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SEXUAL DIMORPHISM AND PARENTAL ROLES IN THE THORN-TAILED RAYADITO (FURNARIIDAE)

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Abstract. Sexual dimorphism, mating system, and parental care are known for only a few species of the large passerine family Furnariidae. We conducted a study of sexual dimorphism in morphology, coloration, and parental roles during incubation and chick-rearing in the Thorn-tailed Rayadito (*Aphrastura spinicauda*), a characteristic resident ovenbird of the southern temperate rainforests of Chile and Argentina. Through molecular sexing, morphological measurements, and spectrophotometric analysis of body plumage and rectrices of reproductive adults captured on Chiloé Island (southern Chile), we determined that males were between 2% and 10% larger than females in mass, tarsus length, and wing length, while no difference was found for the length of the bill or the two longest central rectrices and their characteristic spines, or in plumage coloration. Heavy males were paired with heavy females and light males with light females. Males and females participated equally in all reproductive activities during the incubation and nestling phases, except removal of nestling feces, in which females were twice as active as males. In a study of habitat use on Navarino Island (extreme southern Chile) we found that the extended graduated tail, with rectrices that end in spines, which gives the species its name, was not used as a support while foraging and could be related to another function such as sexual or social signaling. The absence of sexual dimorphism in plumage and parental roles in rayaditos may be related to the use of the long, graduated tail as a signal of quality by both sexes, although this hypothesis requires confirmation through future mate choice studies.

Key words: monogamy, parental care, parental roles, plumage coloration, sexual dimorphism, sexual selection, tail length.

Dimorfismo Sexual y Roles Parentales en *Aphrastura spinicauda* (Furnariidae)

Resumen. El dimorfismo sexual, el sistema de apareamiento y el cuidado parental solo se conocen para unas pocas especies de la gran familia de paseriformes Furnariidae. Realizamos un estudio del dimorfismo sexual en morfología, coloración y roles parentales durante la incubación y la crianza de los polluelos en *Aphrastura spinicauda*, un furnárido residente característico de los bosques lluviosos templados de Chile y Argentina. Por medio de sexado molecular, medidas morfológicas y análisis espectrofotométrico del plumaje corporal y de las rectrices de adultos reproductores capturados en la Isla de Chiloé (Chile meridional), determinamos que los machos eran entre un 2% y un 10% mayores que las hembras en peso y longitudes de tarso y ala, mientras no se encontraron diferencias en las longitudes del pico y de las dos rectrices centrales más largas a cada lado de la cola así como de las características espinas terminales de las rectrices. Machos pesados estuvieron emparejados con hembras pesadas y machos ligeros con hembras ligeras. Los machos participaron tanto como las hembras en todas las tareas reproductivas durante las fases de incubación y crianza, excepto en cuanto a la retirada de sacos fecales, en que las hembras se mostraron el doble de activas que los machos. En un estudio en la Isla de Navarino (extremo meridional de Chile) comprobamos que la larga y graduada cola con las rectrices terminando en espinas no fue empleada como soporte durante la búsqueda de alimento, por lo que podría estar implicada en alguna otra función como señalización sexual o social. La ausencia de dimorfismo sexual en plumaje y roles parentales en el Rayadito puede estar relacionada con la utilización de la larga cola como señal de calidad en ambos sexos, aunque esta hipótesis requiere confirmación a través de futuros estudios de elección de pareja.

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INTRODUCTION

Detailed information about sexual dimorphism and the role of each sex in parental care is lacking for the great majority of species in the large passerine family Furnariidae (Remsen 2003). Furnariids are characteristically sexually monochromatic, and in most species both sexes have brown coloration and complex plumage patterns, which are exhibited during the displays of some species. Sexual dimorphism in size is also slight. For the few species studied in detail, males are on average only slightly larger in linear measurements (Winker et al. 1994, Remsen 2003). This is in accordance with the presumed social monogamy of many species, and the apparent equality between the sexes in parental care: the few existing studies suggest that both members of the pair contribute to nest-building, incubation, and feeding of nestlings and fledglings (Kendeigh 1952, Fraga 1980, Nores and Nores 1994, Skutch 1996).

Many furnariids have exceptionally long tails, in some cases among the longest tails with respect to body size for any passerine (Remsen 2003). These tails are often graduated, with rectrices ending in spines. The use of these tails for support on trunks or vertical branches has been proposed for several species in which the rachises are stiffened and the distal ends function as braces during climbing (Remsen 2003). However, a stiffened rachis is not always evidence of climbing behavior while foraging (Skutch 1967, Remsen 2003), and tails in some species are too long to be useful in foraging (e.g., the extremely long tail of des Muir's Wiretail [*Sylviorthorhynchus desmursii*]). This suggests to us that sexual selection has emphasized tail development instead of body coloration in furnariids.

We studied sexual dimorphism, the role of each sex in parental care, and foraging behavior in a furnariid characteristic of southern temperate forests in Chile and Argentina, the Thorn-tailed Rayadito (*Aphrastura spinicauda*). Rayaditos are small, active, insectivorous birds that glean prey items from tree branches and trunks, and forage from the understory to the canopy (Vuilleumier 1967). They are resident cavity-nesters, with low fecundity and prolonged parental care of eggs and chicks (Moreno et al. 2005). In winter, rayaditos travel in mixed-species flocks, in which they are the main species around which other birds congregate (Ippi and Trejo 2003). They show an apparent lack of sexual dichromatism and size dimorphism, although no quantitative morphological study on this species has been conducted to date. No detailed information about the role of each sex in parental care in this species has been published. The characteristic long and graduated spiny tail of rayaditos suggests that it may function as a brace and support while foraging or as a sexually selected ornament in both sexes. Graduated tails incur an aerodynamic cost through increased drag (Thomas 1993), and are often sexually selected by acting as handicaps (Andersson 1982, Grafen 1990, Johnstone 1995). Using molecular sexing, morphological measurements, detailed spectral analyses of plumage coloration, and observations of parental provisioning at the nest and of foraging and habitat use, we aimed to establish: (1) if tails are normally used for support while foraging, and (2) the degree of sexual dimorphism in morphology, coloration, and parental care in this socially monogamous species.

METHODS

FORAGING BEHAVIOR

In December 2005, we conducted a study of habitat use by three local populations of Thorn-tailed Rayaditos foraging in mature *Nothofagus* forests on the island of Navarino (54°55′S, 67°40′W). Our aim was to elucidate the function of the tail while foraging. In each study site, we walked slowly through the forest along linear transects and stopped as soon as we observed a foraging rayadito. After 10 sec of observation, we began to record on tape the following data: type of substrate (ground, trunk, thick branch directly protruding from trunk, thin outer branch growing from a higher order branch, or foliage), height of substrate above ground, rayadito posture (climbing upward, climbing downward, hanging upside down, horizontally moving along a branch), and the position of the tail (in the air or leaning against the substrate). In cases where the tip of the tail leaned against the substrate, we noted if it barely touched the substrate or was pressed against it. Recordings were made every 5 sec. We made $\leq$10 records per observation (mean number of records per observation = 5.4 $\pm$ 0.4 SE, range = 2–10). To avoid repeating ob-

servations on the same individual, we left the immediate area and continued along the transect for at least 40–50 m before making further observations. For each individual observed, we calculated the proportion of records per observation on different substrates and in different postures, when the tail was in the air or touching the substrate, and the average height of the records. As sex was unknown in this study, we did not make any statistical comparison, and instead present average values for individuals to describe the use of the tail by foraging rayaditos.

MORPHOLOGY AND COLOR MEASUREMENTS

The study of morphology and parental roles was conducted on Chiloé Island, Chile (41°52′S, 73°39′W), in the austral spring (November–December) of three years (2002–2004). Although rayaditos on Chiloé are considered a different subspecies than birds in central Chile and Navarino (Johnson and Goodall 1967), they are morphologically very similar (RAV et al., unpubl. data). Adults were captured in the context of a study of the breeding biology of rayaditos using nest boxes (Moreno et al. 2005). For a description of the study area, see Moreno et al. (2005). Adults were captured with nest-box traps when chicks were 13 days old (hatching day = day 0). Birds were banded with individual combinations of color and metal bands (National Band and Tag Co., Newport, Kentucky, model 1242–3). Following Svensson (1984), we measured tarsus length and bill length (using digital calipers, to the nearest 0.1 mm), flattened wing chord (to the nearest mm with a stopped ruler), and the two central rectrices on the right side of the tail (to the nearest mm with a stopped ruler designed for tail measurements). The two central rectrices on each side of the graduated tail are the longest, while all rectrices have a spine (Fig. 1). We measured total rectrix length and length excluding the spine. All measurements were taken by the same person. There was no obvious difference between the sexes at this stage of the breeding cycle, as all birds showed signs of a brood patch and there was no detectable difference between mates in the size of the cloacal protuberance (differences may possibly be evident during earlier breeding stages). Mass was recorded with a Pesola (Baar, Switzerland) spring balance to the nearest 0.1 g. As all individuals were captured in the same nesting stage, it was not necessary to control for stage-dependent mass changes. A drop of blood was obtained by brachial venipuncture, and blood was stored in a buffer solution (100 mM of Trishydroxymethylaminomethane [TRIS] pH = 8.0, 100 mM of Ethylenediaminetetraacetic acid [EDTA] and 2% Sodium Dodecyl Sulfate [SDS]) for DNA preservation until analysis. The exact age was known for only

FIGURE 1. Thorn-tailed Rayadito with its characteristic graduated tail.

two breeding adults, banded as chicks the previous year.

In 2004, we measured plumage color with a portable battery-driven Minolta spectrophotometer (model CM-2600d) that covered the range 360–700 nm. There is probably variation in color in the UV range below 360 nm that should be considered in future studies if furnariids are shown to respond to wavelengths in the UV range (Ödeen and Håstad 2003). Tail feathers were analyzed in the laboratory with a spectrophotometer that included the entire reflectance range (see below). The target mask of the spectrophotometer, with a diameter of 1 cm, was placed directly on the breast, top of the head, and middle of the back and rump. Reflectance spectra for each part of the body were calculated as the mean of three sequential measurements obtained by the spectrophotometer. The apparatus was moved slightly between measurements. Reference calibrations against a white standard were performed periodically according to the manufacturer's specifications. We used brightness, chroma, and hue from the CIELAB color space (Commission Internationale de l'Eclairage 1976) to describe body color in the human visible spectrum. The L*a*b*, or CIELAB, color space was used to denote brightness (L*) and chromaticity (a*, b*). In the chromaticity diagram, a* goes from green (negative values) to red (positive values), and b* goes from blue (negative values) to yellow (positive values). The farther away from zero, the more saturated the color. Chroma in the L*C*h* (brightness, chroma, hue) color space is a composite measure of chromaticity and was calculated according to the formula: Chroma = $\sqrt{(a^*)^2 + (b^*)^2}$. Hue in this space is calculated as $\tan^{-1}(b^*/a^*)$. Geometric distances in the CIELAB color space approximate intuitive color differences.

In 2004 we collected the right central rectrix of each individual by cutting it at the base and stored it away from light until analysis. The dorsal side of rectrices was measured in the laboratory with a nonportable Ocean Optics S2000 fiber-optic spectrophotometer (Ocean Optics, Inc., Dunedin, Florida) using a 200 micron fiber-optic probe with a 2 mm diameter reading area held at a 90° angle to the feather surface. Reflectance spectra curves (300–700 nm) were generated with a Spectralon white standard (Labsphere, Inc., North Sutton, New Hampshire) as a reference. We did not use the CIELAB color space with respect to tail feathers because it disregards reflectance in the UV part of the reflectance spectrum. Three consecutive measurements were taken on each of the proximal, middle, and distal parts of the feather (not including the spine) to obtain repeatabilities of reflectance spectra. Principal components analyses (PCA) were performed on the three spectra obtained for each feather. Repeatabilities of PC1 and PC2 for all parts of the feather were significant (all $R > 0.47$, all $P < 0.001$), so PCA was performed on a single reflectance spectrum for each feather calculated as the average of the reflectance spectra for the three feather parts. To reduce the number of variables in relation to the number of individuals, we grouped the 36 10 nm intervals presented by the apparatus into 18 intervals of 20 nm each by taking the average of every two intervals (Cuthill et al. 1999).

SEX DETERMINATION

DNA was isolated from blood samples using proteinase K digestion and ethanol precipitation by means of the "UltraClean DNA BloodSpin Kit" (Mo Bio Laboratories, Carlsbad, California). PCR reactions were performed in 20 µl of final volume using 0.5 U Taq Polymerase (Biotools, Madrid, Spain), 200 µM dNTP's, 1 mM Taq Buffer with $MgCl_2$, and 10 pmol of primers 2550F (5′-GTTACTGATTCGTCTACGAGA-3′) and 2718R (5′-ATTGAAATGATCCAGTGCTTG-3′). The forward and reverse primers amplified the CHD1 (chromo-helicase-DNA binding protein) sequence, present in both W and Z avian chromosomes (Fridolfsson and Ellegren 1999). The PCR reaction consisted of an initial denaturing step at 94°C for 90 sec, followed by 30 cycles of denaturation (94°C for 30 sec), annealing (48°C for 45 sec) and extension (72°C for 45 sec), and two final cycles of 48°C for 60 sec and 72°C for 5 min. PCR products were separated by electrophoresis at 90 V in 2% agarose gels in Trishydroxymethylaminomethane-acetate [TAE] buffer. The amplification products corresponded to CHD1W of 450 bp and CHD1Z of 600 bp. Birds were sexed as females (heterogametic, WZ) when both fragments were amplified and as males (homogametic, ZZ) when only the 600 bp band was visible.

TABLE 1. Mass and morphological measurements (means ± SE, *n* in parentheses) of female and male Thorn-tailed Rayaditos on Chiloé Island, Chile, with coefficients of variation (CV). Significant differences between the sexes after sequential Bonferroni correction are denoted with an asterisk.

	Female	CV	Male	CV	*t*	*P*
Mass (g)	10.3 ± 0.1 (29)	4.9	11.3 ± 0.1 (26)	5.4	7.0	< 0.001*
Tarsus length (mm)	19.5 ± 0.1 (29)	4.3	20.0 ± 0.1 (25)	2.3	2.8	0.008*
Wing length (mm)	55.0 ± 0.3 (29)	3.2	58.0 ± 0.3 (27)	3.0	6.4	0.001*
Bill length (mm)	13.9 ± 0.1 (29)	4.0	14.3 ± 0.2 (27)	6.8	2.3	0.03
Longest rectrix (mm)	71.6 ± 0.9 (29)	6.3	70.0 ± 0.9 (27)	7.2	1.2	0.22
Spine of longest rectrix (mm)	19.8 ± 0.8 (29)	20.9	18.3 ± 0.9 (27)	25.1	1.3	0.19
Second-longest rectrix (mm)	57.6 ± 0.7 (23)	6.8	58.1 ± 0.7 (24)	4.5	0.5	0.59
Spine of second-longest rectrix (mm)	8.9 ± 0.3 (23)	18.3	8.9 ± 0.3 (24)	19.7	0.01	0.99

PARENTAL CARE

Most observations of parental care by banded pairs were obtained on day 3 ($n = 5$) and days 14–17 after hatching ($n = 18$). Observations of banded pairs during the nestling stage were used to compare parental care between the sexes. Two observations of banded pairs and nine observations of unbanded pairs during incubation were also obtained. Observations of incubating pairs were used for descriptive purposes only, as sex of individuals could not be established in most cases. Activity at nest boxes was recorded with video cameras for periods of 4 hr in 2003 (all observations on day 3 and 12 observations on days 14–17) and 90 min in 2004. In total, 104 hr of observations were obtained in 2003 and 33 hr in 2004. The number of feeding visits and the number of times fecal sacs were removed were obtained from the videotapes. The time spent inside the nest box when chicks were three days old was also recorded.

STATISTICAL ANALYSIS

As several individuals were measured and observed in more than one year, we used data from only the last year in which an individual was studied. Similarly, for pairs that bred together in more than one year, only data for the last year were used in statistical comparisons. Different sample sizes for the two sexes in comparisons between sexes are due to elimination of some observations to avoid pseudoreplication. Comparisons between the sexes were conducted both independently of mates (using ANOVA) and within pairs (paired *t*-tests). All parental care variables are expressed per hour of observation. Sequential Bonferroni corrections for multiple tests were applied when two or more associated tests were conducted (Rice 1989). Means are presented ± SE.

RESULTS

FORAGING BEHAVIOR

In total, 46 individuals were observed for periods of less than one minute. Substrates were used in the following proportions of records per observation: 0.25 ± 0.05 foliage, 0.25 ± 0.05 thin outer branches, 0.22 ± 0.04 primary thick branches, 0.21 ± 0.04 trunk, and 0.04 ± 0.02 ground. The mean height per observation at which rayaditos foraged was 7.7 ± 6.5 m. The proportions of records per observation in which foraging postures were used were: 0.53 ± 0.05 for horizontal movement along branches, 0.28 ± 0.04 for hanging upside down, 0.17 ± 0.04 for climbing upward along trunks or steep branches, and 0.02 ± 0.01 for climbing downward. Rayaditos held their tails in the air in 0.96 ± 0.01 of the records per observation, and they leaned their tails against the substrate in the remaining 0.03 ± 0.01 of the records per observation. All records of rayaditos leaning their tails against the substrate were made when they climbed upward on trunks. In all these cases, the tip of the tail only briefly touched the trunk and appeared to be used for balance, not support.

MORPHOLOGY

Males were larger than females with respect to tarsus length, wing length, and mass (Table 1). However, no differences with respect to bill length or the length of the two longest rectrices and their protruding spines were found (Table 1). Within-pair comparisons returned similar results as the general comparisons between sexes, with differences in all morphological

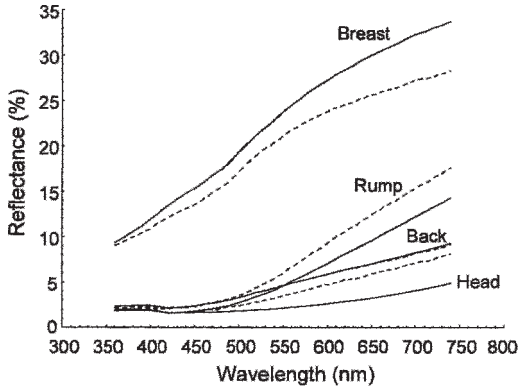

FIGURE 2. Reflectance spectra of four body parts of female (solid lines) and male (dotted lines) Thorn-tailed Rayaditos on Chiloé Island, Chile. Only reflectance in the wavelengths visible to humans was measured. Data are means for all measured individuals ($n = 9$ for females, $n = 10$ for males).

variables except rectrix and spine lengths (paired t-tests: all $t_{23–26} > 3$, all $P < 0.01$), for all variables except tail variables (all $t_{21–26} < 1.5$, all $P > 0.10$). Coefficients of variation were similar for all variables, except that the lengths of the central rectrices showed slightly higher values (Table 1). Tail spine lengths showed very high coefficients of variation, as is expected for parts of a structure compared with whole structures (Lande 1977). We took measurements from four females and four males in more than one year. Of these, three females and two males showed increases with time in the length of the longest rectrix, while one female showed no change and two males showed decreases. Significant within-pair correlations were found with respect to mass only ($r_{23} = 0.5$, $P = 0.009$; for other traits all $r_{20–25} < 0.3$, all $P > 0.10$), indicating that heavy males were paired with heavy females.

COLOR

Reflectance spectra of head, back, and rump plumage were typical of dark-brownish colored objects, while breast plumage showed reflectance spectra typical of whitish-brown objects (Fig. 2). No evidence of high reflectance close to the UV range was detected. There was no difference between the sexes in body plumage color as represented by brightness, chroma, and hue in the CIELAB color space (Table 2). Within-pair comparisons showed the same results as the independent comparisons between sexes (all $t_{5–8} < 1.8$, all $P > 0.10$). There were no within-pair associations with respect to body color after correcting for multiple tests (all $r_{4–7} < 0.4$, all $P > 0.33$).

Reflectance spectra of tail feathers were similar to those for body plumage, with reflectance in the UV range very low. Two principal components explained more than 92% of the variation in reflectance spectra for the longest tail feathers (PC1: 82%, eigenvalue = 29.3; PC2: 16%, eigenvalue = 5.8). PC1 was related to achromatic brightness and was flat with respect to wavelength (high values represent dark feathers and low values pale feathers), and PC2 was associated with hue and declined monotonically with wavelength, with the high-

TABLE 2. Comparisons between body plumage color measures (means ± SE, number of individuals in parentheses) in the CIELAB color space of female and male Thorn-tailed Rayaditos on Chiloé Island, Chile. L* (lightness) ranges from 0 (extremely dark) to 100 (extremely light), C* (chroma) ranges from 0 (achromatic) to 60 (fully saturated color), and h* is an angular variable going from 0° (red) to 90° (yellow), 180° (green), 270° (blue), and full circle to red again (360°). No tests were significant after Bonferroni correction.

	Females	Males	t	P
L* Head	15.6 ± 1.9 (9)	17.9 ± 4.0 (10)	0.5	0.63
C* Head	6.2 ± 1.4 (9)	10.2 ± 3.2 (10)	1.1	0.28
h* Head	45.2 ± 7.0 (9)	53.8 ± 3.5 (10)	1.1	0.27
L* Breast	53.1 ± 2.8 (10)	52.2 ± 1.8 (10)	0.3	0.80
C* Breast	15.4 ± 2.3 (10)	15.7 ± 1.7 (10)	0.1	0.93
h* Breast	80.6 ± 1.3 (10)	80.9 ± 0.9 (10)	0.1	0.89
L* Back	25.4 ± 0.9 (10)	25.3 ± 1.4 (10)	0.1	0.93
C* Back	14.7 ± 1.4 (10)	15.1 ± 1.2 (10)	0.2	0.82
h* Back	71.0 ± 1.2 (10)	71.5 ± 0.8 (10)	0.3	0.75
L* Rump	26.1 ± 1.1 (10)	30.1 ± 1.1 (10)	2.5	0.02
C* Rump	23.1 ± 2.6 (10)	24.6 ± 3.1 (10)	0.4	0.71
h* Rump	64.4 ± 2.1 (10)	64.8 ± 1.5 (10)	0.1	0.88

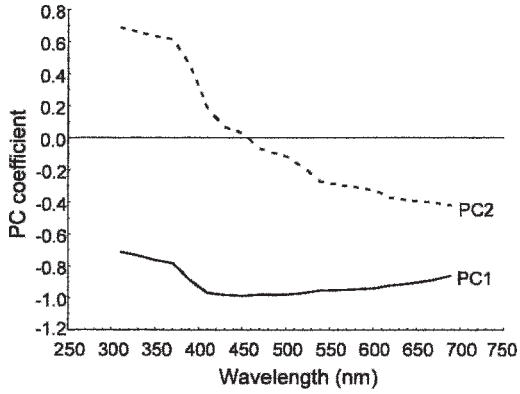

FIGURE 3. Coefficients for the two main principal components derived from PCA in relation to wavelength for the right longest rectrices of Thorn-tailed Rayaditos on Chiloé Island, Chile. Multiplying these coefficients by reflectance at a certain wavelength interval gives the PCA scores.

est values at the UV end and the lowest values at the red end of the spectrum (Fig. 3). No difference was found between the sexes for PC1 ($t_{20} = 1.9$, $P = 0.07$) or PC2 ($t_{20} = 0.7$, $P = 0.83$) of the longest rectrix. The same result was obtained from within-pair comparisons (PC1: $t_9 = 1.5$, $P = 0.17$; PC2: $t_9 = 1.2$, $P = 0.28$). No within-pair correlations were found with respect to color of the longest rectrix (all $r_8 < 0.01$, all $P > 0.90$).

PARENTAL CARE

Parental attendance at the nest during incubation was very high, with an adult present in the nest box for 55.1 ± 2.9 min hr^{-1} ($n = 11$ nests). Most incubation sessions (52%) were terminated by the other member of the pair assuming incubation duty. Absences of both mates from the nest were short, with an average duration of 3.5 ± 1.2 min ($n = 11$). Incubation sessions had an average duration of 16.8 ± 3.1 min ($n = 11$).

No differences in parental care between the sexes were detected when chicks were three days old (Table 3). However, within-pair comparisons revealed a significant difference in duration of brooding sessions ($t_4 = 5.6$, $P = 0.005$), with males brooding longer per session than females. There were no within-pair differences for other variables (all $t_4 < 2.1$, all $P > 0.11$). Both sexes visited the nest at similar rates when chicks were approximately two weeks old (Table 3). However, females removed fecal sacs at rates twice as high as males at this stage of the nestling period (Table 3). Within-pair comparisons at this stage were similar (provisioning days 14–17: $t_{16} = 0.4$, $P = 0.71$; fecal sac removal days 14–17: $t_{16} = 4.0$, $P < 0.001$). No within-pair correlations with respect to parental care variables were significant after Bonferroni correction at day 3 (all $r_3 < 0.93$, all $P > 0.03$), although this was probably due to low sample size. On days 14–17, within-pair correlations were not significant either (all $r_{15} < 0.06$, all $P > 0.85$). There were no significant associations after Bonferroni correction between tail length and parental care variables (all $r_{5-32} < 0.2$, all $P > 0.63$), or between tail color (PC1 and PC2) and parental care variables (all $r_{11} < 0.6$, all $P > 0.03$) on days 14–17.

DISCUSSION

Thorn-tailed Rayaditos exhibit an absence of obvious sexual dimorphism in color and morphology characteristic of furnariids (Remsen 2003). In addition, males exhibit brood patches and there is no detectable difference with respect to cloacal protuberance between the sexes during the nestling stage, making it necessary to use molecular methods to sex

TABLE 3. Hourly number of provisioning visits and removal of fecal sacs at 3 and 14–17 days of nestling age, and hourly brooding time and mean brooding session duration at 3 days of age (means ± SE, number of individuals in parentheses), by female and male Thorn-tailed Rayaditos on Chiloé Island, Chile. Significant differences between the sexes after Bonferroni correction are denoted with an asterisk.

	Female	Male	F	P
Provisioning rates, 3 days (hr^{-1})	10.6 ± 1.6 (5)	10.1 ± 1.7 (4)	0.04	0.85
Fecal sacs, 3 days (hr^{-1})	1.1 ± 0.3 (5)	1.7 ± 0.4 (4)	1.3	0.29
Brooding time, 3 days (min hr^{-1})	13.1 ± 1.4 (5)	17.3 ± 1.6 (4)	3.9	0.09
Mean brooding session (min)	4.7 ± 0.6 (5)	7.1 ± 0.7 (4)	6.0	0.04
Provisioning rates, 14–17 days (hr^{-1})	21.2 ± 1.5 (18)	20.6 ± 1.7 (15)	0.1	0.79
Fecal sacs, 14–17 days (hr^{-1})	4.2 ± 0.3 (18)	2.1 ± 0.3 (15)	20.0	< 0.001*

adults. However, despite overlap in measurements, males are between 2% and 10% larger than females in size and mass. Given that island populations may experience ecological release (Selander 1966), sexual dimorphism of mainland rayaditos may be less than that reported here. Despite males being larger than females, there is no difference in length of the two longest rectrices or spines, as has been found for ornamental traits in other species (Boland et al. 2004, Kraaijeveld et al. 2004). Females are smaller and weigh less but have longer tails for their body size than males. Both sexes have very similar body plumage coloration, although we cannot confirm this for the UV part of the spectrum. The same is true for tail color, including UV reflectance. As has been reported for other furnariids (Kendeigh 1952, Fraga 1980, Nores and Nores 1994, Skutch 1996), males and females participate equally in incubating eggs and brooding and raising young, except for removal of fecal sacs, which is done predominantly by females. Monomorphism in body plumage and equality of the sexes in parental care suggest the absence of sexual selection for signaling traits in these socially monogamous birds.

All 12 tail feathers of rayaditos end in thin spines, in which the distal portions of shafts are virtually without barbs. The lengths of both the rectrices and their spines decrease gradually from the inner feathers outwards. The two central tail feathers on each side have spines of 9 and 20 mm on average, respectively, with strengthened shafts. However, our observations indicate that rayaditos seldom climb tree trunks by supporting themselves with their tails, and their foraging behavior consists mostly of horizontally moving along branches and hanging upside down while gleaning arthropods from bark and foliage. On the few occasions when we observed a bird leaning the tip of its tail against a trunk while climbing upward, it was during a quick balancing movement. Furnariids with similar tails to rayaditos, like the Spotted Barbtail (*Premnoplex brunnescens*), sometimes move up vertical trunks with the body upright and the tail pressed against the bark, but they seem to depend little upon the strongly barbed tail feathers for support (Skutch 1967). Several genera exhibiting tail spines do not climb on trunks while foraging (Remsen 2003). Furnariid tree-climbing specialists like White-throated Treerunners (*Pygarrhichas albogularis*) have much shorter tails and stronger spines than rayaditos (RAV and JM, pers. obs.). Thus, it is doubtful that tail spines in rayaditos have any utility related to support while foraging. However, our observations were made during a brief period of the annual cycle. It is possible that foraging behavior changes seasonally, reflecting changes in food resource distribution, so our data are not conclusive evidence for the absence of functionality of the tail spines in foraging. The only real way to understanding the function of the tail spines is through experimental manipulation of their length.

Elongated tail feathers of rayaditos had a slightly higher coefficient of variation than other morphological characters, as is characteristic of epigamic traits (Møller and Pomiankowski 1993, Fitzpatrick 1997). Rectrix and spine lengths were similar in both sexes, but males were significantly larger, thus the elongated central rectrices are apparently not a partially sex-limited trait that exists in females merely as a genetically correlated response to selection on males (Lande 1980). The longest central rectrices and spines measured actually belonged to females. The elaborate tails of furnariids may be an expression of mutual sexual selection in this family that is characterized by social monogamy and the absence of plumage dimorphism. The long tail of rayaditos could also function in social contexts affecting both sexes, for example in competition for food or territories (West-Eberhard 1983, Kraaijeveld et al. 2004). Only experimental tail manipulations and detailed studies of social behavior and mate choice in this and other furnariids can confirm if tails play a role in signaling in this large, understudied family.

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