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# Variation in nest predation among arid-zone birds

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I examined the nesting habits and success of 11 co-existing species in an arid, sub-tropical habitat in South Africa. Nesting success ranged from 3.5% to 75.4% among species, with predation by mammals and snakes accounting for 94% of nest losses. Differences in predator avoidance behaviour (deserting the nest vs sitting tight) may explain markedly different daily nest predation risk experienced by the Double-banded Courser *Rhinoptilus africanus* (0.5%) and Namaqua Sandgrouse *Pterocles namaqua* (9.2%). Nest predation was inversely related to nest density, but this reverse density dependence may reflect a seasonal effect, as predation decreased as the breeding season progressed from spring to mid-summer. Overall, daily egg predation rates were higher than daily nestling predation rates among nine altricial species, contrary to the widely-held view that increased activity at the nest during the nestling period increases predation risk. The prediction of higher daily nest predation rates on ground-nesting species than on shrub/tree-nesting species in an open habitat was supported. Among ground-nesting species, territorial residents suffered significantly lower daily nest predation rates than nomads, suggesting that residents may use experience of local predator activity to place their nests in safer sites.

## Introduction

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

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

Research on the modification of predation risk by parental behaviour has focused on active nest defence behaviours, such as distraction displays and attack (see reviews by Montgomerie and Weatherhead 1988 and Martin 1992), with little attention to passive, predator avoidance behaviours. Nest predation has also been linked to variation in a number of life history traits, including clutch size (Slagsvold 1982, Martin 1995, Martin and Clobert 1996, Julliard *et al.* 1997) and rate of development (Martin 2002, Remeš and Martin 2002). A trait that has received little attention in relation to nest predation is that of residency vs migration or nomadism. Birds that are year-round residents on fixed territories could be expected to develop detailed knowledge of nest-predator activity within their territories. Such birds could be expected to place their nests in safer sites, when compared to migrant or nomadic birds that spend less time within the area selected for nesting. The suggestion that migrants or nomads might benefit from a predator swamping effect (e.g. Welty 1982: 553) is not well supported (e.g. Summers and Underhill 1987).

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

This study examined nest predation rates among a variety of species in relation to nest site, nest density, predator

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

## Methods

The study was conducted over four early-summer seasons (August–December 1993–1996) in an area of 10 000ha on the farm Droëgrond (29°07'S, 20°16'E), Northern Cape Province, South Africa. A description of study site attributes is given elsewhere (Lloyd 1999). Intra-seasonal variation in nest predation and nest density was examined for the 1996 season only, when two exceptional cold-front rainfall events (53.5mm on 23–25 July, and follow-up rains of 77.5mm on 7–8 November) stimulated an influx of nomadic species, particularly sparrowlarks, and intense breeding activity among all species present (Lloyd 1999). Nests of 13 species were found randomly through the nesting period, either by flushing birds while cycling through the study area or, in the case of Namaqua Sandgrouse *Pterocles namaqua*, by following birds flying to the nest to relieve their mates. Nests were visited at intervals of 1–6 days: precocial species were visited the most frequently. A parallel study found that frequent nest visits did not affect nest predation rates (Lloyd *et al.* 2000a). Predation was assumed to have occurred when eggs or nestlings (too young to fledge) disappeared. Identification of nest predators was attempted for only the Namaqua Sandrouse (whose nests were generally visited on a daily basis) and Chat Flycatcher. The Rhombic Egg-eating Snake *Dasypeltis scabra*, which feeds exclusively on birds' eggs, was identified as the predator when crushed shells were found near the nest and/or when eggs disappeared one at a time. Small mammals were identified either by their tracks in the sandy substrate, or their habit of biting a chunk out of the side of the egg. Larger mammals were identified by their tracks alone. There were no avian nest predators 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 nests found at the nestling stage.

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

success = (1 – [losses/exposure])$^{np}$

where *exposure* is the total number of active nest days, and *np* is the period in the nesting cycle being considered.

Overall nesting success (at least one precocial chick hatching or one altricial nestling fledging) was calculated as the product of success during the laying and incubation periods combined, and the nestling period. The variance of Mayfield's estimator was derived from the expression:

([exposure – losses] x losses)/([exposure]$^3$)

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

The original nest records (in the collection of the Nest Record Card Scheme at the Avian Demography Unit, University of Cape Town) of Maclean (1967, 1968, 1970a, 1970b) from the Kalahari Gemsbok National Park (KGNP) (now Kgalagadi Transfrontier Park), 300km to the north of the present study site, were re-analysed using the Mayfield method for comparison with the present study. Maclean's nests were not visited frequently enough to determine separate incubation- and nestling-stage predation rates, so overall daily nest predation rates were calculated.

When determining the length of the incubation or nestling periods, the laying of the last egg or fledging of the last chick was assumed to have occurred midway between two visits no more than two days apart. While the calculated periods for individual nests are therefore subject to some error, the species' average is considered a reasonable approximation (cf. Mayfield 1975).

For ground-nesting species, the following characteristics were recorded for each nest site for a random sample of nests of each species in 1996: (a) a subjective estimate of nest camouflage evaluated as the degree to which the rim of the nest matched its immediate surroundings (1 = poor, 2 = fair, 3 = good, 4 = excellent), (b) the proportion of the nest edge concealed by objects at the nest edge greater than the height of the incubating bird (0%, 1–25%, 26–50%, 51–75% or 76–100%), (c) the dominant substratum around the nest (1 = sand alone, 2 = sand with pebbles or scattered stones, or pebbles alone, 3 = pebbles with scattered stones, 4 = stones/rocks with pebbles), and (d) the number of objects >3cm high within a 1m radius of the nest. The substratum codes served as an index of complexity of the nest environment. The object totals served as an index of both complexity and cover around the nest.

Rainfall was measured at a rain-gauge located centrally in the study site. Daily average temperatures were obtained from the weather station at Upington, 120km to the north-east of the study site but which experiences similar weather conditions. Statistical comparisons were performed using SPSS software.

## Results

### Nest site
Species-specific breeding data of the various species studied at Droëgrond are summarised in Table 1. Nest site characteristics are summarised in Tables 1 and 2. Several ground-nesting species sited their nests on the southern to eastern side of small plants to gain some shade during the heat of the day. Lark-like Bunting *Emberiza impetuani* nested in more concealed situations than the other species; there were more objects within 1m of the nest and a greater proportion of the nest edge was concealed (Table 2). This species' nests were, however, among the easiest to locate, being predictably sited in rocky habitat and along road verges. Furthermore, the substantial rim of twigs of most nests did not often match the general substratum of sand, pebbles and stones.

**Table 1:** Summary of nesting parameters of species nesting at Droëgrond (1993–1996). Average incubation (inc.), nestling (nslg.) and nesting (nest — includes laying, incubation and nestling) periods (prd) were calculated to the nearest half-day. Hatching success (Hatch %) was the percentage of eggs surviving to hatch that hatched. Overall nesting success (Nest succ.) was calculated as the product of success during the laying/incubation and nestling periods, using the method of Mayfield (1975) and mortality rates summarised in Table 3. Nestling deaths from the rains of 7–8 November 1996 were excluded from the nest success calculations. Fledging success (Fledg. succ.) is the average number of young fledging per successful nest

| Species | Nest site and nest type | Avg. clutch size ± SD range (n) | Avg. inc. prd (n) | Avg. nslg. prd (n) | Avg. nest. prd | Hatch % (n eggs) | Nest succ. (%) | Fledg. succ. ± SD (n) |
|---|---|---|---|---|---|---|---|---|
| Double-banded Courser[1] | ground — no nest exposed in open terrain | 1 ± 0 (12) | 28.0 (1) | – | 28.0 | 75.4 | 1 | |
| Namaqua Sandgrouse[2] | ground — shallow scrape exposed in open terrain | 2.88 ± 0.33 2–3 (224) | 21.0 (2) | – | 25.0 | 94 (173) | 8.2 | 2.76 ± 0.50 (59) |
| Spike-heeled Lark[3] | ground — sunken cup S-E of small plant | 2.70 ± 0.66 2–4 (46) | 13.0 (4) | 11.0 (2) | 25.5 | 92 (63) | 22.1 | 2.55 ± 0.69 2.55 (11) |
| Sclater's Lark[4] | ground — sunken cup exposed in bare patch | 1 ± 0 (34) | 11.0[a] | 11.5 (9) | 22.5 | 80 (25) | 19.8 | 1 |
| Grey-backed Sparrowlark[5] | ground — sunken cup S-E of small plant | 2.72 ± 0.62 1–5 (245) | 9.6 (15) | 8.9 (22) | 20.0 | 86 (365) | 23.4 | 2.31 ± 0.79 (71) |
| Black-eared Sparrowlark[6] | ground — sunken cup S-E of small plant | 2.67 ± 0.51 1–4 (113) | 10.2 (7) | 8.6 (16) | 21.0 | 87 (182) | 31.4 | 2.17 ± 0.70 (41) |
| Tractrac Chat[7] | ground — sunken cup S-E of small plant | 3 ± 0 (6) | 14.0[b] | 16.0[b] | 32.0 | | 26.0 | 3 ± 0 (4) |
| Lark-like Bunting[8] | ground — sunken cup S-E of object, concealed | 3.26 ± 0.69 2–5 (23) | 12.5[b] | 12.5[b] | 27.5 | 85 (41) | 3.5 | 2.33 ± 1.15 (3) |
| Rufous-eared Warbler[9] | shrub — closed oval mean ht 0.6m (0.1–1.5m) | 4.67 ± 1.00 4–7 (9) | 11.5[b] | 12.0[b] | 27.0 | | 44.6 | 3.75 ± 0.96 (4) |
| Chat Flycatcher[10] | shrub — open cup mean ht 1.0m (0.5–1.8m) | 3 ± 0 (15) | 14.0[b] | 12.0[b] | 28.0 | 93 (29) | 24.8 | 1.91 ± 0.83 (11) |
| Cape Sparrow[11] | shrub — closed ball mean ht 1.9m (1.5–2.5m) | 4.38 ± 1.15 2–7 (16) | 13.0[b] | 19.0[b] | 35.5 | | 19.8 | 3.00 ± 1.31 (8) |

[a] Calculated (cf. Mayfield 1975) as twice the mean incubation before hatching for nests found randomly through the incubation period (n = 20)
[b] From Maclean (1993)
Species: [1] *Rhinoptilus africanus*, [2] *Pterocles namaqua*, [3] *Chersomanes albofasciata*, [4] *Spizocorys sclateri*, [5] *Eremopterix verticalis*, [6] *E. australis*, [7] *Cercomela tractrac*, [8] *Emberiza impetuani*, [9] *Malcorus pectoralis*, [10] *Melaenornis infuscatus*, [11] *Passer melanurus*

**Table 2:** Nest site characteristics of ground-nesting species at Droëgrond in 1996, summarised as the percentage of nests within each sub-stratum, camouflage and concealment category, with the number of objects within a 1m radius of the nest and the distance to the closest shrub >50cm high. Sub-stratum codes: 1 = sand alone, 2 = sand with pebbles or scattered stones, or pebbles alone, 3 = pebbles with scattered stones, 4 = stones/rock with pebbles. Camouflage codes (the degree to which the rim of the nest matched its immediate surroundings): 1 = poor, 2 = fair, 3 = good, 4 = excellent. Concealment is given as the proportion of the nest-edge concealed by objects greater than the height of the incubating bird

| Species (n nests) | Substratum | | | | Camouflage | | | | Concealment (%) | | | | | Objects |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | 0 | 1–25 | 26–50 | 51–75 | 76–100 | Mean ± SD |
| Double-banded Courser (5) | 0 | 80 | 20 | 0 | | | | | 100 | 0 | 0 | 0 | 0 | 2 ± 2 |
| Namaqua Sandgrouse (20) | 30 | 10 | 50 | 10 | | | | | 35 | 50 | 15 | 0 | 0 | 19 ± 13 |
| Spike-heeled Lark (30) | 50 | 33 | 17 | 0 | 7 | 13 | 50 | 30 | 0 | 77 | 17 | 7 | 0 | 10 ± 8 |
| Sclater's Lark (10) | 0 | 40 | 60 | 0 | 0 | 10 | 0 | 90 | 90 | 10 | 0 | 0 | 0 | 5 ± 3 |
| Black-eared Sparrowlark (105) | 41 | 37 | 22 | 0 | 1 | 7 | 37 | 55 | 0 | 83 | 16 | 1 | 0 | 13 ± 10 |
| Grey-backed Sparrowlark (242) | 33 | 42 | 22 | 3 | 0 | 5 | 31 | 64 | 0 | 86 | 13 | 1 | 0 | 14 ± 14 |
| Lark-like Bunting (29) | 33 | 3 | 40 | 23 | 60 | 13 | 13 | 13 | 0 | 0 | 50 | 41 | 9 | 32 ± 17 |

Both Namaqua Sandgrouse and Double-banded Courser *Rhinoptilus africanus* nested in the same, open habitats, but their nest micro-environments differed to a subtle extent. Whereas Namaqua Sandgrouse generally placed their nests within a local concentration of objects, most of them less than 15cm high, Double-banded Coursers nested in more exposed situations with fewer objects within a 1m radius of the nest (Table 2).

**Predator avoidance strategy**

Predator avoidance strategies were characterised for only the Double-banded Courser and Namaqua Sandgrouse, and are based largely on the birds' reactions to the approach of a human observer. The incubating Double-banded Courser ran rapidly off the nest 30–100m in advance of an observer, and it was rare for the observer to pinpoint the location of the nest from the movement of the bird even dur-

ing a rapid approach on a bicycle. The non-incubating member of the pair usually remained in the vicinity of the nest, acting as both a sentinel and a decoy. Incubating Namaqua Sandgrouse either walked slowly off the nest in a skulking fashion in advance, or sat motionless, flushing directly off the nest at close range (3–5m). The non-incubating member of the pair never remained in the vicinity of the nest.

## Nest predators

Predation accounted for 93.9% of all complete nest losses (n = 588 failed nests), excluding the losses due to the rains of 7–8 November 1996, which are considered separately below. The identity of nest predators was determined most accurately for Namaqua Sandgrouse (Lloyd *et al*. 2001). Mammalian predators accounted for 80.4% of sandgrouse nest losses, with small mammals, mainly the diurnal Yellow Mongoose *Cynictis penicillata*, Cape Grey Mongoose *Galerella pulverulenta* and Suricate *Suricata suricatta*, and the nocturnal Striped Polecat *Ictonyx striatus*, taking nearly eight times as many nests as nocturnal larger mammals, which included Bat-eared Fox, Cape Fox *Vulpes chama*, Aardwolf *Proteles cristatus* and Aardvark *Orycteropus afer* (Lloyd *et al*. 2001). Egg predators are assumed to be similar for the other ground-nesters, but snakes might take an appreciable proportion of the nestlings of altricial species (see below).

There was definite evidence of mammal predation (displaced or torn nests) in only 7% of predation losses among shrub-nesting species. The blue egg shells of the Chat Flycatcher *Melaenornis infuscatus* were easier to locate than those of the other species and, of 10 nests with eggs lost to predation, definite evidence of Rhombic Egg-eating Snake predation (crushed egg shells on the ground under the nest shrub) was found at seven of them, with two others probably suffering a similar fate. The eggs of other shrub-nesters usually disappeared without disturbance to the nest. I therefore view this specialist snake as the principal egg predator of shrub-nesting species. The egg-eater was also responsible for 13–44% of annual predation on the nests of Namaqua Sandgrouse over four years (Lloyd *et al*. 2001). Eggs and nestlings usually disappeared from ground nests without disturbance signs, so predators could not be identified. In addition to the mammals listed above, a variety of

snakes (Cape Cobra *Naja nivea*, Horned Adder *Bitis caudalis*, Namib Tiger Snake *Telescopus beetzii* and Namib Sand Snake *Psammophis leightoni*) were all observed on the study site and are likely important predators of nestlings.

## Nest predation rates

Daily nest predation rates varied dramatically among co-existing species, ranging from 0.50% to 10.98% (Table 4), resulting in nesting success ranging from 3.5% to 75.4% (Table 1). With the exception of Tractrac Chat *Cercomela tractrac* and Rufous-eared Warbler *Malcorus pectoralis*, daily egg predation rates were higher than daily nestling predation rates for the nine species examined (Table 3). Comparisons were statistically significant for only three species: Sclater's Lark *Spizocorys sclateri*, Black-eared Sparrowlark *Eremopterix australis* and Chat Flycatcher. However, a combined probabilities test (Sokal and Rohlf 1995) indicated that daily egg predation was greater than daily nestling predation among all species combined (P < 0.001).

Daily nest predation rates at Droëgrond were not significantly different from those on the same species in the Kalahari Gemsbok National Park (Wilcoxon paired-sample test: $t_{(2),9}$ = –0.01, P > 0.9; see Table 4). Daily nest predation rates were significantly higher on ground-nesting species than on shrub/tree-nesting species (Mann-Whitney $U$-test: $U_{(1)9,9}$ = 16, P = 0.031; Table 4). Among ground-nesting species, daily nest predation rates were significantly higher on nomads than on territorial residents ($U_{(1)4,5}$ = 0, P = 0.016). There were no true nomads among the shrub-nesting species, but a distinction was made between species occupying territories, and non-territorial species that undertake irregular local movements (ranging species). Daily predation rates were not significantly higher on ranging shrub-nesters than on territorial shrub-nesters ($U_{(1)4,5}$ = 8, P = 0.6).

Excluding week seven as an anomaly, the overall daily nest predation rate decreased through the 1996 season ($F_{10}$ = 10.8, P = 0.009), as average daily temperature rose through spring to summer (Figure 1). Exceptionally high nest predation during week seven occurred in the days after 48 hours of soaking rains also resulted in high nestling mortality from exposure (see under 'Other mortality' below). Nest density increased to an initial peak in weeks four to five, and

**Table 3:** Comparison of daily predation rates during egg (laying and incubation) and nestling periods among species at Droëgrond. Overall, daily egg predation was higher than daily nestling predation (combined probabilities test P < 0.001)

| Species (n nests) | Daily egg predation ± SE (%) | Daily nestling predation ± SE (%) | Egg vs nestling predation Z | P value |
|---|---|---|---|---|
| Double-banded Courser (12) | 0.50 ± 0.50 | – | | |
| Namaqua Sandgrouse (278) | 9.19 ± 0.65 | – | | |
| Spike-heeled Lark (55) | 6.63 ± 1.23 | 3.89 ± 1.44 | 1.447 | 0.075 |
| Sclater's Lark (46) | 8.72 ± 1.96 | 2.19 ± 1.08 | 2.910 | 0.002 |
| Grey-backed Sparrowlark (368) | 7.23 ± 0.63 | 5.79 ± 0.74 | 1.485 | 0.069 |
| Black-eared Sparrowlark (159) | 6.38 ± 0.87 | 3.34 ± 0.73 | 2.668 | 0.004 |
| Tractrac Chat (12) | 3.20 ± 2.23 | 5.04 ± 2.84 | 0.511 | 0.305 |
| Lark-like Bunting (35) | 11.93 ± 2.44 | 9.04 ± 3.05 | 0.740 | 0.230 |
| Rufous-eared Warbler (13) | 1.56 ± 1.10 | 4.65 ± 2.62 | 1.087 | 0.140 |
| Chat Flycatcher (26) | 6.86 ± 2.50 | 1.57 ± 0.99 | 2.026 | 0.022 |
| Cape Sparrow (27) | 6.04 ± 1.95 | 3.06 ± 1.35 | 1.258 | 0.106 |

**Table 4:** Daily nest predation rates compared among species, nest sites (ground or shrub) and degrees of residency (resident, nomadic, ranging). D = Droëgrond, K = Kalahari Gemsbok National Park. Where daily nest predation rates on a species were calculated separately for the two sites, the average of the two values is given on the third line

| Species | Nests | Nest days | Daily nest predation ± SE (%) | | | |
|---|---|---|---|---|---|---|
| | | | Resident, ground | Nomadic, ground | Resident, shrub | Ranging, shrub |
| Double-banded Courser | 12 | D199.5 | (0.50 ± 0.50) | | | |
| | 45 | K475.0 | (0.84 ± 0.42) | | | |
| | | | 0.67 | | | |
| Fawn-coloured Lark[1] | 12 | K106.0 | 3.77 ± 1.85 | | | |
| Spike-heeled Lark | 55 | D587.0 | (5.79 ± 0.96) | | | |
| | 28 | K250.5 | (4.39 ± 1.29) | | | |
| | | | 5.09 | | | |
| Tractrac Chat | 12 | D122.0 | 4.10 ± 1.79 | | | |
| Sclater's Lark | 46 | D389.0 | | 5.66 ± 1.17 | | |
| Namaqua Sandgrouse | 278 | D1 980.5 | | (9.19 ± 0.65) | | |
| | 32 | K149.0 | | 4.70 ± 1.73) | | |
| | | | | 6.95 | | |
| Pink-billed Lark[2] | 42 | K326.0 | | 6.44 ± 1.36 | | |
| Grey-backed Sparrowlark | 368 | D2 700.0 | | (6.70 ± 0.48) | | |
| | 129 | K736.5 | | (8.96 ± 1.05) | | |
| | | | | 7.83 | | |
| Black-eared Sparrowlark | 159 | D1 383.5 | | (5.06 ± 0.59) | | |
| | 47 | K334.0 | | (6.89 ± 1.39) | | |
| | | | | 5.98 | | |
| Lark-like Bunting | 35 | D264.5 | | (10.98 ± 1.92) | | |
| | 33 | K297.5 | | (6.39 ± 1.42) | | |
| | | | | 8.69 | | |
| Rufous-eared Warbler | 13 | D192.5 | | | (2.60 ± 1.15) | |
| | 21 | K251.0 | | | (4.38 ± 1.29) | |
| | | | | | 3.49 | |
| Chat Flycatcher | 26 | D242.0 | | | (3.69 ± 1.22) | |
| | 22 | K173.5 | | | (4.03 ± 1.49) | |
| | | | | | 3.86 | |
| Chestnut-vented Titbabbler[3] | 12 | K110.5 | | | 0.91 ± 0.90 | |
| Black-chested Prinia[4] | 20 | K206.0 | | | 1.46 ± 0.83 | |
| Scaly-feathered Finch[5] | 30 | D+K419.0 | | | | 2.15 ± 0.71 |
| Cape Turtle Dove[6] | 9 | K66.0 | | | | 3.03 ± 2.11 |
| Yellow Canary[7] | 17 | D+K125.5 | | | | 3.19 ± 1.57 |
| Cape Sparrow | 27 | D312.5 | | | | (4.48 ± 1.17) |
| | 27 | K257.5 | | | | (8.54 ± 1.74) |
| | | | | | | 6.51 |
| Namaqua Dove[8] | 20 | K226.0 | | | | 2.65 ± 1.07 |
| Means | | | 3.41 ± 1.38 | 6.92 ± 1.07 | 2.27 ± 1.46 | 3.51 ± 1.73 |

Species: [1] *Mirafra africanoides*, [2] *Spizocorys conirostris*, [3] *Parisoma subcaeruleum*, [4] *Prinia flavicans*, [5] *Sporopipes squamifrons*, [6] *Streptopelia capicola*, [7] *Serinus flaviventris*, [8] *Oena capensis*

then decreased until the rain event in week seven stimulated a second flush of nesting, whereafter nest density increased steadily until the end of the study (Figure 1). In a multiple regression (forward stepwise) setting daily nest predation rate as the dependent variable, and week, mean daily temperature and nest density as three independent variables, only nest density entered the model. Daily predation rate was inversely related to nest density (Figure 2).

The co-efficient of inter-annual variation in nest predation was low (3.9–15.1% within species) in comparison with variation in rainfall over the study period (51.3%: Table 5).

**Other mortality**

Following soaking rains on 7–8 November 1996 (77mm in 48 hours), 58.8% and 42.9% of all nestlings (n = 102 and 49 respectively) of Grey-backed and Black-eared Sparrowlarks died (Lloyd 1999). This is much higher mortality than nestling mortality from other causes, respectively 6.9% (n = 101 hatchlings) and 8.7% (n = 69 hatchlings) for these two species. Of 14 sparrowlark nests with eggs at the time of the November rains, three were destroyed by flooding and 11 survived, although four of the latter were later abandoned.

**Discussion**

**Nest site and degree of residency**
Predation has been reported as greater on ground-nesting species than on open-nest, aboveground-nesting species in
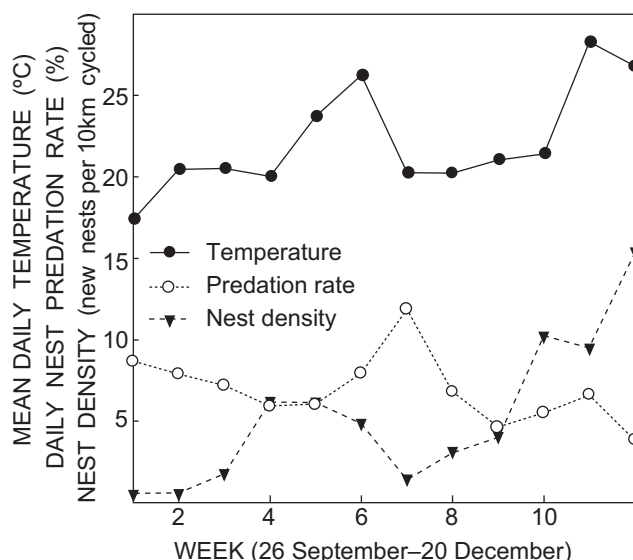
**Figure 1:** Mean daily temperature (°C), daily nest predation rate (%) for nests of all species combined, and nest density (new nests found per 10km cycled) for all species combined during weeks 1–12 (26 September to 20 December) through the 1996 breeding season at Droëgrond. Total distance cycled was 1 788km. Soaking rains (77mm in 48h) fell at the start of week seven



**Figure 2:** Daily nest predation rate (for nests of all species combined) correlated negatively with nest density through the 1996 breeding season at Droëgrond

shrub and grassland habitats, but lower in forest habitats (Martin 1993). The results of the present study support this pattern (Table 4). In addition, the limited data support the prediction of higher nest predation among nomadic ground-nesters when compared to resident ground-nesters, but not in the comparison of ranging and resident shrub-nesters (Table 4). Sample sizes were small, and the analyses did not control for the effects of phylogenetic independence. It would therefore be useful to pursue more rigorously the hypothesis that long-term residency (which could be equated with experience of predator activity in the nest environs) enhances nest survival.

**Predator avoidance behaviour**
A comparison of the predation rates on nests of the Double-banded Courser and Namaqua Sandgrouse illuminate the potential influence of predator avoidance behaviours. These two precocial species of equivalent body size with very similar nesting sites have contrasting predator avoidance behaviours — the Double-banded Courser deserts the nest well in advance of a predator's approach, whereas the Namaqua Sandgrouse tends to sit tight, flushing directly off the nest at close range. Both species nest in exposed situations, but to subtly different degrees, which may relate to their contrasting predator avoidance behaviours. The Namaqua Sandgrouse places its nest adjacent to several low objects, presumably to interrupt the outline of a bird crouching on the nest (Lloyd et al. 2000b, see also Table 2). The Double-banded Courser preferred even greater exposure (see Table 2), possibly to increase its field of view for the early detection of an approaching predator, and thus enhance the effectiveness of its strategy of abandoning the
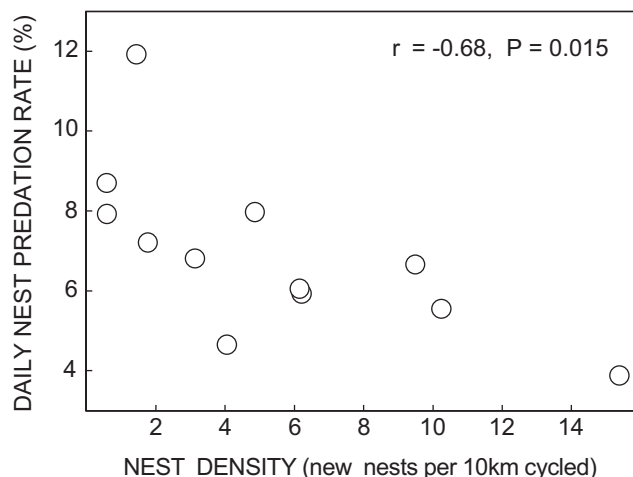
nest. Maclean (1967) noted that all Double-banded Courser nests were sited for clear, all-round horizontal visibility. The incubating courser was assisted by its mate, which usually remained in the general vicinity of the nest, and acted as a sentinel (Maclean 1967, pers. obs.). The prevailing predator-avoidance behaviour of the Namaqua Sandgrouse is to sit tight on the nest during the approach of a predator, relying on its cryptic plumage to avoid visual detection (Maclean 1968, pers. obs.). Three separate observations of the close approach of a small-to-medium-sized mammal to a Namaqua Sandgrouse nest suggest that this species remains on the nest, flushing at a minimum distance of 2m from a predator (Maclean 1968, pers. obs.). Maclean (1968) observed how a Bat-eared Fox *Otocyon megalotis* trotting past a sandgrouse nest used the flushing bird as a cue to locate the eggs. Nest predation rates differed markedly between these two species (Table 4), which I suggest is due largely to the different predator-avoidance behaviours they employ.

Using a predator simulation model, Lloyd et al. (2000b) suggested that it was possible for the high levels of predation experienced by Namaqua Sandgrouse to be largely incidental in nature, if predators use the close-range flushing of the incubating bird as a cue for nest location. It follows that if the incubating bird is able to leave the nest undetected, the predator's nest-detection path width would be narrowed severely, since it could no longer rely on the flushing bird as a cue, and would have to rely on visual and/or olfactory cues from the eggs alone. This possibly explains the lower predation levels the Double-banded Courser experienced, although the potentially greater crypsis of a single egg (Croze 1970) could be a contributing factor. These hypotheses could be more rigorously tested through experimental manipulations on each of the two species.

**Egg and nestling predation**
Despite the increased activity at nests with nestlings, daily predation rates on nestlings were generally lower than those

**Table 5:** Annual rainfall, with percent nest predation (1st line) and success (2nd line, exposure in nest days in brackets), and their co-efficients of variation (CV) for species with sufficient data spanning more than one year at Droëgrond

| Year | 1993 | 1994 | 1995 | 1996 | CV (%) |
|------|------|------|------|------|--------|
| Rainfall (mm) | 83.0 | 126.8 | 75.2 | 214.8 | 51.3 |
| Namaqua Sandgrouse | 85.20 | 91.58 | 90.54 | 93.49 | 3.94 |
| | 13.52 | 7.61 | 9.46 | 5.71 | 36.75 |
| | (299.0) | (1 369.0) | (100.0) | (212.5) | |
| Spike-heeled Lark | | 74.69 | | 79.99 | 4.85 |
| | | 21.97 | | 18.67 | 11.48 |
| | | (187.0) | | (400.0) | |
| Sclater's Lark | 60.84 | | 80.96 | 79.11 | 15.10 |
| | 22.50 | | 11.58 | 20.89 | 32.17 |
| | (171.5) | | (98.5) | (119.0) | |

on eggs of the altricial species (Table 3). Three potential factors could explain this result. Firstly, adults spend less time brooding nestlings than they do incubating eggs, which likely leads to a lower probability of a predator flushing an adult from the nest, and using this behaviour as a cue to nest location. Bowen and Simon (1990) noted that no nocturnal mammal predation on Greater Prairie Chicken *Tympanuchus cupido* nests occurred during egg-laying when females were away from nests, but appreciable predation occurred during incubation, when the females were on the nest all night. If predators use similar cues, this could explain the lower predation rates on nestlings, and add further support to our idea that the absence of adults from the nest can substantially reduce predation risk. Secondly, the relative importance of different nest predators may differ between the two periods, resulting in differences in predation rates. The Rhombic Egg-eating Snake, for example, is an important egg predator, but it does not take nestlings. Thirdly, if more obvious nests are located by predators earlier (i.e. if predation is non-random), a trend of decreasing predation rate over the length of the nesting period is expected (Martin *et al.* 2000). Such a pattern would result in lower predation during the nestling period than the incubation period.

## Nest density

Predation rates at our study site exhibited an inverse relationship with nest density (Figure 2), but nest density *per se* is probably not the primary factor determining this relationship. Predation rates also decreased as the season progressed from spring to mid-summer (Figure 1). A similar decrease in predation through the breeding season was observed among Namaqua Sandgrouse during the 1994 season (Lloyd *et al.* 2001), and has been noted in several other studies, where it has been attributed to changes in the behaviour, diet, density or species of predators (Nolan 1963, Newton 1964, Roseberry and Klimstra 1970, Gottfried 1978). The most plausible explanation for decreasing predation rates through the season in our study area is an increasing availability of alternative food for the principal nest predators. The only specialist nest predator was the Rhombic Egg-eating Snake, and snakes do not appear to respond to nests as prey in a density-dependent manner (Best 1978, Gottfried 1978, Gottfried and Thompson 1978). Although the recorded mammalian predators are general-

ists, if not opportunists, the bulk of their respective diets consists of arthropods (Smithers 1983). Arthropod abundance was not measured in this study, but is known to increase in summer and after appreciable rainfall in seasonal and arid environments (Louw and Seely 1982). If nest predation by these generalist predators is largely incidental (e.g. Vickery *et al.* 1992, Howlett and Stutchbury 1996, Lloyd *et al.* 2000b), then predation rates are expected to decrease as general food abundance increases.

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