because it retards plant development and/or the associated increase in insect abundance (Davies 1977, Wyndham 1980). High temperatures after rainfall ensure rapid grass growth, and finchlarks normally start laying within two weeks of summer rains (Maclean 1970b, this study). Temperature can influence the timing and pattern of breeding by stimulating or inhibiting egg laying to ensure that the nestling period coincides with peak arthropod availability (Newton 1964). Finchlarks line their nests with the awns of grass seeds, particularly those of *Stipagrostis* spp. (Dean *et al.* 1992). The lag period between rainfall and the start of breeding in these species may depend on the rate of grass growth, and thus the availability of nesting material rather than food. *Stipagrostis* spp. take between two weeks (after summer rain) and over two months (after winter rain) to produce seed. The length of the breeding season of finchlarks is probably dependent on the integrated effect that rainfall and temperature have on the length of the growing season of the vegetation. Warm weather and the absence of follow-up rains lead to fairly rapid drying of the soil and early termination of plant growth, particularly among the grasses and annuals that dominate the vegetation in the Nama Karoo and Kalahari.

Nomads (mostly granivores) generally exhibit a more synchronised breeding response than resident species (mostly insectivores), probably because they have a more specific set of breeding requirements that reduces breeding opportunities to short-lived windows in the annual cycle. Finchlarks, for example, appear to require a rain event of at least 40 mm to produce conditions favourable for breeding in the Nama Karoo. In only 14 (36%) of the last 39 years have such conditions occurred at Droëgrond, but being nomadic, these birds would have bred elsewhere in many locally unfavourable years. The requirement for more productive conditions could be a combination of the following: 1) nomads suffer significantly higher nest-predation rates than residents (Chapter 9), which has selected for faster development rates and resulted in a higher brood energy demand (Bosque & Bosque 1995), and 2) nomadic granivores are probably less efficient at finding insects to feed their chicks than are specialist resident insectivores.

Clutch size

Intra-seasonal and inter-annual variations in the clutch sizes of several species have been linked to changes in food availability (Dijkstra *et al.* 1982, Hussell & Quinney 1987, Grant & Grant 1989 and references therein), but not necessarily at the time of laying. Thus some species lay a smaller clutch later in the season, even when food is abundant, in anticipation of a decrease in food availability towards the end of the season when there may still be nestlings to feed (Klomp 1970, Hussell 1972). The immediate increase in clutch size in Greybacked Finchlark following the November rains (Fig. 10.4) was probably not a direct response to increased food availability at the time of laying, but in anticipation of an increase by the time the eggs hatch (Immelmann 1973). Arthropod abundance usually only increases from a week or two after a rainfall stimulus (Grant & Grant 1989, p 70).

Clutch size in many species does not vary in direct response to climatic variables and/or the influence of these variables on food availability (Klomp 1970). An inflexible clutch size may be adaptive in a seasonally predictable or relatively stable environment. Where species have to make maximum use of erratic and unpredictable breeding opportunities that vary greatly in quality, flexibility in clutch size may be selected for. Just over 50% of the species studied at Droëgrond exhibited clutch size fluctuations in response to rainfall (Table 10.2). Other southern African arid-zone species known to produce larger clutches in better seasons include two species of starlings (Hoesch 1936), Monteiro's Hornbill *Tockus monteiri* (Kemp & Kemp 1972), Pygmy Falcon *Polihierax semitorquatus* (Maclean 1970c) and Sociable Weaver *Philetairus socius* (Maclean 1973). Data on clutch size variation for many other species in this region are lacking.

Siegfried and Brooke (1989) examined the extent to which environmental unpredictability correlated with variation in modal clutch size, using a variation of Ashmole's hypothesis (Ashmole 1963, Ricklefs 1980), namely that clutch size should increase with increasing unpredictability. They found no evidence to support the hypothesis among granivores, but some support among insectivores. In contrast, Järvinen (1986) noted a decrease in average clutch size in a harsh (unpredictable) environment, and suggested that laying a small clutch is a compromise between breeding and not breeding. Given the variability in clutch size of many species occupying the unpredictable arid zone, the use of the modal or mean clutch size may not be informative. Future studies on the ecological and evolutionary implications of clutch size among arid-zone birds should aim to gather adequate data on the range of variation in clutch size under different environmental conditions, rather than the average. To understand the relationship between clutch size flexibility and reproductive success, we should compare productivity between species with a fixed clutch size and those with a flexible clutch size, as a function of environmental variation.

CHAPTER ELEVEN

SUMMARY AND SYNTHESIS

This study, initiated to investigate the population dynamics of the Namaqua Sandgrouse and the key ecological factors that influence annual variations in population sizes, in some ways raises more questions than it answers. The very high nest-predation rates that are experienced in a core breeding area within South Africa (Chapter 2) suggest that this apparently density-independent mortality may be the key factor limiting population growth. In fact, the estimates of annual recruitment suggest that this mortality is so high that populations may not be able to replenish themselves, at least not locally. This result is both unusual and unexpected, and raises the concern that anthropogenic disturbances to the predator guild may be a contributing factor. The circumstantial evidence concerning this hypothesis is inconclusive, however. The lack of any definite evidence of a regional population decline in this species raises the possibility that other regions within southern Africa may act as net sources, and that the extreme nomadism of the Namaqua Sandgrouse ensures sufficient movement of birds between regions to mask population declines in sink areas. An alternative hypothesis is that four consecutive years of data from a highly stochastic ecosystem are not enough to detect the range of variation in the breeding success of this species. Although the relatively small variation in nesting success in response to substantial variation in annual rainfall argues against this alternative, the high degree of nesting failure in several other arid-zone species (Chapter 9), again with no evidence of population declines, suggests there is still much we have to learn about the population dynamics of these birds. Future research should aim to establish what annual adult-survival rates are among these species, as this is a key parameter in any population dynamics model.

Namaqua Sandgrouse exhibited substantial variation in nest-site characteristics and clutch-pigmentation variables, but these appeared to be largely subject to neutral selection, despite the very high levels of predation (Chapter 4). Investigator effects were ruled out as a contributing factor (Chapter 3). This result is unusual, given the large number of studies, from regions experiencing lower nest-predation risk, that have demonstrated the adaptiveness of nest-site characteristics and shown that birds can identify nest sites with characteristics that reduce the risk of predation (Schrank 1972, Bowman & Harris 1980, Osborne & Osborne 1980, Hill

1984, Bekoff *et al.* 1987, Martin & Roper 1988, Marzluff 1988, Möller 1988, Kelly 1993, Schieck & Hannon 1993, Gregg *et al.* 1994, Rivera-Milán 1996). The suggestion that much of the nest predation suffered by Namaqua Sandgrouse may be incidental is an intriguing one, but requires further investigation to obtain more definite proof.

This study provides further empirical evidence of the highly nomadic nature of the Namaqua Sandgrouse, and of the partial "east-west" migration pattern across South Africa first identified by Malan *et al.* (1994). However, the finding that this partial migration largely takes place between two late-summer-rainfall regions suggests that direct gradients in food availability are not driving this movement pattern (Chapter 7), contrary to the conclusions of Malan *et al.* (1994). There is no immediately obvious alternative explanation, however. The "western" region receives half the rainfall of the "eastern" region, and has a greater probability of experiencing more widespread and continuous drought, i.e. rainfall inadequate for the growth of annual plants (Tyson 1987, Zucchini *et al.* 1992), and may, therefore, be riskier for the birds to remain nomadic within year-round.

The factors responsible for determining the timing of breeding in the Namaqua Sandgrouse remain obscure (Chapter 7). In some regions (e.g. Namaqualand and the Namib) breeding starts soon after seasonal rains have produced an abundant seed-food supply. In other regions, most notably the Nama Karoo, breeding may start up to five months after seed-set, and often extends into the seasonal rainy season when food supply is expected to decrease to its lowest levels in the annual cycle. This is particularly surprising in the light of the finding that adults may not usually be nutritionally challenged, but that the growing chicks may require a reasonably abundant food supply due to their greater food demands and limited mobility (Chapter 6). The hypothesis that variation in the timing of breeding may be related to not only food supply, but also to seasonal variation in nest-predation risk, requires further study. The possibility that the unusually variable breeding seasons across southern Africa may be related to an, as yet undiscovered, complex pattern of seasonal movements between regions, which may in turn be a strategy to reduce risk in a stochastic environment, could also be examined.

The management of the Namaqua Sandgrouse as a resource for sustainable utilisation will be a complex affair if it is to be approached in a reasonably rigorous and scientific fashion, and if it aims to prevent exploitation leading to commercial extinction (Chapter 8). The first point to be emphasised is that our current knowledge of the population dynamics of this species is inadequate for this task, and will only be improved by wide-ranging and long-term monitoring of breeding success, adult survival and movements. The implications, for the commercial utilisation of this species, of the suggestion that much of the mortality may be density independent, will also have to investigated more thoroughly. Once more complete data on adult survival, and recruitment and movements between regions has been obtained, a metapopulation-type model could investigate the effects of differing degrees of density-dependent population regulation, and different off-take levels, on long-term population survival.

The large range in variation in daily nest-predation rates (0.50-10.98%) among species exposed to equivalent predation risk, suggests that differences in nest-site selection and/or predator-avoidance behaviour have a very marked influence on nest-predation rates (Chapter 9). The comparison of the Namaqua Sandgrouse and the Doublebanded Courser suggests that the behaviour of the birds around the nest is of greater importance than nest-site selection (Chapters 4 & 9). Predator-avoidance behaviours of birds at the nest have been poorly studied, so this could be a productive avenue of future enquiry.

The strategy of nomadism was found to be linked to increased nest-predation risk, but the reasons for this have yet to be determined (Chapter 9). This finding has implications for the life histories of nomadic birds, through the convoluted interactions between nest mortality, clutch size, fecundity, egg and chick development rates, and adult survival (Martin 1995, Juillard *et al.* 1997). This is fertile ground for research, and future studies could examine how the contrasting adaptations of nomads and residents to a highly stochastic environment have influenced their life-history parameters.

Clutch size in many species, both nomadic and resident, was found to be closely tied to rainfall (Chapter 10). A flexible clutch size is expected to be adaptive in an environment where species have to make use of erratic and unpredictable breeding opportunities that vary greatly in quality. Nonetheless, just as many arid-zone birds possess a fixed clutch size. Future studies could compare productivity between species with fixed and variable clutch sizes, as a function of environmental variation, and the possible effects of clutch-size flexibility on other life-history parameters.

The excellent work of Tom Cade, Gordon Maclean, David Thomas and others (Cade & Maclean 1967, Maclean 1968, Ward 1972, Maclean 1976, Dixon & Louw 1978, Thomas & Maclean 1981, Thomas 1984), on the physiological, behavioural and ecological adaptations of the Namaqua Sandgrouse to life in arid lands, paints a picture of a highly successful, nomadic opportunist that is superbly adapted to the rigours of its environment. Many of the most successful granivorous bird species inhabit relatively variable and unpredictable environments, and theory leads to the expectation that such bird populations should express traits which lead to relatively high reproductive output (Wiens & Johnston 1977). Most of the other arid-zone species included in this study display a high degree of efficiency and speed in breeding. They respond rapidly to suitable breeding opportunities following rainfall, and breed continuously while they last (Chapter 10). The rapid development rates and clutch-size flexibility of many species are further adaptations to maximise reproductive output under fluctuating conditions. The Namaqua Sandgrouse does not conform to the expectations of a successful arid-zone specialist, however. The breeding activity of the Namaqua Sandgrouse is not tightly correlated with peaks of food availability following rainfall events. This may be because neither adults nor chicks feed on insects, which generally have a narrower window of increased availability than seeds. What is unexpected though, is the finding that Namaqua Sandgrouse do not make use of every apparently suitable opportunity to breed, i.e. they do not appear to be maximising reproductive output in many years. Furthermore, it is unlikely that pairs manage to successfully raise more than one brood to independence each year, given the high levels of predation that necessitate repeat laying, and the slow rates of development.

In conclusion, this study has revealed much about the breeding biology and success of the Namaqua Sandgrouse and several other arid-zone birds. Although the breeding seasons and population fluctuations of the Namaqua Sandgrouse have been examined in some detail in relation to environmental variables, the development of a thorough understanding of the population dynamics of this enigmatic species is likely to occupy many more years of research effort.

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