

Nest survival rates of Red-crested Cardinals increase with nest age in south-temperate forests of Argentina

Luciano N. Segura^{1,2,3} and Juan C. Reboreda¹

¹Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, C1428EGA, Buenos Aires, Argentina

²Laboratorio de Investigaciones en Sistemas Ecológicos y Ambientales, Universidad Nacional de La Plata, Diagonal 113#469, B1904CCA, La Plata, Argentina

Received 28 November 2011; accepted 18 August 2012

ABSTRACT. The main cause of nest mortality for most bird species is predation and nest survival rates often vary in relation to time-specific variables. Few investigators have examined time-specific patterns of nest survival in Neotropical birds, and most such studies have focused on tropical and subtropical species. To better understand age-related patterns of nest survival, we studied nest survival of Red-crested Cardinals (*Paroaria coronata*, Thraupidae) in a south-temperate forest in Argentina. We modeled daily nest survival rates (DSR) using program MARK. We examined the relationship between nest age and nest survival rate, controlling for the effects of physical characteristics of nest sites and progression of the breeding season. We monitored 367 nests for a total of 4018 exposure days. We found that DSR increased with nest age and was higher in small isolated patches than in large continuous patches of forests. The increase of DSR with nest age could be a consequence of more vulnerable nests being predated early in the nesting cycle or a result of parents defending nests more vigorously as nestlings age because of their increasing reproductive value. Open areas of grassland that surrounded the small isolated patches of forests in our study may have been a barrier to predator movements, possibly explaining the lower predation rates. Nest survival rates in our study were lower than those reported for tropical or Nearctic temperate birds, but similar to those reported in other studies of Neotropical temperate birds. Reasons for the low nest survival rates of Neotropical temperate birds remain unclear, and additional studies of predator communities are needed to help elucidate this topic.

RESUMEN. Las tasas de supervivencia de los nidos de *Paroaria coronata* aumentan con la edad del nido en los bosques sur templados de Argentina

La principal causa de mortalidad de nidos para la mayoría de las especies de aves es la depredación de nidos, y las tasas de supervivencia a menudo varían en relación a variables específicos a ciertos tiempos del ciclo del nido. Pocos investigadores han examinado patrones de la supervivencia de nidos temporalmente específicos en aves neotropicales, y la mayoría de estos estudios se han concentrado en especies tropicales y subtropicales. Para entender mejor los patrones específicos a la edad del nido que son relacionados a la supervivencia de los nidos, estudiamos la supervivencia de los nidos de *Paroaria coronata* (Thraupidae) en un bosque sur templado de Argentina. Modelamos las tasas diarias de supervivencia de los nidos utilizando el programa MARK. Examinamos la relación entre la edad y la tasa de supervivencia del nido, controlando para los efectos de las características físicas de los sitios de anidación y la progresión de la temporada de cría. Monitoreamos 367 nidos para un total de 4018 días de exposición. Encontramos que la tasa diaria de supervivencia aumentaba con la edad del nido y fue mayor en pequeños parches aislados que en grandes manchas de bosque continuo. El aumento de la tasa diaria de supervivencia con la edad del nido podría ser una consecuencia de que los nidos más vulnerables fueron depredados al comienzo del ciclo de anidación, o como resultado de que los padres defienden los nidos con más fuerza a menudo que maduran los pichones, debido a su mayor valor reproductivo. Las zonas abiertas de pastizales que rodeaban los pequeños parches aislados de bosques en nuestro estudio pueden haber sido un obstáculo para los movimientos de depredadores, lo que posiblemente explique las tasas de depredación relativamente bajas. Las tasas de supervivencia de los nidos en nuestro estudio fueron inferiores a los reportados para las aves tropicales o Neártico templadas, pero similares a los reportados en otros estudios de aves neotropicales templadas. Las razones por las bajas tasas de supervivencia de nidos de aves neotropicales templadas siguen siendo desconocidas, y estudios adicionales de las comunidades de depredadores son necesarios para ayudar a dilucidar este tema.

Key words: nest success, *Paroaria coronata*, predation, program MARK, south-temperate forests, Thraupidae

The main cause of nest mortality for most bird species is predation (Ricklefs 1969, Martin

1993a) and nest survival rates of many species vary in relation to time-specific variables, such as nest age (Martin et al. 2000a). For example, studies of several north-temperate birds with altricial young indicate that vulnerability to predation increases with nest age (Briskie et al. 1999,

³Corresponding author. Email: lsegura79@yahoo.com.ar

Martin et al. 2000a, Davis 2005, Lloyd and Martin 2005, Hannon et al. 2009, Kerns et al. 2010). Nest survival rates may decline with nest age due to an increase in the frequency of nest visits by adults when feeding chicks, with predators using parental activity as a cue to find nests (Skutch 1949). In addition, the increasing frequency and volume of vocalizations as nestlings grow may attract predators to nests (Leech and Leonard 1997, Briskie et al. 1999). In contrast, other studies of north-temperate (Peak et al. 2004, Grant et al. 2005) and tropical (Ryder et al. 2008) birds have revealed that nest survival rates increase during the nesting cycle. This increase may occur because more vulnerable nests (i.e., nests located in poor quality sites) are predated early in the nesting cycle (Martin et al. 2000a). Alternatively, parents may defend nests more vigorously as nestlings approach fledging age because their reproductive value increases with age (Montgomerie and Weatherhead 1988).

The Neotropical region has the highest bird biodiversity, but relatively few investigators have examined time-specific patterns of nest survival of these species and most such studies have been conducted with tropical and subtropical species. To better understand the effect of nest age on nest survival, we examined nest survival rates of Red-crested Cardinals (*Paroaria coronata*) in a south-temperate forest in Argentina. We modeled daily survival rate of the nests of Red-crested Cardinals over three breeding seasons to determine if vulnerability to predation increased or decreased with nest age, while controlling for the effects of physical characteristics of nest sites and progression of the breeding season.

METHODS

Study site and species. Our study was conducted in the Biosphere Reserve 'Parque Costero del Sur' (MAB-UNESCO) in Buenos Aires province, Argentina (35°20'S; 57°11'W). Vegetation in our ~400-ha study site consisted of woodlands arranged in several rows (50–100 m wide and up to several km long) parallel to the "de la Plata" river, surrounded by small areas of native grasslands and non-native pastures. In addition, small patches of forest (10–70 m diameter) were located further from the river (range = 700–1800 m) and were surrounded by large areas of grassland. Woodlands were dominated

by Tala (*Celtis ehrenbergiana*, Cannabaceae) and Coronillo (*Scutia buxifolia*, Rhamnaceae) trees and, secondarily, by Molle (*Schinus longifolius*, Anacardiaceae) and Ombú (*Phytolacca dioica*, Phytolaccaceae). Potential terrestrial nest predators in our study area included white-eared opossums (*Didelphis albiventris*), lesser grisons (*Galictis cuja*), tree-climbing snakes (*Philodryas* spp.), and small rodents. Potential avian nest predators included Chimango Caracaras (*Milvago chimango*), Guira Cuckoos (*Guira guira*), and Narrow-billed Woodcreepers (*Dendrocopos angustirostris*).

Red-crested Cardinals inhabit semiopen areas with scattered trees and shrubs from central Argentina to southern Brazil, Paraguay, eastern Bolivia, and Uruguay (Ridgely and Tudor 2009). In our study area, these cardinals are present year-round (Segura and Arturi 2012) and breed from October to February. Cardinals nest primarily in Talas and secondarily in Coronillos and Molles (Segura and Arturi 2009) at a height of 2–7 m (mean \pm SE of nests and trees: 3.7 ± 0.1 and 6.2 ± 0.1 , respectively; Segura 2011). They build open-cup nests, modal clutch size is three eggs, incubation starts after the laying of the second egg (even in clutches of four eggs), and nestlings hatch after 12 d of incubation and fledge 14 d after hatching (Segura 2011).

Nest monitoring. We collected data from October to February 2005 – 2008. We found nests by systematically searching potential nest sites and observing the behavior of territorial pairs (Martin and Geupel 1993). We visited nests daily during egg-laying and at the time of hatching, and every two days during the incubation and nestling stages. After nestlings were 10 days old, we inspected nests from a distance of 1–3 m to minimize the risk of premature fledging. We checked nests until they failed or young fledged. We considered a nest deserted if eggs were cold and no parental activity was observed near the nest during the visit (i.e., 15–20 min), or when all chicks died as a result of botfly (*Philornis seguyi*) parasitism (Segura and Reboresda 2011). We considered a nest predated if nest contents disappeared between consecutive visits and there was no parental activity near the nest.

Data analysis. A priori, we selected two temporal factors that might influence nesting success: (1) nest age (day 0 = day the first egg of the clutch was laid) and (2) time of breeding

(i.e., date the first egg of the breeding season was laid; day 1 = 1 October). We were able to determine clutch-initiation dates for nests found during construction and egg-laying ($N = 177$ nests). Clutch-initiation dates were assigned by backdating from hatching dates ($N = 95$ nests) for nests found during incubation and, for nests found after hatching, by using nestling weights ($N = 40$ nests). For 55 nests found and that failed during incubation, we estimated clutch-initiation dates (± 1 –5 days) by assuming that the observed period was halfway between the end of laying (nest age = 3) and hatching (nest age = 13; i.e., if a nest was observed for 3 d, we considered it was observed between nest ages 7–9; if it was observed 6 d, we considered it was observed between nest ages 5–11). In addition, we included year in our models to control for differences in nest survival among breeding seasons.

Because the characteristics of nest sites may influence nest survival, our models also included: (1) tree species in which a nest was built (Tala, Coronillo, and Molle trees), (2) nest height above ground (m), (3) distance from a nest to the nearest edge of the tree canopy (cm), and (4) type of forest (rows if the nest tree was in a row of trees parallel to the river, and patches if located in a isolated forest patch more distant from the river). We included tree species because Coronillo and Molle trees are perennial whereas Tala trees are deciduous, and Coronillo trees have denser foliage than Tala and Molle trees (Arturi 1997). We measured nest height using a pole with marks every 10 cm, and horizontal distance from the center of the nest to the edge of the tree canopy with a tape measure.

We monitored 367 nests found during the construction, egg-laying, incubation, and nestling stages. Because we did not band cardinals in our study, we cannot exclude the possibility that some nests were not independent among seasons (i.e., breeding attempts by the same pair). However, because adult survival rates for north-temperate shrub/canopy nesters between years is ~ 0.55 (Martin 1995) and adult survival rates of south-temperate birds are similar (Martin 1996), the proportion of nests that could have been nesting attempts by the same pair in different breeding seasons is relatively low (i.e., 30%, assuming that survival rates of males and females were independent and the divorce rate was 0%). We considered

a nest successful if one or more chicks fledged. We standardized the observation period for each nesting attempt by setting a maximum length of 27 d (13 d for the egg-laying and incubation stages, and 14 d for the nestling stage; Segura 2011). Observation periods started either the day the first egg was laid (for nests found during construction) or the day a nest was found.

We estimated daily survival rates (DSR) using program MARK (White and Burnham 1999, Dinsmore et al. 2002). We coded encounter histories following Dinsmore et al. (2002) and calculated the number of days in each encounter history relative to a date before the earliest nest found during our study (day 1 = 1 October). We examined linear and quadratic effects of nest age and time of breeding, and then used the best of these models as a base to incorporate models with the physical characteristics.

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 covariates and with the logit-link function (Dinsmore et al. 2002). The list of candidate models was based on combinations of factors that we assumed a priori may affect Red-crested Cardinal nest survival. We ranked and compared models using δAIC_c (estimated as the relative difference between the top ranked model and each other model). We considered models with $\delta\text{AIC}_c \leq 2$ to be equally parsimonious (Burnham and Anderson 2002, 2004). We also report parameter estimates from single best models (Burnham and Anderson 2002). For each parameter of best fitting model, we report 95% confidence intervals. We estimated daily survival rates using parameters of the best-supported model. Values are presented as means \pm SE.

RESULTS

We found 367 nests, including 108 in 2005–2006, 120 in 2006–2007, and 139 in 2007–2008. Eighty-six nests were found during construction, 91 during egg-laying, 150 during incubation, and 40 after chicks hatched. Most nests ($N = 249$, or 68%) were in Tala trees, with 30% ($N = 111$) in Coronillo trees and 2% ($N = 7$) in Molle trees. Nests were located at a mean height of 3.7 ± 0.1 m (range = 1.5–7.7 m). Mean distance from nests to the edge

of the canopy was 59 ± 2 cm (range = 15–260 cm). At least one young fledged from 94 of 367 nests (26%), 232 nests (63%) were predated, and 41 (11%) were abandoned. The proportion of successful nests did not differ among breeding seasons ($\chi^2_2 = 0.1$, $P = 0.94$).

We monitored nests for 140 d (11 October–28 February) for a total of 4018 exposure days. Nest age and time of breeding (expressed as linear trends) were important covariates in modeling DSR (Table 1). Models including type of forest and tree species had lower AIC_c values than the null model, but only models including type of forest contributed to the best model (Table 1). AIC_c values for other models were higher than the AIC_c 's null model. The best-fitted model included the additive effects of nest age, time of breeding, and type of forest ($w_i = 0.74$; Table 1). DSR increased linearly with nest age, decreased linearly with time of breeding, and was higher in small isolated than in large continuous patches of forests (Fig. 1, Table 2). Based on the MARK estimator, an average nest (i.e., initiated on 20 November, in the middle of the incubation period) had an estimated DSR of 0.935 ± 0.004 (range = 0.924–0.941). DSR was higher for an average nest located in isolated patches of forests (0.939 ± 0.004) than for nests in the rows of forest parallel to the river (0.918 ± 0.004).

DISCUSSION

We found that daily survival rates of Red-crested Cardinal nests increased linearly with nest age. Similarly, studies of north-temperate passerines have found that DSR increased from nest initiation through fledging (Peak et al. 2004, Grant et al. 2005). One possible explanation for increased DSR with increasing nest age is that predators find more vulnerable nests (i.e., located in poor-quality sites) early in the nesting cycle and nests that remain active are less detectable by predators (Martin et al. 2000a). For example, Cresswell (1997) found that less conspicuous Blackbird (*Turdus merula*) nests were more likely to survive longer or succeed. Some studies of north temperate birds have also found that variation in nest site characteristics may influence nest predation rates (Martin and Roper 1988, Kelly 1993, Martin 1998, Martin et al. 2000a). Thus, if nests in poor-quality sites are found by predators earlier in the nesting cycle (i.e., during egg-laying or incubation), this

Table 1. Support for models predicting daily survival rate for Red-crested Cardinal nests in Argentina ($N = 367$ nests during the breeding seasons of 2005–2006, 2006–2007, and 2007–2008). AIC_c value of the top model = 1705.9. 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, and w_i = Akaike weight, a measure of each model's relative support within the set of candidate models. $S(\cdot)$ is the general model that assumes a constant DSR among nests and over time, $S(\text{tree})$ is the model including the tree species where the nest was built, $S(\text{date})$ is the model where the DSR has a linear relationship with time of breeding (day 1 = 1 October), $S(\text{age})$ is the model where the DSR has a linear relationship with age of the nest (day 0 = laying of the first egg), and $S(\text{forest})$ is the model including the type of forest where the nest was located. We only included models with AIC_c values lower than the $S(\cdot)$ model.

Model	Deviance	ΔAIC_c	K	w_i
$S(\text{age} + \text{date} + \text{forest})$	1695.9	0.00	5	0.739
$S(\text{age} + \text{forest})$	1700.6	2.66	4	0.194
$S(\text{date} + \text{forest})$	1704.4	6.48	5	0.029
$S(\text{age} + \text{date})$	1706.9	7.06	3	0.021
$S(\text{forest})$	1707.3	7.41	3	0.018
$S(\text{age})$	1711.7	9.84	2	0.005
$S(\text{date})$	1717.9	16.01	2	0.000
$S(\text{tree})$	1716.4	16.51	4	0.000
$S(\cdot)$	1720.7	16.78	1	0.000

would result in higher predation rates during the egg-laying and incubation stages than the nestling stage.

The increase in survival rates with increasing nest age could also be the result of parents defending nests more vigorously because the reproductive value of young increases with age (Montgomerie and Weatherhead 1988). Consistent with this interpretation, Segura (2011) reported that Red-crested Cardinals attacked a taxidermic mount of a nest predator (Guira Cuckoo) significantly more often during the nestling stage than during the incubation or egg-laying stages, and more often during incubation than egg-laying. Similarly, Ryder et al. (2008) found that DSR gradually increased as nests aged for two species of manakins and suggested that greater nest vigilance during the nestling stage may have contributed to this increase. Halupka and Greeney (2009) evaluated the importance of parental care on nest survival in tropical thrushes

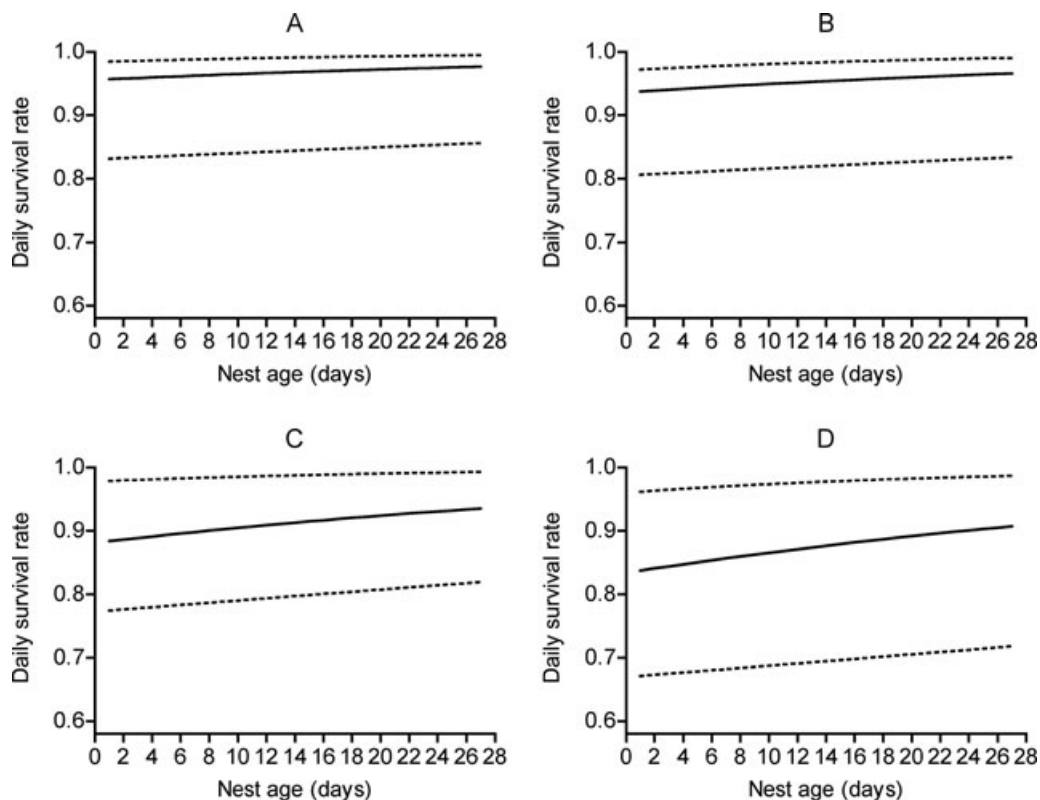


Fig. 1. Daily survival rates (DSR) of Red-crested Cardinal nests as a function of age of the nest (day 0 = laying of the first egg). Estimates were generated from the logistic-regression equation of the top model (Tables 1 and 2). The continuous lines indicate the estimated daily survival rate and the dotted lines the corresponding 95% confidence intervals. Graphs in the upper row represent an early nest (first egg laid on 20 October) in small isolated (A) and in large continuous (B) patches of trees. Graphs in the lower row represent a late nest (first egg laid on 20 December) also in small isolated (C) and in large continuous (D) patches of trees.

and found that parents provide some protection for eggs and young, increasing nest survival (but see Meilvang et al. 1997). However, an increase in levels of nest defense as nests aged would only explain an increase in nest survival if predators could be deterred by the aggressive behavior of Red-crested Cardinals. This may be possible for some opportunistic aerial predators like Guira Cuckoos and Narrow-billed Woodcreepers that destroy clutches in the absence of adults, but not for most terrestrial predators (see also Weidinger 2002, Remes 2005).

We also found that nest daily survival rates decreased linearly with time of breeding. This temporal pattern has also been observed for some passerines in North America and is generally attributed to an increase in the local abundance

of predators (Grant et al. 2005). Because we do not have data on seasonal variation in predators, we cannot test this hypothesis.

Although several studies have revealed a positive association between forest fragmentation and nest predation rates (reviewed in Chalfoun et al. 2002, Stephens et al. 2003), we found that Red-crested Cardinal nests in small isolated patches of forest had higher nest survival rates than those in the rows of forests parallel to the river. Weldon (2006) found that nest predation rates for Indigo Buntings (*Passerina cyanea*) were higher in linear habitats (e.g., fencerows and corridors) than in unconnected fragments. Other authors (i.e., Ambuel and Temple 1983, Paton 1994, Blouin-Demers and Weatherhead 2001) have also found that the abundance of

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

Parameter ^a	Estimate (β) \pm SE	95% confidence interval	
		Lower	Upper
Intercept	3.055 \pm 0.227	2.611	3.499
Age	0.025 \pm 0.009	0.007	0.042
Date	-0.004 \pm 0.002	-0.008	-0.0004
Forest	-0.342 \pm 0.201	-0.762	-0.084

^aAge is the age of the nest expressed as a linear trend (day 0 = day the first egg was laid), Date is the time of breeding expressed as a linear trend (day 1 = 1 October), and Forest is the type of forest (i.e., continuous row or isolated patch) where the nest was located.

nest predators is higher in edges associated with linear habitats. Similarly, the rows of forests parallel to the river may provide suitable habitats for predators of Red-crested Cardinal nests. For such predators, the open areas of grassland that separate the isolated patches of forests from the rows of forests parallel to the river could be a barrier to predator movements (Newbury and Nelson 2007), and that may explain the lower predation rates in isolated patches.

Based on the MARK estimator, an average Red-crested Cardinal nest had an estimated chance of survival of 14% (range = 11–18%). This value is lower than those reported for some open-cup nesting species of birds in Nearctic temperate regions (~50%, Martin 1993b) and tropical regions (~35%, Skutch 1985; 31%, Robinson et al. 2000, ~25%, Alves-Borges and Marini 2010), but is similar to values reported for other south-temperate open-cup nesters (14%, Mermoz and Reboreda 1998; ~18%, Mezquida and Marone 2001; 15%, Astié and Reboreda 2006) in the Neotropics. The lower nest survival rates of south-temperate species compared to that of tropical or north temperate species are mainly the result of differences in predation rates (Martin 1996) and may reflect differences in predator communities. Neotropical birds are characterized by low nest survival rates, but a high number of nesting attempts (five or more) per breeding season (see Martin 1996). Red-crested Cardinals can have up to five nesting attempts (mean = 4.3 \pm 0.1) during a breeding season (Segura 2011) and, therefore,

the probability of having a successful nesting attempt during a breeding season is considerably higher than 0.14.

Many investigators have reported that nest survival rates are lower for tropical than for north-temperate species of birds (Skutch 1949, Martin 1996, Sæther 1996, Martin et al. 2000b, Robinson et al. 2000, Stutchbury and Morton 2001), but additional data concerning nest survival rates of south-temperate Neotropical birds (i.e., birds inhabiting Uruguay, and central and southern Chile and Argentina) are needed (Martin 1996, 2004). Nest survival rates in our study, as well as those reported in other studies of Neotropical temperate birds (Mermoz and Reboreda 1998, Mezquida and Marone 2001, Astié and Reboreda 2006), are lower than those of tropical birds. Such results suggest that nest survival rates of Neotropical temperate birds tend to be lower than those of tropical birds, but additional studies of more species in a wider variety of habitats are needed to confirm this pattern.

ACKNOWLEDGMENTS

We are grateful to L. Sotto and E. Torres for allowing us to conduct this study in Estancia 'La Matilde'. We thank R. McNutt, D. Castle, S. Fee, K. Masterson, A. Formoso, D. Masson, D. Isaldo, R. Jensen, T. Mika, R. Crandall, M. Kalamaras, R. Buxton, A. Nixon, L. Marshall, Y. Obed, and M. Diferdinando for help with data collection and nest monitoring. We are also grateful to M. C. De Mársico and I. Berkunsky for helpful suggestions about program MARK, and to three anonymous reviewers for helpful comments on a previous version of this manuscript. LNS was supported by a fellowship from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). JCR is Research Fellow of CONICET.

LITERATURE CITED

- ALVES-BORGES, F. J., AND M. A. MARINI. 2010. Birds nesting survival in disturbed and protected Neotropical savannas. *Biodiversity and Conservation* 19: 223–236.
- AMBUEL, B., AND S. A. TEMPLE. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64: 1057–1068.
- ARTURI, M. F. 1997. Regeneración de *Celtis tala* Gill ex Planch en el NE de la provincia de Buenos Aires. *Disertación de Tesis Doctoral*, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.
- ASTIÉ, A. A., AND J. C. REBOREDA. 2006. Costs of egg punctures and Shiny Cowbird parasitism on Creamy-bellied Thrush reproductive success. *Auk* 123: 23–32.

- BLOUIN-DEMERS, G., AND P. J. WEATHERHEAD. 2001. Habitat use by Black Rat Snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82: 2882–2896.
- BRISKIE, J. V., P. R. MARTIN, AND T. E. MARTIN. 1999. Nest predation and the evolution of nestling begging calls. *Proceedings of the Royal Society B* 266: 2153–2159.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, NY.
- , AND ———. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261–304.
- CHALFOUN, A. D., M. J. RATNASWAMY, AND F. R. THOMPSON III. 2002. Songbird nest predators in forest-pasture and forest interior in a fragmented landscape. *Ecological Applications* 12: 858–867.
- CRESSWELL, W. 1997. Nest predation rates and nest detectability in different stages of breeding in Blackbirds *Turdus merula*. *Journal of Avian Biology* 28: 296–302.
- DAVIS, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *Condor* 107: 605–616.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPE. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.
- GRANT, T. A., T. L. SHAFFER, E. M. MADDEN, AND P. J. PIETZ. 2005. Time-specific variation in passerine nest survival: new insights into old questions. *Auk* 122: 661–672.
- HALUPKA, K., AND F. H. GREENEY. 2009. The influence of parental behavior on vulnerability to nest predation in tropical thrushes of an Andean cloud forest. *Journal of Avian Biology* 40: 658–661.
- HANNON, S. J., S. WILSON, AND C. A. MCCALLUM. 2009. Does cowbird parasitism increase predation risk to American Redstart nests? *Oikos* 118: 1035–1043.
- KELLY, J. P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodland. *Condor* 95: 83–93.
- KERNS, C. K., M. R. RYAN, R. K. MURPHY, F. R. THOMPSON, AND C. S. RUBIN. 2010. Factors affecting songbird nest survival in northern mixed-grass prairie. *Journal of Wildlife Management* 74: 257–264.
- LEECH, S. M., AND M. L. LEONARD. 1997. Begging and the risk of predation in nestling birds. *Behavioral Ecology* 8: 644–646.
- LLOYD, J. D., AND T. E. MARTIN. 2005. Reproductive success of Chestnut-collared Longspurs in native and exotic grassland. *Condor* 107: 363–374.
- MARTIN, T. E. 1993a. Nest predation, nest sites and birds: new perspectives on old patterns. *BioScience* 43: 523–532.
- . 1993b. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141: 897–913.
- . 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65: 101–127.
- . 1996. Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology* 27: 263–272.
- . 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79: 656–670.
- . 2004. Avian life-history evolution has an eminent past: does it have a bright future? *Auk* 121: 289–301.
- , AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64: 507–519.
- , AND J. J. ROPER. 1988. Nest predation and nest site selection of a western population of the Hermit Thrush. *Condor* 90: 51–57.
- , J. SCOTT, AND C. MENGE. 2000a. Nest predation increases with parental activity: separating nest site and parental activity. *Proceedings of the Royal Society B* 267: 2287–2293.
- , P. R. MARTIN, C. R. OLSON, B. J. HEIDINGER, AND J. J. FONTAINE. 2000b. Parental care and clutch sizes in North and South American birds. *Science* 287: 1482–1485.
- MEILVANG, D., A. MOKNES, AND E. RØSKAFT. 1997. Nest predation, nesting characteristics and nest defence behaviour of Fieldfares and Redwings. *Journal of Avian Biology* 28: 331–337.
- MERMOZ, M. E., AND J. C. REBORDA. 1998. Nesting success in Brown-and-yellow Marshbirds: effects of timing, nest site and brood parasitism. *Auk* 115: 871–878.
- MEZQUIDA, E. T., AND L. MARONE. 2001. Factors affecting nesting success of a bird assembly in the central Monte Desert, Argentina. *Journal of Avian Biology* 32: 287–296.
- MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defense by parent birds. *Quarterly Review of Biology* 63: 167–187.
- NEWBURY, R. K., AND T. A. NELSON. 2007. Habitat selection and movements of raccoons on a grassland reserve managed for Imperiled Birds. *Journal of Mammalogy* 88: 1082–1089.
- PATON, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8: 17–26.
- PEAK, R. G., F. R. THOMPSON III, AND T. L. SHAFFER. 2004. Factors affecting nest success of songbirds in riparian corridors. *Auk* 121: 726–737.
- REMES, V. 2005. Nest concealment and parental behavior interact in affecting nest survival in the Blackcap (*Sylvia atricapilla*): an experimental evaluation of the parental compensation hypothesis. *Behavioral Ecology and Sociobiology* 58: 326–333.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions in Zoology* 9: 1–48.
- RIDGELY, R. S., AND G. TUDOR. 2009. Field guide to the songbirds of South America: the passerines. University of Texas Press, Austin, TX.
- ROBINSON, W. D., T. R. ROBINSON, S. K. ROBINSON, AND J. D. BRAWN. 2000. Nesting success of understory forest birds in central Panama. *Journal of Avian Biology* 31: 151–164.
- RYDER, T. B., R. DURAES, W. P. TORI, J. R. HIDALGO, B. A. LOISELLE, AND J. G. BLAKE. 2008. Nest

- survival for two species of manakins (Pipridae) in lowland Ecuador. *Journal of Avian Biology* 39: 355–358.
- SÆTHER, B. E. 1996. Evolution of avian life-histories: does nest predation explain it all? *Trends in Ecology and Evolution* 11: 311–312.
- SEGURA, L. N. 2011. *Biología reproductiva del Cardenal Común (Paroaria coronata, Thraupidae) en talares del noreste de la provincia de Buenos Aires*. Disertación de Tesis Doctoral, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.
- , AND M. F. ARTURI. 2009. Selección de sitios de nidificación del Cardenal Común (*Paroaria coronata*) en bosques naturales de Argentina. *Ornitología Neotropical* 20: 203–213.
- , AND ———. 2012. La estructura del hábitat influye en la abundancia del Cardenal Común (*Paroaria coronata*) en un bosque templado de Argentina. *Ornitología Neotropical* 23: 11–21.
- , AND J. C. REBOVEDA. 2011. Butterfly parasitism effects on nestling growth and mortality of Red-crested Cardinals. *Wilson Journal of Ornithology* 123: 107–115.
- SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.
- . 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* 36: 575–594.
- STEPHENS, S. E., D. N. KOONS, J. J. ROTELLA, AND D. W. WILLEA. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation* 115: 101–110.
- STUTCHBURY, B. J. M., AND E. S. MORTON. 2001. *Behavioral ecology of tropical birds*. Academic Press, London, UK.
- WEIDINGER, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology* 71: 424–437.
- WELDON, A. J. 2006. How corridors reduce Indigo Bunting nest success. *Conservation Biology* 20: 1300–1305.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120–138.