MICROHABITAT NEST COVER EFFECT ON NEST SURVIVAL OF THE RED-CRESTED CARDINAL

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ABSTRACT.—We evaluated the influence of microhabitat vegetation cover on Red-crested Cardinal (*Paroaria coronata*) nest survival in natural forests in central eastern Argentina by monitoring 106 nests for 1,262 exposure days. Daily nest survival rates increased with vegetation cover above the nest and decreased linearly as the breeding season progressed. Increased concealment above the nest helped hide and protect nests from predators (mainly aerial predators). Earlier nesting attempts in the breeding season were more successful than those later in the season. This is the first study to evaluate the effect of microhabitat vegetation cover on daily nest survival rates of a south temperate passerine. We highlight the importance of microhabitat nest concealment on nest success of the Red-crested Cardinal. *Received 23 October 2011. Accepted 23 March 2012.*

Predation is a major ecological force influencing biological systems at a multitude of levels (Fontaine et al. 2007). Nest predation has been an important factor in the evolution of avian life histories (Skutch 1985, Ricklefs 2000) and nest site selection (Lima 2009, Martin and Briskie 2009) as egg and chick predation are the main causes of nest failure in birds (Ricklefs 1969, Martin 1993b, Lima 2009).

Nest predation rates of numerous bird species are affected by the physical features of a nesting site (Martin 1993b, Liebezeit and George 2002, Gjerdrum et al. 2005, Eggers et al. 2006, Fontaine and Martin 2006). Many studies have reported vegetation cover in the immediate vicinity of a nest provides greater concealment and lower accessibility to predators, which results in higher survival rates (Kelly 1993, Martin 1995, Howlett and Stutchbury 1996, Flaspohler et al. 2000, Liebezeit and George 2002, Weidinger 2002, Winter et al. 2005, Kelleher and O'Halloran 2007, Rangel-Salazar et al. 2008, Kerns et al. 2010; but see Vergara and Simonetti 2004).

Nest site selection likely affects nesting success (Eggers et al. 2006). Many bird species do not choose nest sites randomly with respect to vegetation characteristics (Martin and Roper 1988, Holway 1991, Knopf and Sedgwick 1992); vegetation cover frequently has a significant effect on predator foraging success (Stinson et al. 1981, Bechard 1982). Some birds choose nest sites offering more protective cover given a

simulated increase of predation risk (Eggers et al. 2006). Birds have been observed to change nest microhabitat following predation to more concealed locations (Lima 2009). The type of nest is also important, as cavity and closed nests are likely to be more protected from both environmental conditions and nest predators than open nests (Ricklefs 1969, Martin and Li 1992, Robinson et al. 2000).

Most studies of nesting success have been conducted in either north temperate or tropical areas (Martin 1996). Some authors have inferred that birds in the Southern Hemisphere have higher nest predation rates than in north temperate areas, based on the presence of certain life-history traits (reviewed in Martin 1996). The contrasts between tropical and temperate birds still remain largely unresolved (Martin 1996, Ricklefs 2000, Ferretti et al. 2005). Vegetation cover has been identified as an important influence on predation risk in bird species of north temperate and tropical areas, but little is known about how these factors may influence reproductive biology and nesting success of birds in south temperate regions (i.e., Mezquida and Marone 2002, Vergara and Simonetti 2004).

The Red-crested Cardinal (*Paroaria coronata*), is the basal species of the Thraupidae (Dávalos and Porzecanski 2009), an emblematic group of neotropical birds. It is distributed from center-eastern Argentina to southern Brazil, Paraguay, eastern Bolivia, and Uruguay (Ridgely and Tudor 2009). Cardinals inhabit semi-open forests (Sick 1997), and build open-cup nests (~13 cm wide) in the tree canopy in small forks or thorny branches between 2 and 6 m height (Segura 2011). They breed from early October to late February, nesting in three different tree species: primarily in Tala

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(*Celtis tala*), and secondarily in Coronillo (*Scutia buxifolia*) and Molle (*Schinus longifolius*) (Segura and Arturi 2009).

Our objective was to evaluate the influence of surrounding vegetation cover on nest survival of Red-crested Cardinals in natural forests of central eastern Argentina. We hypothesized that increased nest cover reduces susceptibility to predation, and predicted higher microhabitat cover would have a significant positive influence on nest survival.

METHODS

Study Site.—We conducted the study at 'Estancia La Matilde' (35° 20′ S, 57° 11′ W) in center eastern Buenos Aires, Argentina. The study site was a flat area of 400 ha within the Biosphere Reserve Parque Costero del Sur (MAB-UN-ESCO). It is semi-open grassland with several low chains of woodlands, mainly dominated by native tree species including *Celtis ehrenbergiana* (Tala, deciduous), *Scutia buxifolia* (Coronillo, evergreen), and *Schinus longifolius* (Molle). Red-crested Cardinals are present in the study area during the reproductive and non-reproductive seasons (Segura and Arturi 2012). Potential terrestrial nest predators in these forests are white-eared opossum (*Didelphis albiventris*), lesser grison (*Galictis cuja*), snakes (*Philodryas* spp.), and small rodents. Potential aerial nest predators are: Guira Cuckoo (*Guira guira*), Chimango Carcara (*Milvago chimango*), and Narrow-billed Woodcreeper (Lepidocolaptes *angustirostris*).

Nest Monitoring.—We collected data over three consecutive breeding seasons from 2005 to 2008. We monitored 106 Red-crested Cardinal nests annually from October through February by extensively searching among suitable nesting habitat. We monitored the nests daily during the egg laying and hatching stages, and every 2 days during incubation and nestling stages. Nesting attempts that did not reach egg laying stage (i.e., nests in construction) and nests abandoned during egg laying or incubation were not considered in the analysis. Nests that failed due to *Philornis* ectoparasitism (Segura and Reboreda 2011) were not considered. We examined nest contents on each visit, by taking all eggs or chicks from the nest (Segura 2011 provides details of the null effect of nest monitoring on nest success). We checked nests until fledglings had left the nest or until predation. We considered a nest successful if

at least one young fledged. Nests with signs of predation or where chicks disappeared before the earliest possible fledging date were considered depredated. The entire breeding cycle was 27 days (egg laying + incubation + nestling stages, Segura 2011).

We recorded physical characteristics of vegetation cover in a 50-cm radius around the nest immediately after fledging. We measured the presence of leaves and branches at intervals of 10 cm in a horizontal straight line in each of the four cardinal directions centering on the nest, and also 50 cm vertically above and below the nest. These measurements were taken twice at each nest, at the northern and southern side of the nest separately. We recorded the absence (0 = 0%), weak presence (1 = 1–50%), and abundant presence (2 = >50%) of leaves and branches covering the nest in each 10 cm interval. We calculated the average for horizontal, above, and below measurements. We assumed vegetation cover surrounding the nest did not change throughout the breeding cycle (27 d). There was no significant association between our measurements of cover and date of the breeding season (Spearman's rank correlation; horizontal: $\rho = -0.04$, $P = 0.66$, above: $\rho = 0.01$, $P = 0.94$, and below: $\rho = -0.01$, $P = 0.95$).

We included date of the season and year as additional variables to control for intra- and inter-annual variation. Age of the nest was included as a variable to control for intra-nesting cycle variation. We also included physical characteristics of the nest site that may influence nest survival: (1) tree species where the nest was built (Tala and Coronillo trees), (2) nest height from the ground (m), and (3) nest location within the forest ('center' if the nest-tree was in the center of the continuous chains of forest parallel to the river, 'border' if it was in the border of the chains of forest, and 'patches' if it was in small isolated forest patches more distant from the river).

Data Analysis.—We estimated daily survival rates (DSR) using Program MARK (White and Burnham 1999, Dinsmore et al. 2002). Encounter histories were coded following Dinsmore et al. (2002). We calculated the number of days in each encounter history relative to a date prior to the earliest initiated nest (1 Oct = day 0). We used Akaike's Information Criterion adjusted for small sample sizes to compare models based on log-likelihood values (Burnham and Anderson 2002). We built all models without standardizing

TABLE 1.   Support for models predicting daily survival rates for microhabitat at Red-crested Cardinal nests at Estancia La Matilde, Argentina (2005–2008).

Model	Deviance	ΔAIC_c	k	w_i
S (above + date)[a]	448.3	0.00	3	0.716
S (above)	452.2	2.01	2	0.252
S (horizontal)	457.4	7.07	2	0.029
S (date)	458.6	8.27	2	0.021
S (site)	459.5	9.61	4	0.009
S (tree)	459.8	9.51	3	0.006
S (age)	460.5	10.23	2	0.004
S (below)	461.4	11.04	2	0.002
S (.)	463.4	11.07	1	0.000

[a] AIC_c value of the top model = 454.35.
    Deviance = difference between each model and the saturated model in −2 log likelihood; ΔAIC_c = difference between each model and the top model in Akaike's Information Criterion corrected for small samples (AIC_c); k = number of parameters in the model; w_i = Akaike weight, a measure of each model's relative support within the set of candidate models. S(.) is the general model that assumes constant DSR among nests and over time. S(below), S(horizontal), and S(above) are the models for the microhabitat cover below, horizontal, and above nests, respectively. S(age) is the model where DSR has a linear relationship with age of the nest. S(tree) is the model including the tree species where the nest was built. S(site) is the model including the nest location within the forest. S(date) is the model where DSR has a linear relation with date of season.

covariates and with the logit-link function (Dinsmore et al. 2002). The list of candidate models was based on combinations of factors that *a priori* may affect Red-crested Cardinal nest survival. We ranked and compared models using $\Delta AICc$ (estimated as the relative difference between the top ranked model and each other model). We considered models with $\Delta AICc \leq 2$ to be equally parsimonious (Burnham and Anderson 2002, 2004). We also examined whether the suspected effect of vegetation cover on nest survival was consistent across tree species (interaction tree × cover). We report parameter estimates from the single best model when the top model was strongly supported ($w_i \geq 0.70$) (Burnham and Anderson 2002). We report 95% confidence intervals for each parameter based on the unconditional variances. We obtained daily survival estimates from the logistic-regression equation of the best-supported model. Survival probabilities were the result of daily survival rate over the assumed duration of breeding cycle (27 d). Reported values are means ± SE.

RESULTS

Thirty-four nests produced at least one fledgling (resulting in an overall apparent nest-survival rate of 0.32) while the rest of the nests were predated (68%, n = 72 nests). The total number of successful nests did not differ between seasons (Chi-square: $\chi^2_2 = 2.82$, $P = 0.24$). Nests were built in Tala (n = 68 nests, 64%) and Coronillo (n = 38 nests, 36%) at a height of 3.6 ± 0.1 m

(range = 1.5–6.8 m). Microhabitat nest cover (i.e., leaves and branches covering the nest) was 42.1 ± 1.9% for horizontal measures, 51.1 ± 1.8% for above, and 29.4 ± 1.6% for below measures. Sixty-four nests (60%) were in the border of the chains of forest, 23 nests (22%) were in the small isolated forest patches, and 19 nests (18%) were in the center of the continuous chains of forest.

We monitored nests over a 131-day interval (from 16 Oct to 24 Feb) for 1,262 exposure days. Nest cover above and date within season were important covariates in modeling DSR (Table 1). Models including horizontal and below nest cover, age of the nest, tree species, and site had a lower AICc value than the null model, but did not contribute significantly to the best model (Table 1). The AICc values of the rest of the covariates were higher than the AICc's null model and they were rejected. Interaction tree × cover showed that effect of vegetation cover on nest survival was consistent across both tree species. The best fitted model contained the additive effects of nest cover above and date throughout the season ($wi = 0.72$; Table 1). DSR improved with increasing nest cover above and when decreasing the date throughout the season (Table 2; Fig. 1).

DISCUSSION

Vegetation cover surrounding the nest and date of reproduction within the breeding season had a significant effect on predation risk of Red-crested Cardinal nests. These results suggest increased

TABLE 2. Estimated coefficients and precision for the top additive model (Table 1) explaining daily survival of Red-crested Cardinal nests.

Parameter	Estimate (β) $\pm$ SE	95% confidence interval	
		Lower	Upper
Intercept	1,161 $\pm$ 0,444	0,291	2,032
Date throughout the season	−0,008 $\pm$ 0,004	−0,228	−0,002
Cover above nests	1,058 $\pm$ 0,319	0,431	1,685

concealment helps hide and protect nests from predators, and earlier nesting attempts within the reproductive season are more successful than those later in the season.

Daily nest survival rates improved significantly in relation to increased nest cover above, possibly because of lower accessibility and less visibility of eggs and chicks. Vegetation above the nest had a significant impact and we speculate the main predators access nests from above (e.g., aerial predators such as the Guira Cuckoo, Chimango Caracara, or Narrow-billed Woodcreeper), and not from the tree trunk (i.e., terrestrial predators such as mammals or snakes). The main key for aerial nest predators to find nests is probably visual, and the more visual barriers, the less likely a predator might detect a nest (Watts 1989).

Dense tree-canopy seems to provide more protection and Coronillo trees should offer high quality nesting sites and be chosen more frequently than Tala trees, which have less leafy canopies. However, Red-crested Cardinals nested more frequently in Tala than Coronillo trees (Segura and Arturi 2009). Some authors have suggested that open nesting birds should have a balance between the advantages of high concealment and the need to maintain visibility from the nest (i.e., the advantages to avoid predators by covering the nest and disadvantages associated with too much concealment (Götmark et al. 1995, Wilson and Cooper 1998). Red-crested Cardinals appear to use this balance, selecting sites with higher cover above the nest to avoid predators and, at the same time avoiding building nests in too concealed sites that may reduce visibility from the nest when predators (or conspecifics) approach the nest. Another possible disadvantage is that nest sites that are too covered may have low ventilation and luminosity, which may increase the frequency of ectoparasites (Loye and Carroll 1998, O'Connor et al. 2010).

The date within the breeding season also had a significant effect on nest survival, indicating the

earliest nests (initiated in Oct/Nov) are less likely to fail than those initiated in January and February. These results are consistent with studies which also found seasonal variation in Passeriformes (Hochachka 1990, Jehle et al. 2004, Grant et al. 2005, Moreno et al. 2005; but see Burhans et al. 2002). The decline in nest success with date, as Grant et al. (2005) suggested, could be the result of an increase in predator abundance and movement later in the reproductive season, by post-reproductive adults and dispersing juveniles.

The cumulative probability of nest survival was 0.17 for a nest initiated in the middle of the breeding season (1 Dec) in a site with 50% cover above the nest. The Red-crested Cardinal has higher nest predation rates than north temperate birds (Martin 1993a), but similar predation rates to south temperate birds (Mermoz and Reboreda 1998, Mezquida and Marone 2001, Astié and Reboreda 2006, Delhey et al. 2010, De Marsico and Reboreda 2010, Di Giacomo et al. 2011). Nest predation appears to be higher in several South American than North American locations, and predation might have had a stronger influence on the evolution of birds' life-history traits in South America. South temperate birds should have strategies that allow them to maximize their reproductive fitness given high predation rates. Segura (2011) reported that, after a predation event, each pair of Red-crested Cardinals at this same study site rapidly made another reproductive attempt in the same territory. Nest intervals in Red-crested Cardinals are as short as 6 days from nest loss to initiation of the next clutch (Segura 2011), and the breeding season is long, from October to February. This allows Red-crested Cardinals to have at least 6–8 reproductive attempts in a single season (Segura 2011).

This is the first study to evaluate the effect of microhabitat vegetation cover on daily nest survival rates for a south temperate passerine. Little is known regarding breeding biology and bird predator communities in south temperate
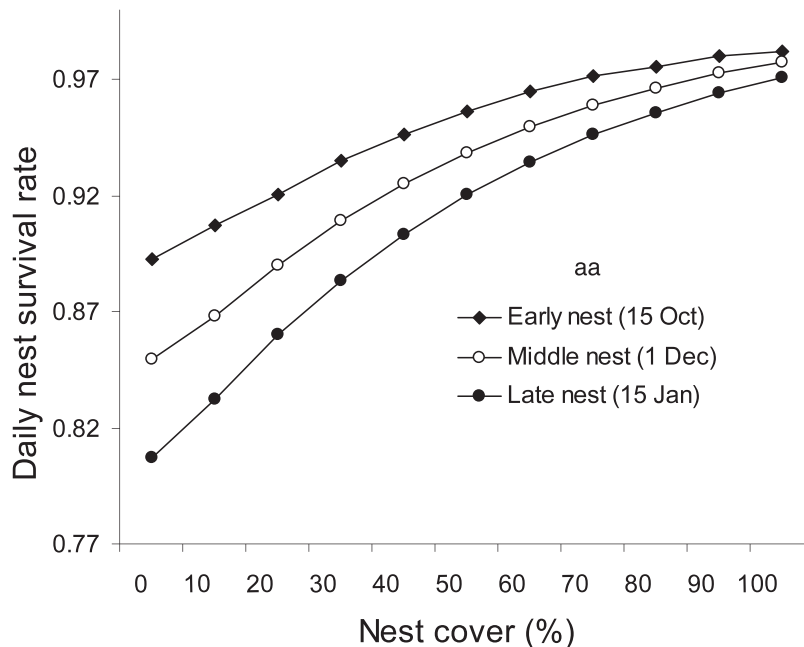
FIG. 1.   Daily survival rate (DSR) of Red-crested Cardinal nests related to the percentage of cover above nests in different periods of the breeding season (15 Oct: early nests, 1 Dec: half of the season, and 15 Jan: late nests).

areas, and future studies should focus in this issue. We highlight the importance of microhabitat nest concealment on nest success of Red-crested Cardinals, and suggest considering these patterns in future conservation and management of this species' natural populations, as well as other bird species with similar life-history traits.

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