

Temporal and spatial patterns of abundance and breeding activity of Namaqua sandgrouse in South Africa

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We examined various measures of temporal and spatial patterns of abundance and breeding activity of Namaqua sandgrouse *Pterocles namaqua* (presumably mostly for *P. n. furvus*) in South Africa. Bird-atlas maps indicating reporting-rates and extensive-counts showed that the majority of Namaqua sandgrouse concentrate in Bushmanland, in the north-western Cape Province, from December to March. From April to July the sandgrouse move north and east of Bushmanland and apparently return to Bushmanland from August to November. This west-east movement occurs at a relatively constant rate of 30–50 km per month. Only 15% of the sandgrouse ringed at an estate within the eastern part of this species range returned the following winter. Follicle diameter and brood-patch measurements increased significantly from July to August, at the time when the majority of birds leave the estate. Belly-soaking was more prevalent in early summer in Bushmanland than in any season in the east. South African populations of Namaqua sandgrouse are partial migrants which breed primarily in early summer (October – November) in Bushmanland.

Temporele en ruimtelike patrone in verspreiding en broei aktiwiteite van die Namaqua sandpatrys *Pterocles namaqua* (vermoedelik meestal *P. n. furvus*) is ondersoek in Suid Afrika. Die voëlatlaskaarte wat rapporteer-skale en ekstensiewe-tellings wys, het aangedui dat van Desember tot Maart die meerderheid sandpatryse gekonsentreer is in Boesmanland. Van April tot Julie het die voëls reeds noord en oos beweeg, net om terugtekeer na Boesmanland van Augustus tot November. Die oos-wes beweging na, en vanaf Boesmanland vind plaas teen 'n relatiewe konstante 30–50 km per maand. Slegs 15% van die geringde sandpatryse wat geoorwinter het op 'n landgoed binne die spesie se oostelike verspreidings gebied, het teruggekeer die opeenvolgende winter. Follikeldeursnee en broeistroommetings het beduidend vergroot vanaf Julie tot Augustus, gedurende 'n periode wanneer die meerderheid voëls die landgoed reeds verlaat het. Pensdeurweking was meer dominant in die vroeë somer in Boesmanland as gedurende enige ander seisoen in die ooste. Die Namaqua sandpatrys populasies in Suid Afrika is gedeeltelik migreerders wat hoofsaaklik in die vroeë somer (Oktober – November) in Boesmanland broei.

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Sandgrouse (Pterocleidae — Brooke 1993) are one of only two families within the Charadriiformes that are exclusively seed eaters (Maclean 1968). According to Maclean (1985), the advantage of a seed-eating specialization is that food is generally spatially and temporally superabundant, depending on the occurrence of suitable rainfall. Therefore, shifts in the distribution and abundance of granivores are usually associated with a variation in local seed supplies, and the success of a particular species rests on its ability to respond to cues indicating the availability of seed in space and time (Wiens & Johnston 1977). It has been suggested that sandgrouse are archetypal granivores, because they inhabit arid and semi-arid regions of Africa and Asia, dispersing, sometimes quite dramatically, to exploit superabundant seeds of ephemeral leguminous plants (Maclean 1976; 1985; Thomas 1984).

The Namaqua sandgrouse *Pterocles namaqua* is endemic to southern Africa and is locally nomadic. However, the southern populations (mostly *P. n. furvus*) are apparently migratory, although their precise movements have not been mapped (Maclean 1993; Maclean & Fry 1986). Clancey (1967; 1979) suggested that the three subspecies of Namaqua sandgrouse could be divided into two broad groups. The north-western, true-desert forms (*P. n. namaqua* and *P. n. ngami*) are largely resident within their range, and the south-eastern form (*P. n. furvus*) is more mobile when not breeding, especially in the Karoo. *P. n. furvus* has been recorded breeding in all months of the year except February, with a more active period from June to January

and peaks in July and November (McLachlan 1985). These seasonal movements and allegedly opportunistic breeding activities may have implications for the management and hunting of Namaqua sandgrouse, because gamebirds should be hunted during the non-breeding season.

The aim of this paper is to test the hypotheses that the southern populations of Namaqua sandgrouse are migratory and that they breed opportunistically. To test these hypotheses we examined five data sets: 1. Reporting-incidence bird-atlas maps, 2. extensive-count surveys, 3. long-term hunting records, 4. ringing returns, and 5. indices of breeding activity.

Methods

Reporting-incidence maps

Maps showing reporting-rates for Namaqua sandgrouse were purchased from the Southern African Bird Atlas Project (SABAP) (Harrison 1992) for the period 1987–1991. These maps represent the atlas cards collected throughout the atlasing period as one data set, and reflect the relative abundance of a species per month within quarter degree squares (QDSs) (Harrison 1989). The proportion of cards on which Namaqua sandgrouse were recorded, within each degree square, was calculated for each of three seasons: December – March, April – July and August – November. These month groupings were chosen to correspond with periods of the year when temporal and spatial differences in the distribution patterns of this species had been detected

during a preliminary unpublished study (Malan, Little & Crowe 1992). The index of relative abundance analysed here was the mean of the percentages for the 16 QDSs comprising a degree square, and ranked from 0 to 8 (0 = <5%; 1 = 5–14,9%; 2 = 15–24,9%; 3 = 25–34,9%; 4 = 35–44,9%; 5 = 45–54,9%; 6 = 55–64,9%; 7 = 65–74,9%; 8 = \geq 75%). We interpreted rank values of 25 as high abundance, and those of <5 as low abundance. Degree squares with fewer than five of their 16 QDSs atlased for any season, or with fewer than five QDSs within South Africa, were excluded from the analysis. We excluded southern Namibia from the analyses because of low atlas coverage in that region (*SABAP News* 13: 10–11). To determine if the index of relative abundance reflected actual sandgrouse numbers within each degree square, we correlated the mean number of birds counted per season per drinking site(s) (counts using the method of Little, Malan & Crowe 1993; see next section) with the index values per degree square, using a log transformation.

Extensive count surveys

Namaqua sandgrouse were counted monthly at watering sites using the method of Little, Malan & Crowe (1993). Counts were done at four localities along a west-east transect, between 28°42'S and 29°30'S in the north-western Cape Province, from April 1990 to June 1992. These localities included five watering sites at Rooipoort Estate (28°38'S / 24°17'E), one site at Plaatjiesdam farm (Middelput, 28°42'S / 22°34'E), one at Droëgrond farm (29°07'S / 20°14'E), and one in the Goëgap Nature Reserve (GNR) (Blou Kokerboom Water, 29°42'S / 18°00'E) (Figure 1). Counts started 90 minutes after sunrise and continued for two hours (Maclean 1968), ending when 10 minutes had lapsed since the arrival of the last bird. Where more than one count was conducted per site per month, a monthly mean was calculated. At Rooipoort, the sum of the monthly means was calculated for the five sites.

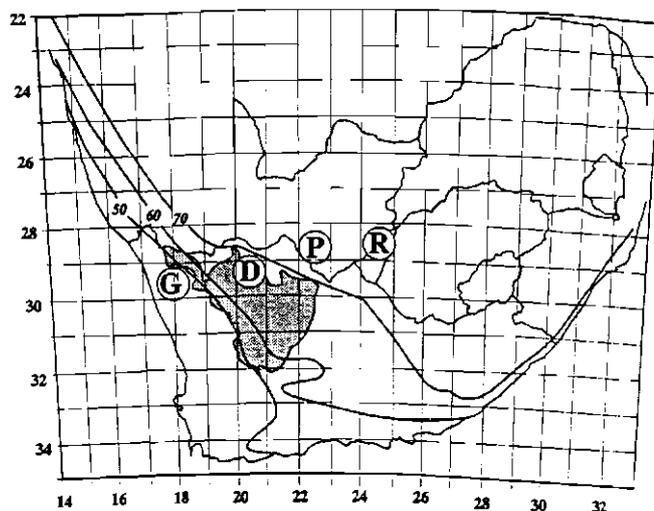


Figure 1 Location of the Namaqua sandgrouse counting sites (G = Goëgap Nature Reserve; D = Droëgrond farm; P = Plaatjiesdam farm; R = Rooipoort Estate), the location of the Nama-karoo Biome (shaded), and isolines for the 50–70% summer rainfall (October – March) percentage of mean annual rainfall.

Long-term hunting records

We analysed data for 85 years (1906–1991) from the Rooipoort hunting book, assuming that numbers shot were correlated with actual sandgrouse densities (Malan, Little & Crowe 1993). We calculated an average bag per hunter per month during the hunting season (May – August) by dividing the number of birds bagged per month by the number of hunter-days for that month.

Ringed returns

Namaqua sandgrouse were caught and ringed during 14 capture operations conducted at Rooipoort from 1988 to 1991 (McGregor, Museum unpub. records; Lewis 1989; Malan, Little & Crowe 1992). The place and date where ringed birds were recovered from 1988–1991 were recorded.

Breeding activity

Measurements of breeding activity were collected from birds shot by hunters during the hunting season (May – July) and by one of the authors (GM) during the rest of the year. We recorded gonad size, brood-patch width and belly-soaking to investigate within-year and between-year variation in breeding activity at Rooipoort. Gonadal development of adult sandgrouse was measured as the length of the longest testis or diameter of the larger ovarian follicle. A female was regarded as reproductively active if a follicle of >10mm was measured, or if an egg was present in the oviduct. Because of small sample sizes during the summer, data for birds collected from September 1990 to April 1991 were pooled. Brood-patch half-width was measured on the left side of the breast, 2 cm from the anterior end of the sternum, and perpendicular to the first line of feathers. Belly-soaking reflects the period when adult sandgrouse provide water for flightless young (Cade & Maclean 1967). We correlated the mean monthly counts with the mean monthly rates of belly-soaking at Rooipoort. We also recorded the number of sandgrouse belly-soaking at Plaatjiesdam, at the GNR, and during counts in the Kalahari Gemsbok National Park (Leeudril, 26°24'S / 20°41'E) and at Kangnas (42 km east of Springbok, 29°35'S / 18°22'E).

Results

Reporting-incidence maps

On a South African scale, maps of reporting-incidence indicate that Namaqua sandgrouse concentrate in Bushmanland and to the north-east from December to March (Figure 2). From April to July, accompanying an apparent northerly movement, there is an eastward shift into the Orange Free State and Karoo (Figure 3). From August to November, sandgrouse return to Bushmanland and the fringes of the Nama-Karoo, which represents a large-scale movement westwards within South Africa (Figure 4). Bushmanland is defined as a biogeographical area within the Nama-Karoo Biome (Figure 4) (Hilton-Taylor & Le Roux 1989). The western boundary of Bushmanland closely follows the 50% summer-rainfall isoline. This isoline separates the predominantly summer-rainfall Nama-Karoo Biome from the winter-rainfall Succulent Karoo Biome.

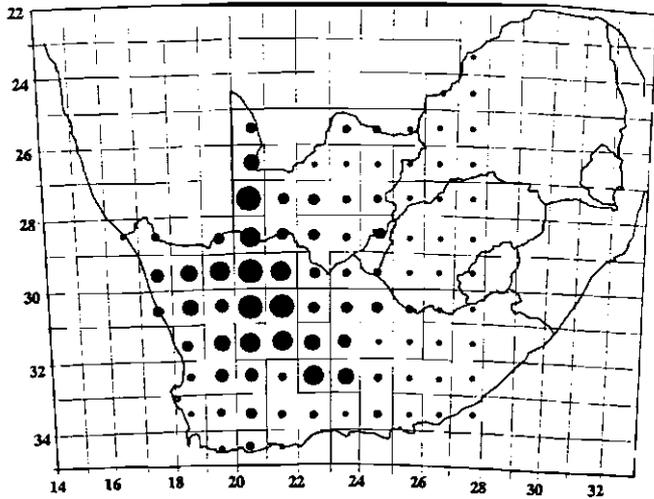


Figure 2 Distribution of relative abundance of Namaqua sandgrouse in South Africa between December and March. Source: Southern African Bird Atlas database (1987–1991). Variable-sized shaded circles reflect ranked indexes of relative abundance, with larger circles reflecting higher abundance (see methods text).

The mean number of sandgrouse counted per locality per season was positively but not significantly correlated with the reporting-incidence index ($r = 0,65; p = 0,11; n = 7$).

Extensive-count surveys

The temporal distribution of sandgrouse fluctuated seasonally at all four localities (Figure 5). At Rooipoort, in the east, the arrival was abrupt and the departure was gradual, whereas further west, at Droëgrond, the arrival was gradual and the departure abrupt. Moreover, the alternating high numbers of sandgrouse from east to west between May 1991 and January 1992 reflected large-scale movement of these birds. Numbers peaked in May and June at Rooipoort, and during July at Plaatjiesdam (145 km west of Rooipoort). At Droëgrond (230 km west of Langberg) numbers peaked

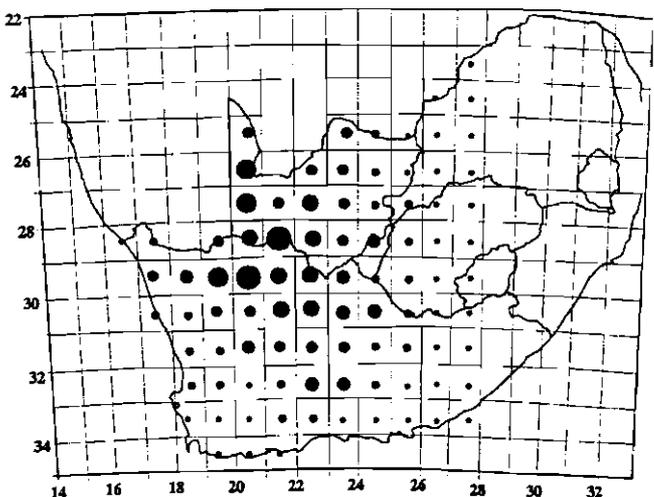


Figure 3 Distribution of relative abundance of Namaqua sandgrouse in South Africa between April and July. Source: Southern African Bird Atlas database (1987–1991). Variable-sized shaded circles reflect ranked indexes of relative abundance, with larger circles reflecting higher abundance (see methods text).

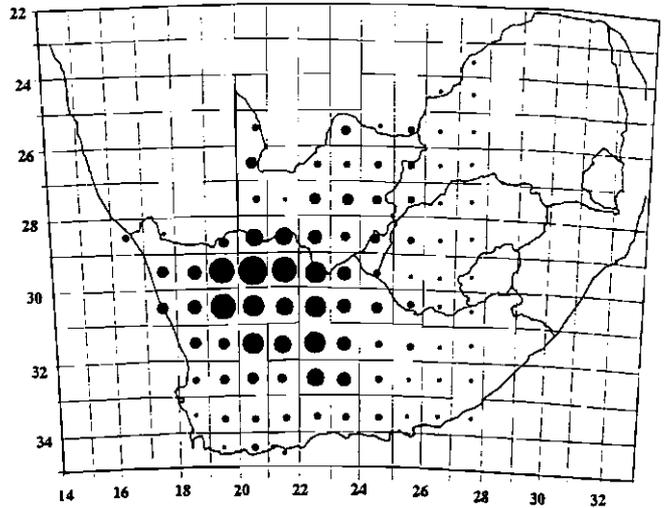


Figure 4 Distribution of relative abundance of Namaqua sandgrouse in South Africa between August and November. Source: Southern African Bird Atlas database (1987–1991). Variable-sized shaded circles reflect ranked indexes of relative abundance, with larger circles reflecting higher abundance (see methods text).

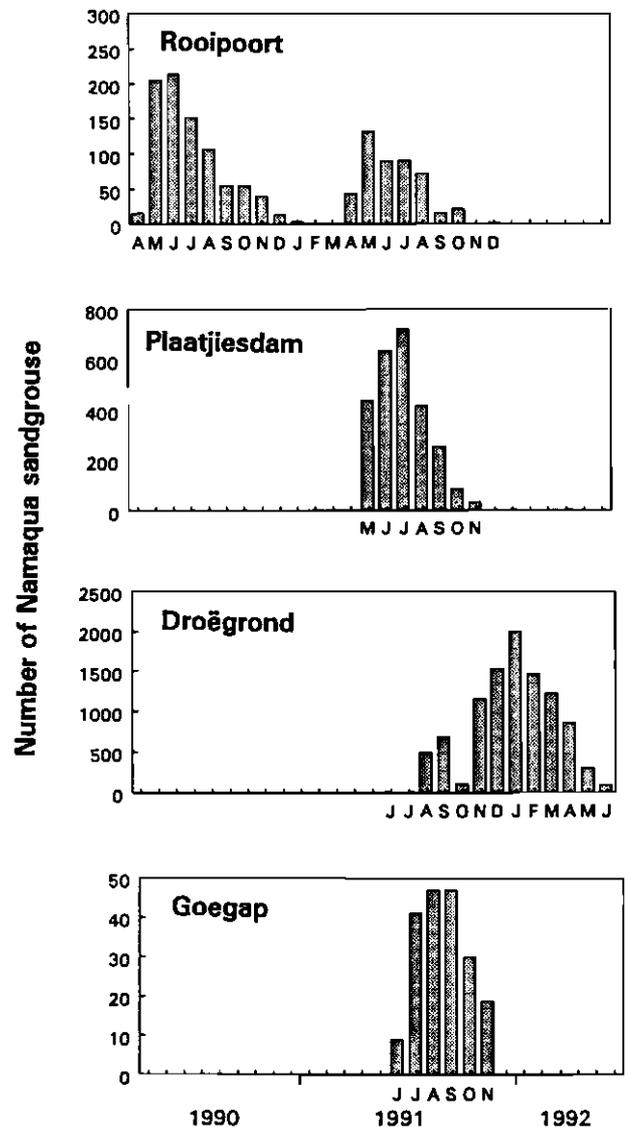


Figure 5 Frequency distributions of Namaqua sandgrouse counted at four localities in the northern Cape Province, South Africa. Only months when birds were counted are shown.

in January. The west-east movement is at a relatively constant rate of 30–50 km per month. However, the pattern at the GNR (230 km west of Droëgrond) did not correlate with the patterns at the other sites. Nevertheless, the sandgrouse departed from the GNR from October to November, in parallel with the larger movement to the north-east. Maximum numbers per month were recorded at Droëgrond (2000, January 1990), followed by Plaatjiesdam (721, July 1991) and Rooipoort (214, June 1990), with the lowest number being recorded at the GNR (47, August and September 1991).

Long-term hunting records

The mean number of sandgrouse bagged per hunter at Rooipoort was significantly higher during May and June than during July and August (May = 10, June = 12, July = 7, August = 4; $p < 0,05$; ANOVA; $n = 85$ years).

Ringing returns

Of the 85 sandgrouse ringed from 1988 to 1991, two were shot more than one year after capture, one 384 days after capture at the same watering site of release, and the other 726 days after release and 4 km from the site of capture, i.e. back to the same area at the same time of year, almost exactly one year and two years from the date of first capture.

Breeding activity

Mean testis diameters of sandgrouse at Rooipoort showed no significant variation between months nor between years ($p > 0,05$; t -test; Table 1). However, the frequency of reproductively active females in the population increased significantly from June to August during 1990 ($p < 0,01$; $\chi^2 = 10,56$), but was not significantly different between

August and summer (September – December) of that year ($p > 0,05$; $\chi^2 = 0,10$). In 1991, there was no significant difference between June and July ($p > 0,05$; $\chi^2 = 0,10$), but frequency once again increased significantly from July to August ($p < 0,05$; $\chi^2 = 5,48$). The frequency of reproductively active females did not differ significantly between June 1990 and June 1991 ($p > 0,05$; $\chi^2 = 1,36$), nor between August 1990 and August 1991 ($p > 0,05$; $\chi^2 = 0,01$) (Table 2). Mean monthly brood-patch measurements were weakly, but significantly positively correlated with mean monthly gonad development ($r = 0,19$; $p < 0,05$ for males; $r = 0,37$; $p < 0,001$ for females). Mean brood-patch measurements of both sexes did not vary significantly between August 1990 and the summer months, nor between the winter months for 1991 ($p > 0,05$; t -test) (Table 1). However, brood patches were significantly larger in both sexes in 1990 than in 1991 (males: $\bar{x} = 18,3$ & 15,0 mm, respectively; females: $\bar{x} = 18,4$ & 15,5 mm, respectively; $p < 0,001$; t -test). Moreover, in 1991, the brood-patch measurements decreased from June to July and increased in August.

Belly-soaking at Rooipoort peaked between August and October, but was not significantly correlated with sandgrouse numbers ($r = -0,25$; $p = 0,48$) (Table 3). At Plaatjiesdam, belly-soaking was recorded only during September and October, with a combined maximum of 7/81 (8%). At Leeudril, only 5/550 (1%) belly-soaked on 10 July 1991, and none of 104 birds belly-soaked on 20 August 1991. However, on two occasions at the GNR, 51% (24/47) and 40% (19/47) of the few birds that visited the watering site belly-soaked, and the proportion of flocks with at least one bird that belly-soaked was 36% for Kangnas and 40% for Droëgrond.

Discussion

Seasonal patterns of distribution of Namaqua sandgrouse (*P. n. furvus*) in South Africa conformed to normal patterns of avian migration, in that populations moved seasonally in predictable patterns in space and time (Baker 1978; Maclean 1990). However, the breeding-activity patterns were less well defined in time and in locality than those of other migratory birds. Although, on a South African scale, the maps showing reporting-rates and extensive-counts suggest a 'pendulum' of movement from west to east during autumn, and a return shift from east to west during spring, the population remains dispersed, with a seasonal shift in the area of highest concentration. Indeed, the first arrivals and

Table 1 Mean brood-patch half-width and testis length measurements (± 1 SD) for Namaqua sandgrouse *Pterocles namaqua* collected at Rooipoort Estate, northern Cape Province, South Africa (sample size in parentheses)

Date	Brood-patch half-width (mm)		Testis length (mm)
	Males	Females	
June 1990			7,6 \pm 2,0 (134)
July 1990			7,3 \pm 1,1 (10)
August 1990	18,3 \pm 2,8 (56)	18,2 \pm 2,8 (51)	7,3 \pm 1,6 (63)
Summer 1990/1991	18,6 \pm 2,4 (25)	18,2 \pm 2,4 (23)	7,0 \pm 1,3 (24)
June 1991	15,1 \pm 2,3 (11)	15,8 \pm 2,2 (10)	5,4 \pm 1,6 (13)
July 1991	14,6 \pm 1,9 (24)	15,2 \pm 2,6 (22)	6,9 \pm 1,1 (69)
August 1991	15,8 \pm 2,1 (9)	16,2 \pm 2,1 (8)	6,9 \pm 0,8 (34)

Table 2 Proportion of reproductively inactive (follicle diameters ≤ 10 mm) and reproductively active (follicle diameters > 10 mm) female Namaqua sandgrouse *Pterocles namaqua* at Rooipoort Estate, northern Cape Province, South Africa

Follicle diameter	1990			1991		
	June	August	September–December	June	July	August
	$n = 98$	24	17	24	32	81
≤ 10 mm	97%	75%	71%	92%	94%	74%
> 10 mm	3%	25%	29%	8%	6%	26%

Table 3 Mean monthly counts of Namaqua sandgrouse *Pterocles namaqua* at Rooipoort Estate, Plaatjiesdam farm and Goegap Nature Reserve (number of individuals that recorded belly-soaking in parentheses). For Rooipoort the sum of five watering sites is presented

Date	Rooipoort Estate	Plaatjiesdam farm	Goegap Nature Reserve
1990			
April	81 (0)		
May	1026 (0)		
June	1069 (0)		
July	762 (8)		
August	533 (13)		
September	278 (28)		
October	276 (25)		
November	201 (13)		
December	69 (5)		
1991			
January	18 (1)		
February	0 (0)		
March	0 (0)		
April	219 (0)		
May	666 (0)	438 (0)	
June	453 (0)	635 (0)	9 (0)
July	455 (0)	721 (0)	41 (1)
August	366 (0)	416 (0)	47 (24)
September	81 (3)	254 (7)	47(19)
October	108 (2)	85 (7)	30 (13)
November	4 (1)	32 (0)	19 (2)
December	11 (0)		0 (0)

the last departures at any one place overlapped with peaks of abundance at other places, and the occupation of a locality at the eastern end of the migration during the non-breeding season was spread over seven to ten months. These patterns of shift suggest partial migration, because less than the total population was moving at any one time (Baker 1978).

However, because there are no records of time and distance moved by individual birds, we do not know how far individuals actually migrate and if they move in predictable directions. Furthermore, because we studied the migration only in a subset of the range of this species, it is still not known whether these populations are migratory while others are resident.

Although Clancey (1979) predicted that the southern subspecies of the Namaqua sandgrouse, *P. n. furvus*, would be a summer breeder (September – February) in the Karoo districts of the Cape Province and Griqualand West, and may over-winter in the north of its range from April to August, there is an apparent lack of strict temporal or geographical separation between breeding and non-breeding activity. However, the breeding activity of reproductively active females increased significantly just before their departure from the eastern areas and remained high, with high rates of belly-soaking, in the west during the summer.

Therefore, these birds probably breed further west in Bushmanland. Three factors support this hypothesis. Firstly, the sandgrouse concentrate in Bushmanland between August and March, overlapping largely with the period when most sandgrouse have been recorded with eggs (McLachlan 1985). Secondly, although low levels of belly-soaking were generally recorded, similar to those recorded by Maclean (1968) for the Kalahari Desert, the highest rates of belly-soaking were recorded at the Goegap Nature Reserve, at Kangnas and at Droëgrond, indicating high breeding activity in Bushmanland and adjacent areas in early summer. Thirdly, brood-patch measurements decreased from June to July, and increased in August at Rooipoort, just before departure of the sandgrouse, indicating that Rooipoort is probably a non-breeding area for Namaqua sandgrouse.

Furthermore, Namaqua sandgrouse in the northern Cape Province apparently follow the anticipated availability of seed, tracking the predominantly summer rainfall in the east, and predominantly winter rainfall in the west. Indeed, Knight (1989) found that the abundance of Namaqua sandgrouse at two watering sites in the Kalahari Gemsbok National Park were significantly positively correlated with the rainfall of the previous two months. The apparent movement of sandgrouse to the north from April to July, and the reasons for it, need further investigation. Sandgrouse that breed outside Bushmanland possibly use pockets of suitable habitat in poorer environments. Another factor that favours breeding in Bushmanland is the sandy soil characterized by grassy, dwarf shrubland (Rutherford & Westfall 1986; Hilton-Taylor & Le Roux 1989), since that habitat might offer good camouflage as well as early predator detection. Furthermore, the species diversity of food plants is higher in Bushmanland than in areas to the east (Hilton-Taylor 1987) and seed size of plants may be positively correlated with soil-particle size (Chambers, MacMahon & Hafner 1991), which might offer sandgrouse chicks greater seed availability, by volume, in Bushmanland than in the eastern Karoo.

The management implications of these temporal and spatial patterns of abundance and breeding activity of Namaqua sandgrouse (probably mostly *P. n. furvus*) are that hunting should be restricted to the eastern portion of their range and only during the non-breeding, autumn and winter months (1 April – 15 July).

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