

# Patterns of brood division and an absence of behavioral plasticity in a neotropical passerine

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**Abstract** Studies of parental behavior in various habitats provide an opportunity to gain insight into how different environments may mold strategies of parental care. Brood division by parents has been hypothesized to occur facultatively within and among species. Brood division occurs when each parent cares for specific offspring within a brood. We studied brood division in a neotropical passerine, the western slaty antshrike (*Thamnophilus atrinucha*). Our results present a unique picture of a highly specialized example of avian brood division. Division was a fixed behavioral pattern in the population studied: all broods divided by fledging and remained divided during the entire post-fledging period. Brood division before fledging, a previously unreported phenomenon, occurred in 40% of nests observed. Parents that preferentially fed a certain offspring (defined as their focal offspring) in the nest fed the same individual after fledging. Each parent fed only its focal offspring in broods of one and two. The male parent cared for the heavier offspring and the first offspring to leave the nest. Siblings were segregated spatially during the time of highest predation risk. These observations suggest that a consistently high risk of predation on offspring has favored initial spatial segregation and inflex-

ibility of brood division behavior in this species. Factors other than predation risk alone may explain the observed patterns of long-term, perfect brood division. Because high predation is common and relatively predictable in the tropics, selection for fixed brood division may be stronger in tropical birds than in the temperate zone.

**Keywords** Behavioral plasticity · Brood division · Neotropical · Parental care · *Thamnophilus atrinucha*

## Introduction

Strategies of parental care are adaptive responses to environmental factors, such as food availability, threat of predation, and time available for reproduction (Lack 1947, 1968; Burley 1980; Clutton-Brock 1991; Stearns 1992). Contrasting environments can lead to different strategies (Clutton-Brock 1991; Stearns 1992), such as reduced feeding rates to offspring in areas of higher predation risk (Martin et al. 2000b; Ghalambor and Martin 2002).

A flexible behavior in birds is brood division whereby each parent cares for only certain offspring within a brood (Smith 1978; Harper 1985; McLaughlin and Montgomerie 1985). The patterns of brood division are variable. Even within one population, broods may vary in when they divide, for how long, and whether division occurs. Brood division has only been observed during the post-fledging period (Weatherhead and McRae 1990; Anthonisen et al. 1997), varying in timing from fledge day (McLaughlin and Montgomerie 1985) until a few weeks after fledging (Leedman and Magrath 2003). Broods may be divided between male and female parents based on the size or sex of the offspring, or randomly (reviewed in Lessells 2002; Vega et al. 2007). In multi-brooded species, breeding pairs

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often divide broods only in their last nesting attempt of the season or broods are initially divided, but then males subsequently take over care of all fledglings (Nolan 1978; Zaias and Breitwisch 1989; Weatherhead and McRae 1990). Both these patterns allow females to initiate a new nest quicker.

A number of hypotheses attempt to explain the function of brood division: (1) Avoidance of whole brood predation by spatially segregating young (Smith 1978; McLaughlin and Montgomerie 1985). This hypothesis predicts that broods are divided and young segregated spatially during the time of highest mortality for offspring (McLaughlin and Montgomerie 1985; Leedman and Magrath 2003). (2) Conflicts of interest between parents, leading to division by a particular type of offspring (size or sex; reviewed in Lessells 2002). If offspring differ in their feeding requirements (often due to their size or sex), this leads to conflicts between parents over which one feeds the individual requiring more care (reviewed in Lessells 2002). (3) Conflicts between siblings over a particular parent (Slagsvold 1997; Draganioiu et al. 2005). If parents differ in amount of food provided to offspring, this leads to conflicts between siblings over the parent that provides more care (reviewed in Lessells 2002). The dominant (often larger) offspring is predicted to win the conflict (Slagsvold 1997). (4) A parental strategy to reduce conflicts between siblings. Division may decrease the ability of certain offspring to obtain more of the food resources and decrease the number of siblings young compete with by separation into subfamilies (Harper 1985). If sibling competition is reduced, little aggression between siblings is expected. (5) A parental strategy to increase provisioning efficiency of the parents, reducing the amount of time and energy parents spend feeding young (Smith 1978; Moreno 1984; McLaughlin and Montgomerie 1985). Provisioning efficiency may increase if the offspring a parent is feeding remains in closer proximity than the other offspring (Smith 1978; Moreno 1984). (6) A strategy that increases the efficiency of interactions between a parent and focal offspring (the specific offspring that a parent is feeding) through the learning of each others alarm calls and foraging behaviors (Leedman and Magrath 2003; Draganioiu et al. 2005; Vega et al. 2007). This hypothesis (social specialization) predicts long-term, extreme brood division, with one-on-one care between a parent and focal offspring, even in broods of one.

Most studies of avian brood division have observed species breeding at temperate latitudes (reviewed in Lessells 2002; but see Price and Gibbs 1987; Leedman and Magrath 2003; Vega et al. 2007). Environmental conditions for breeding birds differ significantly by latitude (Lack 1947, 1968; Skutch 1949, 1950; Martin 1996). Thus, studies of parental behavior in tropical regions provide an opportunity to gain insight into how different environments

may mold strategies of parental care. Long breeding seasons with multiple breeding attempts, long post-fledging periods, and a small clutch size (“typical” tropical traits) are generally observed in tropical and southern hemisphere passerines when compared with their temperate-zone counterparts (Martin 1996; Stutchbury and Morton 2001; Ricklefs and Wikelski 2002; Russell et al. 2004). Data are few, but the threat of predation to offspring appears to be comparatively high in the tropics (Ricklefs 1969; Skutch 1985; Robinson et al. 2000) and is viewed as the predominant selective pressure on avian life histories in the tropics (Skutch 1949; Martin et al. 2000a). Because of the higher predation environment experienced by tropical birds, predation may play an important role in brood division.

The present study is the first detailed examination of avian brood division in a “typical” tropical species, living in a contiguous, mainland tropical forest with a high abundance of predators (Skutch 1985; Sieving 1992). We studied parental care in a neotropical passerine, the western slaty antshrike (*Thamnophilus atrinucha*). This species has been hypothesized, via one anecdotal account, to exhibit brood division during the post-fledging period (Oniki 1975). We asked the following questions: (1) What is the timing of brood division? (2) How does the brood divide; by offspring size, sex, fledge order, or randomly? (3) Are the patterns of division fixed throughout the year or does the occurrence of division vary with breeding attempt? (4) What are the potential functions of brood division?

## Materials and methods

### Study population and site

We observed slaty antshrikes from February to September in 2003 and 2004 on a 100-ha study site in Parque Nacional Soberanía: a 22,000-ha lowland, tropical moist forest in the Republic of Panama (for details, see Karr 1971; Robinson et al. 2000). Slaty antshrikes are a resident insectivore endemic to the Neotropics with a modal clutch size of two (Oniki 1975; Roper 1996). We captured adult birds and marked them with unique combinations of color and numbered metal leg bands. We observed 29 breeding pairs in 2003 and 45 pairs in 2004. Including renesting attempts, we observed 98 nests in 2003 and 175 nests in 2004. We weighed (mass to the nearest 0.1 g) nestlings on the seventh day after hatch (2 days before fledging) and banded them with metal and color leg bands.

### Sampling parent and offspring behavior

We used video camcorders in 2004 to assess whether brood division occurred in the nest and feeding rates of parents.

Identification of the sex of the feeding parent was by sexual dimorphism in plumage color. Individual nestlings were differentiated by marking the back of the nestlings' heads with different colors of acrylic paint. Nests that were too high to individually mark nestlings were used to compare feeding rates of parents. Video camcorders were camouflaged and placed at least 2 m away from the nest. We videotaped nests continuously from 7 A.M.–2 P.M. during three stages of the nestling period: early (days 1–2 after hatch), mid (days 3–4), and late (days 6–7). Observer effects appeared minimal as adults typically returned to feed within 15 min of setting up the video camcorder. We observed 23 nests on videotape; of these, six contained one nestling and 17 contained two. Broods of one were observed to examine whether one or both parents fed the single offspring, testing the social specialization hypothesis. We identified which nestling was fed by which adult and the number of feeding trips by each parent by reviewing the videotapes.

After young fledged, we conducted 2-h observations on families one to two times per week until fledglings were no longer present on the natal territory. Thirteen broods (three broods of one and ten broods of two) were observed in both the nestling and post-fledging periods. Thirty-two broods of two and 11 broods of one were observed during the post-fledging period. The average number of observation periods per family was 7.6 (SE±0.68,  $n=43$ ) and ranged from 1 to 20 depending on the length of the post-fledging period and survival of young. Each observation period was separated by at least 3 days.

Due to dense vegetation and individuals often foraging up high (greater than 10 m), individual birds constantly went in and out of view during the observation periods. Therefore, individuals were observed opportunistically. The following observations were taken (in parentheses is each hypothesis for brood division that was tested by the specific observation): number of feeding visits (conflicts of interest between parents and between siblings and social specialization hypotheses), distances between siblings (predation), aggression between siblings (reduction in sibling competition), and how closely offspring followed parents (provisioning efficiency). We observed feeding events, offspring begging, and other interactions between parents and offspring to assess if brood division occurred.

We attempted to resight fledglings and parents on a weekly basis. If a fledgling disappeared before 35 days, we classified the individual as dead because fledglings cannot forage independently before this age (Tarwater, unpublished data). If the individual disappeared after 35 days, we considered the individual to have dispersed. We never resighted fledglings that disappeared before 35 days despite searching the surrounding area. Results from radio-telemetry support this assumption (Tarwater, unpublished data).

Determination of the occurrence of brood division

Broods were considered divided by two methods. Primarily, brood division was determined based on the feeding events observed during the nestling ( $n=10$ ) and post-fledging periods ( $n=20$ ; see statistical analyses below). During the post-fledging period, in some broods, we were unable to observe enough feeding events to statistically test for division. This was either due to mortality of one offspring ( $n=7$ ) or difficulty in observing feeding events ( $n=5$ ). These broods were considered divided (at least initially when both offspring were alive) based on proximity between individuals, parental defense, begging by fledglings, and by the few feeding events observed. All broods of two were observed during more than one time period to determine the occurrence of brood division. In divided broods, one parent is with one offspring, which are hereafter referred to as the “focal” parent and “focal” offspring.

Criteria for how broods were divided between parents

We examined if one parent provisioned a particular type of offspring by assessing three offspring characteristics: nestling size, sex, and fledge order. Siblings were weighed 2 days before fledging to compare nestling size. We observed young leaving the nest (i.e., fledging) for 16 nests in 2004 to compare order of fledging. Young were observed until the sexual dimorphism in plumage was visible (3 weeks after fledging). We did not conduct DNA-based sex determination for offspring that died before sexing by plumage was possible. The sample size for broods where we knew which parent took which offspring and offspring mortality occurred was negligible ( $n=10$ , male and female parents each had five offspring die).

Statistical analyses

*Determination of the occurrence of brood division*

For brood division to occur, two statistical criteria must be met (Harper 1985; Leedman and Magrath 2003). First, different fledglings within a brood must be fed in different proportions by different adults (Leedman and Magrath 2003). Separate chi-squared tests on each brood were used to test the first criteria. Second, within a brood, each offspring must be fed more by one parent than the other parent (Leedman and Magrath 2003; Draganoiu et al. 2005). We used separate two-tailed binomial tests on each offspring per brood, comparing the number of male and female feeding visits to each offspring. If both criteria are met, the brood was considered divided. In a few broods, the chi-squared test for the entire brood was significant and only one of the binomial tests. If the binomial test for the

other offspring was not significant because this offspring was rarely observed being fed (less than five feeding visits observed) and the feeding events to this offspring were not by the parent feeding the other fledgling, the brood was still considered divided. We pooled feeding events observed across all observation periods to see if one parent always fed the same offspring. During each observation period, each fledgling was observed being fed on average 1.6 times ( $SE \pm 0.1$ ,  $n=57$  fledglings). Brood division could still be assessed even when a fledgling was only observed being fed once during an observation period because all fledglings were observed more than one time.

We also tested for the occurrence of preferential feeding. Preferential feeding was tested to examine whether parents that preferred an individual in the nest fed the same individual after fledging. This can occur in: (1) broods of two when only one offspring in a brood is fed more frequently by one parent (unlike brood division where each offspring is fed by a different parent) and (2) broods of one, when one parent feeds the offspring more than the other parent. In broods of one, whether a parent fed the offspring more frequently because it was the better feeding parent or because the parent actively preferred the offspring was difficult to differentiate. Nevertheless, the long-term extreme associations found between one parent and the offspring suggest an active preference (see “Results” below). We used two-tailed binomial tests on each offspring per brood, comparing the number of feeding visits by male and female parents to the offspring.

#### *Criteria for how broods were divided between parents*

To assess if division was based on offspring traits (size, sex, or fledge order), we used Pearson  $\chi^2$  exact tests with tail probabilities estimated by Monte Carlo routines (StatXact6.0).

#### *Hypotheses for the function of brood division*

The predation hypothesis predicts broods should be divided and siblings segregated spatially during the time of highest offspring mortality. Therefore, we examined changes in spatial segregation with offspring age and how this corresponded to changes in offspring mortality with age. We determined the spatial segregation of young [the distance (in meters) between two siblings from the same brood] by calculating the mean distance between siblings for each observation period per brood. We then calculated the average spatial segregation of young across all broods for each time point. We used repeated-measures analysis of variance (ANOVA) to evaluate if spatial segregation changed with offspring age (in weeks). Observed percent of fledglings dying during each week period was calculated

by dividing the number of offspring that died during the week from the total number of fledglings alive at the beginning of the week.

A conflict of interest between parents over how the brood is divided is predicted if offspring differ in their feeding requirements (we examined the amount of food offspring received). A conflict of interest between siblings is predicted if parents differ in amount of food provided. We used feeding rate and food load to examine amount of food provided. We observed during the post-fledging period observations which individuals were in or out of view. We then used the total time in view and number of feeding observations to calculate feeding rates. During the nestling period, feeding rate was calculated by number of feeding observations divided by the total time a nest was videotaped. Differences in feeding rates between parents and between different types of offspring in broods of two were tested using Wilcoxon-signed ranks tests. Prey size was estimated by comparing the length and depth of the prey item to the length and depth of the bill of the adult with prey. Food load was calculated by multiplying length by depth. Males and females do not differ in these bill measurements (Tarwater and J.P. Kelley, unpublished data). Differences in food load between parents were tested using a Wilcoxon-signed ranks test.

The reduction in sibling competition hypothesis predicts little aggression between siblings should be observed. We recorded the number of times during the post-fledging period that siblings chased one another to examine aggression. The provisioning efficiency hypothesis predicts that offspring should follow their focal parent more often than their non-focal parent. We used a paired  $t$  test to determine whether fledglings followed focal parents more often than non-focal parents. Following an individual is defined as staying in close proximity (less than 5 m apart) and following the movements of the parent (not including during feeding events).

## Results

### Timing of division

We accumulated 391 h of videotaped observations from 23 nests (17 nests with two nestlings, six nests with one nestling) during the nestling period. In contrast to all previous reports on the timing of brood division, we observed division during the nestling period. To test for division, we used only nests with two nestlings and where individual nestlings could be identified accurately for at least two time periods (occurred in 10 of 17 broods with two nestlings). All feeding events used to assess brood division were from the mid and late nestling stages because the paint on the nestlings' heads was not visible during the

early stage. Brood division was found unambiguously in three of ten nests ( $\chi^2$  tests,  $P < 0.03$  in all three tests, and binomial, two-tailed,  $P < 0.11$  in all six tests; Fig. 1). Because feeding rates during the nestling period were low ( $< 1.1$  feeding visits per hour per offspring), we considered two-tailed binomials at  $P < 0.11$  to indicate offspring were fed by different parents. In these three divided broods, each parent had a primary offspring, and each offspring had a primary feeder. Additionally, one adult was associated with the same nestling across all time periods sampled. In one nest (Fig. 1, brood 4), the  $\chi^2$  test was significant; however, one of the binomial tests was not. In this brood, each parent had a primary offspring, but one nestling was fed equally by both parents. Whether this brood is considered divided depends on if brood division is classified based on the parent's point of view (having a primary offspring) or the offspring's (having a primary feeder). In this brood, each parent had the same primary offspring during both the nestling and post-fledging periods, suggesting that the brood divided during the nestling period.

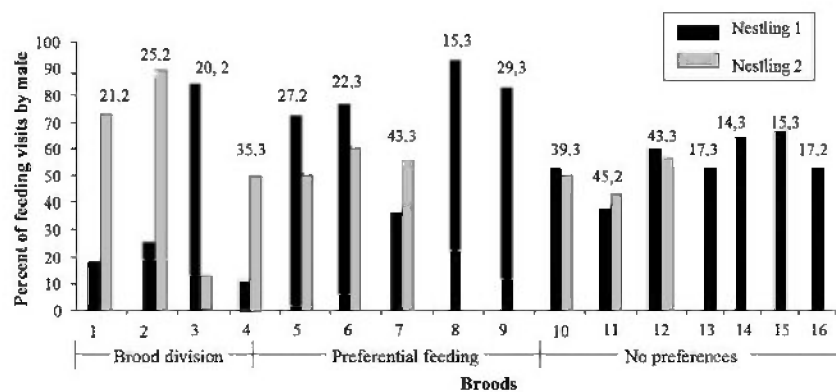
All broods observed were divided upon fledging. Our observations at the time of fledging indicated that parent and focal offspring form pairs immediately ( $n = 16$  broods). One parent fed the offspring in the nest, while the other parent led the fledged offspring away. We conducted observations on 32 families with two fledglings (Table 1). All broods were observed on fledge day and on at least one other day to test for brood division. The average number of observation periods per family was 8.1 (SE  $\pm 0.68$ ,  $n = 32$ ), with each observation period separated by at least 3 days. In 20 broods, the  $\chi^2$  test was significant, indicating that parents fed different young in different proportions. In 15 of these 20 broods, brood division was found in all cases (binomial, two-tailed,  $P < 0.03$  in all 30 tests; Table 1); however, in the remaining five broods, only one binomial

test (for one of the fledglings) was significant. Few feeding events were observed for the other fledgling. These broods were still considered divided based on the number of feeding events for both fledglings and the interactions observed between the parent and focal offspring. In 12 broods, there were not enough feeding observations to test for brood division either because one offspring died early in the post-fledging period ( $n = 7$ ) or too few feeding events were observed ( $n = 5$  broods). These broods were considered divided at least in the beginning of the post-fledging period (when both offspring were alive) based on behaviors of parents and offspring. Broods where both offspring survived and observations were conducted from fledge day until apparent natal dispersal ( $n = 17$ , broods 1–9, 11–18 in Table 1) remained divided the entire post-fledging period.

We tested the cases where either brood division or preferential feeding in the nest occurred and the offspring fledged to determine whether the association between a parent and specific nestling persisted into the post-fledging period. Preferential feeding in the nest occurred in three broods of two (binomial, two-tailed,  $P < 0.08$  in all cases; Fig. 1) and in two broods of one (binomial, two-tailed,  $P < 0.001$  in all cases; Fig. 1). In eight of nine cases (binomial, one-tailed,  $P < 0.03$ ), the parent that preferentially fed the nestling took the same individual after fledging.

Strict one-on-one care in broods of one and two

Not only was brood division ubiquitous by fledging but perfect brood division was also observed (all feedings to one offspring are by one parent). In broods of two (where both offspring survived), out of 476 total feeding observations, only six observations of a parent feeding a non-focal fledgling were observed (Table 1). Even in single young broods, offspring were fed by only one parent. Out of 231 total feeding observations of single young broods [includ-



**Fig. 1** Percent of feeding visits by male to individual nestlings (number of feeding visits by male to one nestling out of total number of visits by male and female to same nestling). *Two bars above a brood* indicate a brood of two, and *one bar (black only)* indicates a brood of one. Broods: 1–3: exhibit unambiguous brood division, 4:

ambiguous brood division (see text), 5–9: preferential feeding by male or female to one nestling, 10–16: no division or preferential feeding. *Numbers above each brood* represent the number of total feeding events observed and number of observation periods each nest was videotaped

**Table 1** The number of feeding visits by the male out of the total number of feeding visits (by male and female) to particular fledglings during the post-fledging period

Brood no.	No. of observation periods	$\chi^2$	Fledgling 1			Fledgling 2		
			Feeding visits		<i>P</i>	Feeding visits		<i>P</i>
			Total #	Average/day		Total #	Average/day	
1	8	—*	12/12	1.5	0.001	0/10	1.4	0.001
2	12	—*	12/12	1.7	0.001	0/20	1.0	0.001
3	7	—*	6/6	1.2	0.03	0/8	1.3	0.008
4	6	—*	12/12	2.0	0.001	1/22	3.5	0.001
5	12	—*	14/14	3.5	0.001	0/14	3.5	0.001
6	11	—*	14/15	1.6	0.001	1/17	1.5	0.001
7	12	—*	21/22	1.8	0.001	0/17	1.5	0.001
8	5	—*	7/7	1.5	0.02	0/6	1.3	0.03
9	10	—*	22/22	2.2	0.001	0/11	1.1	0.001
10	3	—*	8/8	2.7	0.008	0/10	3.3	0.002
11	12	—*	15/15	1.3	0.001	0/11	0.9	0.002
12	9	—*	10 /10	1.1	0.001	0/13	1.4	0.001
13	10	—*	11 /11	1.2	0.001	0/17	1.9	0.001
14	9	—*	17/17	1.9	0.001	0/9	1.0	0.001
15	13	—*	20/20	1.7	0.001	0/19	1.6	0.001
16	10	—*	12/12	2.0	0.001	0/4	0.7	— <sup>c</sup>
17	6	—*	12/13	1.7	0.003	0/3	1.0	— <sup>c</sup>
18	7	—**	9/9	1.8	0.004	0/3	0.6	— <sup>c</sup>
19	20	—**	0/12 <sup>b</sup>	1.7	0.001	3/3 <sup>b</sup>	1.5	— <sup>c</sup>
20	12	—**	16/ 16	2.0	0.001	0/2 <sup>b</sup>	1.0	— <sup>c</sup>
21	2	NS	1/1	0.3	— <sup>c</sup>	0/3	1.0	— <sup>c</sup>
22	2	NS	4/4	2.0	— <sup>c</sup>	0/2	1.0	— <sup>c</sup>
23	4	NS	3/3	0.8	— <sup>c</sup>	1/2	0.3	— <sup>c</sup>
24	2	NS	2/2	1.0	— <sup>c</sup>	0/3	1.5	— <sup>c</sup>
25	5	NS	1/6	0.8	— <sup>c</sup>	1/1 <sup>b</sup>	1.0	— <sup>c</sup>
26	2	— <sup>a</sup>	6/6	3.0	0.03	0/0		— <sup>c</sup>
27	5	— <sup>a</sup>	0/7 <sup>b</sup>	1.4	0.02	0/0 <sup>b</sup>		— <sup>c</sup>
28	15	— <sup>a</sup>	0/23	1.6	0.001	0/0 <sup>b</sup>		— <sup>c</sup>
29	12	— <sup>a</sup>	17/17	1.7	0.001	0/0 <sup>b</sup>		— <sup>c</sup>
30	5	— <sup>a</sup>	0/6 <sup>b</sup>	2.0	0.03	0/0 <sup>b</sup>		— <sup>c</sup>
31	14	— <sup>a</sup>	1/14	2.6	0.001	0/0 <sup>b</sup>		— <sup>c</sup>
32	7	— <sup>a</sup>	16/17	2.3	0.001	0/0 <sup>b</sup>		— <sup>c</sup>

*Total #* total number of feeding visits observed across all observation periods. *Average/day* average number of feeding visits observed per observation period. *P* two-tailed binomial tests based on number of feeding visits by male and female parent to one fledgling.

\* $P < 0.001$ , \*\* $P < 0.01$ ; NS:  $P > 0.05$

<sup>a</sup> Unable to perform test because one fledgling died before was observed being fed.

<sup>b</sup> Fledgling died early in the post-fledging period.

<sup>c</sup> Too few feeding visits observed to statistically test for brood division.

ing both broods where one fledgling died early in the post-fledging period ( $n=9$ ) and broods that fledged only one young ( $n=11$ ), 225 were by the fledgling's focal parent.

Adults are predicted to maximize reproductive fitness by decreasing inter-clutch intervals. Thus, the expectation is that either males would care for the single fledgling or adults would share in care to allow the female to initiate a new nest. In 11 of 43 broods, only one young fledged and males and females were equally likely to care for the fledgling (males cared for 6 of 11 fledglings). In the nine broods where two young fledged but one died within the

first few days of the post-fledging period, the parent that lost its focal fledgling did not help in provisioning the surviving fledgling (Table 1). Additionally, males may be more likely to take the single fledgling if the pair initiated another nest. We found no association between the occurrence of reneating and sex of parent caring for the single fledgling (Fisher's exact test,  $P=1.00$ ,  $n=20$ ). To determine if sex of parent providing care to the fledgling influenced timing of reneating, inter-clutch intervals were calculated. Inter-clutch interval is the number of days between fledge day of the first nest and lay date of the

second nest. No difference was observed in mean ( $\pm$ SE) inter-clutch interval length based on which sex of parent cared for the fledgling (male=47.0 $\pm$ 3.87 days,  $n=5$ , female=52.1 $\pm$ 6.46 days,  $n=7$ , Mann–Whitney  $U$  test,  $U=20.00$ ,  $P=0.75$ ). Thus, regardless of which parent provided care to the single fledgling, breeding pairs did not alter the timing of the subsequent nest attempt.

#### Criteria for how broods were divided between parents

Male (fathers) and female (mothers) parents were equally likely to select male or female offspring as their focal young (Table 2). We only included broods with different sexed offspring in the analysis because in these broods parents have an option of which sex to feed. Parents appeared to divide broods based on offspring size, with fathers taking the heavier offspring (Table 2). Offspring sex was independent of offspring size ( $\chi^2=0.036$ ,  $df=1$ ,  $P=1.0$ ,  $n=33$ ). Parents also divided broods based on order of fledging. Fathers tended to take the first to fledge and mothers the last to fledge (Table 2). Heavier offspring were the first sibling to fledge in 10 of 15 cases ( $\chi^2=2.13$ ,  $df=1$ ,  $P=0.14$ ,  $n=30$ ). Thus, fathers took the heavier offspring, which tended to be the first offspring to leave the nest.

#### Variation in brood division with breeding attempt

Out of 18 breeding pairs observed (where both offspring survived and enough feeding visits were observed to test for brood division, broods 1–18 in Table 1), ten attempted another nest after the first successful brood. Previous studies found that brood division either occurs only in the last broods of the year or broods initially divide but then males switch to caring for all fledglings. We found that regardless of whether the pair had another nesting attempt, all broods were divided (as shown above). Eight of the 10 second nest attempts overlapped with the post-fledging

care period of the previous nest. Adults alternated between caring for the new nest and their focal fledglings.

#### Tests of the hypotheses for the function of brood division

##### Predation

The predation hypothesis predicts that broods will be divided and young segregated spatially during the time of highest mortality for offspring (McLaughlin and Montgomerie 1985; Leedman and Magrath 2003). Slaty antshrike siblings were spatially segregated for the first week out of the nest, and after this initial week, the two fledglings remained in close proximity (on average, less than 5 m apart) for the remainder of the post-fledging period (repeated-measures ANOVA  $F_{2,30}=8.76$ ,  $P<0.005$ ,  $n=19$ ; Fig. 2). Slaty antshrike fledglings were more likely to die during the first week after fledging (83 young fledged of which 20.4% died during the first week) then during week 2 (7.8% died), week 3 (5.0%), and weeks 4 and 5 (0% each; Fig. 2). We did not have enough broods where siblings did not spatially segregate the first week to explicitly test whether segregation reduced the chances of predation. Nevertheless, all broods were divided and spatially segregated during the time of highest mortality, consistent with the predation hypothesis.

##### Conflicts of interest between parents over how broods divide

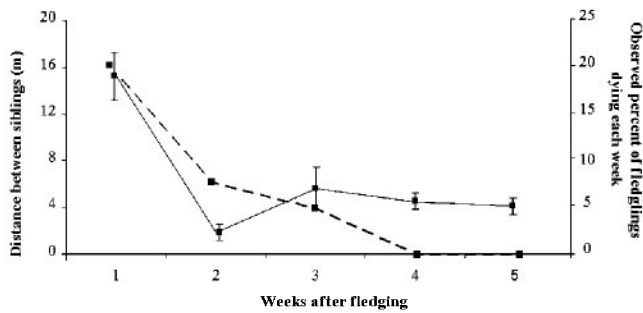
If division by offspring type is due to conflicts between parents, differences between siblings in amount of food received should be observed. Parents fed light and heavy offspring at similar rates during the post-fledging period (Wilcoxon-signed ranks test:  $Z=-0.2$ ,  $P=0.85$ ,  $n=24$ ; Fig. 3). Because heavy and light offspring did not receive different amounts of food, the conflicts of interest between parents hypothesis was not supported.

##### Conflicts of interest between siblings over how broods divide

If division by offspring type is due to conflicts between siblings, differences between parents in amount of food provided should be observed. Males and females did not differ in their feeding rates during the post-fledging period (Wilcoxon-signed ranks test:  $Z=0.13$ ,  $P=0.91$ ,  $n=26$ ; Fig. 3) or during the nestling period (Wilcoxon-signed ranks test:  $Z=1.19$ ,  $P=0.25$ ,  $n=16$ ; Fig. 3). Additionally, average food load/feeding trip did not differ between parents during the post-fledging period (Wilcoxon-signed ranks test:  $Z=0.710$ ,  $P=0.48$ ,  $n=17$ ) or during the nestling period (Wilcoxon-signed ranks test:  $Z=-1.04$ ,  $P=0.33$ ,  $n=14$ ).

**Table 2** The number of fledglings male and female parents had as focal offspring based on offspring sex, size, and fledge order

	Parent sex		$\chi^2$	$df$	$P$
	Female	Male			
Offspring sex			0.14	1	0.7
Male	8	6			
Female	6	8			
Offspring size			7.81	1	0.01
Heavy	10	21			
Light	21	10			
Offspring fledge order			4.80	1	0.03
First	4	11			
Second	11	4			



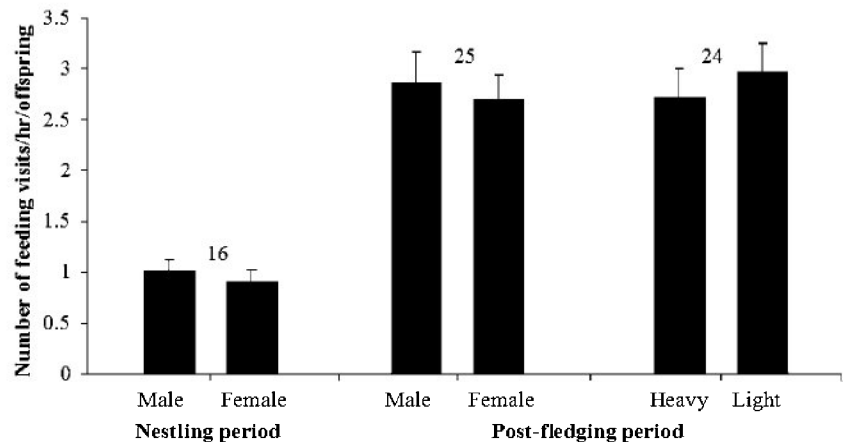
**Fig. 2** Mean ( $\pm$ SE) distance between siblings (solid line,  $n=19$  broods) and observed percent of fledglings dying each week (dashed line,  $n=83$  fledglings) for the first 5 weeks after offspring fledge

These results indicate parents fed offspring equally. Thus, the hypothesis that division arises due to conflicts between siblings over the better feeding parent was not supported.

#### Parental strategy to reduce sibling competition

If sibling competition is reduced due to brood division, little aggression between siblings should be observed. We could not directly test whether aggression was reduced because both divided and undivided broods were not found. Nonetheless, aggression between siblings in the form of chasing or displacement was only seen three times in all broods watched during the post-fledging period. Because we observed that parents never fed non-focal fledglings, we also examined how often offspring attempted to get food from non-focal parents. We observed a fledgling trying to get food from a non-focal parent in only 13 out of 476 feeding events. This observation was rare despite the fact that the entire brood traveled together after the first week out of the nest. By offspring only begging to focal parents (and offspring never having more than one sibling), sibling competition is essentially nonexistent.

**Fig. 3** Mean ( $\pm$ SE) feeding rates by male and female parents and received by heavy and light offspring across the nestling and post-fledging periods. Numbers above bars are the sample sizes for each paired comparison



#### Provisioning efficiency

Provisioning efficiency may increase if the offspring a parent is feeding remains in closer proximity than the non-focal fledgling. Fledglings followed focal parents more often than they followed non-focal parents (paired  $t$  test,  $t=5.944$ ,  $df=30$ ,  $P<0.001$ ,  $n=31$ ). By fledglings staying close to focal parents, parents did not travel far to feed offspring.

#### Social specialization

We observed perfect, long-term brood division and strict one-on-one care in broods of one (as shown above). These patterns are consistent with the social specialization hypothesis.

#### Discussion

Overall, our results present a unique picture of a highly specialized example of avian brood division. High variability among species occurs in the percent of individuals that divide broods. Slaty antshrikes appear to be at the extreme end of this distribution, with no variation in the occurrence of division. Brood division was ubiquitous in slaty antshrikes by the time young left the nest. All broods were observed on fledge day, and both parents were either observed feeding different offspring ( $n=25$  broods) or parents were defending separate areas, suggesting each parent was feeding a different fledgling (broods where one fledgling was not observed being fed,  $n=7$ ). Each parent fed only its focal offspring in broods of one and two. The male cared for the heavier offspring upon fledging and the first offspring to fledge. Our observations are the first account of avian brood division in the nest. Moreover, we are the first study supporting predation as a potentially key factor in the initial spatial segregation and division of the brood.



### Division during the nestling period

Our observations of division in the nest leads to interesting questions of why broods divide early, why parents feed the same offspring after fledging and how discrimination in the nest occurs. Preferential feeding in the nest has been demonstrated in a number of species; however, these studies did not explicitly test for brood division (reviewed in Lessells 2002). Brood division is an extreme form of preferential feeding, and thus, division in the nest should not be unexpected. Studies on preferential feeding indicate that nestling position, begging intensity, and size influence the allocation of food, and male and female parents may differentially respond to these nestling traits (Gottlander 1987; Leonard and Horn 1996; Kilner 2002). Sex differences in provisioning rules in the nest may reduce the ability of offspring to monopolize food resources (Kolliker et al. 1998). This hypothesis is equivalent to the reduced sibling competition hypothesis of brood division. Competition between siblings in the nest occurs when larger nestlings outcompete smaller nestlings for the better position or for the better feeding parent (Gottlander 1987; Kilner 1995; Slagsvold 1997). Brood division may ensure that the smaller nestling gets fed. In slaty antshrikes, the observation that parents fed the same individual in both the nestling and post-fledging periods is unique. Parents either have the same decision rules, favoring large or small offspring before and after fledging, or parent–offspring recognition develops during the nestling period. Additionally, because a parent feeds the same individual, this suggests that there is a benefit to maintaining the relationship between a parent and offspring across both time periods. One potential benefit may be to facilitate division at fledging, particularly because siblings leave the nest at different times. These questions call for further investigation.

### Division by offspring size

In slaty antshrikes, males cared for the heavier offspring and first offspring to fledge. Other studies have similarly shown the male parent feeding the larger offspring (Bengtsson and Ryden 1981; Slagsvold et al. 1994). This is generally attributed to the male choosing to feed the offspring that requires less care, or larger offspring choosing to be fed by the parent that provides more care (reviewed in Slagsvold 1997). Neither of these is supported by our results. Heavier offspring did not appear to require less food than lighter offspring (they were fed equally), and male and female parents did not differ in their feeding rates. Even when evaluating provisioning on a per nest basis, only in 2 out of 17 nests did one parent have a higher feeding rate (and fed the lighter offspring). Division by size and fledge order may occur because parents have a rule of thumb on how to divide the brood to facilitate division

(Harper 1985; Vega et al. 2007). Nevertheless, further evaluation of other potential hypothesis for division based on offspring size is necessary.

### Variation in care with number of breeding attempts

In slaty antshrikes, all broods divided and remained divided, regardless of renesting. Yet in other multi-brooded, pair breeding species, brood division does not occur until the last nesting attempt of the season or males take over care of older fledglings, reducing inter-clutch interval length (Nolan 1978; Zaias and Breitwisch 1989; Weatherhead and McRae 1990). Interestingly, in one cooperatively breeding species, both early and final broods were divided (Leedman and Magrath 2003). By having extra caregivers, cooperative breeding may allow broods to remain divided and the female to renest rapidly (Leedman and Magrath 2003). Due to the long breeding seasons of tropical birds, selection favoring rapid renesting after a successful first brood may be reduced (Russell et al. 2004). Additionally, fledglings require extended post-fledging parental care (Russell 2000; Russell et al. 2004). Breeding pairs wait to initiate a second clutch until fledglings (from broods of one and two) are independent (Tarwater, unpublished data). Due to long breeding seasons and extended post-fledging parental care, antshrike parents do not appear to be in a rush to nest again after the first successful brood.

### Broods of one

The fixed behavior of one-on-one care in broods of a single offspring is uncommonly observed in other species (but see Leedman and Magrath 2003). Males are predicted to provide more care to fledglings only if females initiate a new clutch sooner as a result (Weatherhead and McRae 1990). Yet, this was not observed in antshrikes. Male care did not decrease inter-clutch interval length and occurred regardless of whether the female initiated another nest. When only one nestling fledged, males and females were equally likely to care for the offspring. How it is decided which sex of parent cares for the fledgling requires further investigation. Sole care by one parent in single young broods suggests that there are benefits to having one-on-one care, irrespective of brood division. This result lends support to the social specialization hypothesis as an important factor in brood division.

Why does long-term, seemingly obligatory brood division occur in slaty antshrikes?

The absence of behavioral plasticity in brood division has not been reported elsewhere and implies unusually strong

selection for this behavior in slaty antshrikes. The result that all broods divided precludes the direct testing of hypotheses. Thus, our approach is correlative, and we acknowledge the need for experimental studies to explicitly test causation. Nevertheless, this is the first study to support avoidance of predation as part of the explanation for why brood division with initial spatial segregation occurs. This may be due to the higher predation risk on offspring (during the nestling and post-fledging periods) compared to other species studied. Results from radio transmitters placed on nestlings just before fledging ( $n=14$ ) suggest that the primary cause of mortality in the first few days of the post-fledging period is predation (Tarwater, unpublished data).

Spatial segregation upon fledging and comparatively early and universal brood division may reflect a high risk of nest mortality and high risk of predation immediately after fledging. Species subject to frequent nest predation tend to have shorter nestling periods and leave the nest at a lower body mass relative to adult body mass (Ricklefs et al. 1998; Remes and Martin 2002). This leads to young fledging in a relatively undeveloped and immobile state, making them especially vulnerable to predators after fledging. In antshrikes, fledgling mortality was greatest during the first week when young had poor mobility and were likely less capable of escaping predators. Predators may cue into parental activity when provisioning (Skutch 1949; Martin et al. 2000b; Eggers et al. 2005) or begging intensity of offspring (Briskie et al. 1999). Separating spatially the newly fledged young reduces activity at any one location because of the fewer feeding visits to one location when only one fledgling is present. This reduced activity decreases the chances of predation on the whole brood.

Because of the low probability of offspring surviving to fledge in tropical birds (due to high nest predation), if they do fledge, the offspring should be of extremely high value to parents (Ricklefs 1969). Thus, while most species (regardless of latitude) experience the highest fledgling mortality the first week after fledging, the low probability of reaching fledging in many tropical birds (5–15% probability in slaty antshrikes) is expected to heighten selection on behaviors to increase fledgling survival. One such behavior is ubiquitous division with spatial segregation upon fledging.

Whereas predation on offspring is likely a key selective force in the development of obligatory brood division and initial spatial segregation, which environmental factors/life history traits necessitate long-term, perfect division is less clear. Although tests are indirect, our results appear consistent with the social specialization, reduction in sibling competition, and provisioning efficiency hypotheses. Parents feeding the same individual before and after fledging, single parent care in broods of one, and perfect

brood division all suggest that maintaining a one-on-one relationship between a parent and offspring is itself beneficial. Leedman and Magrath (2003) suggested through the “social specialization hypothesis” that this type of care increases the efficiency of interactions among the brood by the focal parent and offspring learning each others individual alarm calls and foraging behaviors.

Social specialization may not necessarily be the factor initially causing broods to divide but rather may enhance the benefits of brood division (such as increasing provisioning efficiency and reducing sibling competition; Leedman and Magrath 2003; Vega et al. 2007). For example, with perfect division, parents know the exact amount of food individual offspring receive. This decreases the ability for offspring to manipulate parents for additional resources and for dominant siblings to obtain more food than other siblings (Leedman and Magrath 2003). Because parents never fed non-focal fledglings, offspring rarely begged or followed non-focal parents, and siblings were rarely aggressive to one another. Once mobile, fledglings followed their focal parents closely, and thus, parents spent less time looking for their focal offspring. Sibling competition is predicted to be more important as siblings get older and become more mobile (Harper 1985). By maintaining perfect one-on-one care, sibling competition is essentially nonexistent. If sibling competition plays a role in division, this suggests that parents maintain some control over intra-brood competition. Parents have been shown to control competition in other parental care behaviors. For example, hatching asynchrony, whereby parents influence sibling competition by controlling the onset of incubation (Magrath 1992; Ricklefs 1993; Smiseth et al. 2003).

Strict one-on-one care is not commonly observed; thus, the question still remains as to why increased efficiency of interactions is more important in certain environments. Efficiency may be important whenever there is an advantage of rapid offspring growth and close parental attention, such as that found in environments with a high risk of predation on offspring. One-on-one care may lead to a reduction in begging and movement associated with provisioning. This may decrease overall brood activity, beneficial in a high predation environment (Skutch 1949; Briskie et al. 1999; Martin et al. 2000b). Additionally, food abundance is hypothesized to be more limited in tropical habitats than in temperate habitats during the breeding season (Lack 1947, 1968). If food is limited in the environment, increasing provisioning efficiency and reducing sibling competition by dividing broods may be especially important (Slagsvold 1997). Two studies have found that brood division no longer occurred when food was abundant (Harper 1985; Price and Gibbs 1987), demonstrating the role food availability may play in division.

Division appears to be a fixed behavioral strategy in slaty antshrikes. Fixed behaviors are expected when selective pressures such as predation risk either vary predictably (i.e., seasonal variation) or remain a consistently strong pressure in the environment (i.e., consistently high predation risk) (Luttbeg and Warner 1999; Relyea 2003). Additionally, flexibility in behaviors may be costly if individuals cannot reliably track changes in predation levels (Stephens 1987; Luttbeg and Schmitz 2000; Gabriel et al. 2005). Predation to offspring is a considerable and consistent threat in slaty antshrikes (i.e., nest predation rates are consistently above 80%; Oniki 1975; Roper 1996); therefore, strategies to minimize risk should be favored. In antshrikes, the factors influencing brood division and initial spatial segregation may be sufficiently constant to select for a fixed strategy of parental care.

In conclusion, brood division has generally been thought to vary within individuals and populations depending upon environmental conditions. Yet, we observed no variability in the occurrence of brood division. This study indicates that under certain conditions, plasticity in parental care behaviors may not always be selected for. Studying species in different environments clearly enhances our knowledge of the adaptive nature of brood division. Investigation of how selective pressures within an environment shape parental care behaviors will shed light onto the variability in parental care strategies observed across species.

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