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The breeding biology of the Namaqua Sandgrouse, *Pterocles namaqua*

Penn Lloyd, Robin M. Little & Timothy M. Crowe

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7701 South Africa

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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 (\pm 48-hour 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, with the female relieving the male 151 min (\pm 21 S.D.) after sunrise and the male relieving the female 105 min (\pm 21 S.D.) before sunset. The incubation period is 21 days from clutch completion, and the three chicks normally hatch within 18 hours of one another. 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 of 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-bred 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; Hoesch 1955), several authors remained sceptical (e.g. Archer & Godman 1937; Meinertzhagen 1964; Hüe & Etchécopar 1957; Schmidt-Nielsen 1964) until Cade & Maclean (1967) outlined the special adaptations of the belly feathers of male sandgrouse that allow efficient water absorption and transport. Marchant (1961), studying the Pin-tailed 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 Yellow-throated Sandgrouse, *P. gutturalis* (Tarboton *et al.* 1999), the only data on sandgrouse breeding success.

This paper 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. These data are important for the informed management of the Namaqua Sandgrouse as a commercially hunted gamebird (Lloyd 1999a).

STUDY SITE 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 during 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 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. 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 Egg Eater, *Dasypteltis 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 with fewer than three eggs where definite evidence of Rhombic Egg Eater predation was found.

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

$$\text{success} = (1 - [\text{losses}/\text{exposure}])^{np},$$

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). Using this method, a nest is assumed terminated midway between visits. By way of exam-

ple, a nest first found on day 1, active on day 10, but found empty on day 13, is active for $9 + 1.5 = 10.5$ days. 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 and juvenile males in the drinking population. The average monthly frequencies of belly-soaking males (as a proportion of the total drinking population) were determined for each season. Because the counts of juveniles were too incomplete, 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 a more detailed study of the Yellow-throated Sandgrouse (see Tarboton *et al.* 1999):

$$C = J/B.$$

This approach rests on the assumption that the number of juveniles reaching independence is proportional to the number of males belly-soaking for dependent chicks, and that this proportion is equal for both Namaqua and Yellow-throated Sandgrouse. Use of the constant C assumes that juveniles are distinguishable from adults at the waterhole for one month after they first appear there. Hinsley & Hockey (1989) noted that a captive-bred juvenile Double-banded 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 discussion), this observation suggests that juveniles may be distinguishable from adults in the field for only one additional month. On the other hand, Tarboton *et al.* (1999) were able to distinguish juvenile Yellow-throated Sandgrouse for up to two months after the last belly-soaking males were noted. Use of the constant $C/2$ therefore assumes that juveniles are distinguishable from adults for two months after they first appear, and that they are counted twice during the two-month period. Although minimum and maximum 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. Counts of birds drinking and belly-soaking at other localities across southern Africa (detailed in Lloyd *et al.* 2001) were used to estimate recruitment at these localities.

RESULTS

Nest site and nest construction

Namaqua Sandgrouse generally nest 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. Nest-object orientation is random, indicating that the nest is 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, 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. While the clutch is incomplete, incubation is irregular. On days when an egg was laid, the female arrived at three nests monitored with cameras mid-morning (08h40–11h05), accompanied by the male partner. The female then sat on the nest for between 50 min and 6.5 h, and appeared to be responsible for most 'incubation' on egg-laying days. At one nest monitored by camera, 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 a second nest, the male remained with the female until 12h11, with the female leaving the incomplete clutch at 16h01. At a third nest, the male left the female within 10 min of arrival. 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 all 10 nests monitored sufficiently closely during egg-laying, the female laid an egg every other day, closer to a 48-hour interval than a 24-hour interval. The interval between the laying of the first and third egg is, therefore, approximately four days.

On the alternate days that the female did not lay an egg (days 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 modal clutch size for the Namaqua Sandgrouse is three. The average for 224 nests was 2.88 (S.D. ± 0.33 , range 2–3). As the Rhombic Egg Eater 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.

Incubation

Upon clutch completion, incubation was continuous. The female incubated through the day, flying to relieve the male at the nest an average of 151 min (S.D. ± 21 , $n = 48$) after sunrise. The male returned in the afternoon to relieve the female 105 min (S.D. ± 21 , $n = 126$) 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 during 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 mid-summer (Fig. 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), with 63 drinking in the afternoon (three belly-soaking males and sex

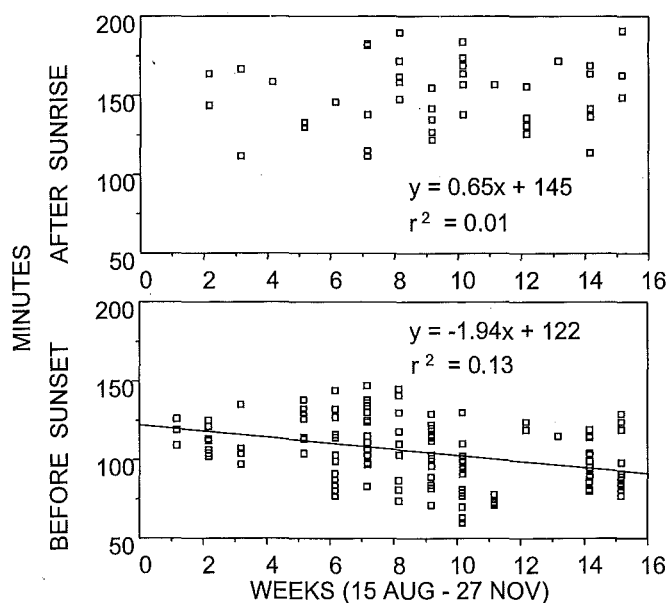


FIG. 1. Morning and afternoon nest relief times of Namaqua Sandgrouse at Droëgrond recorded during the breeding seasons of 1993–1996.

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, considering the small numbers 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.

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. Hatching rarely, if ever, occurs at night. In cases where one or two chicks hatched in the afternoon, the remaining two or one usually hatched the next morning. In some cases, the three chicks hatched during 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.

On the first morning when there were 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 h of the last chick hatching, and may do so within an hour in the presence of an observer.

Nest predation and nesting success

Predation accounted for 96% of all nest losses (Table 1). The nocturnal Rhombic Egg Eater, 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. Rhombic Egg Eaters 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 Rhombic Egg Eaters 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, with small mammals taking nearly eight times as many nests as larger mammals. Smaller mammal predators which occur commonly on the study site include the diurnal Yellow Mongoose, *Cynictis penicillata*, Small Grey Mongoose, *Galerella pulverulenta*, and Suricate, *Suricata suricatta*, and the nocturnal Striped Polecat, *Ictonyx striatus*. Larger mammals (all nocturnal) include Bat-eared Fox, *Otocyon megalotis*, Cape Fox, *Vulpes chama*, Aardwolf, *Proteles cristatus*, and Aardvark, *Orycteropus afer*. The two termite-eating specialists, Aardvark and Aardwolf, are relatively unimportant nest predators – the Aardvark accounted for the predation of only three nests.

Nesting success (to hatching) ranged between 5.7% and 13.5%, averaging 8.2% over the four years studied (Table 2). 1992 was an exceptionally dry year (20.5 mm), with the largest single rain

TABLE 1. 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.

	Rhombic Egg Eater	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 excluding 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.

TABLE 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				Overall	KGNP* 1965/66
	1993	1994	1995	1996		
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 \pm SE (%)	7.36 \pm 1.51	9.42 \pm 0.79	9.00 \pm 2.86	10.35 \pm 2.09	9.19 \pm 0.65	4.59 \pm 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.

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 (Appendix 1), and nesting success (13.5%) was higher than over the following three years.

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 (Lloyd *et al.* 2001). Large numbers of Namaqua Sandgrouse moved nomadically into the area in April, to exploit super-abundant seed-food supplies. The increased population size during the 1994 breeding season, which started in August, resulted in elevated nest densities (Table 3). As nest density increased as the season progressed from spring into summer (Table 3), predation rates decreased (Fig. 2).

The following year (1995) was relatively dry (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 during the breeding season. Nest densities were therefore low, but nest predation rates remained high.

Good rains fell during 1996 (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 3). Nest predation rates on this species were surprisingly high in 1996 (Table 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 ($z = 0.14$ – 1.21 , all $P > 0.05$), but were significantly higher at Droëgrond than in the Kalahari Gemsbok National Park ($z = 2.53$, $P < 0.01$).

Chick development and survival

This study collected only limited data on chick development. 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. Adults were never seen feeding a chick

TABLE 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 1993	–	–	–		
	4	1	0.25		
Oct 1993	11	2	0.18		
	15	5	0.33		
Nov 1993	14	6	0.43		
	12	6	0.50		
1993	56	20	0.36	1196	0.67
Aug 1994	–	–	–		
	23	18	0.78		
Sep 1994	–	–	–		
	20	31	1.55		
Oct 1994	15	23	1.53		
	15	19	1.27		
Nov 1994	–	–	–		
	9	9	1.00		
1994	72	100	1.39	1385	3.68
Sep 1995	13	1	0.08		
	–	–	–		
Oct 1995	6	2	0.33		
	–	–	–		
1995	19	3	0.16	–	–
1996				1798	0.72

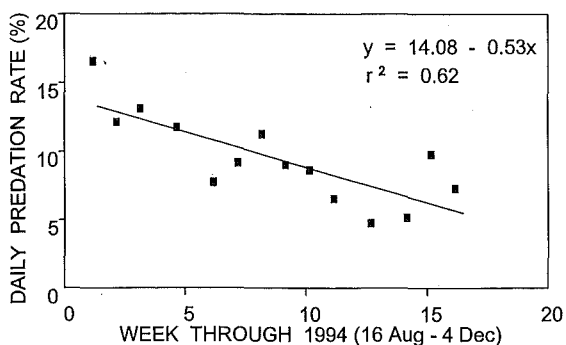


FIG. 2. Daily predation rates on Namaqua Sandgrouse nests through the 1994 breeding season. Regression $F_{1,12} = 19.57, P < 0.001$.

directly.

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 1). 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 3), the total number of belly-soaking males was approximately the same by the start of December in each year (Appendix 1). 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 1).

Annual recruitment estimates for the Namaqua Sandgrouse varied substantially between localities and between seasons at the same locality (Table 4, Appendix 2). 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).

The average number of juveniles per family group (the adult pair with juveniles) observed at waterholes in Bushmanland and the Kalahari during the period of the study was 1.69 and no family included three juveniles ($n = 16$ groups).

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. A 48-hour laying interval has similarly been observed in Pin-tailed (Marchant 1961, Frisch 1970), Double-banded (Hinsley & Hockey 1989) and Pallas's Sandgrouse, *Syrhaptes paradoxus* (Grummt 1985), and longer than the 24-hour laying interval suggested by Maclean (1968) for the Namaqua Sandgrouse. 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, with the male incubating at all times of the day, but our observations do not support this. The presence of a bird on incomplete clutches during only hot, sunny weather suggests that the bird is present only to prevent the eggs from overheating. It was not determined whether the birds actually incubated the eggs during this time. Captive Double-banded 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). In the Chestnut-bellied Sandgrouse *P. exustus*, the incomplete clutch was covered by the male during the day, but after clutch completion, the female incubated during the day and the male at night (J. F. Reynolds in Cramp *et al.* 1985). No mention was made of overnight incubation during the laying period. The incomplete clutch is left unattended overnight in both the Pin-tailed and Spotted Sandgrouse (Marchant 1961). Marchant (1961) noted that the incomplete clutch of both species

TABLE 4. Estimated annual sandgrouse recruitment from monthly adult:juvenile ratios in waterhole counts (Yellow-throated Sandgrouse = YTS; from Tarboton *et al.* 1999) 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 for details of monthly waterhole counts. KGNP = Kalahari Gemsbok National Park.

	% 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

¹Assumes that the belly-soaking total recorded in Appendix 2 is representative of only half the 1993/94 breeding season.

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. Double-banded 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 incubation 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 we 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 Pin-tailed Sandgrouse that 'once the female is on the eggs during full incubation we never saw the male approach the nest nor even suspected its presence within the range of ordinary observation'. 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 suitable foraging places, which would explain why the birds incubated alone.

Maclean (1968) reported 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 thermoregulation and osmoregulation 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. First, the exploratory movements of the precocial chicks around the exposed nest site could attract the attention of a passing predator. Second, 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

During 1993, Namaqua Sandgrouse at Droëgrond nested during drought conditions towards the end of an exceptionally dry two-year period. Most bird species in this arid-zone study area breed after rainfall (Lloyd 1999b). 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.* 1999). Predation by the Rhombic Egg Eater, 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 varied between years, the magnitude of this variability (C.V. = 4%) was relatively small compared with the variance in annual rainfall (C.V. = 51%) and changes in relative nest density (Table 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 1969; Martin 1993), they were not unnaturally elevated by observer disturbance (Lloyd *et al.* 2000a), and four consecutive years of data suggest that they are sustained over the medium to long term (Table 2).

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 specialize on birds' nests as food, even when nest density increases greatly. The available evidence suggests that they locate the nests accidentally during their daily foraging movements in search of insect food (Lloyd *et al.* 2000b). 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).

Chick development and survival

The chicks are evidently self-feeding from the moment they hatch, although the adults may point out food items at least initially. The chicks feed on the same seeds as the adults (Lloyd *et al.* 2000c). Hinsley & Hockey (1989) noted similar behaviour in captive-breeding Double-banded 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; PL, pers. obs.). 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. Double-banded Sandgrouse chicks can fly strongly at the age of four weeks, however (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 our observations showing that juveniles did not appear at the waterhole until at least two months after nests started hatching. Likewise, Tarboton *et al.* (1999) found that juvenile Yellow-throated Sandgrouse appeared at the waterhole (nearly adult-sized) approximately two months after males in the population started belly-soaking.

At Droëgrond, estimates of annual recruitment varied substantially between seasons (Table 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 Pin-tailed 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 4) in the 1994/95 season, despite an extended breeding season and nesting success of 7.6% (Table 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 1) 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 non-breeding season (1.31:1, $n = 437$ birds; P. Lloyd, unpubl. data), and for the nearby Rooipoort estate (1.38:1, $n = 576$ birds; Malan *et al.* 1992). Tarboton *et al.* (1999) similarly noted a male-biased sex ratio (1.35:1, $n = 7307$ birds) in the Yellow-throated 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 warrant 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 Double-banded Sandgrouse that left her 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 Nama Karoo 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 (Little 1997). The average nest predation rate for Namaqua Sandgrouse at Droëgrond (91.0%) is considerably higher than the 53.9% recorded for a stable Yellow-throated Sandgrouse population (Tarboton *et al.* 1999). Furthermore, estimated annual recruitment for Namaqua Sandgrouse at Droëgrond and several other sites was generally less than half that estimated for Yellow-throated Sandgrouse (Table 4). The only exceptions were at Chyandour and in the Kalahari Gemsbok National Park.

Nest failure rates greater than 70% have been implicated in population declines in shrub-steppe 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 (Lindström *et al.* 1995; Palomares *et al.* 1995; Rogers & Caro 1998; Crooks & Soulé 1999).

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 inter-annual variation in predation intensity despite considerable variation in rainfall, and therefore the productivity of the environment (Table 2). The study site at Droëgrond is, however, in a sheep farming region where top predators (Black-backed 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*, has disappeared from the Bushmanland region within the last 100 years (Boshoff *et al.* 1983).

The Black-backed Jackal, Tawny Eagle and Martial Eagle, *Polematius bellicosus*, are the most important predators of Suricates, and in a comparative study Clutton-Brock *et al.* (1999) found that significantly greater numbers of larger predators in a protected area (Kalahari Gemsbok National Park) in relation to adjoining ranch-land resulted in 1.7 times higher mortality

among Suricates. Crooks & Soulé (1999) found that the loss of a single 'top predator', the Coyote, *Canis latrans*, from habitat patches led to higher extinction rates of scrub-breeding birds, through an ecological release of smaller mesopredators. The available evidence suggests that they locate the nests accidentally during their daily foraging movements in search of insect food (Lloyd *et al.* 2000b).

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 in 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) supports the suggestion of a higher level of nesting success at this site. A case could, therefore, be made for mesopredator release (*sensu* Crooks & Soulé 1999) being responsible for the higher nest predation at Droëgrond, but this hypothesis requires testing.

A possible contributing factor to the high nest predation rates at Droëgrond is the abundance of harvester termites (Hodotermitidae) in the Nama Karoo 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 loose surface mounds to expose worker termites. Not only are these termites very abundant in the 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 Nama Karoo region, a population decline is a likely 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 artifact 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. Whereas their annual productivity, within the Nama Karoo 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. 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.

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APPENDIX 1. 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 1993	323		1		
28 Sep 1993	344		5		
11 Oct 1993	480		8		42:27
22 Oct 1993		40	5		26:13
28 Oct 1993	889		67		
05 Nov 1993	945		66		189:67
18 Nov 1993	1048		105		180:90
02 May 1994	8700		6		120:120
17 May 1994	10800				
15 Jun 1994	5000				
24 Jun 1994	3002	2623	10		
13 Jul 1994	5600				68:57
05 Aug 1994	4100				
18 Aug 1994	5872	2370	6		
21 Aug 1994		3300	3		40:33
27 Aug 1994	11052				
13 Sep 1994	7150		13		
22 Sep 1994		697	5		
28 Sep 1994	7027				
05 Oct 1994		886	11		103:89
15 Oct 1994		410	5		
24 Oct 1994		945	14		
12 Nov 1994	6858	1237	35		244:198
21 Nov 1994		680	29		105:66
24 Nov 1994		604	26		69:54
29 Nov 1994	8376				
03 Dec 1994	9032		115	4	
10 Mar 1995	8430	280	4	0	108:89
16 Mar 1995		3600	20	2	64:63
08 Apr 1995	1817	449	5	3	144:118
14 Apr 1995	719	246	3	2	120:115
02 May 1995	65		0	0	
05 Jun 1995	48		0	0	
08 Sep 1995	287		1	0	99:86
04 Oct 1995	309	222	5	0	44:33
17 Oct 1995	319		6	0	152:120
31 Oct 1995	243		10	0	119:93
12 Nov 1995		295	23	1	92:83
14 Nov 1995		656	13	7	222:182
04 Dec 1995	64		2	4	39:25
20 Jan 1996	917	59	19	1	131:89
03 May 1996	422		3	1	29:24
10 May 1996	419	136	6	2	64:51
24 Sep 1996	1269	661	0	0	289:256
30 Sep 1996		2258	6		
16 Oct 1996	2098	493	1	0	222:193
29 Nov 1996		283	2	2	152:131
14 Dec 1996		640	12	3	
					3276:2565
					1.28:1

APPENDIX 2. Counts of adults and the frequencies of belly-soaking males and juveniles (Yellow-throated Sandgrouse only) for the Yellow-throated Sandgrouse (1988–1992; from Tarboton *et al.* 1999) and Namaqua Sandgrouse at various localities.

Month	Yellow-throated Sg.			Droëgrond '93/94		Droëgrond '94/95		Droëgrond '95/96		Droëgrond '96/97		Soetdoring '94/95		Soetdoring '95/96	
	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		
Total		58.91	35.97		15.61		9.04		16.62				16.93		12.94

Month	KGNP '95/96		KGNP '96/97		Pioneer '94/95		Chandour '94/95		Langberg '94/95		Langberg '95/96	
	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*
Total		107.50				32.26		41.72		8.87		33.32

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