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Sex-biased help and possible facultative control over offspring sex ratio in the Rufous-fronted Thornbird, *Phacellodomus rufifrons*

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RESUMO: **Possível controle facultativo na razão sexual de ajudantes no joão-graveto, *Phacellodomus rufifrons.*** Foi examinada a estrutura social e a demografia de uma população de joão-graveto *Phacellodomus rufifrons,* uma espécie de furnarídeo que exibe reprodução cooperativa. Foram estudados aspectos potencialmente associados aos mecanismos seletivos que caracterizam a reprodução cooperativa: a origem do sexo dos ajudantes, a razão sexual de jovens e adultos e os padrões de dispersão de cada sexo. O trabalho foi feito no Parque Nacional da Serra do Cipó, estado de Minas Gerais no sudeste do Brasil. Foram monitoradas oito a 10 famílias entre os anos de 2000 e 2003 em uma área de cerrado de aproximadamente 80 ha. Amostras de tecido sanguíneo foram coletadas nos indivíduos marcados com anilhas coloridas. Foi aplicada a técnica molecular para determinar o sexo dos filhotes e adultos, uma vez que o dimorfismo sexual é ausente nesta espécie. A população estudada apresenta reprodução cooperativa de parentesco, com grupos sociais compostos de um casal reprodutor e seus filhotes que prorrogam a dispersão. O comportamento de ajuda foi detectado principalmente entre os jovens machos. As fêmeas jovens tendem a dispersar antes, permanecendo no território natal por não mais que um ano. Os machos jovens prorrogam a dispersão, permanecendo nos territórios natais por pelo menos três anos. A razão sexual desviada a machos resulta principalmente da tendenciosidade do recrutamento de jovens. A primeira ninhada de casais reprodutores é tendenciosa em relação a machos, o sexo ajudante. Estas descobertas sugerem que as fêmeas de *P. rufifrons* podem estar exibindo controle facultativo sobre a razão sexual dos seus filhotes.

PALAVRAS-CHAVE: Cuidado parental, dispersão tardia, filopatria, reprodução cooperativa, suboscines.

ABSTRACT: We examined the social structure and demography of a cooperative breeding population of the Rufous-fronted Thornbird*Phacellodomus rufifrons,* a neotropical ovenbird that inhabits open scrublands in South America. We focused on aspects potentially associated with the selective mechanisms underlying cooperative breeding: the origin and sex of helpers, the sex ratio of young and adult population, and the dispersal patterns of young of each sex. The study was conducted at 'Parque Nacional da Serra do Cipó', a natural reserve in southeastern Brazil. Eight to ten social groups were monitored on a scrubland area of about 80 ha, during 2000-2003. Individuals were color-banded and blood or feather shafts were sampled. Molecular techniques were used to determine the sex of adult and fledgling, as sexual dimorphism is absent in the species. Kin-based cooperative breeding occurs, with social groups composed of a breeding pair and offspring that delayed dispersal. Help was mainly due to young males. Female offspring tended to disperse earlier and remain in the natal territory up to one year, while males, delayed dispersal for up to three years. Sex ratio skews towards male in the adult population resulted mainly from biases in the sex ratio of recruited young. The first brood of breeding pairs was biased towards males, the helper sex. Our findings suggest that Rufous-fronted Thornbird female may exhibit facultative control of offspring sex ratio.

KEY-WORDS: Cooperative breeding delayed dispersal, parental care, philopatry, suboscines.

Cooperative breeding occurs whenever more than two individuals help rear the offspring of one pair (Emlen and Vehrencamp 1985), and has been reported for 308 bird species across 27 families, accounting for ~3% of all 9672 bird species described (Arnold and Owens 1998). Despite this generally accepted definition, cooperative breeding includes a diverse array of mating and social systems (Ligon and Burt 2004).

A general observation in cooperative species is that one sex usually helps more than the other (Cockburn 1998). Helping is often expressed by sons (Emlen 1997, Ewen *et al.* 2001), but may also be exhibited predominantly by daughters or by both sexes (see references in Cockburn 2004). Sex ratio biases towards the sex that helps to rear offspring were previously reported for cooperative breeders such as the red-cockaded woodpecker *(Picoides borealis)* (Gowaty and Lennartz 1985) and the Seychelles warbler *(Acrocephalus sechellensis)* (Komdeur 1996, Komdeur *et al.* 1997). The control over offspring sex ratio gives support to the local resource enhancement hypothesis (review in Komdeur 1996), which predicts biases in offspring sex ratio when one sex contributes more to the parental fitness through the helping behavior.

The Rufous-fronted Thornbird *Phacellodomus rufifrons,* an endemic neotropical Furnariidae (ovenbird) is a cooperative breeder, where more individuals than just the breeding pair helps in territory maintenance, nest building and feeding the nestling (Rodrigues and Carrara 2004). Here, we investigate the structure of cooperative breeding system and demography of the population studied by Rodrigues and Carrara (2004). We focused on those aspects of greater relevance to understanding the mechanisms of expression or maintenance of cooperative breeding in this species, namely: 1. The sex and origin of helpers: is one sex more prone to help than the other, and is helping behavior expressed by retained offspring only? 2. Dispersal behavior of young: do male and female offspring have similar dispersal patterns, is there a philopatric sex? 3. The sex ratio of the adult population and recruited young: is there a bias towards the helper sex in any of these levels?

METHODS

The Species – The Rufous-fronted Thornbird is a monomorphic ovenbird that inhabits thorny scrublands of South America (Ridgely and Tudor 1994). It lives in pairs or groups of up to ten individuals, on all-purpose territories maintained throughout the year. Territory size ranges from about two to four ha (Rodrigues and Carrara 2004). Rufous-fronted Thornbirds build one of the largest nests of the Neotropical ovenbirds (Sick 1993); nests may be up to 2 m long and approximately 0.4 m wide. The nest is made of sticks and usually has two or three independent chambers, each with its own entrance. Nests are usually at the extremities of thin branches of isolated trees. More than one nest can be built and maintained in a single territory. They are used not only for breeding, but also as an overnight roosting site throughout the year (Carrara and Rodrigues 2001). In southeastern Brazil, the breeding season starts at about mid September and lasts until early April. Nests are very asynchronous, clutch size ranges from 2 to 3, and reproductive success is generally low (Carrara and Rodrigues 2001). Several group members participate in territory defense, nest-building, nest-lining, and nestling provision (Rodrigues and Carrara 2004).

The study was conducted from June 2000 to June 2003 at 'Parque Nacional da Serra do Cipó', city of Jaboticatubas, in the central region of Minas Gerais state, southeastern Brazil. The study site (19°12' to 19°35'S and 43°27' to 43°38'W) encompasses about 80 ha of area within the park, and includes gallery forests and cerrado (an open scrub savannah-like vegetation, see Rodrigues *et al.* 2005 for details).

With a dry period from April to September and a wet period from October to March, the average annual precipitation is approximately 1500 mm, falling primarily between December and March. Mean annual temperature varies between 17°C-18.5°C (Antunes 1986).

Sixty-three individuals occupying twelve territories were captured with mist-nets and banded with metal bands provided by the Brazilian Environmental Agency (CEMAVE-IBAMA). A unique combination of color plastic bands was assigned to each bird.

As nests chambers are almost closed, with only a small opening, nestlings could only be captured after they had left the nest. They were captured during the first week out of the nest to enable tissue sampling, as the first month is the period of highest mortality among the young (Carrara and Rodrigues 2001).

Group Composition and Parental Care – During the breeding seasons (September to April), ten territories were monitored every two weeks. Group composition was determined by observation of activities on territories during the day, and nest roosting behavior, which was important for confirming the identity and number of territory occupants.

Feeding activity of young was monitored from early morning and sessions ranged from four to six hours. Attempts were made to reduce the influence of the investigators by hiding behind shrubs or woodpiles, when possible, and artificial hides 10 m from the nests were used in some cases.

Dominance Status – Dominance was attributed to breeding pairs in territories that most actively fed the young. Other birds were referred to as subordinates, as they usually consisted of offspring, and presumably were not involved in breeding attempts in their natal territory. When a subordinate individual helped dominants in feeding the young, it was referred to as a helper (Rodrigues and Carrara 2004).

Molecular Sexing – One of the problems faced by researchers studying social behavior in the Furnariidae is the lack of sexual dimorphism in almost all species of the family (Remsen 2003, Faria *et al.* 2007, but see Roper 2005). To overcome this drawback, here we employed molecular technique for sexing individual birds.

Feather shafts or blood samples were taken from 60 birds. Blood samples of 25 to 50 µL were collected by wing venipuncture, using BD 30x3 dischargeable needles and capillary tubes. The samples were stored in 1.5 mL tubes containing 500 µL of absolute ethanol (Caparroz *et al.* 2001) that were kept at 4°C until being processed. Feather shafts were stored in 70% ethanol at room temperature.

DNA was extracted from blood and feather shafts by standard phenol-chloroform methods and stored in TE buffer (Sambrook *et al.* 1989). DNA samples were used in molecular sexing method with P2 and P8 primers for PCR as described by Griffiths *et al.* (1998). Following the PCR reaction, 5 µl were submitted to electrophoresis in an 8% native polyacrylamide gel in TBE 1X, at 125V for about four hours, after which they were visualized by silver staining (Santos *et al.* 1996).

Statistical analysis – We tested for a bias in adult sex ratios during the three years with the log likelihood ratio test (the G-test). Differences in dominance turnover rates and the sex ratio of recruited young were analyzed using the Student's t-test.

Fisher's exact test was used to test for a bias in the sex ratio of the young produced in first broods compared with that found in broods produced by pairs with tenure, accompanied by male offspring. We defined tenured pairs as those that had already produced one brood together in the study site.

RESULTS

Mean observation time of feeding activity of young was 6.3 (± 6.08) hours/group in the first two years. In the third year it was increased to 24.3 (± 12.8) hours/group, as fieldwork efforts could be enlarged.

Sex and the Origin of Helpers – Only subordinate males were observed acting as helpers, with one exception during an unusual circumstance of brood parasitism. During the three breeding seasons, eight males were observed helping the dominant pair feed the young: of these, six were certainly young that delayed dispersal, two of which expressed helping behavior already in the same breeding season they were produced (Table 1).

Subordinate females were present in the study site in one breeding season. These were three one-year-old females that delayed dispersal and were in the natal territory when their parents reproduced again. No subordinate female helped in the rearing offspring, although two were seen near the nest with food in their beaks; this food was either consumed or was dropped.

Social groups were composed of one breeding pair and offspring that delayed dispersal, and remained in the natal territory. Sometimes, immigrants associated with family groups for short periods, such as overnight roosting. In one instance, an immigrant male was in a territory when nestlings were being reared, and while seen adding sticks to the nest, he did not help feed the nestlings. This was the only instance in which a subordinate male did not feed the nestlings

When Daughters Helped – A female offspring helped in one unusual circumstance, which was when a parasitic cuckoo was being reared by the group. The group involved included the dominant pair (third year breeding here) and offspring (one yearling female and two young born in the same year). Although the dominant female used the nest for overnight roosting, she was not seen feeding the cuckoo. The dominant male delivered food, helped by two daughters (observation effort = 28 hours). When females were not found in the group, males exclusively cared for the young. This occurred in two territories when the dominant female disappeared during the nestling period.

DISPERSAL PATTERNS

Among young – Female offspring dispersed predominantly just before or during the breeding season following their birth (11.1 ± 5.2 months; n = 7), while males tended to remain in the natal territory for periods ranging from one to three years (16.5 ± 10.8 months; n = 11; Fig. 1). We observed 14 dispersal events: offspring dispersal, change of territories by adults and immigration. In most cases, individuals occupied the territory as dominants (79%). In three cases, immigrants in occupied territories with a dominant pair were subordinate and briefly stayed in the territory (three to four months). The only female in the latter group became dominant in an adjacent territory.

Routes to become dominant – Thornbirds became dominant by following one of at least three different ways: 1) dispersal in the first year and immediate occupation of an unoccupied territory, only females (n = 2); 2) delayed dispersal and occupation of a nearby territory as dominant, seen in both, males and females (n = 2); 3) dispersal and occupation of subordinate position in an alien territory until finding a nearby vacancy, observed only in one female. Territory inheritance may also have occurred twice in the study area, but no breeding was observed. These territories were occupied by a mother and her male offspring.

Males that delay dispersal may benefit from the security provided by the use of their parental territory while searching for territory vacancies. In his third year in his natal territory, a subordinate male crossed two territories and was captured in an area where the dominant single male had recently lost its mate. During the same breeding season, this subordinate male was successful in occupying a neighboring territory as dominant after the previous dominant male disappeared. Also, a return to the natal territory occurs, as noted for a male helper that had left its original territory early in a breeding season, returning two months later at the end of the breeding season.

Turnover rates of dominant individuals – Eighteen dominant individuals disappeared from the study site: 11 females, and seven males. Disappearance rate of dominant females was twice that of males in the first two years, reaching 50% of dominant females in the third year (Table 2). Average turnover rates, however, were equal among the sexes ($t = 1.29$, n = 6, d.f. = 4, $p > 0.05$). Territory openings as dominants occurred at 38% per year for females and 24% per year for males. Dominance positions for females became vacant on an annual mean rate of 38% of existing territories, while for males this value was 24%.

Sex Ratio – With P2 and P8 primers, males and females were successfully distinguished. The PCR products showed two bands for females and a single band for males, corresponding to distinct gene targets: CHD-Z from Z chromosomes which

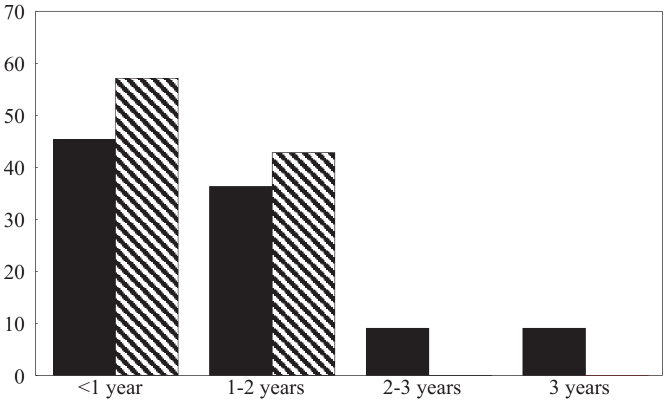

FIGURE 1. Age of dispersal or disappearance of Rufous-fronted Thornbird offspring. Full bars represent males (n = 11) and striped bars represent females (n = 7). Frequency was determined for the total young sample. The figure is incomplete. Axes need to be labeled better, the importance of this figure needs to be emphasized here, and so on.

TABLE 1. Behavior of subordinate Rufous-fronted Thornbird individuals, as recorded along the nestling-feeding period. Only events of co-specific broods were considered.

Breeding season	Number of breeding groups sampled	Helpers		Non-helpers	
		Males	Females	Males	Females
2000/01	02	04	0	0	0
2001/02	03	04	0	0	0
2002/03	04	04	0	01	03

TABLE 2. Disappearance rate of dominant Rufous-fronted Thornbird males and females at the study site.

Year	Territories occupied	Disappeared Dominants		Frequency (%)	
		Females	Males	Females	Males
2000/01	10	4	2	40.0	20.0
2001/02	8	2	1	25.0	12.5
2002/03	10	5	4	50.0	40.0
Average (SD)	—	3.67 (1.53)†	2.33 (1.53)	38.3 (12.6)	24.2 (14.2)

(†) *t* = 1.29, n = 6, d.f. = 4, p > 0.05

TABLE 3. Sex ratio of the Rufous-fronted Thornbird adult population at the study site. Sex ratio is described as the proportion of males in the population.

Year	Number of territories	Number of subordinates		Total number		Adult sex ratio
		Males	Females	Males	Females	
2000/01	10	9*	1	19	11	0.63
2001/02	8	6*	1	14	9	0.61
2002/03	10	7	4	17	14	0.54

(*) G test: D = 7.24, n = 10, d.f. = 01, p < 0.05 (2000/01); D = 3.88, n = 07, p < 0.05 (2001/02)

TABLE 4. Total number of Rufous-fronted Thornbird males and females recruited in territories at the study site. Recruitment means offspring survival until the end of the breeding season.

Year	Recruited young		Ratio of males
	Males	Females	
2000/01	05	02	0.71
2001/02	04	03	0.57
2002/03	04	02	0.67
Total	13**	07	0.65

(**)T test: t = 5.08, n = 06, d.f. = 04, p < 0.01

appear as a pair in males, and CHD-W from W chromosomes which appear only in females that bear also a copy of the Z chromosome. The size difference between the distinct chromosome genes is about 20 base pairs.

The adult sex ration was 50:50 (G = 2.12, n = 30, d.f. = 1, p > 0.05 (2000/01); G = 1.07, n = 23, d.f = 1, p > 0.05; G = 0.29, n = 31, d.f. = 1, p > 0.05 (2002/03). In subordinates, a bias toward males occurred in the first two years [G = 7.24, n = 10, d.f. = 1, p < 0.05 (2000/01); G = 3.88, n = 07, d.f. = 01, p < 0.05 (2001/02); G = 0.82, n = 11, d.f = 1, p > 0.05 (2002/03)]. In the three years of the study, the frequency of subordinate males was 0.9, 0.86, and 0.64, respectively.

The difference in the frequency of subordinate males and females is due to the sex ratio of recruited young (Table 4). Thirteen males were recruited over the three breeding seasons, while only seven females were recruited. More males than females were recruited in every year. On average, 65% of the young recruited in any one year were males, a percentage significantly higher than that of females (t = 5.08, n = 6, d.f. = 4, p < 0.01). Stronger deviations were recorded in the first (0.71) and the third year (0.67) of the study.

TABLE 5. Sex ratio (at fledgling) of first broods, and broods of tenured breeding pairs. Pairs were sampled only once in each condition. Only broods for which all fledglings were sampled were considered. Sex ratio is described as the proportion of males in the brood.

	Brood sex ratio	
	Pairs first brood	Tenured pairs brood
Broods sampled	1.0	0.0
	1.0	0.5
	1.0	1.0
	1.0	0.5
	1.0	0.0
Average (SD)	1.0 (0)**	0.4 (0.42)

(**) Fisher exact test: n = 21, p = 0.01

Sex ratio biases produced by non-tenured pairs – The analysis of offspring sex ratio data taking into account the tenure of breeding pairs (namely, if individuals had already bred in the area) revealed a striking bias towards males in the broods produced by non-tenured pairs (Table 5). Pairs that matched this condition produced young males in a higher frequency than tenured pairs, whose brood sex ratio averaged equality, with a slight deviation towards female production (Two-tailed Fisher exact test: n = 21, p = 0.0124). All first broods generated by monitored pairs were composed exclusively by males, in clutches of 2,0 ± 0,71 young (n = 5).

DISCUSSION

The Rufous-fronted Thornbird exhibits kin-based cooperative breeding, with social monogamy (*sensu* Hasselquist and Sherman 2001). The social groups were composed of a breeding pair and undispersed offspring, usually males. Female offspring dispersed up to one year from birth, sooner than males, which remains for up to three years. Male biased sex ratio in the adult population resulted mainly from biases in the sex ratio of recruited young. Biases in the sex ratio of young were high among the first brood of breeding pairs, favoring males, the helping sex. Our findings thus suggest that females may exhibit facultative control of offspring sex ratio.

Sex-biased Helping Behavior – In the Rufous-fronted Thornbird, male offspring are essentially the only young that help. Accordingly, it has been shown that in cooperative species usually one sex helps more than the other (review in Cockburn 1998).

Female Rufous-fronted Thornbird apparently may help, as seen in one case, but even so, it is rare. Additional efforts are necessary to verify the extent of bias in helping behavior between offspring of both sexes under different social circumstances, for instance, after a dominant (male or female) disappearance. Here, female offspring became helpers when their mother was not involved in rearing young activity, what suggests that dominant behavior may play a determinant role in the expression of helping behavior by the offspring.

Dispersing Patterns – Delayed dispersal is a very frequent strategy in cooperative breeders, largely considered as a prerogative for the development of kin-based cooperative systems (Koenig *et al.* 1992, Dinckinson and Hatchwell 2004). It reflects the common interests of the offspring and their parents, which usually results in increased parental productivity through higher young or parental survival (Cockburn 1998). In the Rufous-fronted Thornbird, all observed young (12 males, 6 females) had a great tendency to remain in the natal territory during most of the non-breeding season. This prolonged association with the natal territory and parents may bring important benefits to the offspring (Emlen 1982), especially along the dry season when insect availability, the main diet component of this species (Sick 1993), may be severely reduced in the area (Ekman *et al.* 2004). The retained offspring may have access to those feeding areas used by their parents or familiar group, and may benefit from an elevated protection against predators offered by an efficient group guarding, as indicated by the immediate alarm vocalizations produced when observers were located (Rodrigues and Carrara 2004).

Constraints to Adult Dispersal and Independent Breeding – Delayed dispersal is often associated with shortage of resources required to independent breeding, such as vacant areas or mates (Emlem 1982a, Koenig *et al.* 1992, Hatchwell and Komdeur 2000). Cooperative breeding populations frequently live in saturated habitats (Arnold and Owens 1998), where breeding vacancies constitute a limiting resource to reproduction (Pruett-Jones and Lewis 1990, Komdeur 1992, Walters *et al.* 1992). The availability of breeding vacancies seems indeed to play an important role in dispersion decision of the Rufous-fronted Thornbird offspring. When dominance positions became available in neighbor territories, yearling females left their natal group and moved to these territories. The same was noted for a male that dispersed – after having spent 36 months in the natal territory – to acquire a breeding vacancy in a neighbor group. The shortage of this resource in the study site is a consequence of the low turnover rates of dominants and the scarcity of suitable areas for the establishment of new territories. Habitat saturation thus could be a key factor inducing Rufous-fronted Thornbird young to delay dispersal.

In the population studied, male offspring is probably facing higher constraints to obtain breeding opportunities than females, as suggested by the strong contrast between the number of subordinates of both sexes in the area and the frequency of dominance vacancies arising. Not only was the number of individuals competing for a breeding vacancy much higher among males, but also the likelihood of a dominance position to become available was lower. These conditions probably promote the longer permanence of male offspring with their parents, favoring the expression of helping behavior.

Skutch (1969), who was the pioneer in studying the Rufous-fronted Thornbird breeding system, did not detect cooperative breeding in a population inhabiting the Venezuelan scrubland. Territories were occupied predominantly by one pair, but in some cases groups of three birds were formed by the retention of young for up to one year. This finding sharply contrasts to the high cooperative breeding levels detected in the population studied here, that ranged around 60% of extant territories. In the carrion crow *(Corvus corone),* another species with kin-based cooperative breeding, helping behavior was demonstrated to respond to environmental conditions. In a transplantation experiment, Baglione *et al.* (2002) transferred carrion crow eggs originated from a population of non-cooperatives to a population with high level of cooperative breeding. Five out of six transplanted young delayed dispersal, and two of those expressed helping behavior in the following breeding season. Variation in cooperative breeding between Rufous-fronted Thornbird populations indicates that helping behavior in this species is flexible, and probably arises from differences in ecological circumstances, as habitat saturation and territory quality, experimented by young.

Sources of Imbalance in the Sex Ratio of the Adult Population – The sex ratio of the adult population was biased towards males, especially in the first two years of the study. Although the observed biases did not significantly differ from the expected frequency of 1:1 when the adult population was considered as a whole, significant biases were detected among subordinate individuals in the first two years. This finding indicates that sources of imbalance in the sex ratio were present and to some extent influenced the population studied. Some of potential sources are the sex ratio of young produced, the turnover rate of adults (resulting from death or secondary dispersals), as well as immigration and dispersal rates.

Immigration into the monitored area occurred in low frequencies (three males and five females along the three years), mainly to fill dominance vacancies, and did not contribute to the observed skews, as immigrant females exceeded immigrant males in number. In contrast, adult turnover rates played some role in biasing the sex ratio towards males, with dominant females yearly disappearing from the study site with a frequency 1.75 times higher than that observed males. Such a turnover rate contributed to the reduced number of subordinate females in the area. The strongest factor inducing biases in the sex ratio of adults, however, was the skewed sex ratio of young produced. Male offspring surpassed female offspring in all the monitored breeding seasons. Their frequency was significantly higher than that of females, averaging 65% of the annual recruited young. At the end of the study, young males had been produced in numbers almost twice as high as females.

These observations indicate that offspring sex ratio and adult turnover rates additively influenced the sex ratio of the Rufous-fronted Thornbird adult population, producing biases of varying strength towards males along the years.

Facultative Control over Brood Sex Ratio – Despite the small number of broods sampled in this study, we observed a significant difference between the sex ratio of offspring raised by tenured and non-tenured pairs. The latter raised offspring composed exclusively of males. In contrast, the sex ratio of the offspring of tenured pairs averaged equality.

The biases detected in the sex ratios of those broods from non-tenured pairs may have resulted from an adaptive strategy of sexual allocation. Pairs that were breeding for the first time in the study area used to live alone in their territories. It is noteworthy that in their first brood all of them have favored young males, the sex prone to remain in the natal territory and to help rearing the nestlings. The assistance of helpers seems to have a positive effect on parental productivity, enhancing their success in raising young (Rodrigues and Carrara 2004). Philopatric males also have an important role in group enlargement, enhancing territory defense, nest building (Carrara and Rodrigues 2001), and vigilance (Rodrigues and Carrara 2004). By overproducing young males in their first brood, breeding pairs increase their chances of obtaining benefits from the helpers' presence in the following years, thereby increasing their likelihood of reproductive success.

Biases in the sex ratio of young were not evident among tenured pairs. All the birds sampled on this breeding class were being assisted at least by one subordinate male, supporting the idea that the probability of helper assistance in the breeding season following the first brood is high. The balance achieved in the sex ratio of young on subsequent breeding may reflects the influence of ecological and demographic constraints over the allocation strategy of females, possibly the food availability (territory quality) or sibling competition for vacancies. Successive overproductions of males (the more philopatric sex) would quickly strengthen both limitations, reducing female reproductive success.

Strong biases in the sex ratio of the first brood were previously reported for two cooperative breeders, the red-cockaded woodpecker *(Picoides borealis)* (Gowaty and Lennartz 1985) and the Seychelles warbler *(Acrocephalus sechellensis)* (Komdeur 1996, Komdeur *et al.* 1997). As observed in the Rufous-fronted Thornbird, in both species the biases favored the helper sex, reaching levels of absolute presence of only this sex in the brood (brood composed 100% by the helping sex).

Both in the red-cockaded woodpecker and in the Seychelles warbler, the presence of helpers has a marked influence on the reproductive success of parents. In the red-cockaded woodpeckers, helping behavior seems to increase considerably the fledgling success of females that breed for the first time in a given area, but not of those females with prior tenure (Gowaty and Lennartz 1985). In the Seychelles warbler, individual fitness is affected both by the number of helpers and by territory quality. The presence of helpers enhances the reproductive success of pairs living in high quality territories, but decreases the fitness of parents in low quality areas, as a result of food depletion (Komdeur 1994). Accordingly, intensive skews toward helpers (females) were recorded in brood sex ratios of pairs on high quality territories, while breeding pairs on low quality territories invested more in the dispersing (male) sex (Komdeur 1996).

The skews in offspring sex ratio described for those species clearly have an adaptive role, suggesting that facultative control over the sex ratio of broods was possibly occurring (Gowaty and Lennartz 1985, Komdeur 1996). Experimental evidences confirmed that Seychelles warbler female indeed has the ability of adjusting the offspring primary sex ratio in an adaptive manner (Komdeur 2002). The facultative variation of brood sex ratio seems to occur in some other cooperative breeding species (references in Komdeur 2004), and was additionally demonstrated in the Bell miner (*Manorina melanophrys:* Ewen *et al.* 2003). Rufous-fronted Thornbird females may exhibit facultative control over their offspring sex ratio, supporting the local resource enhancement hypothesis (Clark 1978, Emlen *et al.* 1986, Lessells and Avery 1987, Komdeur 1996), which predicts biases in offspring sex ratio when one sex contributes more to the parental fitness through the helping behavior.

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REFERENCES

Antunes, F.Z. (1986) Caracterização climática do estado de Minas Gerais. *Inf. Agropec.* 12:9-13.

Arnold, K.E. e I.P.F. Owens (1998) Comparative breeding in birds: a comparative test of the life history hypothesis. *Proc. R. Soc. London Ser. B.* 256:739-745.

Baglione, V., D. Canestrari, J.M. Marcos, M. Griesser e J. Ekman (2002) History, environment and social behaviour: experimentally induced cooperative breeding in the carrion crow. *Proc. R. Soc. Lond. Ser. B.* 269:1247-1251.

Caparroz, R., C.Y. Miyaki, M.I. Bampi e A. Wajntal (2001) Analysis of the genetic variability in a sample of the remaining group of Spix's Macaw (*Cyanopsitta spixii,* Psittaciformes: Aves) by DNA fingerprinting. *Biological Conservation* 99:307-311.

Carrara, L.A. e M. Rodrigues (2001) Breeding biology of the Rufous-fronted Thornbird *Phacellodomus rufifrons,* a neotropical ovenbird. *Int. J. Ornithol.* 4:209-217.

Clark, A.B. (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201:163-165.

Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Ann. Rev. Ecol. Syst.* 29:141-177.

Cockburn, A. (2004) Mating systems and sexual conflict, p. 81-1001 Em: W.D. Koenig and J.L. Dickinson (eds.), *Ecology and Evolution of Cooperative Breeding in Birds.* Cambrige: Cambrige University Press.

Dinckinson, J.L e B.J. Hatchwell (2004) Fitness consequences of helping, p. 48-66. Em: W.D. Koenig e J.L. Dickinson (eds.), *Ecology and Evolution of Cooperative Breeding in Birds.* Cambridge: Cambridge University Press.

Ekman, J., J.L. Dickinson, B.J. Hatchwell e M. Griesser (2004) Delayed dispersal, p. 35-47. Em: W.D. Koenig e J.L. Dickinson (eds.), *Ecology and Evolution of Cooperative Breeding in Birds.* Cambridge: Cambridge University Press.

Emlen, S.T. (1982) The evolution of helping. I. An ecological constraints model. *Am. Nat.* 119:29-39.

Emlen, S.T. (1997) When mothers prefer daughters over sons. *Trends in Ecology and Evolution* 12:291-292.

Emlen, S.T. e S.L. Vehrencamp (1985) Cooperative breeding strategies among birds, p. 359-374. Em: B. Hölldobler e M. Lindauer (eds.), *Experimental Behavioral Ecology.* Stuttgart: Gustav Fischer.

Emlen, S.T., J.M. Emlen e S.A. Levin (1986) Sex ratio selection in species with helpers-at-the-nest. *Am. Nat.* 127:1-8.

Ewen, J.G, R.H. Clarke, E. Moysey, R.L. Boulton, R.H. Crozier e M.F. Clarke (2001) Primary sex ratio bias in an endangered cooperatively breeding bird, the black-eared miner, and its implication for conservation. *Biological Conservation* 101:137-145.

Ewen, J.G, R.H. Crozier, P. Cassey, T. Ward-Smith, J.N. Painter, R.J. Robertson, D.A. Jones e M.F. Clarke (2003) Facultative control of offspring sex in the cooperatively breeding bell miner, *Manorina melanophrys. Behavioural Ecology* 14:157-164.

Faria, L.P., L.A Carrara e M. Rodrigues (2007) Dimorfismo sexual de tamanho no fura-barreira *Hylocryptus rectirostris* (Wied, 1821) (Aves – Furnariidae). *Revista Brasileira de Zoologia* 24:207-212.

Gowaty, P.A. e M.R. Lennartz (1985) Sex ratios of nestling and fledgling red-cockaded woodpeckers *(Picoides borealis)* favor males. *Am. Nat.* 126:347-353.

Griffiths, R., M.C. Double, K. Orr e R.J.G. Dawson (1998) A DNA test to sex most birds. *Molecular Ecology* 7:1071-1075.

Hatchwell, B.J. e J. Komdeur (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* 59:1079-1086.

Hasselquist, D. e P.W. Sherman (2001) Social mating systems and extrapair fertilizations in passerine birds. *Behavioural Ecology* 12:457-466.

Koenig, W.D., F.A. Pitelka, W.J. Carmen, R.L. Mumme e M.T. Stanback (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111-150.

Komdeur, J. (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358:493-495.

Komdeur, J. (1994) Experimental evidence for helping and hindering by previous offspring in the cooperative breeding Seychelles warbler *(Acrocephalus sechellensis). Behav. Ecol. Sociobiol.* 34:31-42.

Komdeur, J. (1996) Facultative sex ratio bias in the offspring of Seychelles warblers. *Proc. R. Soc. Lond. Ser. B.* 263:661-666.

Komdeur, J. (2004) Sex-ratio manipulation, p. 102-106. Em: W.D. Koenig e J.L. Dickinson (eds.), *Ecology and Evolution of Cooperative Breeding in Birds.* Cambridge: Cambridge University Press.

Komdeur, J., S. Daan, J. Tinbergen e C. Mateman (1997) Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* 385:255-525.

Ligon, J. D. e D.B. Burt (2004) Evolutionary origins, p. 5-34. Em: W.D. Koenig e J.L. Dickinson (eds.) *Ecology and Evolution of Cooperative Breeding in Birds.* Cambridge: Cambridge University Press.

Pruett-Jones, S. G. e M.J. Lewis (1990) Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* 348:541-542.

Remsen, J.V. (2003) Family Furnariidae, p. 162-357. Em: del Hoyo, J., A. Elliot e D.A. Christie (eds.), *Handbook of the Birds of the World, vol. 8.* Barcelona: Lynx Editions.

Ridgely, R.S. e G. Tudor (1994) *The Birds of South America: the Suboscine Passerines.* Oxford: Oxford University Press.

Rodrigues, M. e L.A. Carrara (2004) Cooperative breeding in the Rufous-fronted Thornbird *Phacellodomus rufifrons:* a Neotropical ovenbird. *Ibis* 146:351-354.

Rodrigues, M., L.A. Carrara, L.P. Faria e H. Gomes (2005) Aves do Parque Nacional da Serra do Cipó: o Vale do Rio Cipó. *Revista Brasileira de Zoologia* 22:326-338.

Roper, J.J. (2005) Sexually distinct songs in the dueto of the sexually monomorphic Rufous Hornero. *J. Field Ornithol* 76:234-236.

Sambrook, J., E.F. Fritsch e T. Maniatis (1989) *Molecular Cloning. A laboratory Manual.* New York: Cold Spring Harbor Laboratory Press.

Santos, F.R., N.O. Bianchi e S.D. Pena (1996) Worldwide Distribution of Human Y Chromosome Haplotypes. *Genome Research* 6:601-611.

Sick, H. (1993) *Birds in Brazil.* Princeton: Princeton University Press.

Skutch, A.F. (1969) A study of the Rufous-fronted Thornbird and associated birds. *Wilson Bull.* 81:5-43.

Walters, J.R., C.K. Copeyon e J.H. Carter III (1992) Test of the ecological basis of cooperative breeding in red-cokaded woodpeckers. *Auk* 109:90-97.