

The influence of nest-site characteristics on the nesting success of the Karoo Prinia (*Prinia maculosa*)

Dianah Nalwanga¹, Penn Lloyd^{1,2*}, Morné A du Plessis¹ and Thomas E Martin²

¹ Percy FitzPatrick Institute of African Ornithology (DST/NRF Centre of Excellence), University of Cape Town, Rondebosch 7701, South Africa

² Montana Co-operative Wildlife Research Unit, University of Montana, Missoula MT 59812, United States of America

* Corresponding author, e-mail: plloyd@botzoo.uct.ac.za

Choice of nest site has important consequences for nest survival. We examined nest-site characteristics relative to nest success in Karoo Prinias breeding in coastal dwarf shrubland, where high nest predation is the main cause of nest failure. Initially, we compared nests that failed during the building, laying, incubation and nestling stages and those from which young were successfully raised, to test whether nests that survived to progressive stages in the nesting cycle differed in their nest-site characteristics. Subsequently, we compared the characteristics of successful nests with those of unsuccessful nests. The nest-site characteristics considered included nest height, nest-plant height, nest-plant species, distance from lateral foliage edge, nest concealment, nest-patch heterogeneity and vegetation cover at four different heights. We were unable to distinguish between the nest-site characteristics of nests that failed during the various stages of the nesting cycle. Concealment was the main nest-site characteristic that differentiated successful nests from unsuccessful nests, with successful nests being located in more concealed sites. The other variables that contributed to the discrimination between successful and unsuccessful nests by discriminant function analysis included nest-plant type and distance from edge, which are also directly related to concealment. This suggests that nest concealment is the most important variable influencing nesting success at this site, which has a preponderance of visually-oriented predators.

Introduction

Nest predation is the major cause of reproductive loss in birds (Ricklefs 1969, Berry 2001) and is considered a strong selective force in nest-site selection (Martin 1988, 1998, Lloyd *et al.* 2000). Most birds have a wide variety of potential nest sites to select from (Sakai and Noon 1991) and commonly select sites that reduce the probability of clutch predation. Features of nest sites that may affect success include nest concealment, nest site complexity and nest height or accessibility to different predators (Weidinger 2002).

Several studies have suggested that increased concealment in the immediate vicinity of the nest reduces the probability of nest predation (Kelly 1993, Götmark *et al.* 1995, Cresswell 1997). However, some studies have not found a direct relationship between concealment and probability of survival (Best and Stauffer 1980, Holway 1991, Filliater *et al.* 1994, Ford 1999, Lloyd *et al.* 2000). Indeed, for some species, more conspicuous nests may allow adults better visibility, permitting them to detect and respond to predators more effectively (Ford 1999).

Identifying habitat or nesting microhabitat variables associated with higher nest success is important for our understanding of bird–habitat relationships (Kolbe and Janzen 2002). In this study, we test whether there is any relationship between characteristics of the nest microhabitat and nest success in the Karoo Prinia.

Study area and methods

Study area

The study was conducted within a 1.7 km² area in the 3 000 ha Koeberg Nature Reserve (33°41'S, 18°27'E), Western Cape Province, South Africa. It has a Mediterranean climate with hot dry summers (October–April) and cool wet winters (May–September). The vegetation is dwarf shrubland (up to 3 m tall), comprising a mosaic of Strandveld Succulent Karoo, Dune Thicket and Sand Plain Fynbos vegetation types (Low and Rebelo 1996) on a low-lying coastal plain.

The Karoo Prinia is a small warbler (9g) that defends territories throughout the year and lays a clutch of 2–5 eggs. The enclosed nest is oval-shaped, with a relatively small top-side entrance (Maclean 1993). The nest frame is composed of fine strips of green grass leaves woven together and to the supporting vegetation. The interior is then usually thickly lined with plant down, especially the white, cottony seeds of *Eriocephalus* spp. (Dean *et al.* 1990, pers. obs.). Nests are placed at 30–100 cm above ground (Maclean 1993) in spiny grasses, restios (Restionaceae) and a wide variety of shrubs (Rowan and Broekhuysen 1962). Karoo Prinias suffer high levels of nest loss (daily nest predation c. 7.4%, Lloyd and Martin unpubl. data), with greater predation on nests with eggs than nestlings (Rowan and Broekhuysen 1962). Concealment is likely to be important for the survival of Karoo Prinia nests as most of its nest predators locate nests by sight, and the bird is too small to physically defend its nest.

Direct field observation and predation events, captured on video cameras set at nests (Lloyd and Martin unpubl. data), show that the dominant nest predators at the site include at least six species of snake, together with the Cape Grey Mongoose *Galerella pulverulenta* and Pied Crow *Corvus albus*. The principal snake predators include the Rhombic Egg-eater *Dasypeltis scabra*, Boomslang *Dispholidus typus*, Mole Snake *Pseudaspis cana* and Cape Cobra *Naja nivea*. Predators of lesser importance include a variety of small rodents, and three bird species: Fiscal Shrike *Lanius collaris*; Bokmakierie *Telophorus zeylonus*; Black Harrier *Circus maurus*. With the exception of the Rhombic Egg-eater, all the dominant predators are diurnal, using largely visual cues to locate nests. The Pied Crow searches for nests by flying slowly at a height of 5–20m, using either the flushing behaviour of incubating or brooding adults or nest visibility to locate nests. The Rhombic Egg-eater is a strictly nocturnal snake that preys only on eggs, presumably using olfactory or thermal cues.

Data collection procedures

During the breeding season from August to November 2002 nests were located using parental behaviour, usually during the building stage, and monitored at 1–2 day intervals thereafter to determine nest fate. After activity at the nest had ceased, nest-site variables were measured at two spatial scales: at the nest site and in the nest patch.

Nest-site variables included: (1) nest-plant species; (2) nest height above ground; (3) nest-plant height; (4) distance of nest from lateral foliage edge; (5) nest concealment. Concealment was determined by estimating the percentage of the nest that was visible 1m from the nest at nest height in the four cardinal directions and from 1m above the nest.

Variables measured in the nest patch (defined as the area within a 5m radius of the nest) included nest-patch heterogeneity (total number of shrub species in the nest patch) and plant cover at each of four height intervals (10cm, 50cm, 100cm and ≥ 200 cm above ground). Percentage plant cover at each height interval was calculated as the average cover along eight evenly-spaced 5m radii centred on the nest. Using a 5m length of string strung between two vertical poles, percent cover was estimated as the proportion of the string that was surrounded by vegetation within 5cm at each height interval. Nest-patch heterogeneity was obtained from the total number of plant species encountered across all radii.

Data analysis

We first examined the relationship between nest-site characteristics and the length of time the nest survived. Nests were divided into five groups on the basis of whether they failed during the stages of: (1) building; (2) laying; (3) incubation; (4) the nestling period; (5) successfully fledged. We tested the prediction that nests lost to predation earlier in the nesting cycle would include a greater proportion of poorly-concealed nests than those lost later in the nesting cycle or surviving to fledge young. However, the effect of concealment may be less evident in nests that are depredated at the laying and incubation stages as many nests with eggs are taken by the nocturnal Rhombic Egg-eater snake.

We then compared the characteristics of successful nests with those of unsuccessful nests. Habitat variables were subjected to Pearson correlation analysis to reduce the number of variables. Among the nest-site variables, nest height was correlated with nest-plant height ($r = 0.75$, $P < 0.05$), so these were combined to produce a new variable, relative nest height (ratio of nest height to nest-plant height). This new variable was correlated with nest height ($r = 0.52$, $P < 0.05$) but not with nest-plant height, so nest height was excluded from analyses. Overhead concealment was expected to be an important variable with respect to aerial predation by the Pied Crow, but this was correlated with other measures of concealment ($P < 0.05$ in all cases), so we used average concealment (from four sides and overhead). All five nest-patch variables were included in the analysis.

Initially, multivariate analysis of variance (MANOVA) was used to test for differences between the five groups of nests. Thereafter, univariate analysis of variance (ANOVA) was used to test for overall differences between habitat variables for the nest sites in the five categories. A student's t-test was used to compare the nest-site habitat variables of successful vs unsuccessful nests. A chi-square test was used to compare the choice of nest-tree species between the five nest categories in the first analysis and also between the successful and the unsuccessful nests.

Stepwise Discriminant Function Analysis (SDFA) was used to search for complex differences between the nest-site habitat characteristics of successful vs unsuccessful nests. Wilks' Lambda and F-tests were used to determine the combination of variables providing the best group separation. Co-variance matrices were tested for homogeneity using Box's M criterion. The between-group matrices often showed significant heteroscedasticity ($P < 0.05$). We therefore based the SDFA on pooled within-group co-variance matrices. Mahalanobis distance (minimum D^2) between group centroids was used as the criterion for maximising separation of groups. Standardised co-efficients were obtained from SDFA to determine the partial contributions of each variable to the discriminant function, and factor structure co-efficients to determine correlation of variables with the discriminant functions. Habitat variables used in the SDFA included nest-plant height, nest-plant species (coded as dummy variables), relative nest height, nest distance from lateral foliage edge, average concealment, nest-patch heterogeneity and the average percentage vegetation cover at each of the four height intervals.

All analyses were performed using STATISTICA software version 6 (Statsoft Inc. 2002). Significance levels were set at $P < 0.05$ for all analyses. Proportions were arcsine-transformed to meet assumptions of normality.

Results

Nest-site characteristics were measured for 98 Karoo Prinia nests, 20 of which successfully raised young to fledging. A total of 26 different plant species were used as nesting substrates, listed in Appendix 1.

Comparison of nest sites for the nests in the five groups

The initial MANOVA found that the five groups of nests differed significantly with respect to their nest characteristics (Wilks' Lambda = 0.43, $F = 1.48$, $P = 0.025$). However, there was no significant difference in any of the 10 variables examined for the five categories of nests (Table 1). Although the choice of substrate types did not differ significantly among the five categories ($X^2 = 114.7$, $df = 100$, $P = 0.15$), different proportions of nests for each category were placed in the various nest-plant species (Appendix 1).

Comparisons between nest sites of successful and unsuccessful nests

Nest height, nest-plant height, relative nest height and vegetation cover at each of the four height intervals did not differ significantly between successful and unsuccessful Karoo Prinia nests (all $P > 0.05$, Table 2). Similarly, the unsuccessful vs successful groupings did not differ with respect to nest-plant species ($X^2 = 24.1$, $df = 25$, $P > 0.05$), although nests in certain species such as *Eriocephalus racemosus*, *Metalasia muricata*, *Chrysanthemoides incana*, *Olea exasperata* and *Euphorbia mauritanica* were markedly more successful (29–50% of nests in these species were successful) than those in all other 21 plant species used (success 0–17%; Figure 1). Nests placed in restios all failed within the first three stages of the breeding cycle (Appendix 1).

Average nest concealment was the only variable that differed significantly between successful and unsuccessful nests ($t = -2.14$, $P = 0.035$). Successful nests were associated with higher nest concealment (Figure 2). S DFA yielded

one significant canonical axis that differentiated successful from unsuccessful nest sites ($X^2 = 25.5$, $P = 0.002$, Mahalanobis: $F_{8,89} = 3.55$, $P = 0.002$). This axis was influenced by distance from lateral foliage edge, concealment and nest-plant species (Table 3). In general, S DFA used eight of the 10 variables (Table 3) and classified 81.6% of the nest sites correctly as belonging to either successful or unsuccessful nests, which is better than the expected classification success of a random classification of 67.5% (Table 4).

Discussion

The lack of significant differences in the nest-site characteristics of Karoo Prinia nests that survived to the five different stages of the nesting cycle (see Table 1) suggests that predation may be largely random. However, this analysis may be complicated by heavy predation by the nocturnal and presumably non-visual Rhombic Egg-eater during the laying and incubation periods. With a mix of visual and non-visual predators in such a situation, large samples of nests are likely needed to detect differences. After aggregating nests into just two groups (unsuccessful vs successful), the ANOVA found that successful nests were located in more concealed sites than unsuccessful nests (Figure 2), as one could expect in a situation where visual predators predominate. Furthermore, the S DFA suggests that the variables nest-plant type and distance from edge were important in distinguishing successful from unsuccessful nests (see Table 4). That successful nests tended to be both more concealed

Table 1: Comparison of nest-site variables (means \pm SD) among Karoo Prinia nests that failed at each of the building, laying, incubation or nestling stages, and those that were successful, with ANOVA test statistics

Nest-site variables	Building (n = 30)	Laying (n = 21)	Incubation (n = 18)	Nestling (n = 9)	Successful (n = 20)	F	P
Nest height (cm)	97.0 \pm 37	80.2 \pm 26.4	87.8 \pm 22	84.8 \pm 32.7	84.5 \pm 20.3	1.2	0.3
Nest-patch heterogeneity	5.3 \pm 1.7	5.05 \pm 1.7	5.9 \pm 1.8	4.4 \pm 0.9	4.6 \pm 1.6	2.2	0.08
Nest-plant height (cm)	129.7 \pm 52	110.8 \pm 24	121.2 \pm 36	115.1 \pm 30	128.8 \pm 27	1.0	0.4
Relative nest height	0.8 \pm 0.1	0.7 \pm 0.1	0.8 \pm 0.1	0.7 \pm 0.1	0.7 \pm 0.2	1.2	0.3
Distance from edge (cm)	54.9 \pm 46.1	56.7 \pm 60.4	50.6 \pm 46.3	55.6 \pm 24.6	33.4 \pm 35.4	0.9	0.5
Concealment (%)	46.0 \pm 26.6	47.5 \pm 23.7	35.3 \pm 30.5	38.1 \pm 25.7	58.3 \pm 22.5	1.7	0.2
Cover at 10cm (%)	67.1 \pm 14.6	71.8 \pm 14.3	68.9 \pm 14.5	69.4 \pm 16.1	63.1 \pm 16.1	0.4	0.8
Cover at 50cm (%)	56.1 \pm 21.2	59.2 \pm 20.1	60.2 \pm 18.7	57 \pm 12.6	50.7 \pm 19.5	2.1	0.08
Cover at 100cm (%)	20.4 \pm 22.3	14.4 \pm 16	17.9 \pm 21.8	24.8 \pm 25.6	15.2 \pm 13.5	0.3	0.9
Cover at 200cm (%)	1.17 \pm 4.2	0.42 \pm 1.7	1.68 \pm 7.1	6.97 \pm 20.9	1.19 \pm 5.3	0.8	0.5

Table 2: Comparison of nest-site variables (means \pm SD) among successful and unsuccessful Karoo Prinia nests, with t-test statistics for pairwise comparisons

Nest-site variables	Unsuccessful (n = 78)	Successful (n = 20)	t	P
Nest height (cm)	88.9 \pm 31.1	84.5 \pm 20.3	0.60	0.55
Patch heterogeneity	5.28 \pm 1.7	4.60 \pm 1.6	1.66	0.10
Nest-plant height (cm)	120.8 \pm 40.1	128.8 \pm 26.7	-0.83	0.41
Relative nest height	0.74 \pm 0.13	0.67 \pm 0.16	1.94	0.06
Nest distance from edge (cm)	54.5 \pm 47.9	33.4 \pm 35.4	1.84	0.07
Average concealment (%)	43.0 \pm 26.7	58.3 \pm 22.5	-2.14	0.03
Cover at 10cm (%)	69.1 \pm 14.5	63.1 \pm 16.1	0.55	0.58
Cover at 50cm (%)	58.0 \pm 16.3	50.7 \pm 19.5	1.27	0.20
Cover at 100cm (%)	18.7 \pm 20.9	15.2 \pm 13.5	0.51	0.61
Cover at 200cm (%)	1.75 \pm 8.2	1.19 \pm 5.3	-1.55	0.13

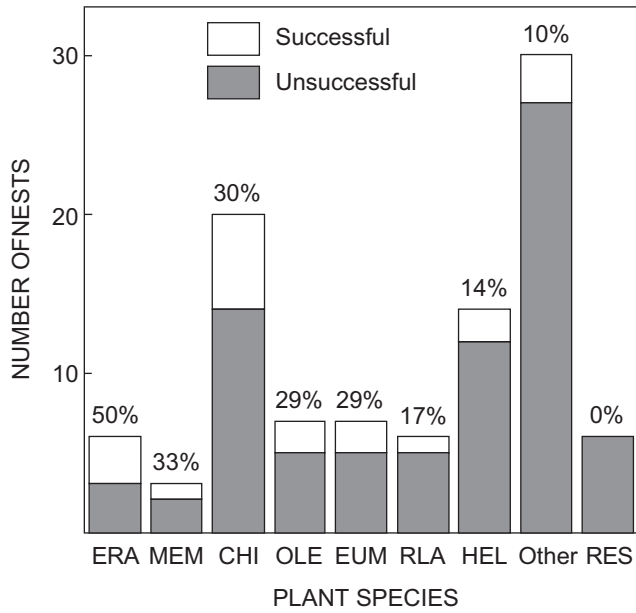


Figure 1: Number of successful and unsuccessful nests of Karoo Prinia placed in the most commonly used plant species at Koeberg Nature Reserve. Percent successful nests for each species indicated above each bar. ERA = *Eriosephalus racemosus*, MEM = *Metalasia muricata*, CHI = *Chrysanthemoides incana*, OLE = *Olea exasperata*, EUM = *Euphorbia mauritanica*, RLA = *Rhus laevigata*, HEL = *Helichrysum revolutum*, RES = restios, Other = all other (19) species

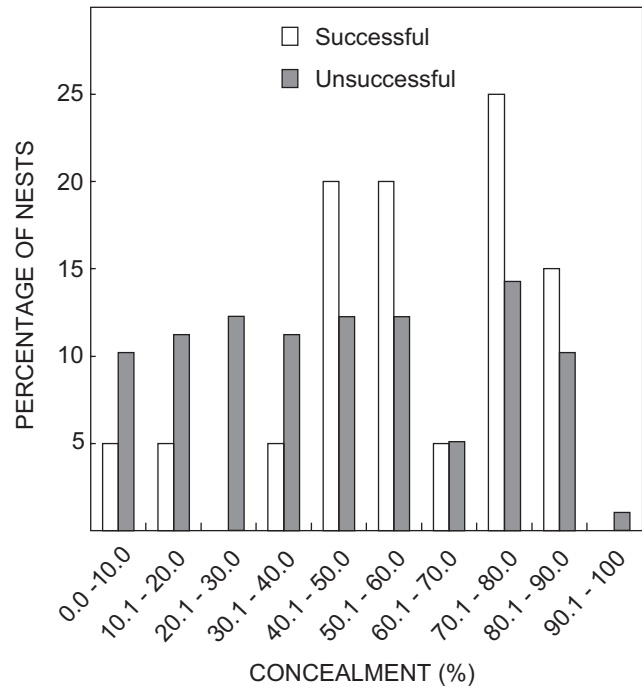


Figure 2: Percentage of successful (n = 20) and unsuccessful nests (n = 78) of Karoo Prinia assigned to each class of concealment (t = -2.14, P = 0.035)

Table 3: Habitat variables important in discriminating between nest sites of unsuccessful and successful Karoo Prinia nests using Stepwise Discriminant Function Analysis. Variables are listed in the order in which they were entered into the model

Nest site variables	Wilks' partial lambda	P	Standardised co-efficients	Factor structure co-efficients
Distance from edge	0.929	0.011	-0.578	-0.333
Concealment	0.940	0.020	0.525	0.387
Nest-plant type	0.942	0.021	0.511	0.454
Nest-patch heterogeneity	0.977	0.149	-0.319	-0.301
Cover at 200cm	0.978	0.159	0.312	0.279
Cover at 50cm	0.980	0.186	-0.295	-0.230
Nest-plant height	0.981	0.198	0.291	0.149
Relative nest height	0.989	0.319	-0.223	-0.350

and situated closer to the lateral edge of the plant suggests that greater concealment is acquired by the bird weaving the nest into the denser foliage at the edge of the plant. All plants used by Karoo Prinia in this study were mature, perennial evergreens, so the greater concealment of successful nests was not due to them experiencing greater foliage growth around them during the typical 28-day nesting cycle.

The selection of thorny plants for nesting has been suggested as an adaptation to reduce nest predation risk (Lazo and Anabalón 1991). The two particularly thorny plants that occur commonly at our study site were *Asparagus capensis* and *Putterlickia pyracantha*. *Asparagus* was infrequently used, probably because this plant is generally too small to function as an appropriate nesting substrate. Despite the

extreme thorniness of *Putterlickia*, this plant is rarely used by Karoo Prinia as a nest site (none in the present sample), possibly because the foliage density of this species is relatively low and thus not conducive to providing good nest concealment from predators that are not deterred by plant thorniness (e.g. snakes).

These results support those of other studies that have found a reduction in the probability of predation, especially from diurnal predators that use visual cues, with increased nest concealment (Murphy 1983, Kelly 1993, Cresswell 1997). However, they are contrary to studies that suggest no relationship between nest concealment and nest success (Best and Stauffer 1980, Holway 1991, Filiater *et al.* 1994, Howlett and Stutchbury 1996, Ford 1999, Lloyd *et al.* 2000), probably as a consequence of random predation (Howlett

Table 4: The correct classification of nest sites to unsuccessful vs successful categories on the basis of 10 nest-site variables, using Stepwise Discriminant Function Analysis, was better than a random classification for both unsuccessful (96.2% vs 79.6%) and successful (25% vs 20.4%) nests

Group	Predicted classifications	
	Unsuccessful	Successful
Unsuccessful	96.2%	3.8%
Successful	75.0%	25.0%
	Random classifications	
	79.6%	20.4%

Total correctly classified = 81.6% vs random = 67.5%

and Stutchbury 1996, Lloyd *et al.* 2000). Because the available evidence suggests that most nest predators at Koeberg Nature Reserve are diurnal, relying largely on visual cues to locate nests, our finding of greater success among more concealed nests is consistent with predictions. Visual cues important to predators will include both the visibility of the nest structure and adult activity and behaviour at the nest. The extent to which vegetation obscures both nest structure and adult activity is therefore expected to be important to nest success in an environment with visually-oriented predators.

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Appendix 1: Percentage of Karoo *Prinia* nests in each nesting-stage category (building, laying, incubation and nestling-stage failure, and successful) that were placed in each plant species used as a nest substrate in Koeberg Nature Reserve

Nest-plant species	Building	Laying	Incubating	Nestling	Successful	Average %
<i>Agathosma bisulca</i>	0.0	0.0	0.0	0.0	5.0	1.0
<i>Aspalathus</i> sp.	3.3	0.0	0.0	0.0	0.0	1.0
<i>Chrysanthemoides incana</i>	3.3	28.6	5.6	33.3	30.0	17.3
<i>Cissampelos capensis</i>	0.0	4.8	0.0	0.0	0.0	1.0
<i>Eriocephalus racemosus</i>	0.0	0.0	5.6	11.1	15.0	5.1
<i>Euphorbia mauritanica</i>	10.0	9.5	5.6	0.0	10.0	8.2
<i>Euclea racemosa</i>	3.3	4.8	0.0	0.0	0.0	2.0
<i>Helichrysum revolutum</i>	10.0	28.6	11.1	11.1	10.0	14.3
<i>Metalasia muricata</i>	10.0	0.0	0.0	0.0	5.0	4.1
<i>Nylandtia spinosa</i>	0.0	0.0	11.1	0.0	5.0	3.1
<i>Olea exasperata</i>	3.3	9.5	11.1	0.0	10.0	7.1
<i>Othonna coronopifolia</i>	0.0	0.0	0.0	11.1	0.0	1.0
<i>Passerina vulgaris</i>	0.0	4.8	0.0	22.2	0.0	3.1
<i>Phyllica stipularis</i>	3.3	0.0	0.0	0.0	0.0	1.0
<i>Asparagus capensis</i>	3.3	0.0	5.6	0.0	0.0	2.0
<i>Pterocelastrus tricuspidatus</i>	0.0	0.0	5.6	0.0	0.0	1.0
Restios (Restionaceae)	13.3	9.5	5.6	0.0	0.0	7.1
<i>Rhus laevigata</i>	13.3	0.0	11.1	0.0	5.0	7.1
<i>Rhus rigida</i>	0.0	0.0	0.0	0.0	5.0	1.0
<i>Senecio halimifolius</i>	6.7	0.0	0.0	0.0	0.0	2.0
Unidentified species (6 spp.)	16.7	0.0	22.2	11.1	0.0	10.2