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# Nest-site selection, egg pigmentation and clutch predation in the ground-nesting Namaqua Sandgrouse *Pterocles namaqua*

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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-to-object orientation was random, indicating that the nest was sited close to objects neither for shade nor shelter from prevailing winds. A stepwise logistic regression analysis, using nine different object type, height and distance category totals as variables of nest-site complexity and concealment, found no effect of these variables on nest fate (survival vs mammal predation). 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 were highly variable in appearance, but intra-clutch variability was 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.

Clutch predation is a major cause of reproductive loss in birds (Ricklefs 1969, Martin & Clobert 1996) and is considered 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, Møller 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 macro-habitat 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 1984, 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 1970, 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.

The Namaqua Sandgrouse *Pterocles namaqua* is a ground-nesting bird of the arid interior of southern Africa that suffered nest predation rates of 85–93% over four consecutive breeding seasons, primarily by small mammal predators (71% of nest losses; Lloyd *et al.* in press a). This study examines nest-microhabitat and egg-appearance variables in relation to clutch

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predation to test hypotheses concerning the adaptiveness of nest-site selection and clutch pigmentation in this species.

## STUDY AREA AND METHODS

The study was conducted over the summer breeding season August–December 1994 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. 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.

The Namaqua Sandgrouse lays a clutch of three eggs (rarely two) in a shallow scrape on the ground (Fig. 1). Nests were located at random through the 25-day nesting period (four days laying and 21 days incubation) by following birds flying to the nest-site to relieve their mates. Nests were marked as inconspicuously as possible, some 10–20 m from the nest, with either a small folded square of white 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. Because the precocial chicks may leave the nest within hours of hatching, nests were monitored once a day to determine their fate. 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. The incubating bird was either flushed or induced to walk off the nest; the contents being checked from a distance of 5–10 m using binoculars.



Figure 1. Namaqua Sandgrouse on nest.

## 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 within a 1-m radius of the nest (none, pale stones only, dark stones only, or mixed pale and dark stones), and substratum surrounding the nest (sand, coarse sand, pebbles, or stones/rock) were noted. In addition, the height of and distance to all objects ( $\geq 3$  cm in height) 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 were compared for each of two distance classes (0–29 cm and 30–100 cm) between the nest-sites and control points.

To investigate the adaptive importance of a concentration of objects around the nest to crypsis and concealment, we ran a stepwise logistic regression analysis testing the effect of nine variables describing the number of objects of different type (solid or sparse), height (3–9 cm or  $\geq 10$  cm) and distance from the nest (0–29 cm or 30–100 cm) on nest fate (hatched vs mammal predation). Solid objects were distinguished from sparse objects due to their differing ability to conceal the nest-site. A 10-cm height threshold was used because an incubating sandgrouse sat approximately this high. A 30-cm distance threshold was used because 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 Egg-eating Snake *Dasypeltis scabra*, we compared nests lost to mammal predation 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.

We tested the hypothesis that relatively more cryptic clutches should have a greater probability of surviving mammal predation using two analyses. In the first, predation frequencies were compared among clutches of different dominant egg-pattern coarseness (speckled or spotted) on substrata of different coarseness (fine sand, coarse sand or pebbles/stones). We assume that clutches exhibiting a closer match between pigment-pattern coarseness and substratum coarseness are more cryptic. In the second analysis, we ran a stepwise logistic regression using five variables: (1) average pigment cover for the clutch; (2) the sum of 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; (3) diversity in pigment cover, calculated as the largest difference in pigment cover between eggs within the clutch; (4) the number of wreathed eggs within the clutch; and (5) the presence or absence (coded 1 or 0) of within-clutch differences in any one of background colour, pigment intensity or pigment pattern. Darker clutches were expected to survive better than lighter clutches because the substratum was invariably darker than the eggs. Visual diversity within the clutch was expected to enhance clutch crypsis, and hence clutch survival. All the above analyses considered three-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, P. Lloyd pers. obs.). Three separate observations of the close approach of a small-to-medium sized mammal to a Namaqua Sandgrouse nest suggest that this species normally remains on the nest, flushing at a minimum distance of 2 m from a predator (Maclean 1968, P. Lloyd pers. obs.). Maclean (1968) observed how a Bat-eared Fox *Otocyon megalotis* used the flushing bird as a cue to locate the eggs. We developed a simple, random-walk model to explore the possible impact of

mammal predators locating sandgrouse nests opportunistically during their daily movements by flushing the incubating birds, using the Yellow Mongoose *Cynictis penicillata* as a model predator. The Yellow Mongoose has a primarily insectivorous diet (Smithers 1983), but was one of the principal nest predators at the study site (Lloyd *et al.* in press a).

In habitat largely similar to that of our 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 ten nests were randomly placed, was divided into 640 000 cells 1.25 m × 1.25 m. 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 ( $P = 0.15$  for each side) and rarely ( $P = 0.05$ ) backtracked on its path. 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

Orientation had no observable effect on the number of objects in each of four orientations (north, east, south, west) within 1 m of nests (Table 1). The object totals differed significantly between the nest-site and the point 2 m to the north for both the 0–29 cm and

**Table 1.** Object means ( $\pm$  sd;  $n = 146$  sites) in different distance and height classes, within a 1 m radius of Namaqua Sandgrouse nests, and a point 2 m to the north of each nest (control), and in each of four orientations within a 1 m radius of Namaqua Sandgrouse nests ( $n = 146$ ). A general linear model (GLM) testing the effect of orientation on the total number of objects (all  $\geq 3$  cm high) was non-significant ( $F_{3,435} = 0.40$ ,  $P > 0.7$ ). The GLM controlled for significant differences in the total number of objects between nest-sites ( $F_{145,435} = 2.53$ ,  $P < 0.0001$ ). GLMs testing the effect of nest position (nest vs control) on the total number of objects around the nest ( $\geq 3$  cm high) were significant for both the 0–29 cm ( $F_{1,145} = 289$ ,  $P < 0.0001$ ) and 30–100 cm ( $F_{1,145} = 69$ ,  $P < 0.0001$ ) distance classes. The GLMs controlled for significant effects of nest-site ( $F_{145,145} = 1.43$ ,  $P < 0.02$  and  $F_{145,145} = 4.35$ ,  $P < 0.0001$  for the 0–29 cm and 30–100 cm distance classes respectively).

Distance classes (cm)	Height classes					Totals
	3–4	5–9	10–14	15–29	$\geq 30$	
<b>Nest-site</b>						
0–29 (a)	1.81 $\pm$ 2.09	2.46 $\pm$ 1.98	0.84 $\pm$ 1.06	0.55 $\pm$ 0.79	0.27 $\pm$ 0.76	5.93 $\pm$ 2.85
30–100 (b)	5.83 $\pm$ 5.86	6.34 $\pm$ 5.39	1.55 $\pm$ 2.62	1.02 $\pm$ 1.67	0.32 $\pm$ 0.95	15.05 $\pm$ 9.74
Totals	7.64 $\pm$ 7.20	8.80 $\pm$ 6.72	2.39 $\pm$ 3.14	1.58 $\pm$ 2.14	0.59 $\pm$ 1.51	20.99 $\pm$ 11.4
<b>2 m north (control)</b>						
0–29 (c)	0.68 $\pm$ 1.05	0.50 $\pm$ 0.85	0.16 $\pm$ 0.55	0.18 $\pm$ 0.51	0.04 $\pm$ 0.20	1.56 $\pm$ 1.88
30–100 (d)	4.14 $\pm$ 4.70	3.90 $\pm$ 4.39	0.80 $\pm$ 1.36	0.47 $\pm$ 1.04	0.23 $\pm$ 0.71	9.55 $\pm$ 8.71
Totals	4.83 $\pm$ 5.32	4.40 $\pm$ 4.90	0.96 $\pm$ 1.55	0.64 $\pm$ 1.30	0.27 $\pm$ 0.77	11.12 $\pm$ 9.92
Ratio a/c	2.6	4.9	5.3	3.2	6.7	3.8
Ratio b/d	1.4	1.6	1.9	2.2	1.4	1.6

Distance classes (cm)	Orientation around nest			
	N	E	S	W
<b>All objects (<math>\geq 3</math> cm high)</b>				
0–29	1.49 $\pm$ 1.01	1.45 $\pm$ 1.14	1.49 $\pm$ 1.07	1.51 $\pm$ 1.08
30–100	3.34 $\pm$ 2.90	4.08 $\pm$ 3.32	3.80 $\pm$ 2.88	3.84 $\pm$ 2.91
Totals	4.82 $\pm$ 3.30	5.53 $\pm$ 3.93	5.29 $\pm$ 3.11	5.35 $\pm$ 3.40
<b>Objects <math>\geq 15</math> cm high</b>				
0–29	0.23 $\pm$ 0.47	0.21 $\pm$ 0.41	0.22 $\pm$ 0.45	0.18 $\pm$ 0.40
30–100	0.33 $\pm$ 0.68	0.34 $\pm$ 0.62	0.36 $\pm$ 0.88	0.32 $\pm$ 0.72
Totals	0.55 $\pm$ 0.91	0.54 $\pm$ 0.81	0.58 $\pm$ 1.00	0.49 $\pm$ 0.92

30–100 cm distance classes (Table 1). 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 of the nest than 30–100 cm distant (Table 1). 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 oriented to provide shade from the sun (north to northwest during the hottest part of the day) or protection from the prevailing northerly and westerly winds.

A logistic regression analysis was unable to detect an effect of the nine object type, height and distance categories on nest survival (Table 2). The nest-site variables of habitat, substratum and presence of stones around the nest also had no significant effect on nest survival (Table 3).

### Egg pigmentation

Namaqua Sandgrouse eggs were remarkably variable in appearance (Fig. 2). 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. 2). Inter-clutch variation was generally greater than intra-clutch variation. A clutch tended to contain eggs of the same pigment pattern (Table 4), and wreathed eggs were non-randomly distributed among clutches; clutches containing two or three wreathed eggs occurred at a significantly higher frequency than expected (Table 5).

The fate of nests was independent of clutch-pigment pattern and substrate type (Table 6). The logistic

**Table 2.** Summary of object totals within various object type, height and distance classes within a 1-m radius of the nest compared between nests that survived to hatch and those that failed to mammal predation. A stepwise logistic regression analysis testing the effect of the nine variables on nest survival determined that all variables were not significant (Wald Chi-square  $\leq 1.85$ ,  $P > 0.15$ ).

Type	Object		Hatched <i>n</i> = 31	Predation <i>n</i> = 87	Pooled <i>n</i> = 118	Range
	Height	Distance				
Solid	<10 cm	0–29 cm	3.42 (2.64)	3.99 (3.17)	3.84 (3.04)	0–14
Sparse	<10 cm	0–29 cm	0.26 (0.58)	0.37 (0.88)	0.34 (0.81)	0–6
Solid	<10 cm	30–100 cm	9.61 (7.84)	11.17 (8.02)	10.76 (7.98)	0–30
Sparse	< 10 cm	30–100 cm	0.84 (1.32)	1.01 (2.96)	0.97 (2.63)	0–19
Solid	$\geq 10$ cm	0–29 cm	0.45 (0.72)	0.30 (0.57)	0.34 (0.62)	0–2
Sparse	$\geq 10$ cm	0–29 cm	1.19 (1.11)	1.01 (1.40)	1.06 (1.33)	0–6
Solid	$\geq 10$ cm	30–100 cm	0.74 (1.41)	1.00 (1.95)	0.93 (1.82)	0–14
Sparse	$\geq 10$ cm	30–100 cm	1.71 (1.74)	1.82 (3.82)	1.79 (3.41)	0–27
Total			18.23 (9.81)	21.40 (11.77)	20.57 (11.30)	3–62

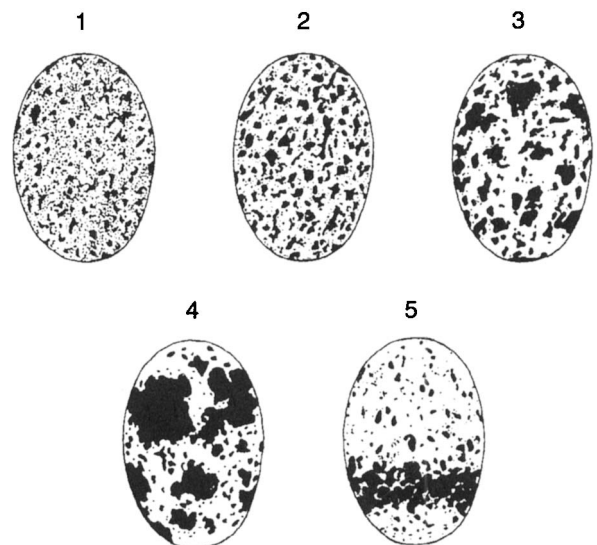
Results are means with  $\pm$  sd in parentheses.

regression analysis was unable to detect an effect of clutch-pigment cover and shade (light–dark) variables on clutch survival (Table 7), 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 8).

**Table 3.** 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). A stepwise logistic regression analysis testing the effect of the three variables on nest survival determined that all variables were not significant (Wald Chi-square  $\leq 0.34$ ,  $P > 0.5$ ).

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



**Figure 2.** Sample of Namaqua Sandgrouse eggs, illustrating the range of variation in egg appearance encountered at Droëgrond.

**Table 4.** 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 5.** The observed versus expected (if random) frequency distributions of wreathed (light or heavy pigment concentration at one end) eggs among three-egg Namaqua Sandgrouse clutches ( $\chi^2_2 = 45.90$ ,  $P < 0.001$ ).

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

### 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 3. The simulated relationship between the proportion of nests found and the number of mongoose predators increased in a non-linear fashion towards a maximum of 1, which can be described by an asymptotic exponential function  $\alpha(1 - e^{-\beta x})$  with upper limit  $\alpha = 1$  (Fig. 4). An increase in the number of predators results in a less than proportional increase in predation

**Table 6.** 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 ( $\chi^2_3 = 0.64$ ,  $P > 0.75$ ).

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	70 (8.75)	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 7.** Summary statistics of clutch appearance variables (clutch-pigment cover, clutch-pigment shade, intra-clutch variability in pigment cover, and the number of wreathed eggs) compared between nests that survived to hatch and those that failed to mammal predation. A stepwise logistic regression analysis testing the effect of the four clutch-crypsis variables on nest survival determined that none of the variables was significant (Wald Chi-square  $\leq 0.48$ ,  $P > 0.48$ ).

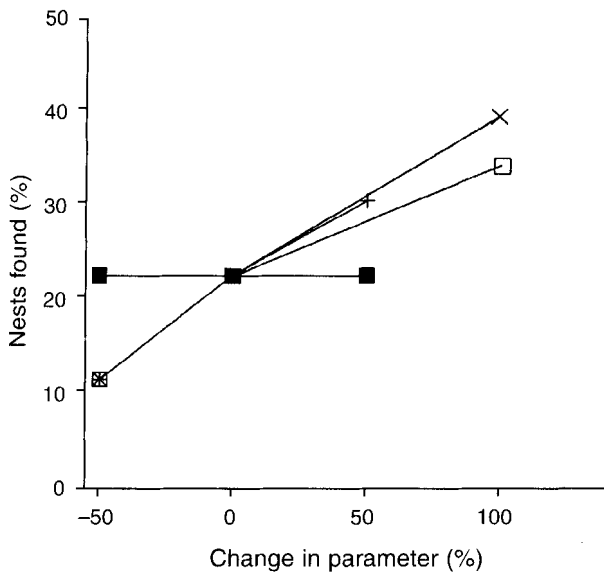
Variable	Hatched $n = 34$	Predation $n = 80$	Pooled $n = 114$	Range
Pigment cover	0.49 (0.11)	0.49 (0.12)	0.49 (0.12)	0.22–0.78
Clutch shade	3.18 (0.72)	3.09 (0.83)	3.12 (0.80)	2–4
Cover diversity	0.17 (0.10)	0.16 (0.08)	0.17 (0.09)	0.02–0.40
Wreathed eggs	0.74 (1.16)	0.60 (0.92)	0.64 (1.00)	0–3

Results are means with  $\pm$  sd in parentheses.

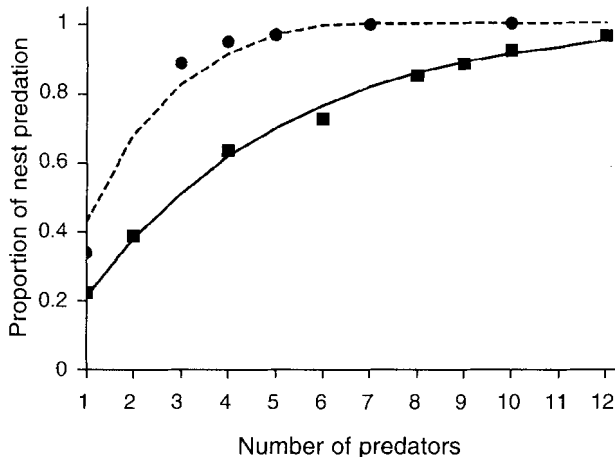
**Table 8.** A  $2 \times 2$  contingency table comparison of mammal predation frequencies between nests exhibiting inter-egg differences in background colour, pigment pattern or pigment intensity codes, and clutches uniform for these variables. Yate's corrected  $\chi^2_1 = 5.60$ ,  $P < 0.02$ .

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

because of the increased overlap in the search areas of the predators. Under the assumptions of the model, predator densities of nine or ten animals per 100 ha can account for predation rates of 88–92%.



**Figure 3.** 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. x, Distance travelled each day; +, detection path width; □, predator destiny; ■, nest density.



**Figure 4.** 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. ■, standard model:  $y = 1 - \exp(-0.24x)$ ; ●, doubled search radius:  $y = 1 - \exp(-0.53x)$ .

## 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 (Table 1). 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 logistic regression analysis failed to detect an effect on nest survival using these variables (Table 2). Increased complexity and/or concealment therefore appeared to have no selective advantage in reducing nest predation among the nests sampled. Such a result might be expected if predators locate nest-sites largely using non-visual cues (e.g. using scent or the close-range flushing behaviour of the incubating bird). Investigator-disturbance effects were ruled out by a parallel study which showed that predation probabilities were not elevated immediately after a nest visit and were unaffected by the frequency of nest visits or the length of time nests were under observation (Lloyd *et al.* in press b).

Nest predation may not be altogether random. 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 1970), 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, for either shade or cover from aerial predators while foraging (Clutton-Brock *et al.* 1999). 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). 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 8),



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 7). 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 9–10 'mongoose units' per 100 ha is required to locate 90% of all sandgrouse nests on a purely incidental (random) basis (Fig. 4). Yellow Mongoose densities are probably higher than assumed in the model; reported densities vary from 2.9 individuals per 100 ha (Howard 1995) to 6–7 individuals per 100 ha (Cavallini & Nel 1995) in similar habitats. Although we lack combined predator-density estimates, our 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*, Bat-eared Fox *Otocyon megalotis*, Cape Fox *Vulpes chama*, Aardwolf *Proteles cristatus*, Aardvark *Orycteropus afer*, Cape Cobra *Naja nivea* and the Rhombic Egg-eating Snake (Lloyd *et al.* in press a), 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 (Lloyd *et al.* in press a), 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 non-specialist predation that occurs by chance.

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### REFERENCES

- Beckoff, M., Scott, A.C. & Conner, D.A. 1987. Nonrandom nest-site selection in Evening Grosbeaks. *Condor* **89**: 819–829.
- Bowman, G.B. & Harris, L.D. 1980. Effect of spatial heterogeneity on ground-nest predation. *J. Wildl. Manage.* **44**: 806–813.
- Cavallini, P. & Nel, J.A.J. 1995. Comparative behaviour and ecology of two sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). *S. Afr. J. Zool.* **30**: 46–49.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., MacColl, A.D.C., Kinsky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. 1999. Predation group size and mortality in a co-operative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* **68**: 672–683.
- Croze, H. 1970. Searching image in Carrion Crows. *Z. Tierpsychol.* **5**: 1–86.
- Dixon, J. & Louw, G. 1978. Seasonal effects on nutrition, reproduction and aspects of thermoregulation in the Namaqua Sandgrouse (*Pterocles namaqua*). *Madoqua* **11**: 19–29.
- Graul, W.D. 1975. Breeding biology of the Mountain Plover. *Wilson Bull.* **87**: 6–31.
- Gregg, M.A., Crawford, J.A., Drut, M.S. & DeLong, A.K. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. *J. Wildl. Manage.* **58**: 162–166.
- Hill, D.A. 1984. Factors affecting nest success in the Mallard and Tufted Duck. *Ornis Scand.* **15**: 115–122.
- Hockey, P.A.R. 1982. Adaptiveness of nest-site selection and egg coloration in the African Black Oystercatcher *Haematopus moquini*. *Behav. Ecol. Sociobiol.* **11**: 117–123.
- Hoffmann, T. 1996. Nama Karoo biome. In Low, A.B. & Rebelo, A.G. (eds) *Vegetation of South Africa, Lesotho and Swaziland*: 52–57. Pretoria: Department of Environmental Affairs and Tourism.
- Howard, P. 1995. The ethology, sociology and interspecific interactions of the Yellow Mongoose *Cynictis penicillata* in the Karoo. Unpublished MSc thesis, University of Pretoria, Pretoria.
- Howlett, J.S. & Stutchbury B.J. 1996. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. *Auk* **113**: 1–9.
- Kelly, J.P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodland. *Condor* **95**: 83–93.
- Lloyd, P., Little, R.M. & Crowe, T.M. in press a. The breeding biology of the Namaqua Sandgrouse *Pterocles namaqua*. *Ostrich*.
- Lloyd, P., Little, R.M. & Crowe, T.M. in press b. Investigator effects on the nesting success of arid-zone birds. *J. Field Ornithol.*
- Maclean, G.L. 1968. Field studies on the sandgrouse of the Kalahari Desert. *Living Bird* **7**: 209–235.
- Maclean, G.L. 1970. The biology of the larks (Alaudidae) of the Kalahari sandveld. *Zool. Afr.* **5**: 7–39.
- Martin, T.E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evol. Ecol.* **2**: 37–50.

- Martin, T.E. & Clobert, J.** 1996. Nest predation and avian life-history evolution in Europe versus North America: a possible role of humans. *Am. Nat.* **147**: 1028–1046.
- Martin, T.E. & Roper, J.R.** 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* **90**: 51–57.
- Marzluff, J.M.** 1988. Do Pinyon Jays alter nest placement based on prior experience? *Anim. Behav.* **36**: 1–10.
- Moller, A.P.** 1988. Nest predation and nest-site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. *Oikos* **53**: 215–221.
- Osborne, P. & Osborne, L.** 1980. The contribution of nest-site characteristics to breeding-success among Blackbirds *Turdus merula*. *Ibis* **122**: 512–517.
- Owen, D.F. & Whiteley, D.** 1986. Reflexive selection: Moment's hypothesis resurrected. *Oikos* **47**: 117–120.
- Preston, F.W.** 1957. Pigmentation of eggs: variation in the clutch sequence. *Auk* **74**: 28–41.
- Ricklefs, R.E.** 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* **9**: 1–48.
- Rivera-Milán, F.F.** 1996. Nest density and success of columbids in Puerto Rico. *Condor* **88**: 100–113.
- Schieck, J.O. & Hannon, S.J.** 1993. Clutch predation, cover, and the overdispersion of nests of the Willow Ptarmigan. *Ecology* **74**: 743–750.
- Shrank, B.W.** 1972. Waterfowl nest cover and some predation relationships. *J. Wildl. Manage.* **36**: 182–186.
- Smithers, R.H.N.** 1983. *The Mammals of the Southern African Sub-region*. Pretoria: University of Pretoria.
- Tinbergen, L.** 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. *Arch. Neerl. Zool.* **13**: 265–343.
- Tomkins, I.R.** 1944. Wilson's Plover in its summer home. *Auk* **61**: 259–269.
- Vickery, P.D., Hunter, M.L. & Wells, J.V.** 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* **63**: 281–288.
- With, K.A. & Webb, D.R.** 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. *Condor* **95**: 401–413.

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