Parental Care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters

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ABSTRACT.—The genus *Sporophila* (Emberizidae) comprises species of small finches characterized by marked sexual dichromatism, which in birds is positively associated with extent of female bias in parental care. We analyzed differences in parental care in Tawny-bellied (*S. hypoxantha*) and Rusty-collared (*S. collaris*) seedeaters. We video-recorded nest activity during incubation and when young were 2–4 and 7–9 days of age. Females of both species built the nest and incubated the eggs alone. Female Tawny-bellied Seedeaters: (1) incubated 59% of the time, (2) had a higher frequency of nest visits than males when chicks were 2–4 days of age, and (3) their visits were longer because after feeding they remained in the nest brooding the chicks. There were no gender differences in frequency of nest visits when chicks were 7–9 days of age, but visits of females were longer than those of males. Female Rusty-collared Seedeaters: (1) incubated 51% of the time and (2) had a higher frequency of nest visits when chicks were 7–9 days of age. Both males and females brooded chicks and there were no gender differences in frequency and length of nest visits when chicks were 2–4 days of age. Parental care in both species is female biased, but the extent of male care is slightly higher in Rusty-collared than in Tawny-bellied seedeaters. *Received 4 February 2008. Accepted 29 April 2008.*

The most common mating pattern among birds is social monogamy with biparental care (Lack 1968, Silver et al. 1985, Neudorf 2004). However, there is a considerable variation in type and extent of male care within monogamous species, as males may or may not defend territories, build the nest, incubate the eggs, brood and deliver food to the nestlings, and assist fledglings after they leave the nest (Clutton-Brock 1991).

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The genus *Sporophila* (Emberizidae) comprises 31 species of small finches that inhabit grassy open and semi-open habitats from Mexico to central Argentina (Meyer de Schauensee 1952, Ridgely and Tudor 1989). All *Sporophila* species are characterized by a marked plumage-color dimorphism with males strongly patterned and colorful, and females duller and similar between species (Ridgely and Tudor 1989). Variation in melanin-based dichromatism in birds is positively associated with extent of gender bias in passive brood defense (Owens and Hartley 1998). Males of dichromatic species are less likely to participate in nest building (Soler et al. 1998) and to share incubation with females (Verner and Willson 1969).

The reproductive biology of *Sporophila* seedeaters is little studied and most research was in Central America (i.e., Gross 1952, Skutch 1954, Alderton 1961, Stutchbury et al. 1996, but see Marcondes-Machado 1997, Francisco 2006). These studies indicate that most *Sporophila* seedeaters are socially monogamous and have biparental care, but do not report details of sexual differences in parental care.

The reproductive biology of Tawny-bellied Seedeater (*S. hypoxantha*) and Rusty collared Seedeater (*S. collaris*) is virtually unknown, except for the work of Di Giacomo (2005). Tawny-bellied Seedeaters are included within the ''capuchinos'', a monophyletic group of 11 species (Lijtmaer et al. 2004) that share a similar male plumage coloration pattern (Ridgely and Tudor 1989). Rusty-collared Seedeaters are included in a different clade than Tawny-bellied Seedeaters (Lijtmaer et al. 2004) allowing us to compare gender differences in parental care between species that are relatively distant within the genus. The objectives of our study were to: (1) analyze the extent of gender bias in parental care in *S. hypoxantha* and *S. collaris,* and (2) compare gen-

der differences in parental care between these species.

METHODS

Study Area.—The study was conducted at Reserve El Bagual (26° 10′ S; 58° 56′ W), in the Province of Formosa, Argentina, during breeding seasons 2004–2005 and 2005–2006. This 3,300-ha reserve is in the region of the eastern or humid Chaco. Average annual rainfall in the area is 1,500 mm with mean monthly temperature varying from 16.9° C in July to 26.7° C in January.

Study Species.—Tawny-bellied Seedeaters are sexually dichromatic but genders do not differ in body size (~8–9 g). They are residents at our study site and nest in dry grasslands of *Elionurus muticus* and *Imperata brasiliensis* or *Andropogon lateralis*, and in wet grasslands of *Paspalum intermedium* and *Sorghastrum setosum*. Laying starts during the second half of October and continues until the second half of March. The nest is a deep semispherical open cup built at a height of ~70 cm above ground level. Clutch size is 2–3 eggs; incubation starts with the laying of the penultimate egg and lasts 11–12 days. Young fledge when they are 9–10 days of age (Di Giacomo 2005).

Rusty-collared Seedeaters are sexually dichromatic and males and females do not differ in body size (~12–13 g.). They are residents at our study site and nest in wetlands of *Cyperus giganteus* from early November to early April. The nest is a semispherical open cup built at a height of 1–1.5 m above ground level. Clutch size is 2–3 eggs; incubation starts with laying of the penultimate egg and lasts 12–13 days. Young leave the nest when they are 9–12 days of age (Di Giacomo 2005).

Data Collection.—We searched for nests during the breeding season and visited nests daily or every other day to identify start of laying and date of hatching. We recorded nest-building activity in 18 nests of Tawny-bellied Seedeaters and 10 nests of Rusty-collared Seedeaters. We recorded the gender of the individual that carried nest material during 3–4 consecutive trips for each nest (~15–25 min of observation/nest). We video-recorded nest activity using a Sony Hi8 CCD video camera placed 1.5–2 m from the nest. Video records lasted between 2 and 4 hrs. We video recorded

six nests during incubation (12 hrs of video records) for Tawny-bellied Seedeaters, 13 nests with chicks 2–4 days of age (36 hrs), and five nests with chicks 7–9 days of age (12 hrs). We video recorded four nests of Rusty-collared Seedeaters during incubation (8 hrs), four nests with chicks 2–4 days of age (8 hrs), and six nests with chicks 7–9 days of age (20 hrs). We observed both members of the pair at all of these nests. We video recorded each nest throughout incubation during morning (between 0700 and 1100 hrs) and afternoon (between 1500 and 1900 hrs). We video recorded nests only during the morning for the chick stages.

Data Analysis.—We watched the videotapes in the laboratory and identified the gender of the parent, number of times (to the nearest sec) it landed at, entered, exited, and departed from the nest, and activity at the nest (incubation, feeding, or brooding). We measured the length of each activity in those visits where there were two different behaviors (i.e., feeding and brooding). We calculated the frequency of visits to the nest (nest visits/hr) for each parent, average length of the visits (sec), time elapsed between visits (sec), and proportion of time spent incubating eggs, and feeding and brooding chicks.

We used nonparametric statistics for analyses due to lack of normality of the data and small sample sizes of the groups. Statistical analyses were performed using StatView Version 5.0 statistical software (SAS Institute 1998). All *P*-values are two-tailed with alpha (α) set at 0.05. Data are presented as means ± standard errors. We provide confidence intervals when comparisons yield a nonsignificant result because of small sample sizes (Colegrave and Ruxton 2003).

RESULTS

Tawny-bellied Seedeaters.—Females built the nest and incubated the eggs alone. We did not find differences in frequency and length of incubation bouts between morning and afternoon (Wilcoxon Signed Rank tests, frequency: $z = -0.94$, $P = 0.35$, $n = 6$; length: $z = -0.10$, $P = 0.92$, $n = 6$). Females spent 59 ± 5% of the time at the nest including observations of morning and afternoon together; frequency and length of incubation bouts were 2.3 ± 0.2 bouts/hr and 16.5 min
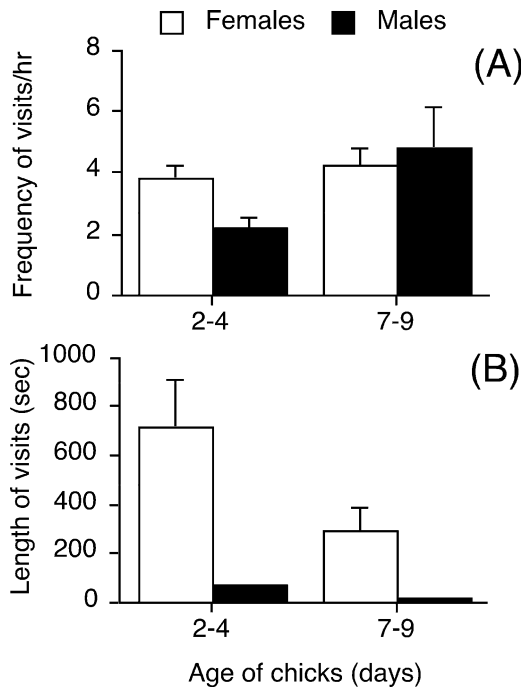
FIG. 1. (A) Frequency and (B) length of nest visits by female and male Tawny-bellied Seedeaters (*Sporophila hypoxantha*) at Reserve El Bagual, Formosa Province, Argentina. Values are mean ± standard errors. The number of nests analyzed was 13 and five for chicks 2–4 and 7–9 days of age, respectively.

± 27 sec, respectively. Males fed females during incubation at three of six nests with a frequency of 0.9 ± 0.5 feedings/hr. Clutch size in nests monitored during incubation was 2.5 ± 0.5 ($n = 6$ nests).

Females had a higher frequency of nest visits than males when chicks were 2–4 days of age ($z = -2.2$, $P = 0.028$, $n = 13$; Fig. 1). Visits of females were longer than those of males ($z = -3.2$, $P = 0.002$, $n = 13$; Fig. 1); the female remained in the nest brooding the chicks after feeding them on 86% of the visits. Females spent $40 \pm 3\%$ of the time brooding chicks while this behavior was not observed in males. The frequency of female's visits with brooding was negatively associated with air temperature (Spearman Rank correlation, $\rho = -0.59$, $z = -2.04$, $P = 0.042$, $n = 13$), but there was no association between length of brooding visits and air temperature ($\rho = 0.19$, $z = 0.67$, $P = 0.51$, $n = 13$). The number of

chicks in nests monitored at this stage was 1.9 ± 0.5 ($n = 13$).

There were no gender differences in frequency of nest visits when chicks were 7–9 days of age ($z = -0.7$, $P = 0.50$, $n = 5$, mean ± SD females: 4.2 ± 1.4, males: 4.8 ± 2.9, 95% confidence interval: $-3.8 - 2.6$; Fig. 1), but females still had significantly longer visits than males ($z = -2.0$, $P = 0.043$, $n = 5$; Fig. 1). Females continued brooding chicks in 21% of the visits and spent $5 \pm 2\%$ of the time in this activity; this behavior was not observed in males. The number of chicks in the nests monitored at this stage was 1.6 ± 0.5 ($n = 5$). Both males and females removed fecal sacs during the chick stage.

Rusty-collared Seedeaters.—Females built the nest and incubated the eggs alone. We did not find differences between morning and afternoon in frequency ($z = -0.37$, $P = 0.72$, $n = 4$) and length ($z = -0.0$, $P = 0.99$, $n = 4$) of incubation bouts. We combined morning and afternoon observations; females spent $51 \pm 8\%$ of the time at the nest with a frequency and length of the incubation bouts of 3.0 ± 0.6 bouts/hr and 12.5 ± 3.2 min, respectively. We observed that in one of four nests the male fed the female during incubation (frequency $= 0.65$/hr). Clutch size in the nests monitored during incubation was 2.7 ± 0.5 ($n = 4$ nests).

The frequency and length of nest visits when chicks were 2–4 days of age did not differ between genders ($z = -0.73$, $P = 0.46$, $n = 4$, mean ± SD females: 3.1 ± 1.7, males: 1.5 ± 2.1, 95% confidence interval: $-2.4 - 5.5$; and $z = -1.46$, $P = 0.14$, $n = 4$, mean ± SD females: 263.8 ± 330.8 sec, males: 56.1 ± 75.2 sec, 95% confidence interval: $-228.1 - 644.1$, respectively, Fig. 2). Females spent $19 \pm 15\%$ of the time brooding chicks. The male brooded the chicks in two of four nests. The number of chicks in the nests monitored at this stage was 2.2 ± 0.5 ($n = 4$).

The frequency of nest visits was higher for females when chicks were 7–9 days of age ($z = -2.0$, $P = 0.046$, $n = 6$; Fig. 2). Females brooded the chicks $13 \pm 8\%$ of the time at this stage, while brooding by males was not observed; we did not detect gender differences in length of nest visits ($z = -1.4$, $P = 0.17$, $n = 6$, mean ± SD females: 364.8 ± 617.8 sec, males: 16.7 ± 2.76 sec, 95% confidence interval: $-299.3 - 995.5$; Fig. 2). The number

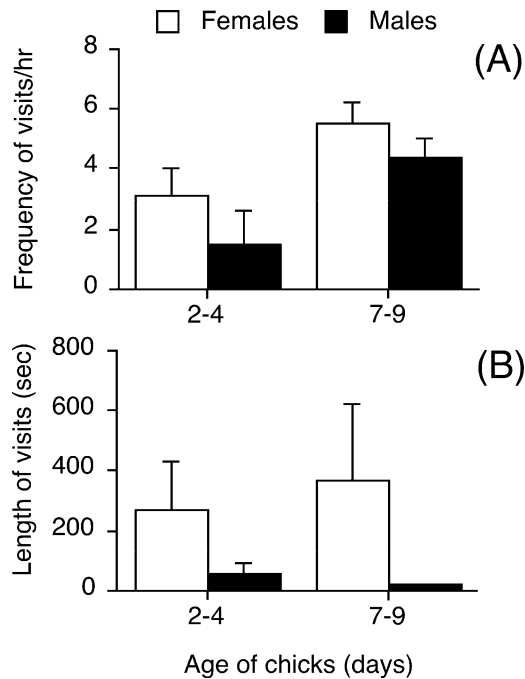FIG. 2.   (A) Frequency and (B) length of nest visits by female and male Rusty-collared Seedeaters (*Sporophila collaris*) at Reserve El Bagual, Formosa Province, Argentina. Values are mean ± standard errors. The number of nests analyzed was four and six for chicks 2–4 and 7–9 days of age, respectively.

of chicks in the nests monitored at this stage was 1.7 ± 0.8 ($n = 6$). Both males and females removed fecal sacs during the chick stage.

DISCUSSION

Parental care is female biased in Tawny-bellied and Rusty-collared seedeaters. The female built the nest and incubated the eggs without assistance of the male in both species. The pattern of parental care after hatching was also similar between species with females spending more time at the nest than males. The main difference between species was that male Rusty-collared Seedeaters brooded the chicks while this was not observed in Tawny-bellied Seedeaters. Other differences between species (i.e., lack of gender differences in frequency and length of visits in the period of 2–4 days of age in Rusty-collared Seedeaters) could be attributed to low power because of small sample sizes.

There are previous studies in other species of seedeaters that provide some qualitative data on type and extent of parental care including: White-collared Seedeater (*S. morelleti*; Skutch 1954), Slate-colored Seedeater (*S. schistacea*; Stutchbury et al. 1996), Variable Seedeater (*S. corvine*; Gross 1952, Skutch 1954), Lined Seedeater (*S. lineola*; Marcondes-Machado 1997), Yellow-bellied Seedeater (*S. nigricollis*; Alderton 1961), and Double-collared Seedeater (*S. caerulescens*; Francisco 2006). The female incubates the eggs and broods the chicks alone in all of these species and males did not participate in nest building, except for Yellow-bellied Seedeaters. Both parents provision the young in most of these species but there is no information on gender bias in provisioning rates (except for Double-collared Seedeater where females have a higher frequency of nest visits than males, Francisco 2006). The only species where males do not participate in chick feeding is Slate-colored Seedeater (Stutchbury et al. 1996). None of the previous studies reported mate feeding by males during incubation (as we observed in Tawny-bellied and Rusty-collared seedeaters) or male brooding (as we observed in Rusty-collared Seedeater). The results for species of seedeaters studied to date indicate this group has female biased biparental care with noticeable differences in the type and extent of male care.

Plumage coloration often has an important role in conspecific interactions (Andersson 1994); Owens and Hartley (1998) reported gender differences in parental care are associated with melanin-based dimorphism. Eumelanin pigments often signal competitive ability and social dominance (Senar 1999), and act as honest signals of male parental quality in a few species (Siefferman and Hill 2003). We did not study the pigments responsible for plumage coloration, but it is likely the rufous rump and underparts of Tawny-bellied Seedeaters, and the black head, black pectoral band, and cinnamon rump and underparts of Rusty-collared Seedeaters are produced by eumelanins and pheomelanins (Gill 1995). Further studies analyzing preference of females for coloration of males, and the association between coloration of males and parental quality may help in understanding the function of sexual dichromatism in this group.

LITERATURE CITED

ALDERTON, C. C. 1961. The breeding cycle of the Yellow-bellied Seedeater in Panama. Condor 63:390–398.

ANDERSSON, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.

CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey, USA.

COLEGRAVE, N. AND G. D. RUXTON. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. Behavioral Ecology 14:446–450.

DI GIACOMO, A. G. 2005. Aves de la Reserva El Bagual. Pages 203–465 in Historia Natural y Paisaje de la Reserva El Bagual. Temas de Naturaleza y Conservación 4 (A. G. Di Giacomo and S. F. Krapovickas, Editors). Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires, Argentina.

FRANCISCO, M. R. 2006. Breeding biology of the Double-collared Seedeater (Sporophila caerulescens). Wilson Journal of Ornithology 118:85–90.

GILL, F. B. 1995. Ornithology. W. H. Freeman and Company, New York, USA.

GROSS, A. O. 1952. Nesting of Hicks' Seedeater at Barro Colorado Island, Canal Zone. Auk 69:433–446.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen Press, London, United Kingdom.

LIJTMAER, D. A., N. M. M. SHARPE, P. L. TUBARO, AND S. C. LOUGHEED. 2004. Molecular phylogenetics and diversification of the genus Sporophila (Aves: Passeriformes). Molecular Phylogenetics and Evolution 33:562–579.

MARCONDES-MACHADO, L. O. 1997. Reproductive behavior of Sporophila lineola (Linnaeus) (Passeriformes, Emberizidae). Revista Brasileira de Zoologia 14:517–522.

MEYER DE SCHAUENSEE, R. 1952. A review of the genus Sporophila. Proceedings of the Academy of Natural Sciences of Philadelphia 104:153–196.

NEUDORF, D. L. H. 2004. Extrapair paternity in birds: understanding variation among species. Auk 121:302–307.

OWENS, I. P. F. AND I. R. HARTLEY. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society of London, Series B 265:397–407.

RIDGELY, R. S. AND G. TUDOR. 1989. The birds of South America. Volume 1. Oxford University Press, Oxford, United Kingdom.

SAS INSTITUTE. 1998. StatView user's guide. Version 5.0. SAS Institute Inc., Cary, North Carolina, USA.

SENAR, J. C. 1999. Plumage coloration as a signal of social status. Proceedings of the International Ornithological Congress 22:1669–1686.

SIEFFERMAN, L. AND G. E. HILL. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male Eastern Bluebirds. Behavioral Ecology 14:855–861.

SILVER, R., H. ANDREWS, AND G. F. FALL. 1985. Parental care in an ecological perspective: quantitative analysis of avian subfamilies. American Zoologist 25:823–840.

SKUTCH, A. F. 1954. Life histories of Central American birds. Families Fringillidae, Thraupidae, Icteridae, Parulidae and Coerebidae. Pacific Coast Avifauna 31:19–49.

SOLER, J. J., A. P. MØLLER, AND M. SOLER. 1998. Nest building, sexual selection and parental investment. Evolutionary Ecology 12:427–441.

STUTCHBURY, B. J. M., P. R. MARTIN, AND E. S. MORTON. 1996. Nesting behavior of the Slate-Colored Seedeater (Sporophila schistacea) in Panama. Ornitología Neotropical 7:63–65.

VERNER, J. AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle. Ornithological Monographs 9:1–76.