



SEASONAL VARIATION IN REPRODUCTIVE OUTPUT OF A NEOTROPICAL TEMPERATE SUBOSCINE, THE FIREWOOD-GATHERER (*ANUMBIUS ANNUMBI*)

KASPAR DELHEY,^{1,5} MARTÍN CARRIZO,² LUCAS C. VERNIERE,³ BETTINA MAHLER,⁴
AND ANNE PETERS¹

¹*Behavioural Ecology of Sexual Signals Group, Vogelwarte Radolfzell, Max Planck Institute for Ornithology, Schlossallee 2, Radolfzell, D-78315, Germany;*

²*Alvarado 845, 5°A, 8000, Bahía Blanca, Argentina;*

³*Bravard 575, 8000, Bahía Blanca, Argentina; and*

⁴*Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EHA Buenos Aires, Argentina*

ABSTRACT.—The risk of breeding failure often varies strongly over the breeding season. If birds optimize production of offspring accordingly, investment in reproduction should be lowest when food for young is scarce or nest predation risk is highest. Evidence for this hypothesis is mixed and stems mainly from studies on northern temperate birds, and it is unclear whether these patterns apply to southern temperate birds with “slow” life histories that resemble those of tropical birds. We studied seasonal variation in reproductive investment and nesting success in a Neotropical temperate suboscine, the Firewood-gatherer (*Anumbius annumbi*). Pairs produced an average of 2.8 clutches over the very long (August–April) breeding season. Clutch size (mean = 5.1 eggs, range: 3–8) was very variable between and within pairs and showed an initial increase followed by a decline, the typical pattern of variation for multibrooded temperate species. The main determinant of breeding success was predation. Although the probability of nest failure increased over the season from 70% to >90%, clutch size was not correlated with failure risk. Egg volume did not show consistent seasonal patterns. Our results suggest that reproductive investment is not optimally adjusted to the seasonal variation in nest predation risk, and more research is needed to assess the influence of food availability. *Received 27 February 2009, accepted 20 August 2009.*

Key words: *Anumbius annumbi*, Argentina, clutch size, egg volume, Firewood-gatherer, Furnariidae, laying date, nest predation.

Variación Estacional en el Éxito Reproductivo de un Suboscino Neotropical de Áreas Templadas, *Anumbius annumbi*

RESUMEN.—El riesgo de fracaso reproductivo a menudo varía fuertemente a lo largo de la temporada de cría. Si las aves optimizan la producción de descendencia en función de este riesgo, la inversión reproductiva debería ser mínima cuando la disponibilidad de alimento para los pichones es baja o el riesgo de depredación es alto. Existe evidencia a favor y en contra de esta hipótesis, que proviene en su mayor parte de estudios realizados sobre aves de zonas templadas del hemisferio norte. Por lo tanto, no existe certeza de que los patrones hallados sean aplicables a especies de zonas templadas del hemisferio sur, que presentan historias de vida similares a las de las aves tropicales (alta supervivencia, baja tasa reproductiva). Estudiamos la variación estacional en inversión y éxito reproductivo en *Anumbius annumbi*, una especie de suboscino neotropical de áreas templadas. Cada pareja de *Anumbius annumbi* realizó en promedio 2.8 posturas durante la muy larga (agosto – abril) temporada de cría. El tamaño de postura (promedio = 5.1 huevos, rango = 3 – 8) varió considerablemente entre y dentro de las parejas y mostró un aumento inicial seguido por una disminución, un patrón de variación típico para especies de la zona templada que realizan múltiples posturas por temporada. El factor determinante del éxito reproductivo fue la tasa de depredación. Si bien la probabilidad de fracaso reproductivo se incrementó a lo largo de la temporada de un 70% a más del 90%, el tamaño de postura no se correlacionó con la probabilidad de fracaso. El volumen de los huevos no presentó un patrón de variación estacional consistente. Nuestros resultados sugieren que la inversión reproductiva no se ajusta estrechamente a la variación estacional en la tasa de depredación y que son necesarios más estudios para determinar la influencia de la disponibilidad de alimento.

⁵E-mail: delhey@orn.mpg.de

REPRODUCTIVE SUCCESS USUALLY varies seasonally in birds, and early broods within a breeding season are generally more likely to succeed than later ones (Perrins 1970, Price et al. 1988). This seasonal variation in success is usually mirrored by seasonal variation in reproductive investment. For example, early broods typically contain more eggs than later ones (Klomp 1970, Crick et al. 1993), and this is to be expected if birds are selected to invest optimally in reproduction to maximize the number of surviving offspring (Lack 1947). Several environmental factors that affect breeding success can vary strongly as the breeding season progresses, causing changes in reproductive success and reproductive investment (e.g., clutch size, egg size, etc.). Two of the most important environmental factors that determine the number of surviving offspring are food available to raise the offspring (Lack 1947, Martin 1987) and nest predation (Martin 1995), and these may determine when, and how much, birds invest in reproduction.

Food availability, which typically shows predictable seasonal variation, is believed to have strong effects on breeding success (Martin 1987), and females are expected to fine-tune laying date and clutch size to match food requirements of the brood with the expected timing and availability of resources (Lack 1947). However, although food availability has been the classic explanation for variation in optimal clutch sizes, recent studies suggest an equal or possibly more important role for nest predation (Martin 1995). Small clutches should be favored when predation rates are high, because they allow for rapid re-nesting (Slagsvold 1982, Farnsworth and Simons 2001) and because fewer nestlings means less activity at the nest to attract predators (Skutch 1949, Martin et al. 2000). Within species, differences in predation rates can explain variation in clutch size between populations (Ferretti et al. 2005) and between breeding seasons in the same population (Julliard et al. 1997, Doligez and Clobert 2003). Even within a season, temporal variation in predation rate has been hypothesized to explain seasonal variation in clutch size (Slagsvold 1982). In this case, optimal clutch size should track temporal variation in predation risk and should be negatively correlated with the likelihood of nest failure over the season.

Seasonal variation in reproductive investment has been widely studied in temperate passerine birds of the Northern Hemisphere (e.g., Murphy 1978, Perrins and McCleery 1989, Hochachka 1990), but it is unclear whether the patterns found are applicable to temperate birds of the Southern Hemisphere. Southern temperate birds, such as South American species, are more similar to tropical birds in that they have a "slow" pace of life (Martin 1996, Russell et al. 2004) characterized by low adult mortality and reduced fecundity. This difference in life-history patterns is even more noticeable among endemic taxa such as suboscine passerines in South America that evolved and diversified during the Tertiary when the subcontinent was isolated (Yom-Tov et al. 1994, Ricklefs 2002). Presumably, reduced seasonality and extremely high rates of nest predation in South America have contributed to the differences in life history (Martin 1996). Whether these profound differences in life histories between northern and southern temperate species also affect seasonal patterns of reproductive investment and success within species remains to be seen. For instance, it could be argued that smaller clutch sizes and less seasonal environments in southern temperate regions would provide less scope for seasonal variation in reproductive investment (Evans et al. 2005). However,

detailed studies on the breeding biology of these species are scarce, and the generality of patterns found in northern temperate model species remains to be established (e.g., Moreno et al. 2005, Massoni et al. 2007). Here, we attempt to help fill this gap by reporting a detailed study of the breeding biology of a widespread Neotropical suboscine, the Firewood-gatherer (Furnariidae: *Anumbius anumbi*). Our main aims were to document seasonal variation in reproductive investment and success and to test the hypothesis that seasonal patterns of reproductive investment (clutch and egg size variation) should be correlated with predation risk (the main determinant of breeding failure), as predicted by current optimal-ity models derived from northern temperate species.

METHODS

Study species.—The Firewood-gatherer belongs to the family Furnariidae, one of the most widely distributed families in the Neotropical region. Found in almost every habitat type from coastal deserts to tropical rainforests (Remsen 2003), the Furnariidae are known for their nesting behavior because many species in the family build large and complex enclosed nests whose diversity in form rivals that found in the rest of the passerines (Collias 1997). The Firewood-gatherer is a common medium-sized (18–20 cm, 27–45 g) insectivore that is distributed over large parts of central-eastern South America (southeastern Brazil, Uruguay, eastern Paraguay, and eastern Argentina to northern Patagonia), where it inhabits forest edges, savannas, and grasslands with shrubs (Remsen 2003). It is a year-round resident and breeds during spring and summer in bulky domed stick nests that are profusely "decorated" with carnivore scat, bones, fur, hair, feathers, and so on (Zyskowski and Prum 1999, K. Delhey et al. pers. obs.). The species is socially monogamous, and males and females share nest-building, incubation, and chick-feeding activities. Males and females are cryptically colored (brown) and are largely sexually monomorphic in size and coloration (Remsen 2003).

Study site.—Between 2006 and 2008, we studied a partially color-banded population (20–25 breeding pairs) of Firewood-gatherers near the city of Bahía Blanca, southwest Buenos Aires province, Argentina, in the southeast of the geographic range of the species. The 170-ha field site is on the slopes of the Napostá stream valley (38°35'S, 62°04'W) at ~100 m above sea level. The yearly rainfall averaged 636 mm in 2006 and 2007, with peaks in autumn (March–May) and spring (September–November). Mean monthly temperatures varied between 5.5°C in winter (July) and 24°C in summer (January). Precipitation and temperature data were obtained from a weather station 16 km from the study site through a website (see Acknowledgments). Vegetation consisted of grasslands interspersed with low shrubs (<3 m) dominated by Manca-caballo (*Prosopidastrum angusticarpum*), Piquillín (*Condalia microphylla*), Cina-cina (*Parkinsonia aculeata*), and Piquillín de Víbora (*Lycium gilliesianum*) and a few scattered Caldén trees (*Prosopis caldenia*). Shrubs were found mainly near the rocky outcrops at the top of the valley sides and were surrounded by grasslands. The study site was subject to low levels of cattle grazing.

Field methods.—Birds were caught under license using mist nets around their nests. Each unbanded bird was fitted with a numbered metal ring and a unique combination of three plastic

color bands. The field site was visited regularly from August 2006 until May 2008. The frequency of visits was higher during the breeding season (August–April, ~3 visits per week) than during the non-breeding season (May–July, ~1 visit per week). During visits we searched for new active nests and examined the contents of known active nests. If a nest was suspected of being active, we cut a small (about 10 × 10 cm) hole in the brood chamber to inspect nest contents. This hole was then plugged with an oversized piece of brownish-beige polyurethane foam following the procedures of Mason (1985) and Nores and Nores (1994). Active nests were visited, on average, every 4 days until fledging or nest failure. Eggs were measured at the start of incubation using calipers (± 0.1 mm), and egg volume was computed using Hoyt's (1979) formula. These procedures did not cause discernible disturbance to the birds, in that no active nest was abandoned after being treated this way. Visual predators can easily detect the very large and unconcealed nests, so it is unlikely that the foam plugs increased their detectability, given that most empty nests were opened and sealed similarly. Additionally, our data suggest that the holes plugged with foam did not provide predators with a point of easy access to the brood chamber, because the foam had been removed in only 4 cases of predation (6%). Moreover, in 3 of these cases, the predator had made additional holes in the nest.

Data analysis.—Nest initiation dates (laying date of the first egg) were back-calculated for nests that were not found on the day the first egg was laid. If a nest was found during laying, initiation date was computed as (initiation date = date found – number of eggs when found × 2), assuming that eggs are laid on alternate days (de la Peña 2005, K. Delhey et al. pers. obs.). For eggs found during the incubation or nestling stage, we computed nest initiation date as (initiation date = hatching date – clutch size × 2 – average incubation period). Hatching date was determined either by direct observation (most of the nests) or by estimating chick age using logistic regressions of chick growth and other cues of chick development (K. Delhey et al. unpubl. data). Because this method of estimating hatching date—and, therefore, nest initiation date—was not very accurate and the breeding season was very long, we grouped nest initiation dates in half-month periods (Fig. 1). These dates were subsequently used as the nest initiation dates (hereafter “lay date”) instead of the actual or estimated day of first egg laying. Nest predation was assumed when all eggs (or all but 1 or 2, which were subsequently abandoned) disappeared from the nest, when all nestlings disappeared from the nest before their expected fledging date, or when nestlings were found dead and injured outside the empty nest. Hatching success was computed as the proportion of laid eggs that hatched, excluding nests that were depredated during the egg phase. Eggs that disappeared during laying and incubation were included as unhatched eggs. These eggs were most likely thrown out of the nest by the parents after being punctured by Shiny Cowbirds (*Molothrus bonariensis*; hereafter “cowbirds”; see below), although we acknowledge that partial predation could also be responsible for some of these losses.

Because a large proportion of our data consisted of repeated breeding attempts by the same pairs, we used mixed models including pair identity as a random variable to avoid pseudoreplication when assessing the effects of date and season on reproductive success and investment. Pairs were identified when at least one

member was marked (94 of 130 nesting attempts). The rest of the nesting attempts were treated as independent observations (even though in a few cases this may not have been the case). This is unlikely to have biased our analyses, because results were qualitatively unchanged if all nesting attempts were treated as independent data points. Clutch size and egg volume were analyzed using mixed models with normal error distribution and identity link. Hatching success and likelihood of partial nestling mortality were analyzed using binomial error distribution and logit link. Explanatory variables were the factor season (2006–2007 or 2007–2008) and the covariates lay date and lay date² to account for possible curvilinear patterns. We also tested for interactions between lay date and season and between lay date² and season. Models were reduced by excluding the variables (starting with the interaction terms) in order of decreasing *P* values until only significant terms (*P* < 0.05) remained in the model.

To examine within-pair consistency in reproductive success and reproductive investment, we computed repeatability following Lessells and Boag (1987) for continuous variables (clutch size, egg volume, and hatching success) for pairs for which we had information on ≥ 2 breeding attempts. Given that in many of the pairs only 1 member was marked, our estimates of repeatability should be treated as conservative, because unbanded birds could disappear and be replaced by another unbanded bird over the season. For dichotomous variables (likelihood of success; i.e., fledged yes–no) we computed logistic regressions incorporating pair identity as a factor. We cannot compute a directly comparable value of repeatability in these cases, but at least we can assess whether there is within-pair consistency. Statistical support is given by the significance of the factor “pair identity,” and the magnitude of the repeatability is estimated by how successful that factor is in classifying breeding events as successful or not.

Nest survival was analyzed using the program MARK (White and Burnham 1999), for which we had all the necessary data from 86 nesting attempts. We built models based on *a priori* biological hypotheses that included the following covariates and factors. (1) Variation within breeding seasons: Nest failure rates have been shown to vary over the season because of differences in predator activity, environmental changes, and other factors. We included the covariate “lay date” as well as “lay date²” in the model to account for possible curvilinear patterns of variation. (2) Variation between breeding seasons: We accounted for this by including the factor “season” in the models. (3) Variation between nest stages: It has been hypothesized that different stages in the nesting period (incubation, nestlings) may experience different predation pressures. Increased activity at the nest during the nestling period should increase nest detectability by predators and raise predation rates (Skutch 1949), but predation rates may be higher during egg stages because the most exposed nests are easily found by predators (Martin et al. 2000). We thus included the factor “nest stage” (egg stage, which includes laying and incubation, and nestling stage) in the models. (4) Cowbird activity: These brood parasites occasionally lay their eggs in nests of Firewood-gatherers and puncture their eggs (K. Delhey et al. unpubl. data), and broken eggs are subsequently thrown out of the nest, presumably by the host (Reboreda et al. 2003). Broken eggs inside or near the nest may attract predators (Arcese et al. 1996), and we modeled this possibility by including the factor “cowbird activity” in the models,

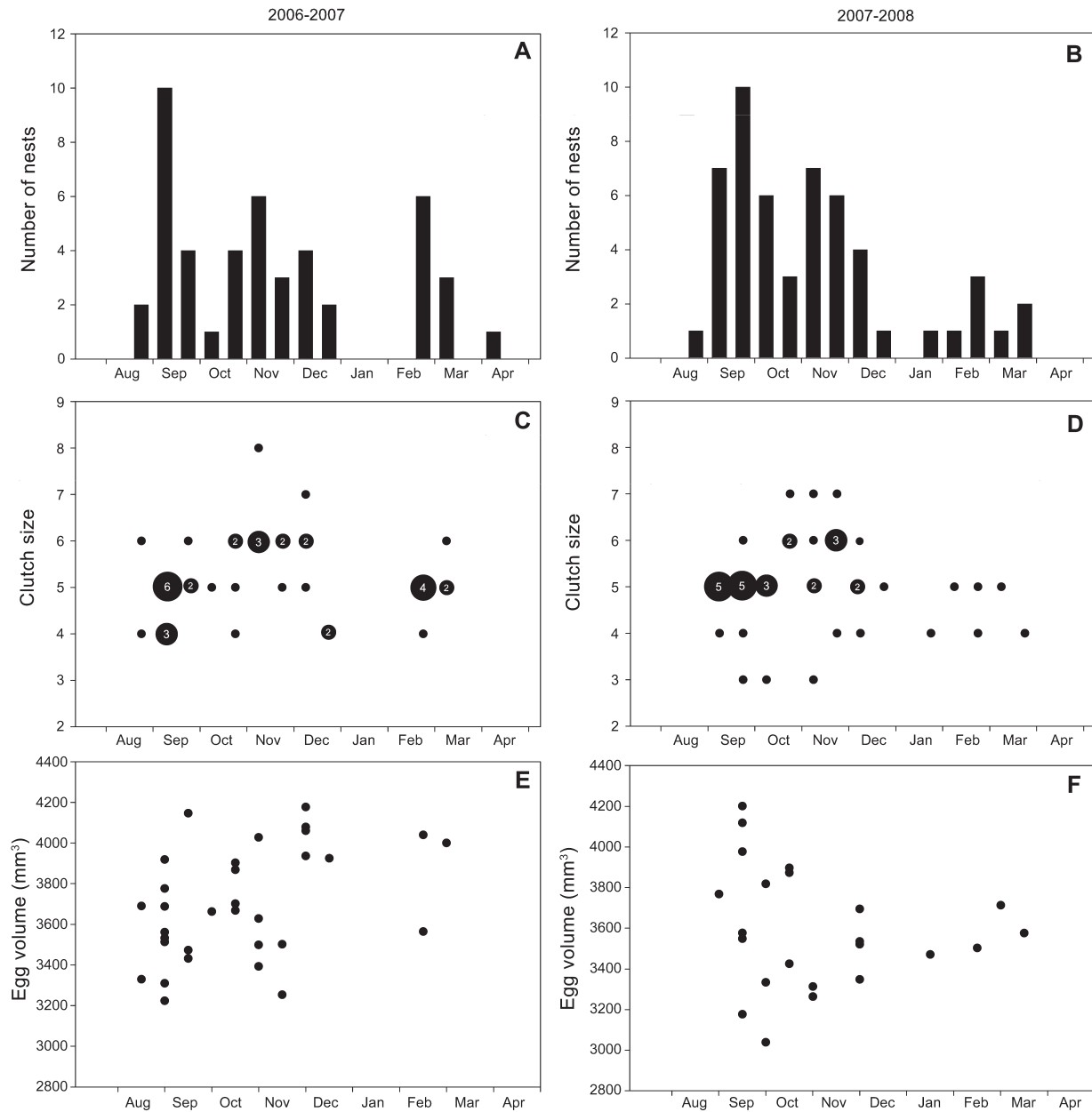


FIG. 1. Seasonal variation in (A, B) number of initiated clutches, (C, D) clutch size, and (E, F) egg volume in Firewood-gatherers in southwest Buenos Aires province, Argentina, grouped by half-month intervals. Left panels (A, C, E) depict breeding season 2006–2007, and right panels (B, D, F) breeding season 2007–2008. In C and D, large symbols with inset numbers represent overlapping data points.

whereby we coded a nest as showing presumed cowbird activity if it presented cowbird eggs, punctured eggs, eggs outside the nest, or eggs that disappeared during laying or incubation. The negative effects of cowbirds on breeding success were restricted to egg losses, because no cowbird chicks survived (K. Delhey et al. unpubl. data). (5) Investigator disturbance: Frequent visits to assess nest contents may attract or deter predators and affect predation rates (e.g., Sockman 1997). We tested this possibility by including the covariate “investigator disturbance,” which is the average number of days between nest visits in the models.

Nest survival models were built in two steps: first we looked for the best model that included only temporal parameters (season, lay date, and lay date²), and later we added the remaining covariates or factors to that best model to find the best overall model. This approach yielded the same best model as constructing and comparing all possible models. Models were compared on the basis of Akaike’s information criterion corrected for small sample size (AIC_c), with lower AIC_c values indicating better fit (Rotella 2009). If models differed by $<2 AIC_c$ units, they were considered equally supported and preference was given to the model with the

fewest parameters (Rotella 2009). Estimates of the daily survival rate (DSR) of nests and other model parameters are given with their 95% confidence intervals (CIs).

Sample sizes for the different analyses vary because of missing data for some nests. In the 2007–2008 season, we performed an experiment on 10 nests to determine the function of “nest decorations.” Because decorations may affect the probability of nest predation (K. Delhey et al. unpubl. data), we removed the experimental nests from the analysis of nest survival. Statistical tests other than nest survival analysis were performed using the programs SPSS (SPSS, Chicago, Illinois) and GENSTAT (VSN International, Hemel Hempstead, United Kingdom), and *P* values are two-tailed.

RESULTS

Breeding phenology.—We found 130 active nests (66 in 2006–2007 and 64 in 2007–2008) in various stages of development (before egg laying = 21, during egg laying = 48, incubation = 49, and chick rearing = 12). First clutches were initiated in the second half of August and last clutches in the first half of April. New nests were initiated throughout this period, but three peaks were identified in both study seasons (September, November, and February; Fig. 1). Numbers of nests initiated in each half-month interval were positively correlated between years (Spearman’s rho, $r_s = 0.66$, $P = 0.005$), which highlights the between-season similarity in the temporal distribution of breeding attempts. The peaks of nest-initiation frequency apparent on Figure 1 are mostly attributable to repeated nesting attempts by the same breeding pairs. Individually marked pairs made 1–6 breeding attempts per season (mean = 2.84, median = 3, 95% CI: 2.43–3.25, $n = 33$ pairs). Incubation lasted, on average, 15.5 ± 0.32 (SE) days (range: 12–19, $n = 26$), nestlings stayed in the nest for 19.6 ± 0.8 days (range: 15–26, $n = 17$), and neither period differed between study seasons (incubation: $t = -0.72$, $df = 24$, $P = 0.47$; nestling period: $t = -1.68$, $df = 7.57$, $P = 0.13$).

Seasonal pattern in clutch and egg size.—Average clutch size was 5.1 eggs (mode = 5, 95% CI: 4.9–5.3, range: 3–8, $n = 106$). Clutch size peaked in the middle of the season in both years, as indicated by the significant quadratic relationship of clutch size with date and the nonsignificant date*season interaction (Table 1). Clutch size also tended to be larger in the 2006–2007 season than in 2007–2008 (Table 1 and Fig. 1). Additionally, clutch size showed significant, but low, repeatability within pairs in the same season ($r = 0.21$, $F = 1.77$, $df = 25$ and 45 , $P = 0.046$). Nonetheless, comparisons of clutch size within pairs (for which we had data on clutch size for ≥ 3 breeding attempts, $n = 9$) showed that the first clutch was smaller than the second (mean difference = -0.88 , 95% CI: -1.35 to -0.42 , paired t -test = -4.43 , $P = 0.002$) and that the second tended to be larger than later clutches, although not significantly so (mean difference = 0.44 , 95% CI: -0.44 to 1.33 , paired t -test = 1.15 , $P = 0.28$).

Egg volume was repeatable within clutches ($r = 0.58$, $F = 7.78$, $df = 77$ and 304 , $P < 0.0001$) and between clutches of the same pair in a given season ($r = 0.50$, $F = 3.77$, $df = 16$ and 29 , $P = 0.001$). Egg volume did not differ significantly between breeding seasons but changed with laying date, although in different ways in the 2 seasons (Table 1 and Fig. 1). Egg volume increased significantly over the season in 2006–2007 but was independent of date in 2007–2008 (Fig. 1). Egg volume was also independent of clutch size in the combined

TABLE 1. Generalized linear mixed models (including pair identity as a random term) analyzing seasonal patterns in reproductive investment (clutch and egg size), hatching success, and partial nestling mortality in Firewood-gatherers in southwest Buenos Aires province, Argentina. Terms in bold are included in the final model. Effect sizes and their 95% confidence intervals (CIs) are given. The interaction terms season*date and season*date² did not reach significance (all $P > 0.25$) except for egg volume (season*date, $\chi^2 = 5.08$, $df = 1$, $P = 0.024$; season*date², $\chi^2 = 3.06$, $df = 1$, $P = 0.08$). In this case we analyzed each season separately.

	Clutch size ^a ($n = 82$)			Egg volume ^a ($n = 55$)			Hatching success (%) ^b ($n = 46$)			Partial mortality (yes–no) ^c ($n = 44$)				
	<i>B</i>	95% CI	χ^2 ($df = 1$)	<i>B</i>	95% CI	χ^2 ($df = 1$)	<i>B</i>	95% CI	χ^2 ($df = 1$)	<i>B</i>	95% CI	χ^2 ($df = 1$)	<i>P</i>	
Season	-0.35	-0.72 to 0.02	3.12	0.077	—	—	0.46	-0.83 to 1.75	0.48	0.48	-0.97	-3.20 to 1.26	0.72	0.39
Date	0.33	0.13 to 0.53	9.93	0.002	33.2^d	6.6^d	0.58	-0.11 to 1.27	2.78	0.95	0.01	-0.19 to 0.20	0.001	0.95
Date ²	-0.02	-0.03 to -0.01	10.37	0.001	-17.1 ^e	1.12 ^e	-0.04	-0.08 to 0.00	2.99	0.084	0.04	-0.02 to 0.09	1.64	0.2

^aNormal error distribution and identity link.

^bBinomial error distribution, logit link, binomial denominator = clutch size.

^cBinomial error distribution, logit link, binomial denominator = 1.

^d2006–2007.

^e2007–2008.

sample ($r = -0.01, P = 0.91, n = 72$) and in 2006–2007 ($r = -0.005, P = 0.97, n = 42$) and 2007–2008 ($r = -0.05, P = 0.80, n = 30$).

Breeding success and causes of failure.—Apparent breeding success was low (25%; 24 of 95 nests with known fate), and predation accounted for 87% of all complete failures (62 of 71 cases). The remaining complete failures were attributable to abandonment (4 nests), nests falling to the ground after a storm (2), and egg puncturing by cowbirds (3). For the subsample of nests of known fate found before or during egg laying ($n = 56$), the pattern was similar: 16 (28%) were successful, 33 (59%) were depredated, 2 (4%) failed because the nest fell, 2 (4%) had eggs punctured by cowbirds, and 3 (5%) were abandoned. Twenty-one nests were depredated during the egg stage (laying and incubation) and 12 during the chick stage. For this subsample of nests found before or during egg laying, there seemed to be low within-pair consistency in the likelihood of success (i.e., fledging young: $\chi^2 = 23.6, df = 15, P = 0.07$; 100% of failed nests were correctly classified by including pair identity in the logistic regression, but only 41.7% of successful nests were; $n = 16$ pairs, 1 with 4, 2 with 3, and the rest with 2 breeding attempts).

The contents of 47 of 62 depredated nests (76%) disappeared without damage to the nest (33 and 28 during the egg and nestling stages, respectively, and 1 at an unknown stage). We assume that these disappearances are attributable mainly to snakes because we witnessed 2 predation attempts by Patagonia Green Racers (*Philodryas patagoniensis*) and in both cases the nest showed no structural damage. In another 6 cases the nest was intact but the entrance was slightly widened, and in the remaining 9 cases the nests presented clear signs of having been broken into. Guira Cuckoos (*Guira guira*) were observed depredating 1 Bay-winged Cowbird (*Agelaioides badius*) nest located inside an old Firewood-gatherer nest (M. Carrizo pers. obs.), which resulted in a widened entrance. Thus, we presume that predation events in which the nest was visibly damaged are attributable to larger predators such as birds (e.g., Guira Cuckoos, Chimango Caracaras [*Milvago chimango*], and Southern Crested Caracaras [*Caracara plancus*] or mammals (e.g., White-eared Opossums [*Didelphis albiventris*] and Little Grisons [*Galictis cuja*]), although we never witnessed mammals depredating Firewood-gatherer nests. The likelihood that a depredated nest had been forced open was higher at the start and at the end of the

breeding season (logistic regression, date: $B = -0.78, 95\% \text{ CI: } -1.45$ to $-0.12, \chi^2 = 5.8, df = 1, P = 0.016$; date²: $B = 0.047, 95\% \text{ CI: } 0.0078$ – $0.086, \chi^2 = 6.03, df = 1, P = 0.014, n = 59$). Taken together, in the first and last 2 months of the breeding season, 40% of the predation events involved nest breakage, whereas in the middle of the season, only 15% of depredated nests had enlarged openings.

Hatching success averaged 84.6% ($n = 49$), and all eggs hatched in 23 of 49 cases (47%). Hatching success in the remaining nests varied between 20% and 86%. Hatching failure was partly attributable to egg puncturing by cowbirds, which was recorded in 27 nests (23% of all nests found during egg stages, $n = 118$). This accounted for 31% of all unhatched eggs (based on the subsample of nests with known hatching success that were found during laying or incubation; $n = 26$). Hatching success did not differ between seasons, but a weak, marginally nonsignificant trend suggests that the likelihood of hatching failure increased in the middle of the season (Table 1). Hatching success was not repeatable within pairs ($r = 0.01, F = 1.02, df = 12$ and $14, P = 0.48$). Overall, hatching success was negatively correlated with clutch size (Spearman's rank correlation, $r_s = -0.33, P = 0.02, n = 49$), but this was the case only in the 2006–2007 season ($r_s = -0.56, P = 0.002, n = 29$; 2007–2008: $r_s = 0.01, P = 0.95, n = 20$). Partial mortality (i.e., largely unexplained loss) of nestlings, which occurred in 7 of 49 nests of known fate, did not vary between or within seasons (Table 1).

To summarize, of all laid eggs of known fate ($n = 369$ from 77 nests), 186 hatched (50.4%), 107 were depredated (29%), 35 were lost to cowbirds (9.5%), 28 failed to hatch for other reasons (7.6%), and 13 were abandoned or the nest fell (3.5%). Of all chicks of known fate ($n = 206$ from 49 nests), 85 fledged (41.2%), 101 were depredated (49%), 13 disappeared singly from the nest or were found dead in the nest (i.e., partial mortality, 6.3%), and 7 were abandoned or died because the nest fell (3.4%).

Daily survival rates.—The DSR of nests in our study was a function of nest stage and date (Table 2). Models that included season as a factor performed less well ($\Delta\text{AIC}_c = 1.8$) than the intercept-only model. Including lay date, on the other hand, substantially improved the fit of the model compared with the intercept-only model ($\Delta\text{AIC}_c = -3.19$). Including lay date² as well did not lead to a better fit of the model ($\Delta\text{AIC}_c = 1$), and we did not consider this covariate further. Adding nest stage

TABLE 2. Summary of models describing variation in daily survival rates of nests of Firewood-gatherers in southwest Buenos Aires province, Argentina.

Model	AIC _c ^a	ΔAIC _c ^b	Weight ^c	K ^d	ΔDeviance ^e	df	P
Intercept + date + nest stage	251.313	0	0.34	3	—	—	—
Intercept + date + nest stage + investigator disturbance	251.711	0.4	0.28	4	1.61	1	0.2
Intercept + date + nest stage + cowbird activity	252.166	0.85	0.22	4	1.15	1	0.28
Intercept + date	254.088	2.78	0.08	2	4.78	1	0.028
Intercept + date + date ²	255.147	3.83	0.05	3	—	—	—
Intercept	257.287	5.97	0.02	1	9.98	2	0.007
Intercept + season	259.088	7.77	0.007	2	—	—	—

^a Akaike's information criterion corrected for small sample sizes.

^b Difference in AIC_c between this and the best model (in bold).

^c Akaike weight, which represents the relative support for the model.

^d Number of parameters in the model.

^e Change in deviance between this and the best model (can be calculated only if models are nested, thus not given in all cases), which follows a chi-square distribution; degrees of freedom and P values are given.

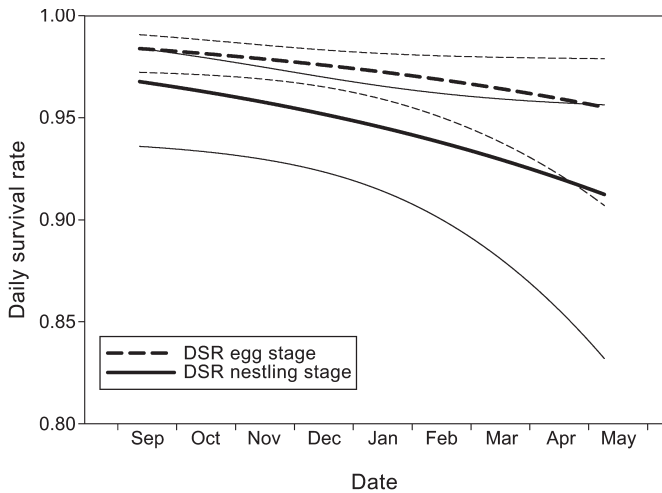


FIG. 2. Seasonal variation in daily survival rate (DSR) of nests during egg stages (laying and incubation) and nestling period in Firewood-gatherers in southwest Buenos Aires province, Argentina, as computed by the best model in Table 2. Means and 95% confidence intervals are shown.

as a factor again improved the fit of the model ($\Delta AIC_c = -2.77$), and this constituted the best model with the lowest AIC_c value. The DSR values decreased as the season progressed ($B = -0.0044$, 95% CI: -0.009 to 0.0001 ; Fig. 2), and DSR was higher during the egg stage (laying and incubation) than during the nestling stage ($B = -0.71$, 95% CI: -1.34 to -0.09 ; Fig. 2). The next-best model ($\Delta AIC_c = 0.39$) included investigator disturbance as an additional variable. Longer intervals (in days) between nest visits tended to be associated with higher DSR, but the 95% CI of effect size clearly included zero ($B = 0.127$, 95% CI: -0.078 to 0.333). Cowbird activity at the nest also seemed to reduce DSR, but the 95% CI was very large ($B = -0.35$, 95% CI: -0.99 to 0.28) and likewise included zero. The parameters from the best model allowed us to calculate the probability of fledging young at different points during the season as $DSR_{\text{eggs}}^{(\text{laying days} + \text{incubation days})} \times DSR_{\text{nestlings}}^{(\text{nestling days})}$. Thus, for a modal clutch size of 5 eggs, the probability of success was 30% (95% CI: 12–51%) for a nest initiated in September and 7% (95% CI: 0.7–25%) for a nest initiated in March.

DISCUSSION

Variation in reproductive effort in our study population was attributable to a combination of multiple breeding attempts and variable clutch sizes, and the main determinant of breeding success was nest predation. The very long breeding season (8 months) provided ample time for pairs to make multiple breeding attempts and, thus, for seasonal changes in reproductive success and reproductive investment. Seasonal changes were evident for most variables describing reproductive success (hatching success and fledging success) and reproductive investment (clutch size and egg volume).

Clutch size is one of the most extensively studied components of avian reproductive investment (e.g., Klomp 1970, Ricklefs 1980, Slagsvold 1982). Clutch size in our study population

is unusual for a Neotropical suboscine, in that it is large (average clutch size in Furnariidae is 3.09 eggs; Yom-Tov et al. 1994) and highly variable. Variation in clutch size over the season was driven, at least in part, by differences in clutch size between repeated breeding attempts by the same pairs, despite consistent differences in clutch size among pairs (i.e., the marginally significant repeatability of clutch size) that may be related to female quality or age. This variation followed a curvilinear pattern with a peak clutch size in the middle of the season (Fig. 1), which is similar to patterns described for multibrooded temperate species in the Northern Hemisphere (Crick et al. 1993). Northern temperate species with more breeding attempts per season show a higher ratio between initial and maximum clutch size, a steeper slope for the increase in clutch size at the start of the season, and later timing of maximal clutch size in relation to the length of the breeding season (Crick et al. 1993). These parameters for Firewood-gatherers in our study were within the range found in multibrooded (>2 breeding attempts per season; $n = 13$) British species (clutch size increase, the ratio between maximum and initial clutch size = 1.2 in *A. annumbi*, British species average = 1.26 [range: 1.0–1.6]; initial slope of clutch size increase = 0.019 in *A. annumbi*, British species average = 0.022 [range: -0.012 to 0.046]; timing of maximal clutch size in relation to length of breeding season = 0.53 in *A. annumbi*, British species average = 0.45 [range: 0.0001–1]; British species data are from appendix in Crick et al. 1993). The curvilinear pattern of variation in clutch size that we observed has, in temperate-breeding passerines, been ascribed to the combination of low food availability for laying females in the early breeding season and a midseason peak in food for feeding young (e.g., Murphy 1978, Crick et al. 1993). We found little evidence to suggest that food limitation influenced breeding success in this species, given that partial nestling mortality was rare and distributed evenly over the season (Table 1) and was apparently not attributable to starvation. However, we did not monitor food availability and cannot address this possibility.

The complete failure of a breeding attempt because of predation was the main determinant of reproductive success in this population. Predation accounted for nearly 90% of complete losses over the season, and the likelihood of predation increased over the season from ~70% to >90% at the end of the season (Fig. 2). This high level of nest predation is similar to that found in another population of Firewood-gatherers (Mason 1985) and comparable with failure rates of shrubland birds in Argentina, where predation risk also increases as the season progresses (Mezquida and Marone 2001). Increases in nest failure rates because of predation have been attributed to increases in predator activity with season (Sperry et al. 2008). In our case, we presume that the most important predators of Firewood-gatherer nests in the area were snakes because they were the only predators that we observed in nests and most (76%) of the depredated nests were intact. Snakes are common in the area and are often found in old Firewood-gatherer nests or depredating nest contents of other bird species that reuse Firewood-gatherer nests (de la Peña 1990, K. Delhey et al. pers. obs.). Snake activity is dependent on temperature (Sperry et al. 2008), which varies over the breeding season. However, because temperature peaked in January in both seasons, temperature alone cannot fully explain the steady increase in predation rates with time (Fig. 2). Alternatively, other predators could

be responsible for late predation events, as suggested by the increased likelihood that depredated nests showed signs that they were broken into at the start and end of the breeding season.

Regardless of predator identity, if predation risk was the sole determinant of clutch size, we would have expected a monotonic decline of clutch size with laying date because of the steady seasonal increase in the probability of nest predation (Skutch 1949, Slagsvold 1982). That we found a seasonal peak in clutch size is inconsistent with this expectation, but it does not necessarily lead to a rejection of the hypothesis that nest predators have no role in the evolution of clutch size in Firewood-gatherers. For instance, feeding nestlings was associated with a lower DSR (Fig. 2), possibly because of greater parental activity that may have attracted the attention of nest predators. Thus, there is ample reason to suspect that nest predation is a potentially strong selective force on clutch size in this species (Skutch 1949, Martin et al. 2000). However, that the smallest clutches were found at the start of the season, when predation risk was lowest, indicates that other factors are at play, and we suggest as one possibility that food resources for laying females may have been limited at the start of the season (e.g., Murphy 1978).

Alternatively, females may be able to more finely adjust their reproductive investment in response to predation risks through modification of egg size (e.g., Fontaine and Martin 2006, Boulton and Powlesland 2008). But as with clutch size, this would predict a seasonal decline in egg size, and we instead observed an increase in 2006–2007 and no relationship with date in the next year (Fig. 1 and Table 1). The discrepancy between seasons is not surprising. Data for several species likewise show strong differences in the relationship with laying date among years (reviewed by Christians 2002). Although none of the studies in Christians's (2002) review were of Neotropical species, egg size did not vary with laying date in most, and if it did, declines in egg size were more common than increases. That we detected an increase in egg size with date in at least 1 of the years is consistent with the possibility that resources for laying females are limited at the start of the breeding season.

To conclude, seasonal variation in reproductive effort (mainly clutch size) followed the pattern expected for similar northern temperate multibrooded species, but our data suggest that this variation is not related in an optimal way to the seasonal variation in nest predation risk, the main determinant of breeding success. To the best of our knowledge, curvilinear patterns of clutch-size variation have not been reported for other Neotropical species. However, similar studies are scarce, and within-season variation in reproductive investment is often not mentioned. In most cases where seasonal variation was examined, no significant changes were detected (Mezquida and Marone 2000, 2003; Robinson et al. 2000; Mezquida 2001a, b, 2002; Moreno et al. 2005; Carvalho et al. 2007; Llambías and Fernández 2009). This may be partly attributable to the fact that some species show relatively invariant clutch sizes (Mezquida 2001b, 2002; Carvalho et al. 2007) or because authors did not test for curvilinear patterns of variation (all the above cited studies). In 4 mainly single-brooded species—Monk Parakeet (*Myiopsitta monachus*; Navarro et al. 1995), Social Flycatcher (*Myiozetetes similis*; Dyrce 2002), Burrowing Parakeet (*Cyanoliseus patagonus*; Masello and Quillfeldt 2004, 2008), and White-rumped Swallow (*Tachycineta leucorroha*; Massoni et al. 2007)—clutch size declined with laying date, whereas in 1

multibrooded species, the Chucao Tapaculo (*Scelorchilus rubecula*; De Santo et al. 2002), late clutches were larger. Whether this variation is adaptive is an open question, because few firm conclusions can be drawn from such a small sample of species. This dearth of information clearly indicates the need for more study of this topic, to establish whether reproductive effort varies with season in Neotropical birds and to assess the presumed causes and adaptive value of seasonal changes in reproductive investment.

ACKNOWLEDGMENTS

We thank the landowner, Cabaña Tres Hojas S.A., and especially its president, G. Sanviti, for permission to work on its property. We are also very thankful to J. Pizá, R. Delhey, and M. Kiehr for vehicle loans, lodging, and child care. C. Pérez, P. Petracci, and J. Pizá provided invaluable help in the field, and R. Scofield gave botanical advice. Our work was made possible by the superb administrative and logistic support provided by G. Rapp of the Max Planck Institute for Ornithology and by the German Embassy in Buenos Aires. This study was supported by the Max Planck Society through a grant of the Program for Advancement of Women in Science awarded to A.P. The manuscript greatly benefited from the comments of two anonymous reviewers, C. Lindell, and M. T. Murphy. Precipitation and temperature data were retrieved from www.tutiempo.net/clima/Bahia_Blanca_Aerodrome/877500.htm.

LITERATURE CITED

- ARCESE, P., J. N. M. SMITH, AND M. I. HATCH. 1996. Nest predation by cowbirds and its consequences for passerine demography. *Proceedings of the National Academy of Sciences USA* 93:4608–4611.
- BOULTON, R. L., AND R. G. POWLESLAND. 2008. Variation in egg size and nest survival with female age in the South Island Robin *Petroica australis*. *Ibis* 150:824–828.
- CARVALHO, C. B. V., R. H. F. MACEDO, AND J. A. GRAVES. 2007. Reproduction of Blue-black Grassquits in central Brazil. *Brazilian Journal of Biology* 67:275–281.
- CHRISTIANS, J. K. 2002. Avian egg size: Variation within species and inflexibility within individuals. *Biological Reviews* 77:1–26.
- COLLIAS, N. E. 1997. On the origin and evolution of nest building by passerine birds. *Condor* 99:253–270.
- CRICK, H. Q. P., D. W. GIBBONS, AND R. D. MAGRATH. 1993. Seasonal changes in clutch size in British birds. *Journal of Animal Ecology* 62:263–273.
- DE LA PEÑA, M. R. 1990. Acción predatora de culebras sobre pichones de aves. *Nuestras Aves* 22:32.
- DE LA PEÑA, M. R. 2005. Reproducción de las Aves Argentinas (con descripción de pichones). L.O.L.A., Buenos Aires.
- DE SANTO, T. L., M. F. WILLSON, K. E. SIEVING, AND J. J. ARMESTO. 2002. Nesting biology of Tapaculos (Rhinocryptidae) in fragmented south-temperate rainforests of Chile. *Condor* 104:482–495.
- DOLIGEZ, B., AND J. CLOBERT. 2003. Clutch size reduction as a response to increased nest predation rate in the Collared Flycatcher. *Ecology* 84:2582–2588.
- DYRCZ, A. 2002. Breeding ecology of the Social (*Myiozetetes similis*) and Rusty-margined (*M. cayanensis*) flycatchers at Barro Colorado island, Republic of Panama. *Ornitología Neotropical* 13:143–151.

- EVANS, K. L., R. P. DUNCAN, T. M. BLACKBURN, AND H. Q. P. CRICK. 2005. Investigating geographic variation in clutch size using a natural experiment. *Functional Ecology* 19:616–624.
- FARNSWORTH, G. L., AND T. R. SIMONS. 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. *Auk* 118:973–982.
- FERRETTI, V., P. E. LLAMBÍAS, AND T. E. MARTIN. 2005. Life-history variation of a Neotropical thrush challenges food limitation theory. *Proceedings of the Royal Society of London, Series B* 272:769–773.
- FONTAINE, J. J., AND T. E. MARTIN. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434.
- HOCHACHKA, W. 1990. Seasonal decline in reproductive performance of Song Sparrows. *Ecology* 71:1279–1288.
- HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77.
- JULLIARD, R., R. H. MCCLEERY, J. CLOBERT, AND C. M. PERRINS. 1997. Phenotypic adjustment of clutch size due to nest predation in the Great Tit. *Ecology* 78:394–404.
- KLOMP, H. 1970. The determination of clutch-size in birds: A review. *Ardea* 58:1–124.
- LACK, D. 1947. The significance of clutch-size, parts 1 and 2. *Ibis* 89:302–352.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116–121.
- LLAMBÍAS, P. E., AND G. J. FERNÁNDEZ. 2009. Effects of nestboxes on the breeding biology of Southern House Wrens *Troglodytes aedon bonariae* in the southern temperate zone. *Ibis* 151:113–121.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics* 18:453–487.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MARTIN, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* 27:263–272.
- MARTIN, T. E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society of London, Series B* 267:2287–2293.
- MASELLO, J. F., AND P. QUILLFELDT. 2004. Consequences of La Niña phase of ENSO for the survival and growth of nestling Burrowing Parrots on the Atlantic coast of South America. *Emu* 104:337–346.
- MASELLO, J. F., AND P. QUILLFELDT. 2008. Klimawandel und Brutverhalten: Erfolgreich brüten in wechselhafter Umwelt? Eine Fallstudie am Felsensittich *Cyanoliseus patagonus*. *Vogelwarte* 46:302–303.
- MASON, P. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. Pages 954–972 in *Neotropical Ornithology* (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). *Ornithological Monographs*, no. 36.
- MASSONI, V., F. BULIT, AND J. C. REBORDA. 2007. Breeding biology of the White-rumped Swallow *Tachycineta leucorrhoa* in Buenos Aires Province, Argentina. *Ibis* 149:10–17.
- MEZQUIDA, E. T. 2001a. Aspects of the breeding biology of the Crested Gallito. *Wilson Bulletin* 113:104–108.
- MEZQUIDA, E. T. 2001b. La reproducción de algunas especies de Dendrocolaptidae y Furnariidae en el desierto del Monte central, Argentina. *El Hornero* 16:23–30.
- MEZQUIDA, E. T. 2002. Nidificación de ocho especies de Tyrannidae en la Reserva de Ñacuñán, Mendoza, Argentina. *El Hornero* 17:31–40.
- MEZQUIDA, E. T., AND L. MARONE. 2000. Breeding biology of Gray-crowned Tyrannulet in the Monte Desert, Argentina. *Condor* 102:205–210.
- 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.
- MEZQUIDA, E. T., AND L. MARONE. 2003. Comparison of the reproductive biology of two *Poospiza* warbling-finches of Argentina in wet and dry years. *Ardea* 91:251–262.
- MORENO, J., S. MERINO, R. A. VÁSQUEZ, AND J. J. ARMESTO. 2005. Breeding biology of the Thorn-tailed Rayadito (Furnariidae) in south-temperate rainforests of Chile. *Condor* 107:69–77.
- MURPHY, E. C. 1978. Seasonal variation in reproductive output of House Sparrows: The determination of clutch size. *Ecology* 59:1189–1199.
- NAVARRO, J. L., M. B. MARTELLA, AND E. H. BUCHER. 1995. Effects of laying date, clutch size, and communal nest size on the reproductive success of Monk Parakeets. *Wilson Bulletin* 107:742–746.
- NORES, A. I., AND M. NORES. 1994. Nest building and nesting behavior of the Brown Cacholote. *Wilson Bulletin* 106:106–120.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242–255.
- PERRINS, C. M., AND R. H. MCCLEERY. 1989. Laying dates and clutch size in the Great Tit. *Wilson Bulletin* 101:236–253.
- PRICE, T., M. KIRKPATRICK, AND S. J. ARNOLD. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240:798–799.
- REBORDA, J. C., M. E. MERMOZ, V. MASSONI, A. A. ASTIÉ, AND F. L. RABUFFETTI. 2003. Impacto del parasitismo de cría del tordo renegrado (*Molothrus bonariensis*) sobre el éxito reproductivo de sus hospedadores. *El Hornero* 18:77–88.
- REMSEN, J. V., JR. 2003. Family Furnariidae (Ovenbirds). Pages 162–357 in *Handbook of the Birds of the World, vol. 8: Broadbills to Tapaculos* (J. del Hoyo, A. Elliott, and D. A. Christie, Eds.). Lynx Edicions, Barcelona, Spain.
- RICKLEFS, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97:38–49.
- RICKLEFS, R. E. 2002. Splendid isolation: Historical ecology of the South American passerine fauna. *Journal of Avian Biology* 33:207–211.
- ROBINSON, T. R., W. D. ROBINSON, AND E. C. EDWARDS. 2000. Breeding ecology and nest-site selection of Song Wrens in central Panama. *Auk* 117:345–354.
- ROTELLA, J. 2009. Nest survival models. In *Program MARK: "A Gentle Introduction," 8th ed.* (E. Cooch and G. White, Eds.). [Online.] Available at www.phidot.org/software/mark/docs/book/.
- RUSSELL, E. M., Y. YOM-TOV, AND E. GEFFEN. 2004. Extended parental care and delayed dispersal: Northern, tropical, and southern passerines compared. *Behavioral Ecology* 15:831–838.

- SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–458.
- SLAGSVOLD, T. 1982. Clutch size variation in passerine birds: The nest predation hypothesis. *Oecologia* 54:159–169.
- SOCKMAN, K. W. 1997. Variation in life-history traits and nest-site selection affects risk of nest predation in the California Gnatcatcher. *Auk* 114:324–332.
- SPERRY, J. H., R. G. PEAK, D. A. CIMPRICH, AND P. J. WEATHERHEAD. 2008. Snake activity affects seasonal variation in nest predation risk for birds. *Journal of Avian Biology* 39:379–383.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 (Supplement 1):S120–S139.
- YOM-TOV, Y., M. I. CHRISTIE, AND G. J. IGLESIAS. 1994. Clutch size in passerines of southern South America. *Condor* 96:170–177.
- ZYSKOWSKI, K., AND R. O. PRUM. 1999. Phylogenetic analysis of the nest architecture of Neotropical ovenbirds (Furnariidae). *Auk* 116:891–911.

Associate Editor: C. A. Lindell