THE PRE-REPRODUCTIVE PERIOD IN A TROPICAL BIRD: PARENTAL CARE, DISPERSAL, SURVIVAL, AND AVIAN LIFE HISTORIES

BY

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DISSERTATION

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ABSTRACT

The period between offspring birth and recruitment into the breeding population is considered one of the least understood components of animal life histories. Yet, examining this period is essential for studies of parental care, dispersal, demography, and life histories. Studies of the pre-reproductive period are particularly few in tropical regions, where the organization of life histories are predicted to differ compared to northern hemisphere species. For my dissertation I used radio-telemetry, mark-resighting, and field observations to study the pre-reproductive period in a Neotropical bird, the western slaty-antshrike (*Thamnophilus atrinucha*), in Panama. First, I found that parental care after offspring left the nest (the post-fledging period) was greater than care during the nestling period. Prolonged care resulted in a clear trade-off for parents as they did not nest again until fledglings from the first brood were independent. Parents fed offspring for a prolonged duration during the post-fledging period and higher post-fledging survival was observed compared to many northern hemisphere species. Second, I observed that offspring that remained with parents for longer periods on the natal territory had higher survival both while on the natal territory and after dispersal compared to those dispersing earlier. Parental aggression towards offspring increased with offspring age and offspring dispersed earlier when parents renested. Contrary to other family living species, only a small proportion of antshrike offspring remained on the natal territory until the following year and all dispersed to float. Floating is when juveniles wander within other breeding pairs' territories. These results suggest that the benefits of delayed dispersal declined with offspring age and with renesting by parents. Third, I observed that survival during the dependent period and first year was greater in slaty antshrikes compared to that of northern hemisphere species. Pre-reproductive survival relative to adult survival was equal or greater than that observed in northern hemisphere species.

The date offspring left the nest, mass, and age at dispersal influenced offspring survival, whereas offspring sex and year did not. Relatively high survival during the pre-reproductive period coupled with comparatively low annual productivity clarifies how many tropical species achieve replacement. High juvenile survival appears to obtain from extended post-fledging parental care, delayed dispersal, low costs of dispersal, and a less seasonal environment. Lastly, I experimentally manipulated begging at the nest to examine changes in parental behavior. Under elevated begging, parents increased provisioning rates and reduced the time between arrival to the nest and feeding of nestlings, potentially to reduce begging sounds. Furthermore, parents switched to preferentially feed the closest offspring during the begging treatment. This suggests parents either allowed sibling competition to influence feeding decisions, or feeding the closer nestling increased the efficiency of provisioning.

In summary, I found that slaty antshrikes have delayed age at reproduction, higher post-fledging and first year survival, extended post-fledging parental care, equal or greater pre-reproductive survival relative to adult survival, and delayed dispersal compared to many northern hemisphere passerines. These results suggest that this tropical species has a strategy of high investment into few offspring. Furthermore, reproductive effort is equal or greater at least in slaty antshrikes compared to northern hemisphere species, suggesting that the latitudinal gradient in clutch size is not explained by a gradient in reproductive effort.

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PREFACE

Chapter 1 is written in first-person singular form. Chapters 2-5 have been written as stand-alone manuscripts for publication and I have retained the plural form in this dissertation. Chapter 2 is in press in *Journal of Avian Biology*, and Chapter 3 is in press in *Animal Behaviour*. Chapter 5 is already published in *Animal Behaviour*. Chapters 2 and 3 were co-authored with my advisor, Jeff Brawn. Chapter 5 was co-authored by Jeff Brawn and a collaborator, J. Patrick Kelley, from University of California, Davis. Patrick Kelley provided help with isolating begging sounds for the experiment and wrote the section in the methods on making begging playbacks.

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CHAPTER 1: INTRODUCTION

The period between birth and recruitment into a breeding population is a critical phase of an organism's life history (Clutton-Brock 1991, Roff 1992). Variation in parental care and dispersal behavior can have long-lasting effects on the fitness of offspring and adults (Clutton-Brock 1991, Green and Cockburn 2001). Moreover, survival until reproduction often has significant effects on population growth and is more sensitive to environmental changes than adult survival (Stearns 1992, Clark and Martin 2007). Despite the importance of the pre-reproductive period, this stage is considered one of the least understood components in demography (Stearns 1992).

In species with parental care, the period between offspring birth and recruitment includes time when offspring are dependent upon their parents followed by an independent period. Owing to high mortality, the pre-reproductive period is subject to intense selection (Clutton-Brock 1991). Parental behaviors that increase offspring survival are predicted (Eggers et al. 2005). Nevertheless, conflict between parents and offspring is also expected over the level of care (Trivers 1974). Parents are predicted to provide parental care as long as the gains in offspring survival outweigh the costs to parents (Clutton-Brock 1991). For example, parents are expected to respond to hungry offspring by increasing provisioning, thus increasing offspring survival (Godfray 1991). Yet, parents may also change the allocation of feeding to favor particular offspring when faced with multiple hungry young (Kilner 2002). This may lead to conflict between parents and offspring and between siblings (Lessells 2002).

Parents can also increase offspring survival by feeding young for a prolonged period (Sunde 2008), by allowing offspring to remain with parents after reaching independence (e.g., delaying dispersal) (Ekman et al. 1999), or both. Parents are predicted to increase care with offspring age until offspring near functional independence (Montgomerie and Weatherhead 1988), after which point conflict may occur over the termination of care (Trivers 1974). Conflicts will be especially pronounced in species where parents breed again the same year because continuing care to the first set of young may reduce the probability of breeding again (Verhulst and Hut 1996). The timing of offspring dispersal depends on the relative costs/benefits of remaining versus dispersing for offspring and for parents, potentially leading to parent-offspring conflict (Ekman 2006). Furthermore, high variation in dispersal is often observed (reviewed in Griesser and Barnaby 2010), yet rarely are the behavioral mechanisms, such as competition, examined. Nevertheless, the outcome of this competition has profound effects on the colonization patterns and genetic structure of populations (Clobert et al. 2009).

Survival of offspring until recruitment is profoundly influenced by parental care, dispersal decisions, and environmental conditions (Green and Cockburn 2001, Ridley 2007). The factors that influence offspring survival may vary depending upon whether offspring are dependent upon their parents or independent (Robles et al. 2007). Survival is often the lowest right after birth in vertebrates (Yackel-Adams et al. 2006) and mortality may peak again after independence or dispersal (Sullivan 1989). Because estimates of survival until reproduction are scarce, population modelers assume pre-reproductive survival is a fraction of adult survival (Ricklefs 1973, Temple and Cary 1988). Yet, small changes in estimates can lead to dramatically different conclusions regarding the stability of populations. Thus further estimates of pre-reproductive survival are needed to evaluate assumptions.

Studying the pre-reproductive period is essential for estimating offspring survival and for examining how, within a population, strategies of parental care and dispersal affects the fitness and behaviors of parents and offspring. Yet, few studies examine this period owing to the difficulty of following juveniles. Furthermore, how the environment leads to variation in these behaviors between species remains an important question in studies of parental investment, group-living, and life history theory.

Understanding how and why life histories differ in contrasting environments has been a dominant focus in life history evolution. One model of life history variation is the “slow-fast” continuum observed in a variety of taxa (Gaillard et al. 1989, Promislow and Harvey 1990). A species may breed early, have high fecundity, short life span, and low adult survival (“fast”) or a species may delay reproduction, have low fecundity, long life span, and high adult survival (“slow”). One of the most well cited examples of this continuum is the latitudinal variation observed in avian life histories. In birds, northern hemisphere species are thought to be on the “fast” end of the continuum and southern hemisphere and tropical species are on the “slow” end (Martin 1996, Ricklefs and Wikelski 2002).

Birds have formed the basis for much of what we know about life history variation because they have been studied across a broader range of habitats than other taxa, making them better suited for comparative studies (Roff 1992, Ricklefs 2000). Nevertheless, studies of tropical and southern hemisphere bird species are limited, hindering our understanding of how the environment shapes life histories and how traits are correlated. For example, differences in seasonality and predation in the lowland tropics compared to northern hemisphere regions are predicted to lead to variation in parental care strategies, dispersal, and age-specific mortality (Ashmole 1963, Ricklefs 2000, McNamara et al. 2008). Yet studies of tropical birds traditionally focus only on estimates of adult survival, clutch size, and parental care in the nest (Martin 2004). Examination of dispersal, parental care, and juvenile survival will help resolve long standing assumptions and questions about tropical birds. For example, estimates of adult survival broadly overlap between northern hemisphere and tropical species, yet clutch size is systematically lower in tropical species (Brawn et al. 1999, Ricklefs and Shea 2007). This raises the question of how tropical populations achieve replacement under the assumption that the population is stable. A finding of higher pre-reproductive survival would resolve this question. Furthermore, a key hypothesis for latitudinal variation in clutch size is based on the assumption that tropical birds have lower reproductive effort (Ghalambor and Martin 2001). Yet estimates of pre-reproductive survival are required to evaluate this assumption (Ricklefs 2010). For my dissertation, I studied the pre-reproductive period in a Neotropical bird, the western slaty-antshrike (*Thamnophilus atrinucha*), to test theory on parental care and dispersal behaviors and to evaluate long-standing assumptions about tropical birds. This species was chosen for practical reasons (common species with nests that could be monitored) and for biological reasons. Western slaty-antshrikes are from a speciose geotropically family, *Thamnophilidae*, and thus have life history traits which are similar to other tropical species. Furthermore, they are "typical" tropical birds with a small clutch size, high adult survival, and long life span (up to 14 years). Therefore, my inferences about antshrikes are generalizable to other tropical species.

A recent review found that tropical and southern hemisphere species have extended post-fledging parental care compared to northern hemisphere species (Russell et al. 2004). The post-fledging period is the period between offspring fledging and independence. This period may require greater care and greater energy expenditure by parents compared to earlier stages (Buitron 1988, Weathers and Sullivan 1991). Despite the importance of the post-fledging period, lack of detailed studies hampers understanding of how care influences parents and offspring. In Chapter 2, "The post-fledging period in a tropical bird: patterns of parental care and survival," I present the results of a five-year study on parental care, trade-offs between current and future breeding attempts, and post-fledging survival. I hypothesized that parental care would be greater during the post-fledging period compared to the nestling period, and parents would continue caring for fledglings at the expense of nesting again. I also estimated survival of offspring after fledging and compared my estimate to those from northern hemisphere species.

Although in tropical birds, offspring delay dispersal for longer than northern hemisphere species (Russell et al. 2004), why delayed dispersal is more commonly observed and how this influences offspring survival remains unresolved. Family living (e.g., delayed dispersal) is predicted in species with high adult survival, where higher lifetime fitness is observed by delaying the age at reproduction (Covas and Griesser 2007). Nevertheless, in many species with high adult survival, offspring do not delay dispersal, and therefore specific benefits of remaining on the natal territory compared to dispersing are required for family living to arise. In Chapter 3, “Family living in a neotropical bird: variation in timing of dispersal and higher survival for delayed dispersers,” I present the results of a six-year study on the patterns of delayed dispersal and the costs/benefits of remaining with parents on the natal territory. I predicted that juveniles that remained with parents longer would have higher survival than those dispersing earlier and renesting by parents would influence offspring dispersal. I also examined how competition between parents and offspring and between juveniles influenced variation in dispersal.

Although delayed dispersal and extended post-fledging parental care are predicted to result in higher first year survival rates in tropical birds, few estimates are available. Furthermore, estimates of pre-reproductive survival are required to examine reproductive effort and demography. In Chapter 4, “Survival until reproduction in a tropical bird: factors influencing survival and implications for life histories,” I present the results of a seven-year study on survival until reproduction, age at reproduction, and the sources of variation in survival during the dependent and independent periods. I hypothesized that survival would be the lowest right after fledging and age at first reproduction would be delayed. I also examined the influence of multiple factors on offspring survival. I compared my estimates of survival during the dependent period, the first year, and from fledging until reproduction to estimates from species in northern hemisphere regions.

In high predation environments, such as the lowland tropics, parents may differ in their response to increased begging compared to lower predation environments because parental activity influences risk of nest predation (Martin et al. 2000, Muchai and du Plessis 2005). In Chapter 5, "Parental response to elevated begging in a high predation, tropical environment," I experimentally manipulated begging sounds at nests to examine parental response. I predicted parents would increase food load to increase total food brought to nestlings, but not increase feeding trips (and therefore not increase risk of predation). I also examined whether parents switched to preferentially feed particular offspring under increased begging.

This is one of the few studies to follow juveniles across the pre-reproductive period and to examine long-standing assumptions about pre-reproductive survival and reproductive effort in tropical birds. My results suggest that reproductive effort is not lower in tropical species and that tropical populations are balanced by having high pre-reproductive survival. Contrary to other studies, I found that parents increased provisioning efficiency and switched to feed the closest begging offspring under elevated begging. Moreover, I found that even in non-cooperatively breeding species, offspring benefit from family living. Furthermore, my results indicate that future studies need to examine how the costs/benefits of delayed dispersal vary with offspring age. This research resulted in one of the most comprehensive studies in any tropical bird, such that we are now able to examine how numerous life history traits are correlated.

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CHAPTER 2: THE POST-FLEDGING PERIOD IN A TROPICAL BIRD: PATTERNS OF PARENTAL CARE AND SURVIVAL[a]

ABSTRACT

How environmental conditions affect the timing and extent of parental care is a fundamental question in comparative studies of life histories. The post-fledging period is deemed critical for offspring fitness, yet few studies have examined this period, particularly in tropical birds. Tropical birds are predicted to have extended parental care during the post-fledging period and this period may be key to understanding geographic variation in avian reproductive strategies. We studied a Neotropical passerine, the western slaty-antshrike (*Thamnophilus atrinucha*), and predicted greater care and higher survival during the post-fledging period compared to earlier stages. Furthermore, we predicted that duration of post-fledging parental care and survival would be at the upper end of the distribution for northern hemisphere passerines. Correspondingly, we observed that provisioning continued for 6-12 weeks after fledging, provisioning rate was greater after fledging, and offspring survival from fledging to independence was 75%, greater than all estimates from north-temperate passerines. Intervals between nesting attempts were longer when the first brood produced successful fledglings compared to nests where offspring died either in the nest or upon fledging. Parents delayed initiating second nests after the first successful brood until fledglings were near independence. Our results indicate that parents provide greater care after fledging and this extended care likely increased offspring survival. Moreover, our findings of extended post-fledging parental care and higher post-fledging survival compared to northern hemisphere species have implications for understanding latitudinal variation in reproductive effort and parental investment strategies.

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INTRODUCTION

The timing and extent of parental care affects the fitness of parents and offspring (Williams 1966, Trivers 1972, Roff 1992). More care often increases offspring survival and subsequently the value of offspring to parents, but can reduce the future reproductive success of parents (Nur 1984, Ekman and Askenmo 1986, Clutton-Brock et al. 1989, Verhulst and Hut 1996). Moreover, depending upon environmental conditions, parents may increase care per offspring or reduce care in favor of producing more offspring in the current breeding attempt (Stearns 1992). How the environment and these costs and benefits mold strategies of parental care is essential to understanding variation in life histories within and among species.

Parents are expected to increase parental care as the energetic needs and reproductive value of offspring increase with age (Winkler 1987, Clutton-Brock 1991, Roff 1992). With the approach of functional independence, however, benefits relative to costs for parents are expected to decline (Montgomerie and Weatherhead 1988, Clutton-Brock 1991). Parental care in altricial birds typically follows the predicted trend of increasing care from the incubation to nestling periods. The post-fledging period is the time between offspring leaving the nest (fledging) and natal dispersal. This period is deemed critical for the survival and reproductive success of offspring (Ridley and Raihani 2007, Sunde 2008). Parental care during this stage may require greater daily energy expenditure of parents (Weathers and Sullivan 1991), greater defense (Greig-Smith 1980, Sergio and Bogliani 2001) and greater provisioning rates compared to earlier stages of offspring development (Buitron 1988, With and Balda 1990, Ogden and Stutchbury 1997). Despite the importance of this period, few studies have examined care after fledging.

In species with prolonged post-fledging care, this long duration of care can reduce the number of young produced annually. For multi-brooded species, trade-offs between current and future reproductive efforts are especially evident (reviewed in Parejo and Danchin 2006). Studies manipulating clutch size of first broods reveal that increased parental care to first broods may prevent or delay parents from initiating another clutch within the same breeding season (Slagsvold 1984, Verhulst and Hut 1996, Siefferman and Hill 2008). Initiating a second nest may be costly to the first brood if this leads to early termination of post-fledging care (Verhulst et al. 1997). Decisions about parental care during the post-fledging period have potentially strong fitness consequences for parents and young.

Comparative studies of avian life histories report a latitudinal trend in duration of the post-fledging period (Ricklefs 1969, Fogden 1972, Skutch 1976, Russell et al. 2004). Relative to north-temperate species, tropical and southern hemisphere passerines tend to delay natal dispersal and time to independence (Russell 2000, Russell et al. 2004). Species at lower latitudes also tend to have smaller clutches; leading to speculation that tropical birds employ a strategy of investing more care into fewer young, increasing offspring survival (Karr et al. 1990, Martin 1996). Most studies on parental care in tropical birds are typically based on clutch size, egg mass, or care to the nest (Ghalambor and Martin 2001, Martin 2002, Martin et al. 2006, Martin et al. 2007). Yet, the post-fledging period is predicted to require the greatest care, particularly in tropical birds. Lack of detailed empirical studies on the post-fledging period in tropical birds hampers understanding of how post-fledging care influences offspring and parents, and its implications on latitudinal variation in avian life histories.

We examined parental care and post-fledging survival in a Neotropical passerine, the western slaty-antshrike (*Thamnophilus atrinucha*); a species known to extend parental care and to be multi-brooded within a breeding season (Tarwater and Brawn 2008). Specifically, we asked: 1) What is the amount and duration of parental care given during the post-fledging period? 2) How does post-fledging care compare with pre-fledging (i.e., nestling period) care? 3) What is survival of offspring from fledging until independence and how does survival of fledglings compare to survival in the nest? 4) Are there trade-offs between successive breeding attempts and how does this influence duration of post-fledging care?

METHODS

Study site and focal species

We observed slaty antshrikes from February to between August and December in 2003-2004, and 2006-2007 on a 100 ha study plot 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. 2000b). In 2005, slaty antshrikes were studied from February to November on Barro Colorado Island (BCI); a 1,562 ha tropical moist forest that was isolated by formation of the Panama Canal (for details see Robinson 1999). BCI and Parque Nacional Soberanía are approximately 8 km apart. We captured adult birds and marked them with unique combinations of colored and numbered metal leg bands. We weighed (mass to the nearest 0.1g) nestlings on the seventh day after hatch (two days prior to fledging), and marked them with unique combinations of metal and color leg bands.

The western slaty-antshrike is an insectivorous passerine averaging 23 g in mass. The antshrike's breeding season in Panama is approximately from January to September (Roper 1996). Slaty antshrikes have a modal clutch size of two (89% of nests), with an incubation period of 16 days and a nestling period of 10 days (Oniki 1975, Robinson et al. 2000a). Antshrikes are socially monogamous, have year-round territories, and often remain with the same mate for multiple years (Roper 2005, Tarwater, unpubl. data).

Estimating parental care in the pre- and post-fledging periods

We used video camcorders to observe nests and estimate provisioning rates and food load (prey size/feeding trip) during the nestling period. Video camcorders were camouflaged and placed at least 2 m away from the nest. We videotaped nests continuously from 0700–1400 h during three stages of the nestling period: early (d 1-2 after hatch), mid (d 3-4), and late (d 6-7). Observer effects appeared minimal as adults typically returned to feed within 15 minutes of setting up the video camcorder. We observed 23 nests (containing one or two nestlings) and accumulated 361 hours of videotaped observations. 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 delivering food (the sexes have similar bill sizes). Food load was calculated by multiplying length of the prey (relative to length of the bill, e.g., 1.25 times length of bill) by depth (relative to depth of bill).

After young fledged, we located and observed families for up to 2 hours one to two times/week (with at least 3 days between observation periods) until fledglings were no longer present on the natal territory or until sampling ceased (between August-December). Families were located by eliciting a response by parents to a slaty antshrike playback or listening for the territorial songs of parents (when parents were responding to other individuals). Observation periods started between 0700-1400 h. Thus the post-fledging period observations spanned the same hours of the day as the nestling period observations. After the initial response by parents, we began the observation period and this continued for two hours. Nevertheless, families were often out of view during the two hours we were on the territories, and thus the amount of time families were observed (and we knew whether an offspring was fed) ranged from 10 minutes to 2 hours (average of 44.8 minutes). Any observation periods that were less than 10 minutes were not included in the analysis. We did not include time of day in the analyses for two reasons.

First, provisioning rates in the nest do not vary systematically throughout the day (ranging from 1.2-1.6 feeding visits/nest/hr), with 0700-0800 being the lowest (1.2 visits) compared to the rest of the day (1.5-1.6 visits/hr). Second, post-fledging observation periods occurred throughout the day for each age of offspring. During these observation sessions, we estimated provisioning rates (number of feeding trips/hr/offspring) and food load. We defined duration of post-fledging care as the age of the fledgling when we last observed a provisioning event (rather than length of time on the natal territory because offspring may remain with parents after reaching independence).

Provisioning rates (in and out of the nest) were calculated by dividing the number of feeding events/offspring out of the total number of hours a nest was videotaped or the amount of time per observation period a fledgling or the parent feeding the fledgling was observed. Brood division is strict in this species; each parent feeds only one offspring (Tarwater and Brawn 2008). During the post-fledging observation period, individuals were observed opportunistically owing to dense vegetation and individuals often foraging up high. Fledgling observation periods were grouped into 3 day intervals (i.e., age 22-24 d). No brood was sampled >1 time during each interval. We compared food load (average prey size per feeding trip) between pre- and post-fledging periods.

We observed 56 focal fledglings (from 37 broods) to determine provisioning rates during the post-fledging period. The average number of observation periods per fledgling was 7.9 (SE ± 0.4) but varied (range = 2-13) due to differential survival of young and timing of dispersal. We observed 38 fledglings (out of the 56 focal fledglings) to determine duration of post-fledging parental care. This sample was smaller because we only included fledglings that were observed after parents stopped provisioning or until natal dispersal. Other fledglings (n=117) were only resighted (no behavioral observations) to estimate the timing of dispersal. Nine broods were observed in both the nestling and post-fledging periods.

Offspring survival

We determined survival of eggs and nestlings by checking nests every 2-3 days. Survival during the post-fledging period was estimated by resighting families one to two times per week from fledge day until offspring were no longer observed on the natal territory. We judged that a fledgling was gone if it was not observed after three checks on the natal territory. We never re-observed a fledgling on the natal territory after three checks. We only included offspring from Pipeline Road (none from BCI in 2005) because most fledglings on BCI had radio-transmitters attached prior to fledging. Our sample included 225 fledglings from families that were resighted throughout the post-fledging period.

Trade-offs between successive breeding attempts

To assess the reproductive status of pairs throughout the breeding season, we searched for nests in territories where adults were banded (between 25 and 48 breeding pairs were observed annually). We estimated renesting interval length; defined as the period between predation of one nest and lay date of the breeding pair's subsequent nest. We also estimated the inter-clutch interval length; defined as the period between fledge day of the first nest and lay date of the subsequent nest. Overlap between broods (if any) was the number of days fledglings from the first brood were still present on the natal territory while the subsequent nest was active. We do not define overlap as the number of days first and second broods overlapped divided by the length of parental care to the first brood (as defined by Burley 1980). This definition usually results in the assumption that length of parental care is equal for all individuals (for example see Smith et al. 1989) because length of parental care is rarely determined for each individual offspring. If duration of care is assumed to be equal, dividing by length of parental care to the first brood does not tell us any additional information than only using number of days of overlap (when comparing the same species). Nevertheless, we did not want to assume duration of care was the same for all individuals. To determine if post-fledging parental care delayed initiation of second nests, we compared the duration of inter-clutch intervals to renesting intervals. These two intervals can differ irrespective of post-fledging care if interval length is positively correlated with how long the nest survived. Therefore, we compared inter-clutch intervals between breeding pairs that had successful fledglings (successful inter-clutch interval) to pairs whose fledglings died between two days prior to fledging (when nestlings were banded) and two weeks after fledging (unsuccessful inter-clutch interval). We also examined if the length of the renesting interval was a function of when the nest was depredated to test the effects of accumulated parental care on time to renest after failure.

Statistical analyses

We assessed changes in provisioning rates with offspring age (for all broods) using mixed model unbalanced repeated-measures ANOVA. Provisioning rates over time (offspring age) was the repeated measure and 75 offspring (56 fledglings and 19 nestlings observed only in the nestling period) were included in the analysis. We also compared provisioning rates and food load between the pre- and post-fledging periods with paired t-tests for broods that were observed in both stages (n=9).

Duration of renesting intervals and unsuccessful inter-clutch intervals were compared with successful inter-clutch intervals using Mann-Whitney tests. A Spearman rank correlation was used to test how length of time the nest survived (up until fledging) influenced length of the renesting interval. We used binary logistic regression to ascertain whether probability of initiating a second nest changed depending on the time in the breeding season the first nest fledged or failed. An analysis of covariance (with fledge date as the covariate) was used to determine if parents changed length of post-fledging parental care (to first broods) when they initiate another nest versus when parents did not.

Survival of offspring in the nest was calculated using the Mayfield method (Mayfield 1961, 1975). Apparent survival of fledglings from fledging to independence was estimated using the Kaplan-Meier estimator. Twenty five offspring disappeared between when we banded them as nestlings and before we resighted them on fledge day. If an offspring disappeared during this period, we do not know whether the offspring died in the nest or early on fledge day. We classified these individuals as dying during the post-fledging period (fledge day). This rule introduces a potential bias in our estimate of post-fledging survival, but a conservative approach to testing our prediction of comparatively high survival rates in the post-fledging period. We considered individuals that were last observed less than 35 days after fledging to have known fates (mortality). Individuals less than 35 days out of the nest are not capable of feeding themselves (see below; Tarwater, unpubl. data) and we never resighted an individual who disappeared from the natal territory at this age elsewhere on the study site. Individuals that disappeared after 35 days and individuals that were observed until independence were right-censored (this was the last age the individual was observed).

RESULTS

Parental care in the pre- and post-fledging periods

The duration of parental care to fledglings varied widely among pairs (range: 31-87 days; Fig. 2.1). The average length of post-fledging parental care was 55.3 ± 1.96 days (mean ($\bar{x}$) ±

SE; n = 38 fledglings, median: 54 days). Overall, duration of post-fledging care was six times longer than the nestling period.

Provisioning rates increased with offspring age (average increase = 0.05 feeds/hr/day/ fledgling) until approximately 41 days after fledging. Rates then declined by, on average, 0.04 feeds/day (repeated measures ANOVA: $F_{37, 386} = 3.18$, P = 0.00; Fig. 2.2). Offspring were fed infrequently after 68 days and the last observed provisioning event was 87 days after fledging. Half of the fledglings (n=117) dispersed between 60-90 days after fledging, coinciding with the period of infrequent or no provisioning by parents (Tarwater, unpubl. data). For broods that were observed during both the nestling and post-fledging periods, provisioning rates were greater during the post-fledging period ($\bar{x} \pm SE = 3.79 \pm 0.27$ feeding visits/hr/offspring) than the nestling period ($\bar{x} \pm SE = 1.2 \pm 0.07$ feeding visits/hr/offspring, paired t-test: t =-9.74, df = 8, P = 0.00). Food load (average load size/feeding trip) did not differ between the two periods (paired t-test: t = 1.21, df = 7, P = 0.27; one brood was not included because prey size could not be seen). Therefore, the amount of food provided per hour and duration of parental care were greater during the post-fledging period than the nestling period.

Offspring survival

Survival during the nest period (incubation and nestling) based on the Mayfield method was 19.9 % (n = 474 nests from Pipeline Road only). Daily survival rate in the nest was calculated using the Mayfield method and then raised to an exponent equal to the total number of days in the nesting cycle to estimate survival during the entire nest period. Survival from fledging until independence (55 days) was 75.1 ± 2.9 % (n = 225 fledglings) (Fig. 2.3). Forty-five out of the 56 fledglings (80.4%) that died during the post-fledging period died within the first day of fledging. Fledglings are vulnerable to predators early in the post-fledging period as they are relatively immobile and remain low to the ground in dense vine tangles. After 1-2 days, fledglings go to the top of the canopy where they fly infrequently for the next two weeks. The latest mortality event observed was 17 days after fledging. If an offspring disappeared after 35 days, we considered this offspring to have dispersed. We have observed individuals at this age off the natal territory and mortality of fledglings is infrequent after the first two weeks out of the nest. Nevertheless, it is possible that some individuals may have died after 35 days rather than dispersed.

The probability of newly laid eggs surviving to independence was 15% based upon their survival probability in the nest (0.20) multiplied by post-fledging survival (0.75). The probability of just fledged young surviving to independence was five times greater than a newly laid egg.

Trade-offs between successive breeding attempts

Parents did not renest until fledglings from the first brood were no longer being fed. We were able to determine if and when a successive breeding attempt was initiated for 69 breeding pairs. Of these, 35 (in which offspring apparently survived to natal dispersal) initiated a subsequent nest with an average inter-clutch interval of 56.1 days (± 2.3). In contrast, the average interval after a failed nest was 11.9 days (± 0.5) (Mann-Whitney U-test: U = 8436.5, df = 1, P = 0.00; Fig. 2.4) and 19.7 days (± 3.9) after the loss of fledged young (offspring died within the first two weeks after fledging) (Mann-Whitney U-test: U = 16.0, df = 1, P = 0.00; Fig. 2.4). Moreover, parents renested quicker after the loss of the nest early on (i.e. eggs) compared to when the offspring were older (i.e. nestlings; Spearman rank correlation: $r_s = 0.14$, P = 0.05). The probability of a pair attempting a second nest decreased during the course of breeding season (Binary logistic regression: $R^2 = 0.58$, df = 1, P = 0.00, odds ratio = 0.94 ± 0.02, n = 69 breeding pairs, Fig. 2.5). If a first nest fledged young between February and April parents always initiated a second nest. If the first nest fledged in May, the probability of parents renesting decreased to 54.5%, and in June the percent dropped to 17.1%. Thus whether extended post-fledging care was a cost to parents (in terms of breeding again within the same season) was conditional upon the time of the breeding season parents cared for fledglings. To distinguish this result from seasonal effects, we examined how the probability of renesting changed throughout the breeding season for pairs that did not have a successful brood. The probability of a pair nesting declined over the breeding season (Binary logistic regression: $R^2 = 0.38$, df = 1, P = 0.00, n = 384 failed nests), with pairs always renesting when the previous nest failed between February and April. Nevertheless if the pairs nest failed in May, 93.5% of pairs still renested, and if the nest failed in June, 64.8% of pairs still renested. Therefore, pairs renested later into the breeding season if they had not had a successful brood compared to when they had a successful brood.

The duration of post-fledging parental care differed between broods that were followed by another nesting attempt (53.4 ± 2.8 days, n = 21) versus those not followed by another attempt (63.2 ± 5.5 days, n = 8; Analysis of covariance with fledge date as the covariate, $F_{1,26} = 7.48$, P = 0.01). Notwithstanding, parents did not nest again until fledglings were near independence. Because broods that were followed by another nesting attempt tended to occur earlier in the breeding season compared to broods that were not followed by another nest, we evaluated the overall influence of fledge date on length of post-fledging parental care and found no relationship (Linear regression: $R^2 = 0.12$, P = 0.5, Fig. 2.6). Instead for broods followed by another nesting attempt, duration of care decreased over the breeding season ($R^2 = 0.56$, P = 0.01) while for broods not followed by another attempt, duration of care increased slightly ($R^2 = 0.54$, P = 0.17, Fig. 2.6).

All breeding pairs that initiated second nests overlapped broods. We defined overlap between broods as the number of days fledglings from the first brood were still present on the natal territory while the subsequent nest was active. Fledglings from the first brood commonly overlapped with the incubation period of the second nest (29 broods with fledglings overlapped during the incubation period, 6 during the nestling period). Mean brood overlap was 10.5 ± 1.3 days (n = 35). Overlap between first and second broods increased over the breeding season (Spearman rank correlation coefficient: $r_S = 0.47$, $P = 0.005$, $n = 35$). Furthermore, the length of the inter-clutch interval declined (thus initiating second nests more rapidly) as the breeding season progressed (Linear regression: $R^2 = 0.48$, $P = 0.00$, $n = 35$ breeding pairs). Breeding pairs exhibited this "time saving" behavior and also decreased the duration of care to fledglings when initiating another nest.

DISCUSSION

The parental strategy of our focal species is clearly to allocate far greater care during the post-fledging period compared to the nestling period, with provisioning continuing for an average of 2 months after fledging. Moreover, offspring survival from fledging to independence was over three times greater than during the nest period. High juvenile survival and the strategy of extended post-fledging care to comparatively few offspring may be common in tropical species and is in sharp contrast to the patterns of parental care observed in many temperate species with altricial young (Russell 2000, Russell et al. 2004).

Allocation of greater care and higher survival in the post-fledging period

We observed that slaty antshrike parents fed offspring for prolonged periods after leaving the nest and provisioning rate was greater compared to the nestling period. Slaty antshrikes exhibit many of the traits associated with prolonged post-fledging parental care; they are insectivorous, forest-dwelling, and live in a tropical environment (reviewed in Langen 2000). Although some studies suggest that prolonged care may be due to slow development of foraging skills (Fogden 1972, Thiollay 1988, Magrath et al. 2000), the species with extended care inhabit a variety of environments (e.g. tropical forests and southern temperate environments) with differing habitat complexities and prey. Instead, prolonged parental care may have allowed for an evolutionary slowing down of offspring foraging development (Langen 2000). If true, then extended parental care during the post-fledging period in antshrikes is likely a strategy by parents to increase offspring survival and competitive ability.

Investment theory predicts that parents will allocate more care and associated risk to older offspring (Clutton-Brock 1991) in part owing to their greater reproductive value (Andersson et al. 1980, Winkler 1987, Montgomerie and Weatherhead 1988). Antshrike offspring at fledging had five times greater probability of surviving to independence than newly laid eggs. We believe that greater care to fledglings is partly due to the lower probability of mortality during the fledgling period compared to the higher mortality observed in the nest. Differences in survival between the nest and post-fledging period in some temperate-breeding species are similar to two-fold higher or lower (Sullivan 1989, Anders et al. 1997, Yackel-Adams et al. 2006) compared to the four-fold difference in survival in antshrikes. Thus, variance in offspring value (e.g., survival differences) between the nest and fledgling periods appears to be large in slaty antshrikes.

Offspring that are fed for longer periods of time may have a higher probability of recruiting into the breeding population owing to increased survival probability, condition-dependent competitive ability (increasing the probability of territory acquisition), or both (Cam et al. 2003, Maccoll and Hatchwell 2004, Becker and Bradley 2007, Ridley and Raihani 2007, Sunde 2008). We observed high survival during the post-fledging period, which reflects both the level of parental care and reduced risk of predation once offspring were mobile. Similar to other studies, we observed that offspring had the highest mortality the first few days after fledging (Sullivan 1989, Anders et al. 1997, Yackel-Adams et al. 2001, 2006). This is when offspring were less mobile and remained low to the ground, making them vulnerable to predators. After two weeks out of the nest, offspring were more mobile and mortality was infrequent. We suggest that offspring mortality early in the post-fledging period is due to predation, as observed by studies using radio-telemetry (Anders et al. 1997, Yackel-Adams et al. 2006). We only observed two cases of offspring starvation, and in both instances one parent went missing, and the other parent could not care for the young fledglings. Furthermore, we previously observed that offspring are segregated spatially during this period of high mortality, and then after two weeks, offspring are brought back together (even though the brood remains divided) (Tarwater and Brawn 2008). This is likely to reduce the probability of both offspring being found by a predator.

Trade-offs between successive breeding attempts

Trade-offs between care to current and future offspring are predicted and often observed (reviewed in Parejo and Danchin 2006). We observed that parents did not attempt new nests until the current offspring were near independence. The apparent costs of parental care to future productivity (within the same season), however, were conditional upon the time in the breeding season. Parents reduced care to fledglings if they initiated a new nest, but the probability of attempting a second brood decreased through the breeding season. Continuing to feed fledglings once they are near independence does not appear worth the cost (in terms of nesting again) if there is time for another nest attempt. Whether this truncation in provisioning reduces first year survival merits study. Parents often used the time-saving strategy of overlapping clutches to feed fledglings and initiate another nest. If the second nest was not depredated, parents became increasingly more aggressive to fledglings, forcing them to disperse before the next nest fledged. Parents increased the amount of clutch overlap and decreased the inter-clutch interval as the breeding season progressed. Our observations suggest that even with a 9 month breeding season, parents often did not have enough time to raise one set of fledglings to independence and then breed again.

Extended care, higher survival, and avian life histories

The duration of post-fledging parental care and the continual increase in provisioning rate until over five weeks out of the nest distinguishes slaty antshrikes from accounts of parental care in north temperate passerines (Russell 2000, Russell et al. 2004). In a review of northern hemisphere passerines, approximately 80% of species had <60 days of parental care during the post-fledging period (median = 15.5 days, n=126 species; Russell 2000). Thus duration of post-fledging care in antshrikes is at the upper end of the distribution for northern hemisphere species. Similar to other studies of tropical birds, we observed high apparent survival rates between fledging and independence (range 0.55-0.69: Cohen and Lindell 2004, Schaefer et al. 2004, Brouwer et al. 2006, Sankamethawee et al. 2009). Furthermore, our estimate of 75% apparent survival during the post-fledging period is outside the range of estimates for north-temperate passerines in all studies known to us (range 0.32-0.64: Stromborg et al. 1988, Krementz et al. 1989, Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001, Yackel-Adams et al. 2001, Berkeley et al. 2007, Kershner et al. 2004, Robles et al. 2007, Wells et al. 2007, Wightman 2009).

A fundamental trade-off for species with parental care occurs between the amount of care (influencing offspring quality) and number of offspring produced (Smith and Fretwell 1974, Stearns 1992). Tropical birds are predicted to invest more care into fewer offspring, increasing offspring survival (Karr et al. 1990, Martin 1996, Young 1996). Different environmental conditions may shift the balance between quantity and quality of young. Selection is expected to favor increased parental care per offspring and decreased clutch size under conditions that may reduce offspring survival (Cody 1966, Fleming and Rauscher 1978, Clutton-Brock 1991, Roff 1992). Less seasonal, tropical environments may promote stronger competition for breeding territories (due to low territory turnover, Ekman 2006) and lower food availability during the breeding season owing to populations being near carrying capacity on a year-round basis (Ashmole 1963, Cody 1966, Ricklefs 1980, McNamara et al. 2008). Furthermore, high rates of nest predation favor reduced clutch sizes (McNamara et al. 2008, Martin and Briskie 2009). These various factors predicted to occur in lowland tropical environments favor increasing offspring quality and reducing offspring quantity.

One common assumption about tropical birds is that they invest less into reproduction on an annual basis and therefore, the value of the current brood is low compared to temperate species (Martin 1996, 2004, McNamara et al. 2008). The value of the current brood to parents and the amount of reproductive effort expected by parents depends upon the survival of offspring to reproduction (Gadgil and Bossert 1970, Schaffer 1974, Stearns 1992). Studies examining brood value often use the number of young that survive to fledging as a proxy for survival to reproduction (Bennett and Owen 2002). Nevertheless, when comparing between species, if post-fledging survival is lower in one species than using number of offspring that fledge is an inaccurate measure of the fitness parents will gain from current offspring (Sullivan 1989, Anders et al. 1997, Robles et al. 2007). At least in slaty antshrikes, one fledgling may be more valuable (compared to northern latitude species) because it contributes more to the fitness of its parents owing to high post-fledging survival. Whether higher survival during the dependent period and extended post-fledging parental care lead to higher survival until reproduction requires more studies of tropical species. Nevertheless, it is clear that post-fledging parental care must be factored into comparative studies of reproductive effort and avian life histories.

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FIGURES

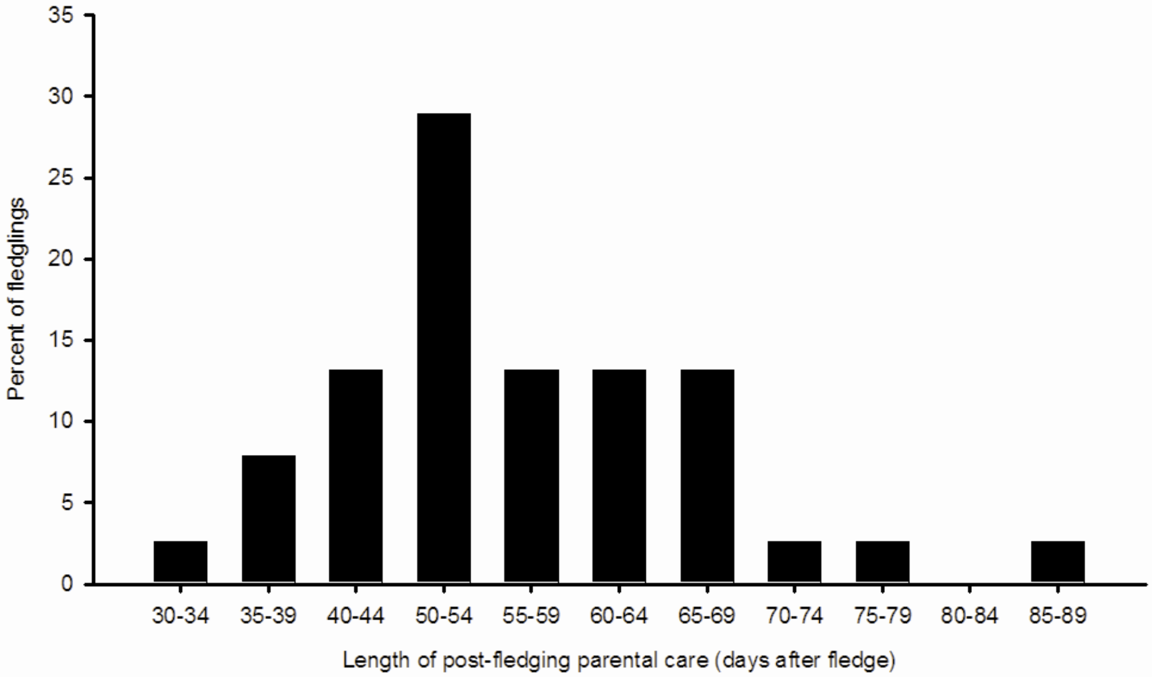

Figure 2.1 Frequency histogram depicting the duration of post-fledging parental care for slaty antshrike fledglings (n = 38 fledglings). Mean observed duration was 55 days

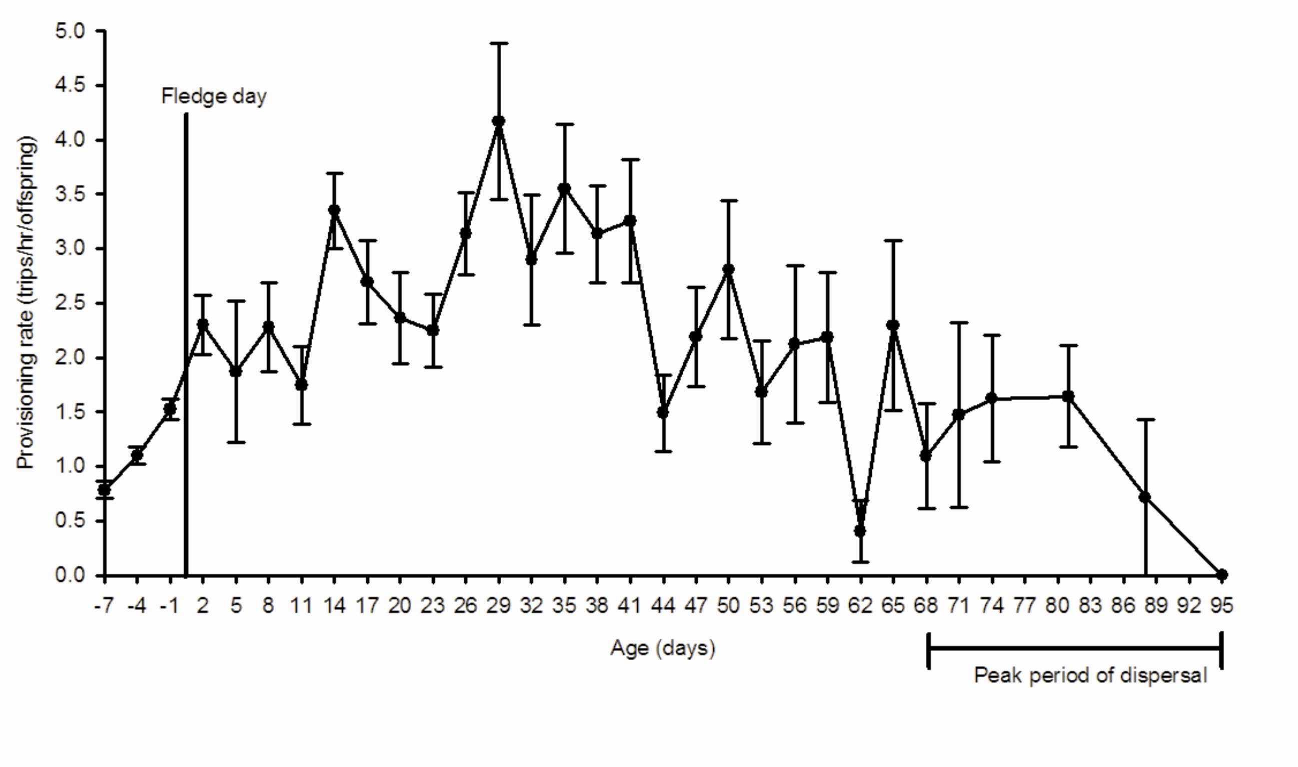

Figure 2.2 Provisioning rates to individual antshrike nestlings and fledglings. Rates are depicted as averages for each age interval (+ 1 SE) (n = 75 individuals for which we observed 19 during the nestling period only, 9 during both periods, and 47 during the post-fledging period only)

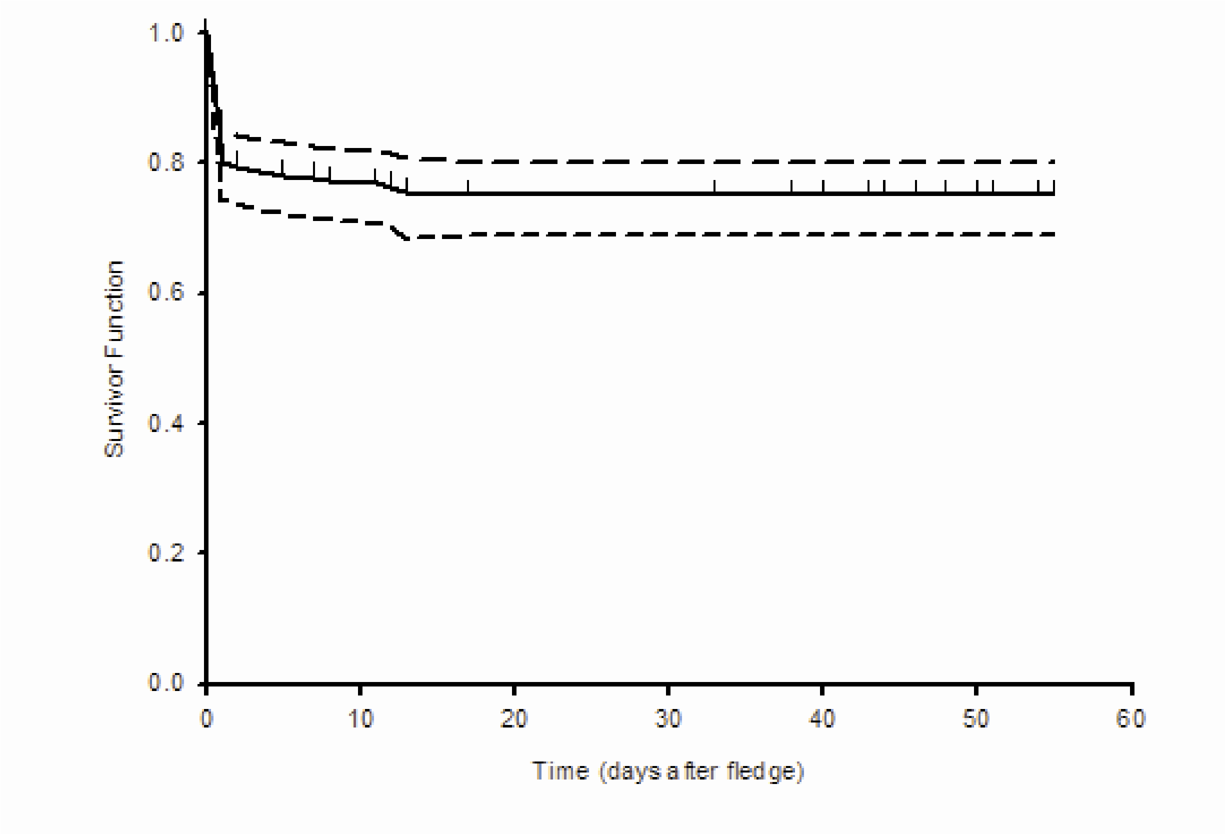

Figure 2.3 Survival of slaty antshrike offspring from fledging until independence (55 days). Dashed lines are the 95% confidence intervals

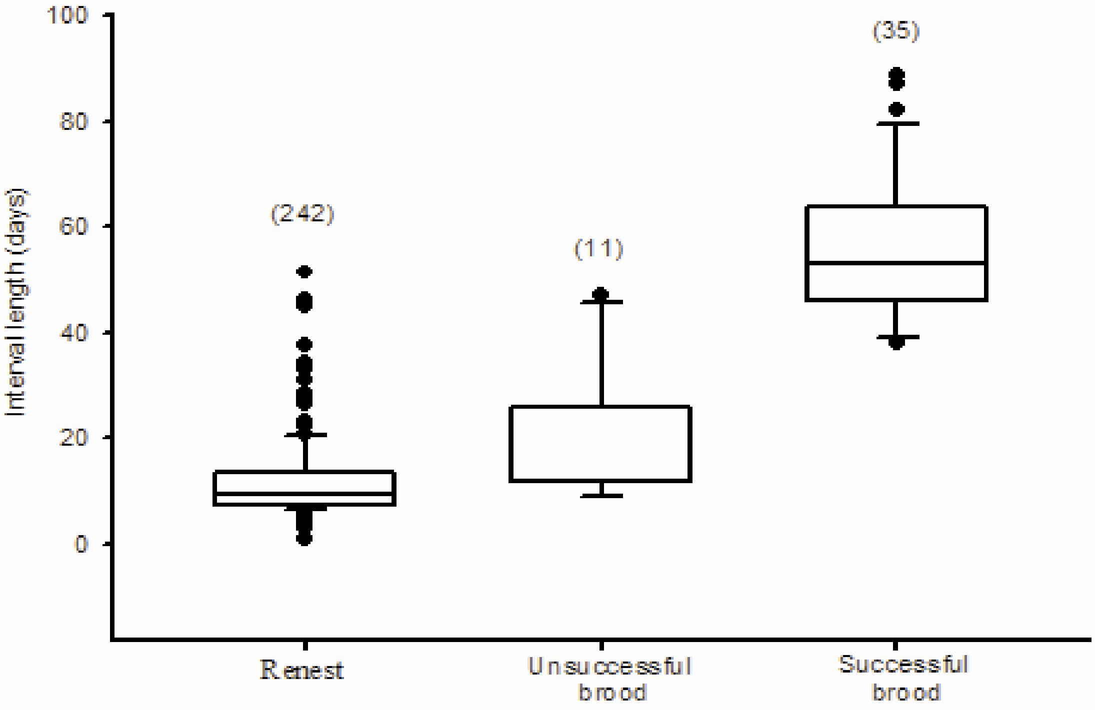

Figure 2.4 Box plots summarizing duration of time between nesting attempts in different contexts. Renest) the interval when a prior nest failed before young fledged. Unsuccessful) the interval when a prior nest failed during the first two weeks of the post-fledging period. Successful) the interval when a prior nest was successful through the post-fledging period. The edges of the box represent 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles, and circles are outliers

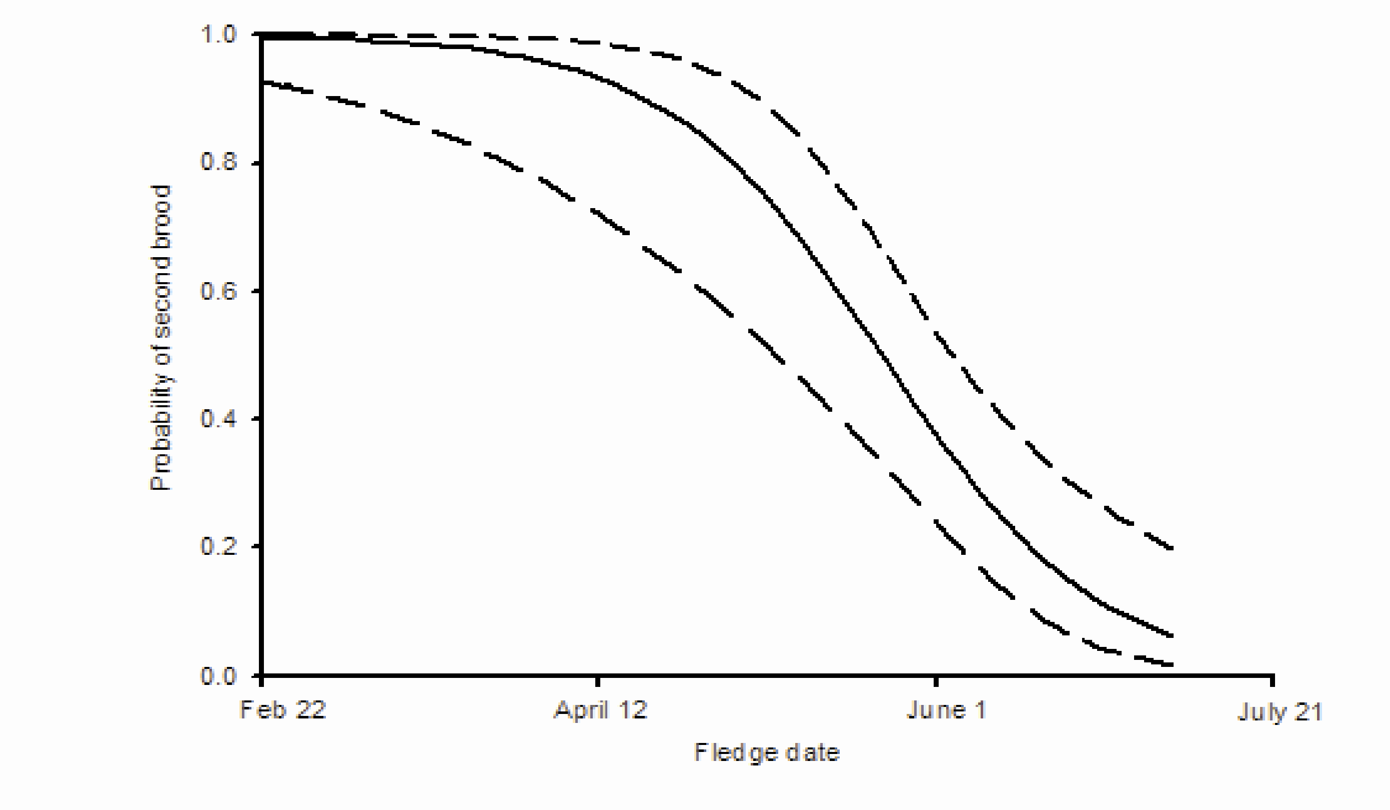

Figure 2.5 Probability of antshrike breeding pairs initiating a second nest as a function of when the previous brood fledged (within the same breeding season). Binary logistic regression was used to estimate probability (1=initiate second brood. 0=do not initiate second brood). Dashed lines: 95% confidence intervals. No second nests were observed after July

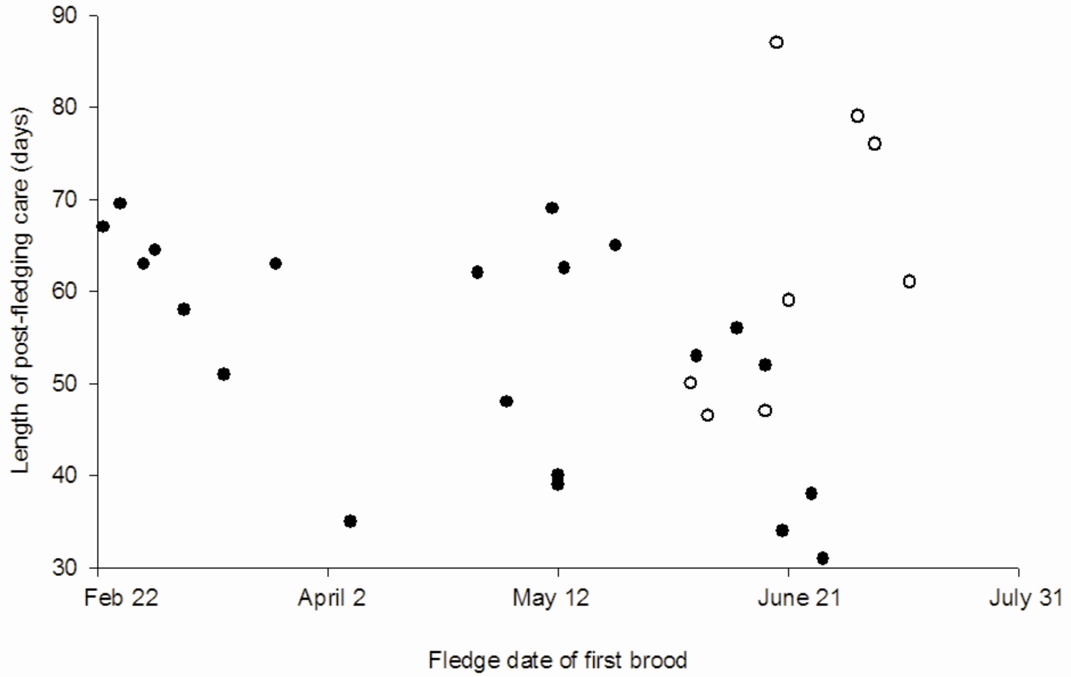

Figure 2.6 Relationship between length of post-fledging parental care and fledge date for slaty antshrike fledglings whose parents initiated second nests (closed circles) and for fledglings whose parents that did not nest again the same year (open circles)

CHAPTER 3: FAMILY LIVING IN A NEOTROPICAL BIRD: VARIATION IN TIMING OF DISPERSAL AND HIGHER SURVIVAL FOR DELAYED DISPERSERS[b]

ABSTRACT

Prompt natal dispersal and reproduction of offspring is viewed as the strategy to maximize lifetime reproductive success. Yet, across many species offspring remain with their parents after independence rather than disperse. Why some species live in family groups and the behavioral mechanisms influencing the extent of family living remain unresolved. Family living is predicted to arise through slow life history traits predisposing certain lineages to family living, and then social and ecological factors resulting in greater benefits of remaining with parents compared to dispersing. We studied family living in the western slaty-antshrike (*Thamnophilus atrinucha*), a bird with a slow life history, in Panama. We quantified the extent of delayed dispersal, and examined the behavioral mechanisms influencing dispersal, and the survival consequences. We observed that offspring survival increased by delaying dispersal. Parental aggression towards offspring increased with offspring age, and in particular when renesting. Thus, offspring dispersed earlier when their parents renested. Fledging date and mass of offspring also influenced timing of dispersal. Although we observed higher survival of delayed dispersers, only a small proportion of offspring delayed dispersal until the next year and all dispersed to float. Our results support theoretical predictions stating that benefits to parents from offspring retention decrease with offspring age and with renesting, leading to natal dispersal. Furthermore, we observed a reduced survival benefit of retention once offspring reached a certain age. Examining parental tolerance, the costs of floating, and how they vary with offspring age are essential to understand the costs/benefits of family living.

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INTRODUCTION

Family living arises when offspring delay dispersal and remain with their parents after reaching independence, that is, after offspring are capable of sustaining themselves (Russell 2000). Family living is observed across a variety of species and taxa, and can lead to complex social behaviors (fish: Taborsky 1994; mammals: Solomon & French 1997; insects: Choe & Crespi 1997; birds: Griesser & Barnaby 2010). Early studies of family living focused on the constraints of dispersal (e.g., inability to breed independently upon dispersal) because prompt dispersal and independent reproduction was viewed as the strategy for maximizing lifetime reproductive success (Emlen 1994; Hatchwell & Komdeur 2000). Recent studies suggest family living may be an adaptive strategy, whereby offspring benefit from philopatry (Covas & Griesser 2007; Griesser & Barnaby 2010). Moreover, although primarily studied in cooperatively breeding species, family living can occur without cooperative breeding, and fitness benefits arise to offspring without helping (Ekman et al. 1999; Griesser et al. 2006; Gill & Stutchbury *in press*).

Family living is predicted to arise first through life history traits predisposing certain lineages to delayed dispersal (e.g., species with slow life histories/medium to long-lived species) and second, through social and ecological factors (Covas & Griesser 2007; Griesser & Barnaby 2010). Medium to long-lived species have higher lifetime fitness by delaying the age at first reproduction compared to shorter-lived species (Stearns 1992; Charlesworth 1994), reducing the costs of delaying for offspring (Covas & Griesser 2007). Correspondingly, delayed dispersal is more commonly observed in tropical and southern hemisphere bird species, which are characterized by a slow life history strategy, compared to northern-latitude species, even when cooperatively breeding birds are excluded (Ricklefs & Wikelski 2002; Russell et al. 2004).

Nevertheless, delaying reproduction does not require offspring to remain with their parents, and therefore, specific benefits of remaining with parents compared to dispersing to float or form juvenile flocks must exist for family living to occur (Ekman 2006). Floating is when offspring wander within other breeding pairs' territories in search of vacancies. By delaying, offspring may gain various benefits such as parental facilitation, group augmentation, and predictable access to resources (Stacey & Ligon 1991; Kokko & Ekman 2002; Griesser & Barnaby 2010).

Even if it might benefit juveniles to delay dispersal, parents have to allow offspring to remain (Ekman 2006). Thus conflict between parents and offspring may arise over the extent to which offspring delay (Trivers 1974). Parents should only prolong investment if this increases offspring survival and outweighs the costs parents incur. Offspring should delay if their survival improves by delaying. Parent-offspring conflict will be especially pronounced in species where parents breed again the same year (Gayou 1986; Le Galliard et al. 2003). Moreover, parents may become less tolerant as offspring increase in age due to the reduction in mortality with age (Clutton-Brock 1991).

In addition to parent-offspring conflict, other behavioral mechanisms may lead to individual variation in the extent of delayed dispersal (Kokko & Ekman 2002; Ekman et al. 2002; Pasinelli & Walters 2002). Although these mechanisms are not well understood (Stamps 2001; Doerr & Doerr 2005), sexual competition between parents and offspring, competition between juveniles, and sibling rivalry may influence when offspring disperse (Ekman et al. 2002; Griesser et al. 2008; Dickinson et al. 2009). Sexual competition may arise when parents are less tolerant of offspring of the same sex (Dickinson et al. 2009) and sibling rivalry is associated with differences in sex and/or dominance between siblings, whereby the more competitive offspring may force early dispersal of their siblings (Ekman et al. 2002; Pasinelli & Walters 2002).

Moreover, males often disperse later than females (Greenwood 1980; Zedrosser et al. 2007; Hanski & Selonen 2009) and offspring that are born earlier in the year may disperse earlier, when competition for breeding patches is reduced (Nilsson 1989).

Despite the common occurrence of family living in non-cooperatively breeding tropical species (Russell et al. 2004), few studies have examined the behavioral mechanisms and consequences of family living in tropical birds (but see Gill & Stutchbury *in press*). We studied a socially monogamous bird, the western slaty-antshrike (*Thamnophilus atrinucha*), in lowland, tropical forests in Panama. This species has a slow life history characterized by high adult survival (0.73 ± 0.04; Brawn et al. 1999), a clutch size of two, delayed age at reproduction, and extended post-fledging parental care (Oniki 1975; Roper 1996; C.E. Tarwater, unpublished data). Antshrikes also have year-round territoriality, multi-brooding, and previous research found that some antshrike offspring delay dispersal until the following year (Roper 1996; Tarwater & Brawn 2008). We quantified the extent of delayed dispersal, and examined the behavioral mechanisms influencing the timing of dispersal, and the survival consequences of delayed dispersal. We predicted that juveniles that remained on the natal territory longer will have higher survival than those dispersing earlier. We also predicted offspring would disperse earlier when parents nested again within the same breeding season. We assessed the behavioral mechanisms of dispersal by examining traits that are associated with sexual competition (parent and offspring sex), competition between juveniles (fledge date, offspring sex, number of siblings within a brood, mass at fledging) and sibling rivalry (differences within broods based on offspring sex and mass at fledging). Because male and female antshrikes both acquire and defend breeding territories, we predicted timing of dispersal would not be sex-biased.

METHODS

Study site and population

We observed slaty antshrikes from January-February to August-December in 2003-2008 on a 104 ha study site within Parque Nacional Soberanía. Soberanía is a 22,000 ha contiguous, lowland, tropical moist forest in the Republic of Panama (for details see Karr 1971; Robinson et al. 2000b). Breeding territories are approximately 0.8 ha in size, with an estimated 106 breeding pairs on the plot (Robinson et al. 2000b). The antshrike breeding season is from January to September, although individuals do not breed this entire time (Roper 1996; C.E. Tarwater, unpublished data). Slaty antshrikes have strict brood division after fledging, with each parent feeding only one of the offspring (Tarwater & Brawn 2008), which hereafter we refer to as the parent's focal offspring. We captured territorial birds using mist-nets and marked them with unique combinations of color and numbered metal leg bands throughout the study. We monitored an increasing number of breeding pairs on the plot each year (25 - 60 breeding pairs). Breeding territories were searched for nests and nests were checked every 2-3 days. Nestlings were color banded prior to fledging.

Extent of delayed dispersal

We used mark - resight and radio-telemetry to quantify extent of delayed dispersal. We define length of time on the natal territory as the period between fledging and dispersal. Transmitters were attached to fledglings that were at least five weeks out of the nest ($N = 26$), by which age they have reached adult body weight and are competent fliers. Transmitters had a battery life of 4 - 9 months and weighed 4 - 5% of body mass (body mass: 22.3 ±0.24 g, transmitter weight: 0.95 g). The transmitters, designed by Sparrow Systems (Fisher, IL), were attached using the leg harness method (Rappole & Tipton 1991). Birds were radio-tracked every

3 - 4 days. For birds without transmitters, we looked for fledglings on their natal territories 1-2 times per week until they were no longer present or until sampling ceased (between August-December). For 27 out of 152 fledglings, we only knew the minimum duration of time offspring were on the natal territory because these birds were still with their parents when sampling ceased. If fledglings were not located during one check, we searched territories at least two more times to confirm disappearance. The average resighting probability for the first two months after fledging was 90% (calculated from the program MARK). Thus, it was rare that we did not find a fledgling when the fledgling was present. If a fledgling disappeared prior to 35 days we classified the individual as dead because fledglings are still dependent upon their parents at this age (C.E. Tarwater & J.D. Brawn, unpublished data). Therefore, these birds were not included in the timing of dispersal analysis. We never resighted fledglings that disappeared from their natal territory prior to 35 days ($N = 56$). Disappearance after 35 days was judged to indicate dispersal and these birds were included in the timing of dispersal analysis. We acknowledge the possibility that fledglings older than 35 days may die rather than disperse. Nevertheless, given the high survival rate of juveniles after 35 days (based on resighting and radio-tagged birds; C.E. Tarwater & J.D. Brawn unpublished data), mortality at this time is rare.

Consequences of length of time on the natal territory on juvenile survival

We used radio-telemetry in 2006-2008 to estimate juvenile survival using the same methods described above (N=26). Because of the small transmitter size, rough terrain, and dense vegetation, the range of the transmitters was roughly 200 m. When a bird went missing, the entire study plot and an additional 400 m from the edges of plot were searched (~ 238 ha in total were searched).

Parental tolerance

We examined renesting by parents to determine if renesting influenced timing of juvenile dispersal. We included only a subset of breeding pairs (*N* = 71 pairs) that were monitored frequently enough to determine if parents initiated another nest after the first successful brood. We examined whether aggression by parents influenced natal dispersal by conducting focal behavioral observations of parents and their focal fledglings (*N* = 56 fledglings) for 2 hour periods 1-2 times/week from fledge day to natal dispersal. We counted the number of times during an observation period parents displaced their fledglings, defined as flying after fledglings and forcing them to leave their current perch. Although we remained on natal territories for 2 hour periods, often the fledglings could not be seen, and therefore we could not determine if the fledgling was displaced. Thus, the average length of time each fledgling was observed (e.g., was in view) during each observation period was 44.8 ± 1.1 min (*N* = 4-49 individuals per week).

Individual variation in extent of delayed dispersal

To examine individual variation in the timing of dispersal, we examined mass at fledging, body condition at fledging (nestling mass divided by tarsus), number of siblings within a brood, offspring sex, parent sex, whether parent and focal offspring were the same or opposite sex, and fledge date. Although antshrikes lay two eggs, only one sibling within a brood may survive to disperse due to mortality of the other sibling during the nestling or early post-fledging period. Sex of parents and offspring were determined by the sexual dichromatism in plumage that can be observed when birds are three weeks out of the nest. We also evaluated variation between siblings within in a brood by comparing relative differences in body mass (heavier/lighter) and sex. Antshrike offspring do not fledge at adult body weight, and we were unable to recapture juveniles to determine if a larger mass at fledging lead to a larger mass near dispersal.

Nevertheless, nestling mass is often correlated with competitive ability and may have long-lasting effects on survival (reviewed in Magrath 1991). In antshrikes, the differences in mass between siblings that arise due to hatching asynchronously persist throughout the nestling period (Tarwater & Brawn 2008). Furthermore, although antshrikes divide broods, male and female parents feed equally (Tarwater & Brawn 2008), and therefore, we do not expect differences in relative mass between siblings to arise due to brood division. We measured nestling mass (to nearest 0.1g using a digital scale) and tarsus length (to nearest 0.01mm) prior to offspring fledging.

Statistical analyses

We used Kaplan-Meier survival analysis in the program SYSTAT to estimate the extent of delayed dispersal. Offspring that were observed until natal dispersal had known fates (125 fledglings) and offspring that were still present on the natal territory when we ceased sampling (27 fledglings) were censored from the data (fate after a certain date was unknown).

We used radio-tagged birds to examine survival consequences of dispersal. We considered mortality to occur when transmitters with the leg harness intact were found on the ground, as it is unlikely that antshrikes could remove a leg harness. Moreover, in 80% of the cases, the transmitter was damaged or bird remains were found adjacent to it. We grouped the duration of time on the natal territory into three categories (short, average, and long) based on our distribution of juveniles with known dispersal times (N=125). This resulted in the following categories: dispersal <69 days after fledging (25.6% of fledglings dispersed at this time), 69-105 days (49.6% of fledglings), and dispersal >105 days (24.8% of fledglings). We used categorical variables because we wanted to compare survival estimates between groups. We had five birds with transmitters that dispersed early (<69 days). Therefore, we only compared juveniles that dispersed between 69-105 days (*N* = 9 birds with transmitters) to ones that dispersed after 105 days (*N* = 12).

Two different survival periods were examined: 1) overall survival, which includes both the time offspring were on the natal territory and after dispersal and 2) survival for the first four months after dispersal. Overall survival was calculated from the time transmitters were attached until the transmitter stopped working or the bird died (up to 9.5 months later). We first tested for significant effects of covariates using Cox proportional hazards survival analysis, none of which were significant. We then used Kaplan-Meier survival analysis to estimate survival. Three out of 26 radio-tagged birds disappeared and these birds were censored from the data, rather than counted as a mortality event. At the time the signals went missing, these birds were on the natal territory <105 days. By censoring these birds, the results are conservative because we predicted higher survival for individuals that remained >105 days. We compared the two dispersal groups using the log-rank test to compare the survival distributions and effect size to compare the point estimates of survival. We used effect size because this compares the magnitude of an effect between groups and is relatively independent of sample size (Nakagawa & Cuthill 2007). We follow the guidelines of Cohen (1988) for classifying effect sizes as small (*d* = 0.25), medium (0.5), or large (0.8).

We used Partial least-squares regression (PLSR) analysis (Wold et al. 1998) to examine the influence, at the population level, of fledge date, nestling mass, offspring sex, parent sex, same/opposite sex offspring, and number of siblings on length of time on the natal territory (response variable). PLSR was used because it can handle smaller sample sizes, correlated independent variables, and does not require normality in the dependent variable. Associations are established with latent factors extracted from predictor variables that maximize the explained variance in the dependent variables. A cross-validation procedure is used to estimate the proportion of variance in the dependent variable that can be explained and predicted by the model (Wold et al. 1998; Carrascal et al. 2009). We retained only 'significant' latent factors, which were defined as those explaining more than 5% of the original variance in the response variable (Carrascal et al. 2009). We did not include the 27 offspring whose timing of dispersal was unknown. This does not bias our results because these individuals are representative of the population. For example, their sex ratio and fledge weight were the same as the average of the population. We did not include body condition in the analysis because nestling mass and body condition were highly correlated (Pearson correlation coefficient=0.76, $P < 0.001$). We used a Mann-Whitney U-test to assess whether renesting by parents influenced dispersal. We used a Pearson correlation coefficient and bootstrapping to examine how age of offspring influenced aggression by parents.

RESULTS

Extent of delayed dispersal

Ninety per cent of offspring remained on the natal territory after the average age of independence from parents (55.3 ± 1.96 days; Tarwater and Brawn, *in press*, Fig. 3.1). The median length of the time on the natal territory prior to dispersal was 84 days after fledging (mean: 118.4 days, range 38 - 346 days, $N = 152$). Only 18 (10 females, 8 males) out of 125 offspring (only including individuals with known dispersal dates) remained on the natal territory until the following breeding season and dispersed between January and May, before parents initiated breeding. Radio-tagged juveniles were followed after dispersal and in all instances juveniles dispersed to float. This pattern was confirmed by the fact that we never saw banded birds acquire a territory upon dispersal.

Consequences of length of time on the natal territory on juvenile survival

Neither fledge date nor age at which transmitters were attached had a significant effect on overall survival (Cox proportional hazards survival analysis: date: $P = 0.17$, age: $P = 0.49$, $N = 21$). Furthermore, dispersal date did not have a significant effect on survival after dispersal ($P = 0.31$, $N = 16$). Based on Kaplan-Meier survival analysis, estimates of overall survival indicated that birds that dispersed after 105 days had higher survival (0.83 ± 0.10) than birds that dispersed between 69 -105 days after fledging (0.46 ± 0.22, $N = 21$; Fig. 3.2a). Although the log-rank test was not significant ($\chi^2 = 2.27$, $P = 0.13$), based on the large effect size observed ($d = 2.1$), differences in survival between the groups were likely to be biologically important. Estimates of survival for the first four months after dispersal indicated that offspring that dispersed later had higher apparent survival (0.80 ± 0.13) than those dispersing earlier (0.44 ± 0.22, $N = 16$; Fig. 3.2b). The log-rank test was not significant ($\chi^2 = 2.71$, $P = 0.10$), however, based on the large effect size ($d = 2.3$), survival after may be higher for offspring that dispersed later. The key period in which survival was greater for retained offspring was the first two months after dispersal. After 50 days, no mortality was observed by early or delayed dispersers. Overall mortality of dispersed juveniles was rare (5 out of 26 transmitters were found on ground).

Parental tolerance

Parents appeared to play an active role in offspring dispersal by forcing young to disperse. If parents initiated another nest after the first successful brood, their fledglings from first broods remained on the natal territory for a shorter duration (median: 69.5, range: 49 - 285.5) than fledglings whose parents did not renest (median: 111.5, range: 52 - 299.5 days, Mann-Whitney U-test, U = 985.5, $P < 0.01$, $N = 71$ breeding pairs). Parents were rarely aggressive towards juveniles less than a month out of the nest, but aggression increased with offspring age (Pearson correlation coefficient: 0.95; Fig. 3.3), and the peak of dispersal (10 - 13 weeks after fledging) coincided with a time when 40% of fledglings were experiencing some form of parental aggression.

Individual variation in extent of delayed dispersal

The PLSR examining the influence of multiple factors on timing of dispersal was significant ($F_{1,123}$=10.70, *P* = 0.001, *N* = 125). We had one significant latent factor explaining 8.0% of the variance. The loadings for fledge date were the highest (8.930), followed by same/opposite sex offspring (4.857), fledging mass (4.142), parent sex (-2.023), offspring sex (1.121), and number of siblings within a brood (0.052). We tested the top three loadings in separate models (none of the factors above were correlated) to further examine their importance. Offspring that fledged later in the year remained on the natal territory longer than those fledging earlier (Spearman Rank Correlation = 0.20, *P* = 0.03, *N* = 125; Fig. 3.4). This relationship was driven by the 18 individuals who remained on the natal territory until the following breeding season and all fledged later in the year. The relationship between fledging mass and length of time on the natal territory was weakly positive (Spearman Rank Correlation = 0.17, *P* = 0.07, *N* = 125). We compared the two groups, opposite and same sex offspring, to length of time on the natal territory and found no differences between the groups (opposite sex: median 80.5, same sex: 76.0, Mann-Whitney U test = 1757.0, *P* = 0.38, *N* = 125). We also looked at male and female parents individually and found neither were more likely to allow the same or opposite sex offspring to remain on the natal territory longer (Female: Mann-Whitney U test: 600.5, P=0.53, df=1; Male: Mann-Whitney U test: 450.0, P=0.62, df=1).

Although siblings often dispersed at different times, there was little evidence that this was influenced by body mass or sex. We observed in 36 out of 48 broods of two (75 %), siblings dispersed at different times. In 26 of these 36 broods, siblings dispersed within six weeks of each other (range: 3 - 47 days). In 9 broods, siblings dispersed during different calendar years (dispersing on average 6.83 months apart). Male and female siblings do not differ in body mass (t-test: $t = 1.41$, $P = 0.16$, $N = 58$). Neither relative nestling mass (binomial exact test: $P = 0.25$, $N = 27$ sibling pairs) nor sex (binomial exact test: $P = 0.62$, $N = 36$ sibling pairs) influenced which sibling dispersed first.

DISCUSSION

This is one of the few studies examining the patterns and consequences of family living in a neotropical bird (but see Robinson et al. 2000a; Gill & Stutchbury *in press*). Offspring delayed dispersal typically for one month after independence and up to 10 months later. Furthermore, offspring that remained on the natal territory longer had higher survival than those dispersing earlier. Parental tolerance influenced offspring dispersal, with fledglings dispersing earlier when parents renested within the same breeding season. Moreover, the pronounced variation in the extent of delayed dispersal observed suggests that alternative strategies for dispersal are utilized by offspring.

Individual variation in extent of delayed dispersal

In species where both sexes benefit from site familiarity, sex-biased dispersal is not predicted (Greenwood 1980). In agreement with this prediction and similar to other studies where both males and females acquire and defend territories, we observed no differences between the sexes in the extent of family living (Gill & Stutchbury *in press*). Furthermore, we found little evidence that sexual competition between parents and offspring influenced dispersal. Reproductive competition in species with year-round territoriality arises when one parent disappears and competition occurs between the remaining parent and offspring over the new mate (Dickinson et al. 2009). In antshrikes, low territory turnover for both sexes likely reduces the opportunity for parents and offspring to compete for a new mate on the natal territory.

In 75% of antshrike broods, siblings dispersed at different times. Contrary to other studies (Strickland 1991; Ekman et al. 2002), we found no evidence that dominance influenced which sibling dispersed first and we observed little direct aggression between siblings. Nevertheless, we observed that fledging mass positively influenced the length of time on the natal territory across the population. Differences in mass between siblings (range of differences: 0 - 3.6 g, mean difference ± SE: 1.2 ± 0.1 g) are typically small, while across the population, the range (mass range: 11.5 - 18.4g) is greater and may lead to differences in juvenile dominance. Furthermore, mass may be correlated with other factors that differ between broods and influence timing of dispersal. For example, larger nestlings may come from higher quality natal territories (van de Pol et al. 2006), where parents are more likely to allow offspring to remain for longer periods and offspring have access to a greater amount of food (Ekman & Rosander 1992; Dickinson & McGowan 2005; Baglione et al. 2006).

In slaty antshrikes, the amount of time offspring remained on the natal territory increased over the breeding season. In particular, only late season offspring remained on the natal territory until the following year. This positive relationship is partly due to the correlation between fledge date and renesting by parents, whereby the probability of renesting declines over the breeding season (C.E. Tarwater & J.D. Brawn, unpublished data). Furthermore, for offspring that queue on breeding territories while floating, fledging early may result in a better position in the queue (Zack & Stutchbury 1992). While it is unclear how antshrike juveniles obtain breeding territories, juveniles float within one area encompassing multiple breeding territories for several months.

Similar to other studies indicating the importance of parental tolerance in delayed dispersal (Ekman & Griesser 2002; Eikenaar et al. 2007), we observed that offspring dispersed earlier when their parents nested again within the same breeding season. Studies of family living (Gayou 1986; Ekman & Rosander 1992) and multi-brooded species (Verhulst & Hut 1996), observe the eviction of fledglings prior to the next breeding attempt. When there is enough time left in the breeding season to renest, allowing independent offspring to remain on the natal territory is thus less beneficial to antshrike parents than attempting another nest.

In conclusion, we found that competition between juveniles and parent-offspring conflict influenced individual variation in the timing of dispersal. Nevertheless, our model explained only a small proportion of the variation in timing of dispersal. Further studies are required to examine variation within broods and how factors, such as territory quality, influence dispersal.

Benefits of family living

Given that in family living species juveniles delay reproduction, family living requires greater benefits of remaining on the natal territory compared to dispersing to join juvenile flocks or float (Brown 1987; Ekman et al. 2002; Ekman 2006). Correspondingly, we observed higher survival for offspring that remained on the natal territory compared to offspring that dispersed to float. These results thus support the hypothesis that family living is an adaptive strategy, whereby offspring receive direct fitness benefits by delaying dispersal (Covas & Griesser 2007). Higher survival may arise through offspring receiving direct benefits from parents, including increased access to resources, and protection from competitors and predators (reviewed in Ekman et al. 2001). Antshrike parents alarmed call in response to predators near offspring and allowed independent offspring access to resources. Direct benefits of family living may also arise through group augmentation, reducing the risk of predation and increasing foraging (Kokko et al. 2001; reviewed in Griesser & Barnaby 2010). Correspondingly, retained antshrike juveniles traveled with their parents and with mixed species understory flocks, while dispersed juveniles traveled alone (C.E. Tarwater, unpublished data). Higher survival after dispersal was also observed for offspring that spent more time on the natal territory. Thus by delaying, offspring receive both the direct benefits that occur while on the natal territory (e.g., parental facilitation and group augmentation), and benefits that arise from dispersing at an older age, such as increased foraging and predator detection skills (Brown 1987; Heinsohn 1991). These skills improve as offspring age (Moreno 1984; Sullivan 1988) and parents may improve juvenile survival by teaching these skills to offspring (Thornton & Raihani 2008). Therefore, by delaying, juveniles may be better able to meet their energetic needs and detect predators once they do disperse.

Why do not more juveniles delay dispersal until the following breeding season?

Although most antshrike juveniles remained on the natal territory after reaching independence, few stayed until the following breeding season and none dispersed directly onto a breeding territory. Given that antshrikes have higher survival by remaining and do not acquire territories upon dispersal, why do juveniles not delay for longer?

The decision to delay dispersal is driven by both the costs/benefits to offspring and to parents (Ekman 2006). Parent-offspring conflict arises because offspring are predicted to delay dispersal at a lower fitness gain compared to their parents (Trivers 1974). In antshrikes, parental behavior influenced the variation in the extent of delayed dispersal, whereby offspring remained with parents for a shorter duration when parents renested. Yet, parents were also aggressive towards older offspring even when they did not renest. This suggests that renesting is more beneficial to parents than allowing independent offspring to remain on the natal territory, and that the benefits of offspring retention decreased with offspring age.

Although we observed higher survival for retained offspring compared to dispersed offspring, no mortality was observed for any offspring >50 days after dispersal and >70 days after transmitters were attached. Thus, once offspring reached 4-5 months of age, remaining on the natal territory did not increase survival compared to floating. Thus the benefits of family living appear to be the most pronounced when offspring are young and still learning skills. Only one study thus far has examined the costs of floating in a group living bird and found greater costs of floating compared to group living (Ridley et al. 2008). Juvenile survival may be correlated with adult survival once offspring are independent (Saether 1989; Ricklefs 2000). Thus in more benign environments, such as that found in the lowland Tropics, and in species with high adult survival, juvenile survival after independence may likewise be high (including the floating period), reducing the costs of floating.

Other studies of delayed dispersal observe that juveniles remain on the natal territory until they acquire their own territory (Green & Cockburn 2001; Morelli et al. 2009), yet we observed that all antshrike juveniles dispersed to float. Our results suggest that the benefits of family living and the costs of dispersal declined with offspring age and with renesting by parents. This study supports the importance of parental tolerance in the costs/benefits of family living and stresses the need for further studies to examine the floating period.

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FIGURES

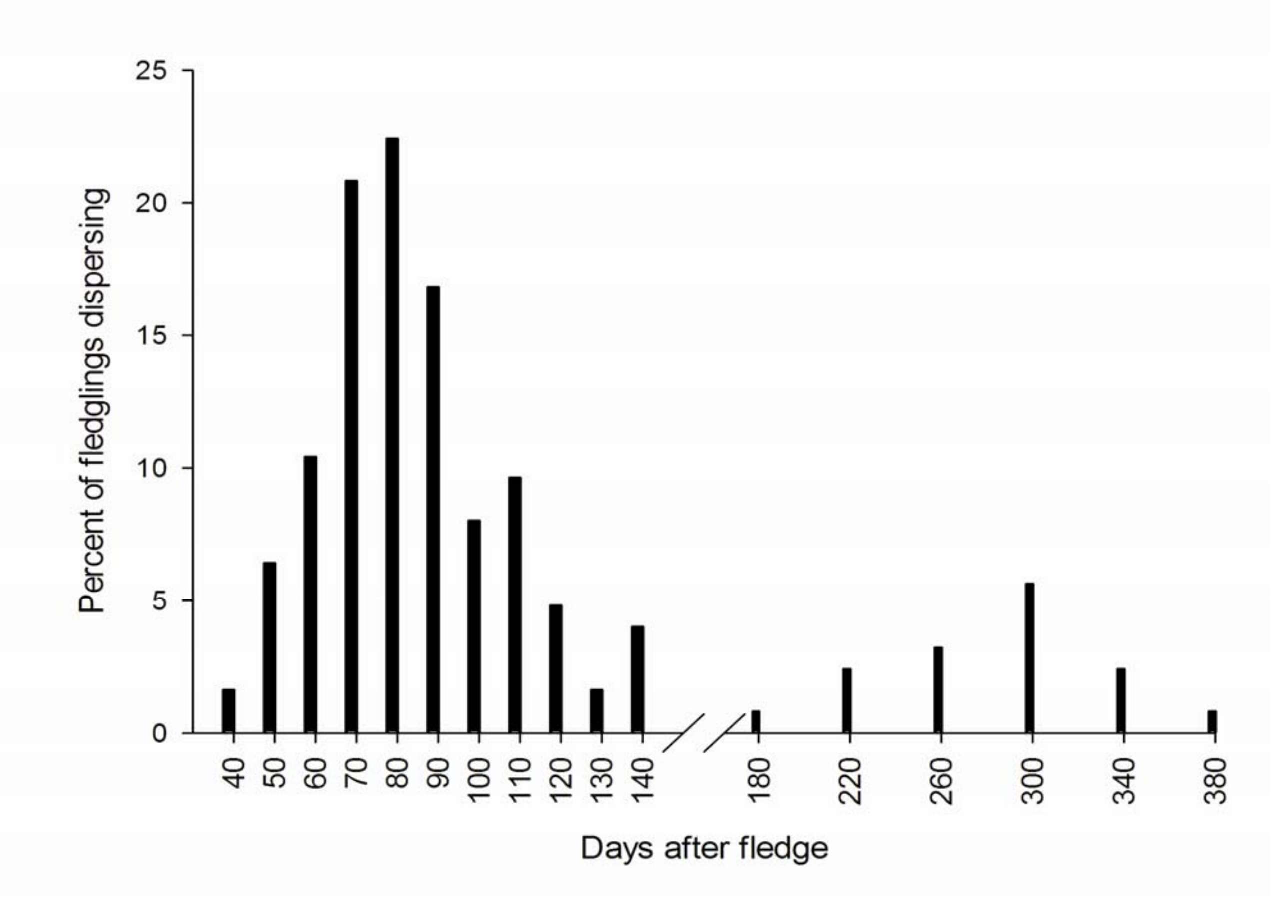

Figure 3.1 Length of time juvenile slaty antshrike offspring remained on the natal territory in Panamanian rainforest. Dispersal of fledglings is grouped into 10 day intervals (e.g. 60 is offspring that dispersed between 51-60 days after fledging) until 140 days, then number of fledgling's dispersing is grouped into 40 day intervals (e.g. 300 is offspring that dispersed between 261-300 days after fledging).

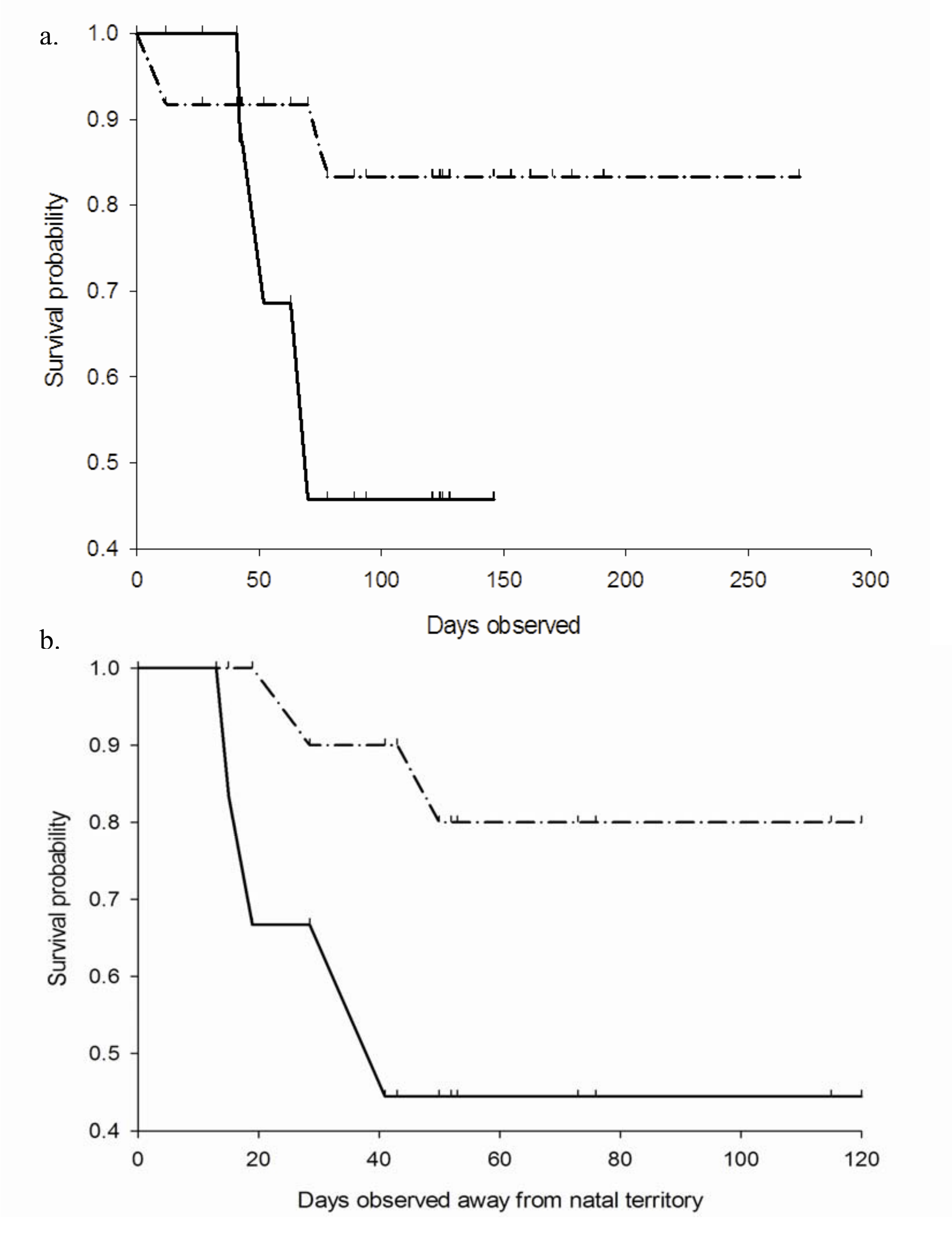

Figure 3.2 Kaplan-Meier survival curves for slaty antshrike juveniles with radio-transmitters that dispersed from the natal territory 69-105 days after fledging (solid line) and > 105 days after fledging (dashed line). Hatch marks are censored individuals. **a**. Survival probability over entire period juveniles observed (from day transmitter attached [day 0] until no longer observed). **b.** Survival probability from dispersal (day 0) until 4 months after dispersal.

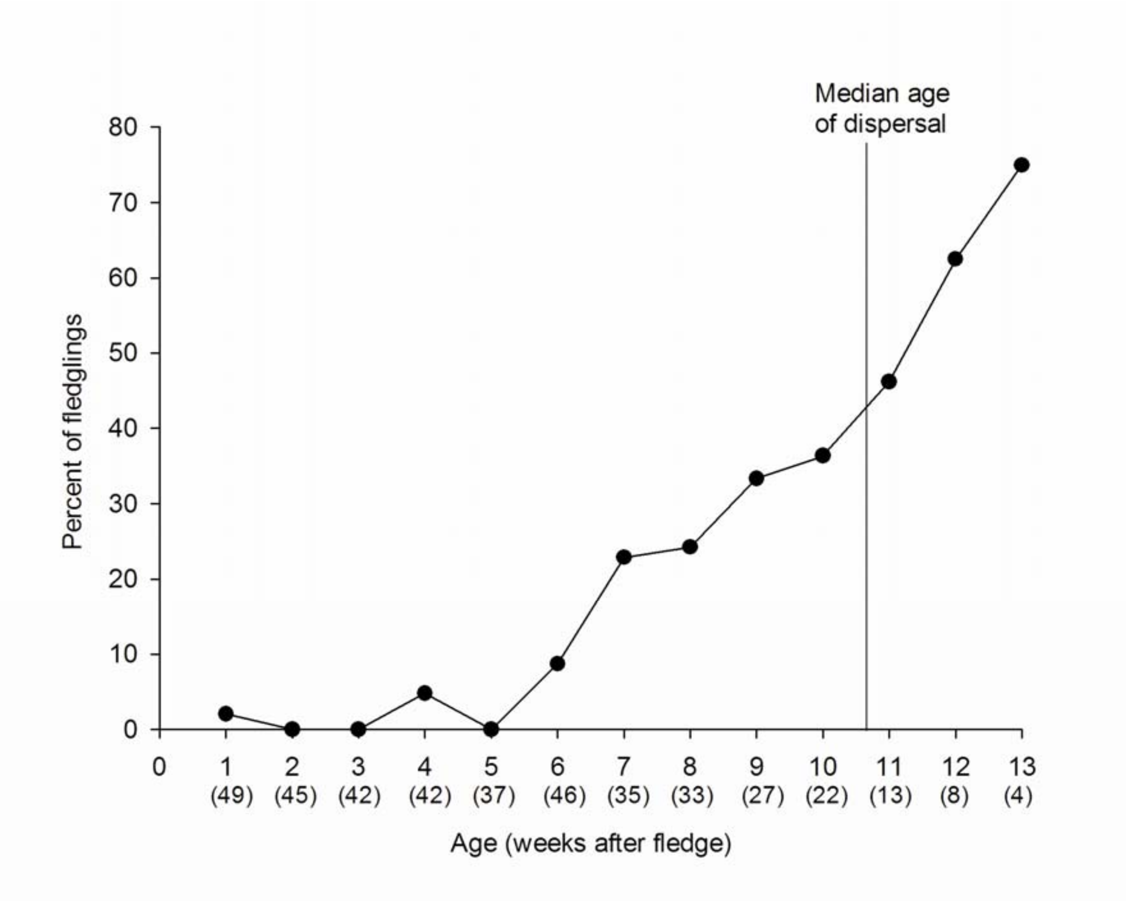

Figure 3.3 The per cent of juvenile slaty antshrikes that experienced aggression from parents as offspring increased in age (week 0 = fledge). Sample sizes are in parentheses below the age of offspring.

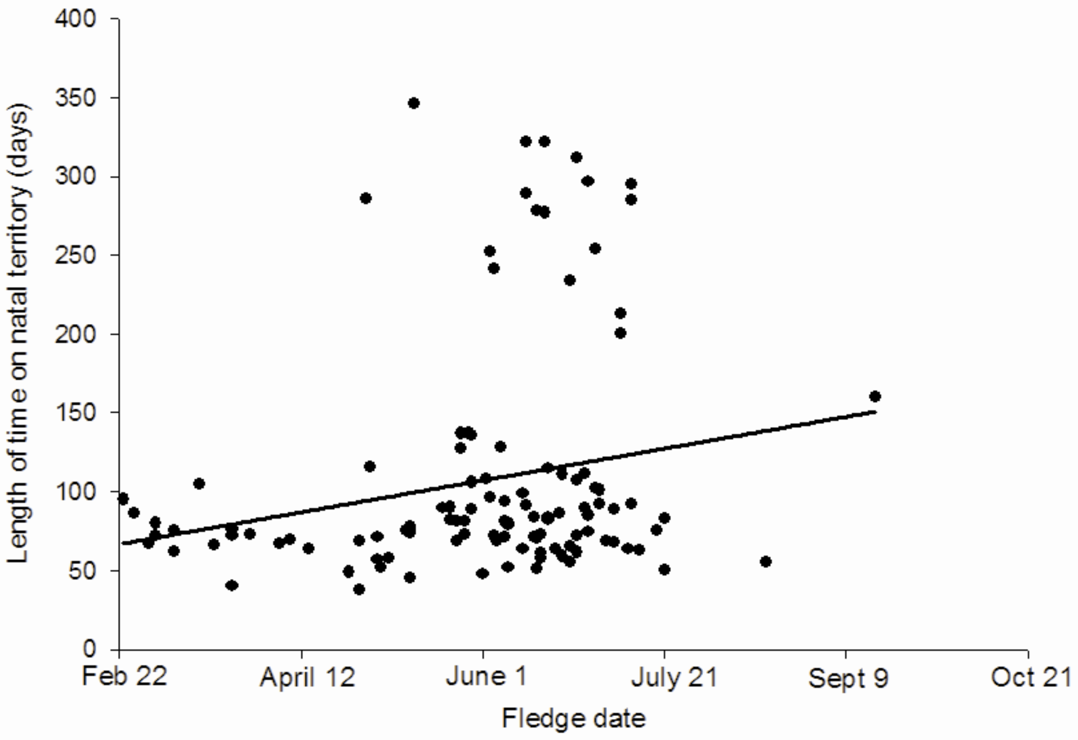

Figure 3.4 The relationship between the amount of time slaty antshrike offspring remained on the natal territory and fledge date ($N = 125$ fledglings).

CHAPTER 4: SURVIVAL UNTIL REPRODUCTION IN A TROPICAL BIRD: FACTORS INFLUENCING SURVIVAL AND IMPLICATIONS FOR LIFE HISTORIES

ABSTRACT

Estimating and knowing the factors that affect survival until reproduction is essential to understanding the organization of life histories within and among species and has strong effects on population growth. Theory predicts, for example, that survival until reproduction influences the optimum level of reproductive investment by parents, which might partly explain prolonged parental care in species with high first year survival. Tests and refinements of life-history theory have been hampered, however, by a lack of field-based data. We estimated survival until reproduction, age at reproduction, and sources of variation in survival in a Neotropical passerine, the western slaty-antshrike (*Thamnophilus atrinucha*), in central Panama. We observed that fledged antshrikes had 77% survival through the dependent period and 49% survival to the age of 1 year; survival rate was lowest during the first week after leaving the nest. Timing of fledging within the breeding season, fledgling mass, and age at dispersal influenced survival, while sex of offspring and year did not. Individuals did not breed until two years of age, and post-fledging pre-reproductive survival was 42% that of adult survival. High survival until reproduction in antshrikes balanced their low annual productivity, resulting in a stable population. Survival during the dependent period and first year in the western slaty-antshrike exceeded estimates for northern hemisphere species. This difference appears to be associated with the extended post-fledging parental care, delayed dispersal, low costs of dispersal, and less seasonal environment of antshrikes.

INTRODUCTION

Survival until reproduction is one of the least understood components of demography, yet estimates are needed to examine population growth, life history evolution, and patterns of variation in life histories (Stearns 1992). Survival at this stage, the outcome of both environmental factors and parental behaviors (Cam et al. 2003), is generally lower and more sensitive to environmental factors than adult survival (Clark and Martin 2007). Therefore, genetic variation in traits that affect pre-reproductive survival potentially is subject to intense selection (Clutton-Brock 1988).

One way of organizing life history variation has been to place species on a slow-fast continuum (Promislow and Harvey 1990), in which "fast" species are characterized by early maturity, high fecundity, and low adult survival, and "slow" species exhibit delayed reproduction, low fecundity, and high adult survival. The latitudinal variation in avian life histories is often cited in this context, with north temperate species occupying the "fast" end of the continuum and tropical and many south temperate species occupying the "slow" end (Martin 1996). Higher first year survival in parallel with higher adult survival is predicted in species with "slow" life histories (McNamara et al. 2008). Yet pre-reproductive survival appears to be similar across species (and independent of adult survival) because species with high adult survival delay reproduction (Ricklefs 2000). Low adult mortality and thus few openings in the breeding population lead to delayed reproduction (>1 year) apparently owing to high costs of breeding early (Stearns 1992, Ricklefs 2000). Furthermore, increased reproductive investment in a brood or litter is predicted when pre-reproductive survival is high or is high relative to adult survival (Gadgil and Bossert 1970, Ricklefs 1977, 2010). These offspring contribute more to their parent's lifetime reproductive success, and are, thus, of higher relative value to parents

(Ricklefs 2010). We define reproductive investment as the additional risk that adults accept to care for their entire brood.

Although adult survival is greater, on average, in tropical compared to north temperate species, estimates broadly overlap between the two regions (Brawn et al. 1999, Blake and Loiselle 2008). Clutch size and annual reproductive success, are, however, consistently lower in tropical species (Lack 1947, Jetz et al. 2008). How, then, do tropical populations achieve replacement under the assumption that the population is stable (e.g., $\lambda = 1$) (Ricklefs 1977)? Finding greater pre-reproductive survival in tropical birds would help answer this question (Martin 1996). Life history observations suggest that extended post-fledging parental care and delayed dispersal of offspring from the natal territory are common in tropical and southern hemisphere species (Russell et al. 2004). Thus theoretical considerations and behavioral data suggest that first year survival and survival until reproduction are greater in tropical compared to temperate regions.

The patterns and sources of variation in offspring survival within a species are essential knowledge for determining when offspring are most vulnerable and for understanding the influence of the environment and parental behavior on survival. The pre-reproductive period encompasses periods during which offspring are dependent upon their parents — when survival is strongly influenced by parental care — and offspring are independent — when survival depends primarily upon environmental conditions (Cam et al. 2003). Low survival soon after birth is common across vertebrates (Clutton-Brock et al. 1987), including the immediate post-fledging period (Yackel-Adams et al. 2006). Furthermore, offspring sex, timing of fledging, age at dispersal, and body mass often influence variation in offspring survival. Sex differences in survival commonly arise when the sexes differ in mass or dispersal behavior (Green and

Cockburn 2001). More generally, offspring that disperse at older ages have higher survival compared to early dispersers (Ekman et al. 1999). The timing of fledging with respect to the breeding season is often a major factor explaining variation in survival; however, how survival changes over the breeding season varies (Clutton-Brock et al. 1987, Naef-Daenzer et al. 2001). Survival has been shown to increase with fledgling body mass in some studies, but not others (Magrath 1991). Contrasting patterns arise in part because mass and timing of fledging may affect survival differently depending on whether offspring are dependent upon parents or independent, yet studies rarely examine both stages.

We estimated survival until reproduction, sources of variation in survival, and age at first reproduction in a Neotropical passerine, the western slaty-antshrike (*Thamnophilus atrinucha*), in the lowland forests of Panama. In a previous paper (Tarwater and Brawn 2010b, *in press*), we estimated survival during the dependent period, from fledging until offspring independence, as 0.75 (± 0.03, using Kaplan-Meier survival analysis). Herein, we present an analysis of pre-reproductive survival and sources of variation in survival across both the dependent (fledging until parents stop provisioning offspring) and independent periods (independence from parents until reproduction). We examined how mass, age at dispersal, timing of fledging in the breeding season, and sex influence survival. We predicted that dispersal at a later age would positively influence subsequent survival based on our previous work with this species (Tarwater and Brawn 2010a, *in press*). Because males and females do not differ in dispersal patterns or mass (Tarwater and Brawn 2010a, *in press*), we expected to find no differences between the sexes in survival. Estimates of survival until reproduction are sparse, and population modelers either assume that pre-reproductive survival is a fraction (0.25-0.5) of adult survival (Ricklefs 1973, Temple and Cary 1988) or calculate survival based on the assumption that in a balanced population recruitment must equal adult mortality (Ricklefs 1973, 1977). We compared our empirical estimate of survival until reproduction to the estimate obtained from assuming the population is stable.

METHODS

Study site and focal population

We studied a population of slaty antshrikes from 2003-2009 on a 104 ha plot in Parque Nacional Soberanía (for details see Robinson et al. 2000). PN Soberanía is a 20,000 ha contiguous, lowland, moist tropical forest. Slaty antshrikes are small, insectivorous passerines (averaging 23g in mass; own observations) from the Neotropical family, *Thamnophilidae*. Females lay a clutch of two eggs, which are incubated (16 days), and the young cared for in the nest (10 days), by both parents. Few nests survive risks of predation and other mortality factors (20% from first egg to fledging during this study). Adults maintain territories year-round, and adult survival at the same study site is high (0.73 ± 0.04) based on mark-recapture modeling that accounted for transient individuals (Brawn et al. 1999). This is similar to our estimate based on resighting of marked territorial pairs (0.75 ± 0.04, Tarwater, unpubl. data). Antshrikes feed their fledged offspring for an average of 8 weeks after leaving the nest, offspring disperse between 38-346 days after fledging (median: 84 days), and brood division occurs during the dependent period (Tarwater and Brawn 2008, 2010a,b). The breeding season lasts from approximately January-September and 106-120 breeding territories occur on the plot (Robinson et al. 2000, Tarwater, unpubl. data).

Juvenile survival

We used mark-resight sampling to estimate survival during the dependent period (8 weeks after fledging) from 2003-2004 and 2006-2007. We color-banded adults (n=119) and searched for nests on their territories. Two to three days prior to fledging, we color banded nestlings (n=198). We resighted juveniles on an approximately weekly basis from fledging until they died or at least until the end of the dependency period (n=178). If fledglings were not located during one period, we search territories at least two more times to confirm disappearance (for further details see Tarwater and Brawn 2010a, b, *in press*).

We did not systematically search for color-marked juveniles after dispersal due to the difficulty of resighting birds that do not defend breeding territories. Therefore, to estimate survival after independence we used only radio-tagged birds (n=28 juveniles) from 2006-2008, of which we were able to monitor 24. The radio-transmitters were approximately 4-5% of the body weight (body mass: 22.3 ±0.24 g, transmitter weight: 0.95 g) and were attached using the leg-harness method (Rappole and Tipton 1991). Transmitters were attached to birds anytime from prior to fledging to 38 weeks after fledging. Dispersal distance was similar between birds located with and without radio-transmitters, suggesting a minimal effect of transmitters, at least on bird movement (Tarwater, unpubl. data). Juveniles were radio-tracked every 3-4 days. Birds were followed for 1 – 9.5 months depending on when the transmitter failed, the bird died, or we lost contact when an individual apparently dispersed from the study area. We judged transmitters found on the ground or in a tree as evidence of mortality. Two of the 24 radio-tagged birds went missing for unknown reasons. We considered these birds to be censored from the data (last known alive, then removed from the study). Juveniles that leave their natal territory earlier disperse further (Tarwater, unpubl. data); the missing birds departed early and thus likely dispersed outside of the study area.

Factors influencing juvenile survival

We assessed the influence of offspring sex, mass at fledging, and fledging date on juvenile survival during the dependent period. For survival during the independent period, we examined the effects of mass at transmitter attachment, fledging date, offspring sex, and age at dispersal (length of time offspring remained on the natal territory prior to dispersal). Two days prior to fledging, a subset of nestlings were weighed (to the nearest 0.1 gram) and measured. Our sample size for nestling mass was greater than for body condition (mass divided by tarsus length); thus, we used only nestling mass in our analysis. Furthermore, body condition and nestling mass are strongly correlated (Pearson correlation coefficient=0.76; Tarwater and Brawn 2010a, *in press*). Age at dispersal from the natal territory was determined by radio-tracking birds. A bird was considered to have dispersed when either a bird was found outside the natal territory or when a bird "dispersed" from their parents. These latter juveniles remained on the edge of their natal territory but did not associate with their parents and the parents did not tolerate the offspring.

Male versus female plumage can be distinguished by three weeks out of the nest. For offspring that died prior to this age we used molecular markers to identify sex (n=44). We collected approximately 40μL of blood from each nestling using tarsal venipuncture and stored the sample in 1mL of Queen's Lysis Buffer (Seutin et al. 1991). We extracted DNA with Qiagen DNEasy kits (Qiagen, Valencia, CA) following the manufacture's instructions. A sequence of the CHD gene on the sex chromosomes was amplified in a polymerase chain reaction using primers 2550F and 2718R. We used 15 μL volumes in a PTC-100 Programmable Thermal Controller (MJ Research, Inc.) using the thermal profile of Fridolfsson and Ellegren (1999). Final concentrations of all reactions were 11.00 mM Tris HCl, 2.50 mM $MgCl_2$, 0.20 mM dNTP, 0.50 μM of each primer, 0.25 U AmpliTaq (Applied Biosystems, Foster City, CA), and 2 μL of the extracted DNA. PCR products were visualized by electrophoresis on a 2% agarose gel.

Age at first reproduction

Age at first reproduction was estimated by resighting juveniles on breeding territories on our study plot. From 2003-2007, we opportunistically resighted juveniles when monitoring the study site. We systematically searched the entire study plot in March and August of 2008, and August/September 2009. We considered the age at reproduction not to be when juveniles acquired breeding territories, but when the juveniles started breeding. Most juveniles (18 out of 27) obtained breeding territories during the non-breeding season (August – January). For these juveniles, we considered the age at reproduction to be the beginning of the following breeding season (1st of April). Breeding between August and December was consistently rare in our population. Whether the population began breeding in January or not until April varied by year. Therefore, by defining 1st of April as the start of the breeding season, we might have increased the age at reproduction by as much as three months. When individuals that were marked as juveniles were found on breeding territories during the breeding season, the day we resighted them was their age at reproduction. We only know the age at first reproduction for individuals that acquired breeding territories on the plot. Nevertheless, we believe our estimate of age at first reproduction is at most a slight underestimate, for two reasons: 1) the duration of the study was long such that we could have observed some juveniles taking up to 6 years to acquire territories; 2) age at first reproduction and dispersal distance appear unrelated (Tarwater, unpubl. data), thus we do not expect any systematic bias due to searching for birds only within the study site.

Comparison of methods to determine survival until reproduction

We compared our estimate of pre-reproductive survival to the estimate obtained by dividing the number of young fledged per individual per year (e.g., annual productivity) by the proportion of adults lost per year (Ricklefs and Bloom 1977). We estimated annual productivity from 2003-2004 and 2006-2007 by monitoring color-banded breeding pairs (2003: 12 breeding pairs, 2004: 28, 2006: 33, 2007: 31). Number of fledged young was the number of offspring in the nest two days prior to fledging (when we banded the nestlings). Slaty antshrikes may be double brooded (Tarwater and Brawn 2008), and thus the maximum observed number of offspring that fledged per year was four.

Statistical analyses

We used the program MARK to estimate survival rates (White and Burnham 1999). We use Akaike's Information Criterion corrected for small sample sizes (AIC_c) to evaluate competing candidate models (Burnham and Anderson 2002). The goodness-of-fit of the global model was assessed using parametric bootstrap procedures in MARK. The variance inflation factor ($\hat{c}$) was calculated by dividing the model deviance by the bootstrapped deviance. When $\hat{c}$ is ≤ 3.0, there is little over-dispersion in the data (Lebreton et al. 1992). Models with a difference (ΔAIC_c) of ≤ 2 are as parsimonious as the best-fit model (lowest AIC_c) and $\Delta AIC_c > 7$ is considered strong evidence that the models differ from one another (Lebreton et al. 1992, White and Burnham 1999, Burnham and Anderson 2002). If the top model did not have >90% of the weight, we derived model averaged estimates to account for model uncertainty (Burnham and Anderson 2002). Model averaging techniques weigh the impact of all models for a given parameter according to its AIC_c weight (Burnham and Anderson 2002). If individual covariates were in the same number of models, we compared the sum of AIC_c weights across all models where each covariate appeared to determine the relative importance of each covariate (Burnham and Anderson 2002).

Juvenile survival was estimated in two ways: we used the Cormack-Jolly-Seber model for mark-resighting data taken during the dependent period and the "known fate" model for survival after independence of radio-tagged birds (White and Burnham 1999). We were interested in how survival changed with age during the juvenile dependency period and in estimating first year survival. Therefore in our analysis, age was equivalent to time, whereby each encounter interval represented a particular age of offspring. Thus for all notations, we use "a" for age rather than the more typical "t" for time to aid in the interpretation of results. During the dependent period, we pooled observations into 7 intervals to generate sufficient sample sizes: 0, when the nestlings were banded; 1, between banding and two days after fledging; 2, three days after fledging to end of week 1; 3, week 2; 4, weeks 3 and 4; 5, weeks 5 and 6; and 6, weeks 7 and 8. The first week after fledging was split into two intervals because most post-fledging mortality typically occurs during the first week out of the nest and changes in fledgling behavior during this time likely lead to differences in resighting probability. We calculated daily survival during the post-fledging period (to make intervals equal in MARK) and then raised daily survival to the number of days in each interval to calculate cumulative survival during each interval. For the first one to two weeks after fledging, offspring are difficult to observe because they are less mobile and hidden in dense vegetation. Thus, we expected that younger individuals would have a lower resighting probability than older offspring. We examined eleven *a priori* models to assess whether survival (Φ) was age-varying and how resighting probability (P) varied with age (Table 4.1a). Our best model, Φ(a)P(a1,2-3,4-6), was survival as age-varying and resighting probability differing between intervals 1, 2-3 (constant within intervals 2-3), and 4-6 (constant within these intervals). We used this best-fitting resighting probability model, P(a1,2-3,4-6), in the rest of the analyses.

We examined annual variation in survival probability (with year as a grouping variable) during the dependent period ($\hat{c} = 1.68$). We were unable to analyze the fully parameterized model, Φ(year*a)P(year*a), due to sample size constraints. Instead, we used Φ(year.)P(year.) (age was constant) as the global model. We found no differences between years in survival probability with survival without year as the top model (with 89.3% of the weight). Therefore we pooled all the data for years to improve precision of our parameter estimates. We analyzed sex independently because 18 of our birds that died were not sexed because we were unable to bleed the nestlings. We did not want to inflate our overall estimate of survival by not including 18 birds that died. Furthermore, we found no apparent relationship between sex and fledging mass (t-test: $t=-0.53$, $df=158$, $P=0.60$). Next, we used the top model from Table 1a to estimate survival and the influence of covariates. We predicted survival would decline linearly with fledging date or that it would peak in the middle of the breeding season. We predicted survival would increase linearly with fledging mass. We also tested for interactions between covariates.

Survival during the independent period was calculated from week 9 (once offspring are independent) until 52 weeks after fledging. Because of sample size restrictions, we only considered survival as constant throughout the independent period and we kept our models simple (Burnham and Anderson 2002). We first tested the influence of sex, and because sex was not strongly supported (see Results), we pooled the sexes together in further analyses. We predicted all three covariates would have linear effects on survival.

We estimated survival to reproduction using our estimates of first year survival and age at reproduction. We considered monthly survival after the first year to be equivalent to our monthly estimate of survival during the independent period. Cumulative survival probabilities were calculated by multiplying the product of all survival estimates. The variance and standard error of cumulative survival was estimated using the delta method (Powell 2007).

RESULTS

Survival during the dependent period and factors influencing survival

Cumulative survival over the period from fledging to independence was 0.77 (± 0.06). After the first week out of the nest, daily survival probability increased over the dependent period (Fig. 4.1). Moreover, survival was lowest (0.85 ± 0.05) the first week after fledging, and then increased to 0.956 (± 0.03) for week 2, 0.978 (± 0.03) for weeks 3-4, 0.998 (± 0.007) for weeks 5-6, and 1.00 (± 0.002) for weeks 7-8. During the first week after fledging, offspring move infrequently and are thus more vulnerable to predation. Resighting probability was the lowest (0.722 ± 0.033) from day 3 to the end of week 2, when offspring are 10+ m up in the canopy, primarily immobile, quiet, and difficult to find. Resighting probability for days 0-2 was 0.874 (± 0.031); this is when offspring are low to the ground, making them easier to find. Resighting probability was the highest in weeks 3-8, when offspring are flying around frequently, following parents, and begging loudly (0.938 ± 0.013).

We tested six *a priori* models to examine the influence of offspring sex on survival. In the top model, with 71.0% of the weight, survival varied with age, but sex exerted only a weak influence (1.90 ΔAICc, Table 4.1b). Resighting probability did not differ between males and females (10.33 ΔAICc). Cumulative survival from fledging until 8 weeks later was 0.77 (± 0.04) for males and 0.76 (± 0.03) for females.

Of the 10 candidate models used to examine the influence of fledging date and mass on survival, the top three models, with 85.7% of the weight, included a quadratic relationship with fledge date (Table 4.1c). Across the population, fledging mass ranged from 11.5 – 18.4g (median: 14.9 g) and fledge date ranged from February 23 – September 21 (median: June 9). Fledging mass was in the third highest model (1.19 ΔAIC_c), and mass had a positive relationship with survival. Nevertheless, the model with fledging mass alone had similar support to the model with no covariates, suggesting a weak relationship between mass and survival. The influence of fledging date on survival changed with offspring age (Fig. 4.2). For the first week after fledging, when mortality was highest, survival peaked in the middle of the breeding season (mid April to early July). The relationship between survival and fledging date was weaker during the last 7 weeks of the dependent period.

Survival after independence and the factors influencing survival

Model averaging estimated survival to be 0.959 (± 0.03) every 4 weeks. Testing two *a priori* models, we observed similar survival probabilities for the sexes during each interval (males: 0.944 ± 0.022, females: 0.946 ± 0.025, with sex >2 ΔAIC_c from the top model). To examine the influence of covariates, we used 8 *a priori* models. The top models (<2 ΔAIC_c) included all three covariates (Table 4.2). For the radio-tagged birds, mass at transmitter attachment ranged from 19.5 – 24.5 g (median: 22.1g), fledging date ranged from February 21 – July 10 (median: May 28), and age at dispersal ranged from 58 - 322 days after fledging (median: 104 days). The sum of AIC_c weights indicated that fledging date had the strongest effect on survival (0.791), followed by age at dispersal (0.621), and then mass (0.502). Model averaging the effect of fledging date indicated that survival declined the later in the season offspring fledged. Model averaging the effects of mass and age at dispersal indicated that survival increased with increased mass and with increased age at dispersal. We found five transmitters on the ground, three of which were damaged, suggesting predation was the cause of mortality. In four out of the five juveniles that died, mortality occurred within the first month after dispersal.

Age at first reproduction

We calculated age at first reproduction for 27 birds (11 females and 16 males). We observed that individuals take on average 1.90 (± 0.13) years (median: 1.82, range: 0.75-2.97) to acquire a territory and begin breeding. No differences were observed between males (1.97 ± 0.17) and females (1.80 ± 0.21; Mann-Whitney U test: U= 75.00, df=1, P=0.51).

First year survival, pre-reproductive survival, and ratio of juvenile to adult survival

Juvenile survival from fledging to one year of age was 0.489 (± 0.06) with most mortality occurring during the first month after fledging (Fig. 4.3). Average survival of juveniles from independence to recruitment was 0.40 (± 0.04). Pre-reproductive survival was calculated by raising monthly survival (during the independent period, 0.959) to the number of months from 1 year of age until reproduction multiplied by first year survival (0.489). Based on the mean age at reproduction (1.9 years), we estimated survival from fledging to reproduction to be 0.309 (± 0.07). To illustrate the relative value of fledged offspring compared to their parent in terms of contributions to future generations, this estimate was 42% of annual adult survival (0.73). Thus, each offspring is 21% (0.5x0.42) as valuable, in terms of contributing genes to future populations, as the parent is to itself. Independent offspring survive 0.40/0.73 = 55% as well as their parents to initial recruitment as adults to the next breeding season.

Comparison of methods to determine juvenile survival

Average annual productivity was 0.91 fledged female young/female (± 0.06, n=4 years) and varied from 0.73-1.0 fledged female young/female. All years were similar (0.91-1.0), except for 2006 (0.73). Calculating juvenile survival based on adult mortality (0.27) and annual productivity (0.91) resulted in an estimate of 29.7% survival until reproduction. This estimate is approximately equal to our estimate based on following juveniles (30.9%).

DISCUSSION

We observed high post-fledging survival, high first year survival, and delayed reproduction in western slaty-antshrikes compared to northern hemisphere passerines. Mass, timing of fledging in the breeding season, and age at dispersal influenced offspring survival, whereas sex of offspring and year did not. Moreover, timing of fledging influenced survival differently depending on whether offspring were dependent upon their parents or independent.

Patterns of mortality and sources of variation

As in other studies, we observed the highest mortality right after and we suspect that predation was the main cause of death (Yackel-Adams et al. 2006). During the first week after fledging, offspring are less mobile than later and are thus more vulnerable to predation. Based on the damage done to the radio-transmitters, mortality during the independent period appeared to be a result of predation. Mortality during this period occurred primarily within the first month after dispersal. Increased mortality after dispersal may arise due to increased movement through new environments (Small et al. 1993) and/or switching from group living to being alone, such as is observed in antshrikes. This transition increases the probability of predation and reduces the efficiency of foraging (Alexander 1974, Ridley et al. 2008).

We observed that offspring mass had a slight positive effect on survival during the dependent period and after independence. Only a slight effect was likely observed during the dependent period because if most mortality during this period was due to predation, as we suggest, differences in mass might not alter the probability of predation on young fledglings (Veasey et al. 2000). A positive effect of mass could arise if heavier offspring are able to acquire more food, survive periods of food shortage, or spend less time foraging and more time watching for predators (Garnett 1981, Green and Cockburn 2001). This may be especially crucial for recently independent juveniles that are less experienced and inefficient foragers (Sullivan 1989).

Timing of fledging within the breeding season had the strongest effect on offspring survival, particularly during the period of highest mortality. We observed that during the dependent period, survival peaked in the middle of the breeding season (mid April to early July). In multi-brooded species, such as antshrikes, the timing of fledging should have no effect or a positive effect on offspring survival compared to single-brooded species, where survival often declines over the season (Daan et al. 1990). These patterns are attributed to changes in food availability (Daan et al. 1990). If food availability had been a key factor, a greater effect of fledging mass on survival should have observed, especially because differences between fledglings often were large (up to 38% larger). Alternatively, changes in predation over the season may lead to variation in survival (Naef-Daenzer et al. 2001).

Nesting success peaked in the middle of the season (Tarwater, unpubl. data). Antshrikes might experience lower predation if the abundance of other alternative prey increased during this same period (Sundell et al. 2003, Elmberg et al. 2009). Many of the common predators at our study site are omnivorous, including various hawks, white-faced capuchins (*Cebus capucinus*), and toucans (Tarwater 2008). In lowland Panama, insect and fruit abundance peaks from May-July (Gradwohl and Greenberg 1982) and peak breeding for bird species is March/April – June/July (Skutch 1950). Thus insects, fruit, and nests and young fledglings of species other than antshrikes are common during this peak. Contrary to our results during the dependent period, survival declined over the breeding season during the independent period. As stated above, insect abundance declines after July (Gradwohl and Greenberg 1982). The inexperience of young juveniles may exacerbate the reduction in food availability later in the breeding season and interact with reduced vigilance behavior to increase predation.

Age at dispersal positively influenced offspring survival during the independent period. In species that delay dispersal, such as antshrikes, offspring survival increases when parents allow offspring to remain on the natal territory after reaching independence (Ekman et al. 1999). By delaying dispersal and remaining on their parents' territory, offspring benefit by living in groups, learning necessary skills prior to dispersal, and by having access to resources and protection from predators (reviewed in Griesser and Barnaby 2010). Previously, we observed that survival for the first four months after dispersal was greater for offspring that dispersed at an older age compared to when younger and parents directly influenced timing of offspring dispersal (Tarwater and Brawn 2010a, *in press*).

Neither offspring sex nor year influenced offspring survival. Evidence for sex-biased juvenile survival is rare except when sex is correlated with other factors, such as mass or age at dispersal (Green and Cockburn 2001). These factors are not correlated with sex in antshrikes (Tarwater and Brawn 2010a, *in press*). In addition to little annual variation in survival, only small differences in nesting success (ranging from 17 - 22% nesting success) and annual productivity were observed across the same years. These results suggest that at least during the years of our study, environmental conditions were relatively consistent.

Parental behavior appears adapted to reduce the probability of nest predation (Martin and Briskie 2009); high mortality commonly observed after fledging may likewise lead to selection on parental behavior. For example, antshrike parents spatially segregate broods during the period immediately after fledging, which might reduce the probability of both offspring being preyed upon in a single predation event (Tarwater and Brawn 2008). Furthermore, two factors directly influenced by parents—fledging date and age at dispersal—strongly influence offspring survival.

Indirect and direct estimates of survival and population stability

High pre-reproductive survival balances low annual productivity in antshrike populations, leading to population stability, with lambda (λ) = 1.009 based on the mean values of all parameters estimated (λ= recruitment [annual productivity*survival until reproduction] + adult survival, Charnov and Krebs 1974). Depending on annual productivity, lambda fluctuated between 0.95-1.04 per year. Pre-reproductive survival often has disproportionate effects on population growth compared to other life history variables (Clark and Martin 2007). Yet, due to the scarcity of empirical estimates, population modelers assume pre-reproductive survival is 0.25-0.5 times that of adult survival in small passerines, with year-round residents on the lower end of this range (Ricklefs 1973, Temple and Cary 1988). In antshrikes, any value less than 41% of adult survival would result in a lambda less than 1.00. Small changes in estimates of survival can lead to drastically different conclusions regarding population stability. Thus we urge caution in using indirect estimates until more studies are conducted that elucidate general patterns.

Higher survival during the dependent period and the first year

We compared our estimates to survival in non-migratory, small (≤100 g) northern hemisphere and tropical and southern hemisphere passerines (Table 4.3). Our estimates of first year survival (0.49) and daily post-fledging survival (0.997) are higher than estimates of first year (pre-reproductive survival in these species, 0.10-0.34, n=7) and daily post-fledging (0.968-0.990, n=5) survival in northern hemisphere species. Our estimate of pre-reproductive survival (0.31) is greater than the pre-reproductive survival estimates for 5 of the 7 northern hemisphere species. Moreover, pre-reproductive survival relative to adult survival (42%) in antshrikes is also at the upper end of the range of northern hemisphere passerines (0.25-0.5; Ricklefs 1973, Temple and Cary 1988). Slaty antshrikes are within the range of estimates of first year survival (0.11-0.66, n=18) and higher than the estimates of daily post-fledging survival (0.972-0.994, n=10) observed in other tropical and southern hemisphere species.

The high survival we observed throughout the pre-reproductive period is likely due to a combination of extended post-fledging parental care, delayed dispersal, low costs of dispersal, and a less seasonal environment. Similar to other tropical and southern hemisphere species, slaty antshrikes have extended post-fledging parental care and delayed dispersal (Russell et al. 2004, Tarwater and Brawn 2010a,b *in press*). Prolonged provisioning increases survival to reproduction (Sunde 2008) and, as discussed above, remaining on the natal territory for longer increases offspring survival and probability of recruitment (reviewed in Griesser and Barnaby 2010). Once young birds become independent, their annual mortality rate is correlated with adult mortality rate, owing to the similar environmental conditions adults and immature individuals experience (Ricklefs 2000). Adult survival is high in antshrikes, and likewise we observed high survival after independence, suggesting agreement with this general pattern. Severe weather, and in particular winter, is often a cause of mortality, particularly in young birds, in northern hemisphere species (Robinson et al. 2007). The less seasonal environment in the lowland tropics may therefore increase survival of offspring through their first year. Dispersal costs also reduce offspring survival (Baker and Rao 2004). Although we observed some mortality of offspring after dispersal, previous work on antshrikes found that survival on the natal territory compared to survival when floating (wandering through other breeding territories) was similar once offspring were 4-5 months old (Tarwater and Brawn 2010a, *in* *press*). Thus, once offspring have reached a particular age, floating does not appear particularly costly.

Juvenile survival rates and latitudinal variation in avian life histories

One of the key hypotheses to explain latitudinal variation in clutch size is based on the assumption that higher adult survival is correlated with lower fecundity, and thus lower reproductive effort (Williams 1966). However, survival of independent offspring to reproduction, relative to adult survival, also influences the reproductive investment: the higher the relative survival of offspring, the higher their contribution to parental fitness and thus the higher the optimum level of investment in them (Ricklefs 1977, 2010). Few studies have parsed the components of adult survival (into reproductive and non-reproductive periods) or juvenile survival (into dependent and independent periods). Nevertheless, rough comparisons can be made based on survival from fledging to reproduction and adult survival. We observed that survival from independence to reproduction was 40% (55% of adult survival) and survival from fledging to reproduction was 31% (42% of adult survival). Because these estimates are at the upper end of the range for northern hemisphere species (Ricklefs 1973, 1977, Temple and Cary 1988), we expect that reproductive investment would be the same or greater in antshrikes compared to northern hemisphere species. If this pattern holds true for other tropical species, the latitudinal gradient in clutch size cannot be explained by variation in reproductive investment. Instead, temperate species might allocate care towards increasing the number of offspring while tropical birds devote care towards improving offspring quality. In less seasonal tropical environments, lower food availability during the breeding season (owing to populations being near carrying capacity on a year-round basis), greater competition for breeding territories (owing to low territory turnover), and high rates of nest predation may favor increasing offspring quality over quantity (McNamara et al. 2008). Furthermore, at northern latitudes, survival of offspring may be more heavily affected by environmental conditions (e.g. winter) that cannot be altered by parental behavior. Conversely, in tropical environments where environmental conditions are more benign, parental behavior might play a greater role in offspring survival.

How tropical populations are balanced when clutch sizes are systematically lower than in north temperate species, but adult survival overlaps broadly is a long-standing question in avian life histories. First year survival in tropical and southern hemisphere regions exceeds that in north temperate regions (Russell 2000, and results presented here), which undoubtedly reflects, at least in part, the extended post-fledging parental care and delayed dispersal observed in tropical species (Russell et al. 2004). Owing to recent studies on post-fledging survival, accurate estimates of survival during this period are slowly becoming available. Yet, robust estimates of first year and survival until reproduction are still scarce. More estimates are needed, particularly in tropical and southern hemisphere species that vary in adult survival, to evaluate latitudinal variation in avian life histories.

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FIGURES AND TABLES

Table 4.1 Summary of model selection results to estimate whether (a) survival probability is age varying and the influence of age on resighting probability (b) the influence of sex (c) influence of fledging date and mass on dependent juvenile slaty antshrikes. Both (b) and (c) use the best-fitting resighting model from (a) P(a1,2-3,4-6).

No	Model[a]	AIC$_c$[b]	Δ AIC$_c$[b]	AIC$_c$[b] wt	K[c]	Deviance
(a) $\hat{c}$ = 2.48						
1)	**Φ(a) P(a1,2-3,4-6)**	**469.53**	**0.00**	**0.594**	**9**	**46.46**
2)	Φ(a) P(a1,2,3,4-6)	471.65	2.12	0.206	10	46.45
3)	Φ(a) P(a1-3,4-6)	472.96	3.44	0.107	8	52.00
4)	Φ(a) P(a1-2,3,4-6)	473.89	4.37	0.067	9	50.83
5)	Φ(a) P(a)	475.80	6.27	0.026	12	46.32
6)	Φ(a) P(a1,2,3-6)	483.97	14.44	0.000	9	60.90
7)	Φ(a) P(a1-2,3-6)	486.23	16.71	0.000	8	65.27
8)	Φ(a) P(.)	487.20	17.68	0.000	7	68.34
9)	Φ(a) P(a1,2-6)	488.82	19.29	0.000	8	67.86
10)	Φ(.) P(a)	507.65	38.12	0.000	7	88.79
11)	Φ(.) P(.)	533.86	64.34	0.000	2	125.30
(b) $\hat{c}$ = 2.35						
1)	**Φ(a) P(a)**	**1120.4**	**0.00**	**0.701**	**9**	**1104.3**
2)	**Φ(a+s)P(a)**	**1122.3**	**1.90**	**0.275**	**10**	**1104.1**
3)	Φ(a*s) P(a)	1129.0	8.56	0.010	15	1102.6
4)	Φ(a)P(s*a)	1130.7	10.33	0.004	16	1102.4
5)	Φ(a+s) P(s*a)	1132.6	12.23	0.002	17	1102.2
6)	Φ(a*s)P(s*a)	1141.4	21.03	0.000	22	1100.7
(c) $\hat{c}$ = 1.99						
1)	**Φ(a*2D)**	**827.54**	**0.00**	**0.395**	**21**	**784.30**
2)	**Φ(a+2D)**	**828.49**	**0.95**	**0.245**	**11**	**806.14**
3)	**Φ(a+2D+m)**	**828.74**	**1.19**	**0.217**	**12**	**804.32**
4)	Φ(a*d)	831.00	3.46	0.070	15	800.36
5)	Φ(a*d + m)	831.45	3.91	0.056	16	798.73
6)	Φ(a+d)	835.29	7.75	0.008	10	817.05
7)	Φ(a+d*m)	836.22	8.67	0.005	10	815.92
8)	Φ(a+m)	837.22	9.68	0.003	10	816.93
9)	Φ(a)	837.43	9.89	0.003	9	819.19
10)	Φ(a+m+d)	837.55	10.01	0.003	11	815.20

[a] Models in bold are the top models (<2 ΔAIC$_c$). a=age (time), d=fledge date, m=fledging mass, 2D= the quadratic effect of date (includes date, date*date in the model) * = interaction, + = additive model, [b] Δ AIC$_c$ = difference between the AIC$_c$ value for the best model and this AIC$_c$ value. [c] K = Number of parameters

Table 4.2 Model selection results for estimation of survival rates of juvenile slaty antshrikes during the independent period (weeks 9-52 after fledging). All models with constant survival.

Model[a]	AIC_c [b]	Δ AIC_c [b]	AIC_c [b] wt	K[c]	Deviance
1) Φ(d+l+m)	**37.75**	**0.00**	**0.378**	**4**	**29.26**
2) Φ(d+l)	**39.25**	**1.50**	**0.178**	**3**	**32.96**
3) Φ(d)	**39.35**	**1.61**	**0.169**	**2**	**35.21**
4) Φ(.)	40.32	2.57	0.104	1	38.27
5) Φ(d+m)	41.24	3.49	0.066	3	34.95
6) Φ(l)	41.95	4.21	0.122	2	37.81
7) Φ(m)	42.27	4.53	0.039	2	38.13
8) Φ(l+m)	43.75	6.01	0.019	3	37.46

[a] Models in bold are the top models (<2 ΔAIC_c). l = length of time on natal territory prior to dispersal, m = mass at transmitter attachment, d = fledge date, + = additive model

[b] Δ AIC_c = difference between the AIC_c value for the best model and this AIC_c value.

[c] K = Number of parameters

Table 4.3 The list of species included in our comparison. All birds are ≤100g non-migratory passerines.

SPECIES	% SURVIVAL	REFERENCE
Daily survival during the dependent period		
Northern hemisphere		
Parus major	0.968	Naef-Daenzer et al. 2001
Parus ater	0.968	Naef-Daenzer et al. 2001
Junco phaenotus	0.974	Sullivan 1989
Turdus merula	0.976	Snow 1958
Sturnus vulgaris	0.990	Krementz et al. 1989
Tropical and southern hemisphere		
Hylophylax naevioides	0.972	Styrsky et al. 2005
Turdus assimilis	0.981	Cohen and Lindell 2004
Sylvia lugens	0.984	Schaefer et al. 2004
Eopsaltria australis	0.987	Zanette 2000
Acanthiza pusilla	0.989	Green and Cockburn 2001
Sericornis frontalis	0.990	Magrath and Yezerinac 1997, Magrath 2000
Climacteris rufa	0.991	Luck 2003
Alophoixus pallidus	0.991	Sankamethawee et al. 2009
Turdoides squamiceps	0.992	Ridley et al. 2007
Sylvia boehmi	0.994	Schaefer et al. 2004
First year survival		
Northern hemisphere		
Parus palustris	0.10	Smith 1993
Turdus merula	0.11	Magrath 1991
Junco phaenotus	0.11	Sullivan 1989
Parus major	0.13	Greno et al. 2008
Zonotrichia leucophrys nuttalli	0.30	Baker et al. 1981
Melospiza melodia	0.32	Smith et al. 2006
Aphelocoma coerulescens	0.34	Woolfenden and Fitzpatrick 1984
Tropical and southern hemisphere species		
Geospiza conirostris	0.11	Grant and Grant 1989
Acanthisitta chloris	0.17	Sherley 1990
Eopsaltria georgiana	0.24	Russell et al. 2004
Malurus cyaneus	0.25	Rowley and Russell 1997
Malurus pulcherrimus	0.28	Rowley and Russell 2002
Malurus splendens	0.31	Russell and Rowley 1993
Nesomimus parvulus	0.35	Curry and Grant 1989
Verio latimeri	0.40	Woodworth et al. 1999
Malurus elegans	0.44	Russell and Rowley 2000
Corvinella corvina	0.44	Grimes 1980
Donacobius atricapillus	0.44	Kiltie and Fitzpatrick 1984

Table 4.3 (cont.)

SPECIES	% SURVIVAL	REFERENCE
Plocepasser mahali	0.47	Lewis 1982
Turdoides squamiceps	0.49	Ridley 2007
Turdoides striatus	0.53	Gaston 1978
Campylorhynchus griseus	0.54	Rabenold 1985
Turdoides caudatus	0.55	Gaston 1978
Acrocephalus sechellensis	0.61	Brouwer et al. 2006
Philetairus socius	0.66	Covas et al. 2004

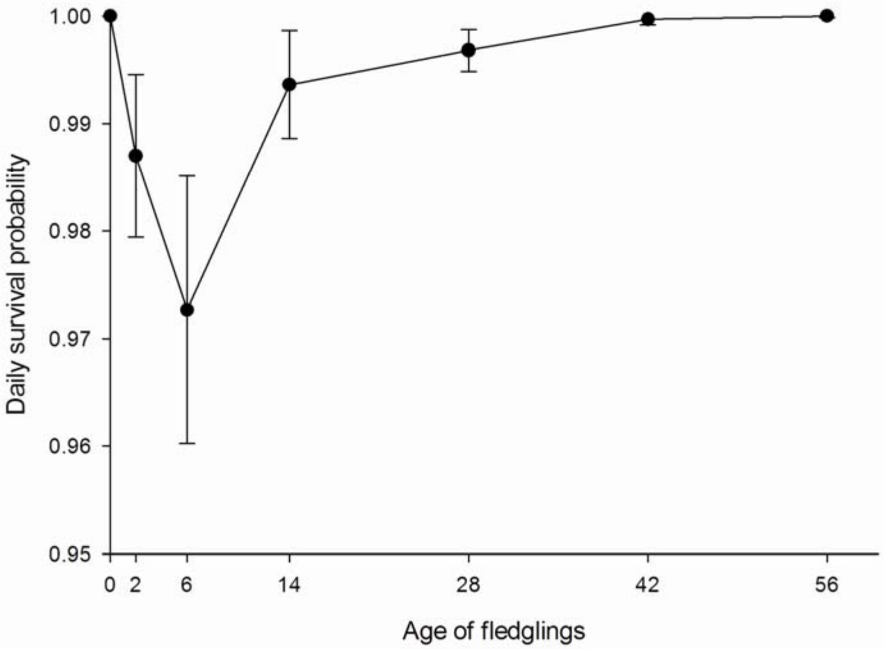

Figure 4.1 Daily survival probability of juvenile slaty antshrike offspring from fledging until the end of the dependent period. Day 0 is fledge day. SE bars shown. No bar is visible for weeks 7-8 due to low error (0.0001).

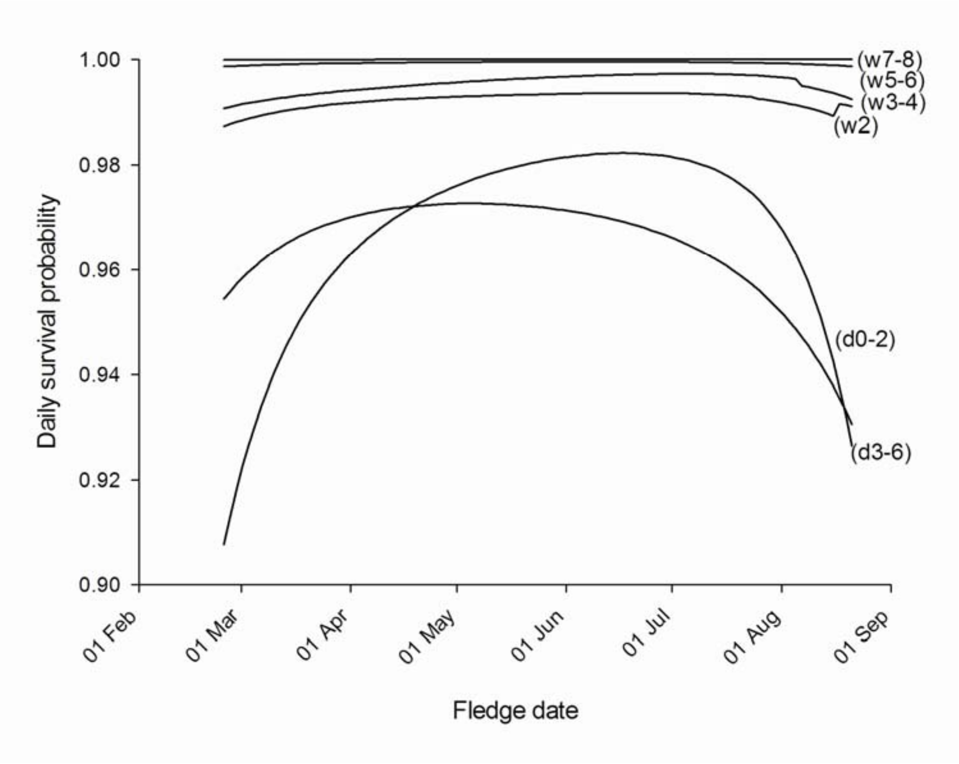

Figure 4.2 The relationship between fledge date of dependent juvenile slaty antshrikes and daily survival probability during days (d) 0-2 and 3-6 after fledging and weeks (w) 2, 3-4, 5-6, and 7-8 after fledging.

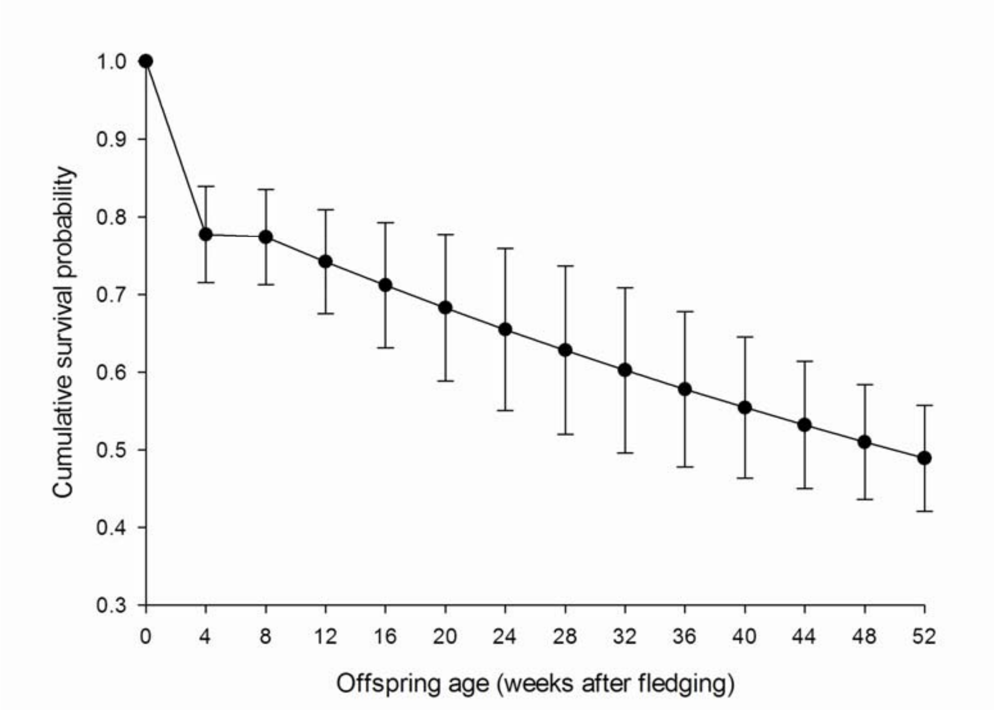

Figure 4.3 Cumulative survival of antshrike offspring from fledging (age 0) until 52 weeks after fledging. Lines are SE bars.

CHAPTER 5: PARENTAL RESPONSE TO ELEVATED BEGGING IN A HIGH PREDATION, TROPICAL ENVIRONMENT[c]

ABSTRACT

Interactions among parents, offspring and the environment are a critical aspect of parental care. Begging by offspring usually results in increased parental provisioning. Yet, parents also vary their behaviours to reduce offspring predation. Both begging sounds and provisioning activity can increase risk of nest predation. We predicted in a high nest-predation environment, parents would satiate young and reduce begging by increasing food load but maintaining the same provisioning rates. We also assessed whether increased begging was beneficial to offspring and whether parents changed the allocation of food to particular nestlings. We increased whole-brood begging via playbacks at nests of a tropical passerine bird, the western slaty-antshrike, *Thamnophilus atrinucha*. We observed that parents increased provisioning rates and reduced food load. Selection may therefore favour feeding hungry nestlings even when predation risk is elevated or begging sounds may place offspring at a higher risk than increased activity. Parents reduced the time between arrival to the nest and feeding of nestlings, potentially to reduce begging sounds. Exaggerated begging did not appear to be beneficial to offspring since parents did not deliver more food. Parents switched to preferentially feed the closest offspring during the begging treatment. This suggests that, under elevated begging, parents either allowed sibling competition to influence feeding decisions, or fed the closer nestling to reduce the time between arrival to the nest and feeding. Studying species in different environments provides insight into how ecological factors such as nest predation influence parental behaviour.

[c] Tarwater, C.E., Kelley, J.P., and Brawn, J.D. 2009. Animal Behaviour 78:1239-1245. Copyright owner has provided permission to reprint. J. P. Kelley provided help with isolating begging sounds for the experiment and wrote the section in the methods on making begging playbacks.

INTRODUCTION

Begging by offspring is observed in a variety of taxa (including invertebrates and vertebrates) and is used as a model system to understand animal communication and conflicts between individuals (reviewed in Kilner & Johnstone 1997). Theory predicts that while parents respond to the needs of their offspring, conflicts between parents and offspring arise over the amount of care provided (Trivers 1974). Assessing food allocation by parents to offspring provides insight on how parents allocate limited resources, how offspring influence these decisions, and how conflicts between siblings and between parents and offspring are resolved. Moreover, the responses of parents to begging are not independent of the environment, and parents may respond differently depending on environmental conditions.

In birds, parents typically increase provisioning rates in response to elevated begging (Bengtsson & Ryden 1983; Whittingham & Robertson 1993; Ottosson et al. 1997; Price 1998; but see Clark & Lee 1998) and this response can have both significant and subtle fitness consequences. For example, parents may change prey choice and food load (prey size per feeding trip), such that prey quality may decline and total amount of food provided may not increase (Lifjeld 1988; Whittingham & Robertson 1993; Price 1998; Wright et al. 1998). If the amount of food does not increase, or prey quality decreases, then exaggerated begging imposes extra costs to offspring and no additional benefits.

Parents may also change the allocation of food within the brood in response to increased begging, such that only particular offspring benefit (Kilner 2002). Such favouritism can promote competition between siblings and conflict between parents and the offspring receiving less care (Lessells 2002). The proximate cues parents use to allocate food may be nestling size, position, or begging behaviours (Smith & Montgomerie 1991; Price & Ydenberg 1995; Leonard & Horn

1996; Leonard et al. 2003; Whittingham et al. 2003). Male and female parents may respond differentially to these nestling attributes (Stamps et al. 1985; MacGregor & Cockburn 2002; Roulin & Bersier 2007). Parents are predicted to either favour the offspring with the greatest marginal fitness returns (one in greatest nutritional need) or the offspring of greatest reproductive value to parents (one with greater survival probability) (Clutton-Brock 1991; Jeon 2008). The offspring in greatest need is often the smaller offspring or the one begging the most intensely (i.e. had the highest vertical position in the nest or was the first to beg) (Gottlander 1987; Kolliker et al. 1998; Leonard & Horn 1998). The offspring with greater reproductive value is often the larger or more competitive offspring (i.e. the one in a better position in the nest) (Clutton-Brock 1991; Jeon 2008).

Nest predation is a major selective pressure on avian life histories (Skutch 1949; Briskie et al. 1999; Martin et al. 2000b). Compared to temperate regions, rates of nest predation in the lowland tropics appear to be higher (Robinson et al. 2000b) and nest predation appears to be most frequent during the day (Libsch et al. 2008). Increased nest activity (Martin et al. 2000a; Badyaev & Ghalambor 2001; Muchai & du Plessis 2005) and increased begging sounds (Leech & Leonard 1997; Dearborn 1999; Haskell 1999) both attract predators to nests. Moreover, the degree to which these factors influence predation depends upon the location of nests (Haskell 1999). Therefore, if parent birds increase feeding rates, predation may increase because of greater activity. Conversely, if parents do not increase feeding rates, the begging sounds of nestlings may also increase the probability of nest predation. Studying a species in an environment with high nest predation will inform on how conflicts between increased risk due to begging and provisioning interact to influence parental response.

We experimentally increased whole-brood begging via playbacks of begging calls at nests of a Neotropical passerine, the western slaty-antshrike, *Thamnophilus atrinucha*, in the lowland forests of central Panama. Studies manipulating begging calls or hunger level typically observe changes in provisioning rates only, yet selection on parental response may act on a suite of behavioural traits. We examined whether elevated begging influenced provisioning rate, food load/trip, prey type, total amount of food brought to nest and allocation within the brood (height of begging, proximity to parent and mass of nestlings). If the total amount of food brought to the nest increased with greater begging, then elevated begging would be beneficial to offspring.

We predicted that parents in a high predation environment, such as lowland Panama, would maintain the same (low) provisioning rates and increase food load in response to elevated begging. This strategy would increase the food given to nestlings (subsequently reducing begging levels and starvation risk), but not increase feeding rate (and thus not attract more predators). Our experiment increased whole-brood begging in broods of two, and thus both nestlings would appear hungry to parents. Parents may not be able to increase food delivery to both nestlings, and then must decide which nestling to feed. This decision may be based upon the begging display, nestling location, or nestling size. We made the following two predictions under elevated begging. (1) If parents prefer the nestling in greatest nutritional need, then the smaller (lighter) and/or more intensely begging (highest begging) offspring would be favoured. (2) If parents prefer the offspring of greater reproductive value (greater survival probability), then the larger and/or more competitive (nestling closest to feeding parent) offspring would be favoured. We also tested whether males and females respond differently to increased begging by young.

METHODS

Study population

We conducted our experiment in 2006 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. 2000a). Slaty antshrikes build open-cup nests in the forks of trees, lay a modal clutch of two eggs and have a nestling period of 10 days (where hatch day is defined as day 0, fledge day as day 9; Oniki 1975; Robinson et al. 2000b). During the course of this study, slaty antshrikes experienced 78.8% nest loss (overall loss based on daily predation rate; Mayfield 1961, 1975). Antshrike nests are depredated by a variety of predators, including snakes, monkeys, raptors, toucans, and small mammals (Roper 1992; Tarwater 2008). Limited evidence suggests that snakes are visually oriented (Weatherhead & Blouin-Demers 2004), birds use visual and auditory cues (Briskie et al. 1999; Santisteban et al. 2002), and mammals use olfaction or auditory cues (Clark & Wobeser 1997; Briskie et al. 1999). In 2003–2004, we banded breeding pairs with unique combinations of colour and metal leg bands and mapped territories. We located nests by searching territories and monitored these nests every 2–3 days.

Experimental methods

Birds can often discriminate between the begging calls of their own versus other young (Stoddard & Beecher 1983). Therefore, we recorded the begging calls of nestlings that were 3–5 days old and then played back these calls at their own nests when nestlings were 6–7 days old. Nestling vocal behaviour was recorded (2–4 h in duration) at a sampling rate of 44.1 kHz using a PMD660 solid-state digital recorder (Marantz Corporation, Kanagawa, Japan), lavalier microphone (ATR-35S; Audio-Technica U.S., Inc., Stow, OH, U.S.A.) and impedence-matcher (plug adaptor/transformer; RadioShack Corporation, Forth Worth, TX, U.S.A.).

From each nest's recording (*N* = 11 nests), five begging bouts were selected on the basis of clarity using Adobe Audition (v1; Adobe Systems Incorporated, San Jose, CA, U.S.A.). We selected a 5–6 s segment of each begging bout (of both nestlings begging). To create the playback stimulus, all five begging bouts were used and these bouts were repeated in random order until a 4 min stimulus file was created. The 4 min file was then repeated on the field playback unit for the duration of the 2 h treatment. A sound file consisting of white noise served as the control stimulus. We adjusted the amplitude of all files (begging and white noise) to a standard level using the 'RMS average' metric in Adobe Audition, which is a measure of the sound's overall loudness. For each experimental trial, playback volume on the playback device was set at the same level for all nests and for both treatments. On a quiet day, the begging sounds were barely audible to observers standing 10 m away. This volume mimicked that of hungry, late-stage nestlings. We observed during the recordings of begging sounds that nestlings begged continuously at a low volume. Therefore, the playback of continuous begging sounds was not more frequent than normal, and the volume was within the normal range for nestlings (similar to hungry nestlings).

Trials were conducted between 24 May and 14 June 2006. Only broods of two were included in the experiment. Each nest received control and begging treatments in randomly assigned order (5 nests received the begging calls first, 6 received them second). We attached Sony headphones (frequency response: 18–22 000 Hz) to the trunk of the nest tree (15–16 cm below the nest) and connected them to a 15 m cable and CD player. A Sony CCD-TRV328 video camcorder was hidden and placed 3–5 m away from the nest to record behaviours.

Trials began between 0800 and 0830 hours. After initial set up, we waited 30 min before beginning the trial to reduce any residual disturbance. To begin a trial, we broadcast 2 h of begging calls or white noise (control), then changed the camcorder videotape. To minimize carryover effects from the first treatment, we included a 1 h period of no playback, followed by 2 h of either begging or white noise (depending on treatment order). At the end of the experiment, nestlings were weighed (mass to nearest 0.1 g). Relative nestling mass within a brood was used as the measure of chick size (larger or smaller). Relative nestling mass tended to remain consistent across the nestling period (in 13 of 15 cases where siblings were weighed on hatch day and 2 days prior to fledging, the larger nestling remained larger). Therefore, we expected that relative mass would remain consistent over the short-term period of the experiment.

Video analyses

We observed six behavioural traits on videotape: (1) the rate of feeding visits by each parent; (2) food load; (3) which nestling was fed; (4) prey type; (5) begging behaviours of nestlings; and (6) the position of nestlings relative to parents. The observers watching the videotapes were blind to nestling size. Prey type was identified (to insect order) from the videotapes by using diagnostic characteristics. We determined food load by comparing the length and depth of the prey with the length and depth of the bill of the adult bird with prey. Two measures of begging display were taken: which nestling begged highest (i.e. had the highest vertical position upon arrival of the parent to the nest with prey) and which was the first to beg. These measures were used because they are correlated with hunger level (with the one begging the highest and begging first being food deprived) and preferential feeding by parents (Price & Ydenberg 1995; Leonard & Horn 1996; Leonard et al. 2003; Whittingham et al. 2003). Furthermore, in a related study where nests were videotaped throughout the nestling period, parents preferentially fed nestlings that begged highest in the nest and that begged first (C. E. Tarwater, unpublished data). Because we were only interested in preferential feeding by parents, we examined relative differences in begging intensity between siblings within a nest. These two begging measures were typically coincident (binary similarity coefficient = 0.91, the nestling that begged the highest was the first individual to beg in 91% of feeding visits). Therefore, we used only 'begging highest' as the begging behaviour in the analysis. The highest-begging nestling is not necessarily closer to the parent, but rather reaches the highest above the nest rim, stretching its neck to try to obtain food.

To evaluate which nestling was closest to the feeding parent, the nest was split into quadrants. When a parent arrived at the nest with food, the closest nestling was the one in the same or closest quadrant to the one the parent was feeding from. Which nestling was closer was used as a measure of competitive ability because studies indicate that this nestling outcompetes its siblings for this position (McRae et al. 1993; Kacelnik et al. 1995). We determined the gender of parents based on sexual dichromatism in plumage colour. On the day that begging calls were recorded, both nestlings were randomly marked with different colours of acrylic paint on the top of their heads for individual identification.

Statistical analyses

We used repeated measures ANOVA to determine whether parent sex or treatment order influenced provisioning rates during begging and control treatments. We also used repeated measures ANOVA (with parent sex as a nested factor) to determine whether provisioning rate, food load and total amount of food brought to the nest differed between treatments. We modeled parent sex as a nested factor within each nest because feeding behaviours of male and female parents are not independent and we were not interested in parent sex alone as a factor (only as an interaction). We calculated the total amount of food brought by summing the prey load per trip across all feeding trips to the nest. We used a chi-square exact test to compare the proportion of prey items brought to the nest between treatments. We compared differences between parents in feeding preferences and changes in provisioning rates to particular nestlings between the two treatments using Wilcoxon signed-ranked tests or paired *t* tests (depending on whether the factors were normally distributed). This test examined whether parental preferences for a particular offspring changed between treatments. We also tested whether parents preferred a particular individual, irrespective of treatment. We compared the allocation of food to particular nestlings to that predicted based on random allocation of food (50% for a brood of two) using one-sample *t* tests. Sample sizes varied for tests because we were unable to observe the size of the prey or the individual nestlings' begging in some nests.

We calculated effect sizes (Cohen's *d*) for nonsignificant statistical tests to determine whether small sample sizes resulted in incorrectly not rejecting the null hypothesis. We used the methods recommended by Nakagawa & Cuthill (2007) and Dunlop et al. (1996) for paired tests and nonparametric data. Nonparametric data were ranked (to normalize data) and then effect sizes were calculated based on the ranked data (Nakagawa & Cuthill 2007). We calculated repeated measures ANOVA effect sizes using partial eta-square (Bakeman 2005). We followed the guidelines of Cohen (1988) for classifying effect sizes as small (0.25), medium (0.5), or large (0.8). For example, a 'large' effect size suggests that the effect of the treatment versus the control is substantial. Debate exists over how to calculate effect sizes for nonparametric data and for repeated measures data (Nakagawa & Cuthill 2007), thus we only report the broader classifications of small, medium and large (rather than giving exact *d* values).

RESULTS

Provisioning rates

In 10 of 11 nests, parents increased the number of feeding visits to the nest during the playback of begging calls compared to the control (RM-ANOVA: treatment effect: $F_{1,21}$= 19.1, $P < 0.001$; Fig. 5.1). Males and females did not differ in their response to the playback of begging calls (RM-ANOVA: sex x treatment interaction: $F_{1,21}$= 0.0, $P = 1.0$, d = small; Fig. 5.1). Order of treatment (whether the begging calls were played first or second) had no effect on response (RM-ANOVA: order x treatment interaction: $F_{1,21}$= 0.04, $P = 0.85$, d = small).

Despite continuous playback of begging calls during the begging treatment, the visual display of nestling begging did not differ between the two treatments. We compared the proportion of visits without the begging display (by either nestling) out of the total number of feeding visits in the treatment versus control and found no difference (begging: 0.0 (always begged); control: 0.008 (begged every time except for once); Wilcoxon signed-ranks test: T = 1.00, N =11, $P = 0.32$).

Food load and total amount of food brought

The average food load size was smaller during the begging treatment than during the control (mean ± SE: begging treatment: 0.91±0.11; control: 1.4±0.21; RM-ANOVA: treatment effect: $F_{1,18}$= 5.65, $P = 0.04$). Changes in food load between the two treatments tended to differ (based on the medium effect size) depending on the sex of the parent (RM-ANOVA: sex x treatment interaction: $F_{8,18}$ = 2.06, $P = 0.14$). Females did not change their food load (paired t test: t_9 = -1.25, $P = 0.24$), however, males did decrease their food load during the begging treatment (paired t test: t_8 = -2.16, $P = 0.06$). In general, males provided larger prey items during the control (1.72±0.57) than females (1.11±0.24) and they provided equal-sized prey during the begging treatment (males: 0.97±0.32; females: 0.86±0.27). The total amount of food brought to nestlings did not differ between treatments (mean ± SE sum of food brought per parent: begging treatment: 4.36 ± 0.66; control: 3.90 ± 0.69; RM-ANOVA: treatment effect: $F_{1,19} = 0.79$, $P = 0.40$, d = small).

Prey type

We were able to classify 44.9% of the total prey items delivered during the begging treatment and 43.6% during the control. Although the smallest prey were less likely to be classified, this was true across both treatments. The most common prey types were the same during both treatments (caterpillars, spiders and katydids). Although the proportions of these prey types differed slightly, overall offspring were not fed different prey during the two treatments (chi-square test: $\chi^2_3 = 5.102$, $N = 68$, $P = 0.18$; Table 5.1).

Allocation of feeding within the brood

Parents did not change the relative proportion of feeding visits to the heavier nestling between the control and begging treatments (both sexes combined; Wilcoxon signed-ranks test: T = 6, $N = 7$, $P = 0.87$, d = small; Fig. 5.2). We observed no overall feeding preference by nestling size during either treatment (Table 5.2). Although not significant, based on a large effect size, parents tended to differ in their feeding preferences based on offspring size (Wilcoxon signed-ranks tests: T = 4, $N = 14$, $P = 0.11$, d = large). Males tended to favour the larger nestling (63.3% of males' total feeding visits went to the heavier nestling) and females tended to favour the lighter nestling (58.3% of females' total feeding visits went to the lighter nestling).

Instead of nestling mass, parents may use begging intensity to allocate food. Parents preferentially fed the nestling begging the highest in both treatments (Table 5.2), but this preference did not differ between treatments (paired *t* test: $t_8 = -0.31$, $P = 0.77$; *d* = small; Fig. 5.2). Males and females did not differ in their preference for the highest-begging nestling (Wilcoxon signed-ranks test: $Z = 0.105$, $N = 20$, $P = 0.92$, *d* = small). Although we observed that the nestling that begged the highest was not more frequently the smaller nestling (one-sample *t* test: $t_6 = 1.89$, $P = 0.11$, *d* = medium), the effect size suggested that there was a tendency for the smaller nestling to beg highest (mean ± SE number of cases = 69.1±10.1%) more frequently than the larger nestling.

Although not statistically significant, based on a medium effect size, parents tended to switch preferences to favour the closest nestling in the begging treatment (paired *t* test: $t_{10} = 1.33$, $P = 0.21$; Fig. 5.2). Moreover, parents fed the closest nestling more frequently than expected during the begging treatment, but not during the control (Table 5.2). Male and female parents did not differ in their feeding preference based on nestling position (paired *t* test: $t_{10} = 0.76$, $P = 0.47$, *d* = small). We examined whether position in the nest was associated with nestling mass or begging behaviour. Across both treatments, the closer nestling was not the larger nestling more frequently than expected (one-sample *t* test: $t_6 = -0.37$, $P = 0.72$, *d* = small), nor did the closer nestling beg higher more frequently than expected (one-sample *t* test: $t_{10} = 0.51$, $P = 0.62$, *d* = small). Similarly, the nestlings did not appear to change their behaviours between treatments. The closer nestling was not the highest-begging nestling more frequently in the begging treatment compared to the control (Wilcoxon signed-ranks test: $Z = -0.73$, $N = 20$, $P = 0.46$, *d* = small).

The average time that parents spent at the nest did not differ between treatments (Wilcoxon signed-ranks test: T= 15, $N = 11$, $P = 0.93$, *d* = small). Nevertheless, based on marginal significance and a large effect size, the time between parent arrival to the nest and feeding of nestlings was reduced in the begging treatment (mean ± SE: 6.8±4.3 s) compared to the control (14.8±10.9 s) (paired *t* test: $t_{10} = -2.0$, $P = 0.07$, d = large).

DISCUSSION

We observed that slaty antshrike parents increased provisioning rates but decreased food load in response to experimentally increased begging by offspring. This resulted in a constant amount of food being brought to the nest. In response to elevated begging, parents did not change the distribution of food within the brood based on nestling mass or begging height; however, parents did switch to preferentially feed the closest offspring.

Increased provisioning in response to elevated begging

Environmental conditions, such as nest predation, may influence parental response to offspring need. Increased provisioning rates or elevated begging sounds can attract predators to nests (Haskell 1994; Dearborn 1999; Martin et al. 2000a; Muchai & du Plessis 2005). We predicted that, in a high predation environment, provisioning rate would not change and that food load would increase in response to elevated begging. This would satiate nestlings, without increasing nest activity. Instead, we observed that provisioning rate increased and food load decreased. Several factors may explain our observations. First, selection to reduce the probability of starvation may be greater than selection to reduce risk of nest predation. In general, begging is considered an honest signal of need (Smith & Montgomerie 1991; Mondloch 1995; Villasenor & Drummond 2007). Thus, by immediately responding to begging, parents may avoid long-term negative consequences (i.e. decreased condition, developmental problems, reduced survival probability) on offspring if they do not respond (Lifjeld 1988). Second, nest predation may not increase with the level of response in provisioning rate we observed. A clutch manipulation experiment (in the same location as this study) found that nest predation did not increase when parents fed an additional nestling (Styrsky et al. 2005).

Third, in our study location, begging calls may place nests at a greater risk of predation than does increased feeding rates because parents in our study responded quickly to reduce begging. Predator type, nest location, and cues that predators use to locate nests determine whether begging calls or provisioning trips place nests at greater risk of predation. Although a diverse suite of nest predators have been observed in our study site (Robinson & Robinson 2001; Tarwater 2008), it is not yet known which nest predators are the most common (and thus whether visual or auditory cues are more important). The intensity of begging vocalizations varies with hunger level (Leonard & Horn 2001). Therefore, even though increased provisioning rates by parents probably do not satiate nestlings (because the total amount of food did not increase), the loudness of begging may be reduced, subsequently reducing risk of nest predation. Parents altered their behaviour under elevated begging conditions in other ways as well. Upon arrival to the nest with food, parents fed nestlings more rapidly in the begging treatment compared to the control. Parents did not use this behaviour to reduce the amount of total time at the nest (which would be beneficial when provisioning rates are increased). Instead, this tactic may be used to reduce begging sounds (and thus predation risk), because begging remains intense until offspring are fed (and until parents no longer have food). Experimental studies are needed to determine the effect of begging sounds versus provisioning rates on nest predation risk.

Similar to other studies, we found that increased provisioning rate was negatively correlated with prey size (Tinbergen 1981; Lifjeld 1988; Grieco 2001). Higher provisioning rates reduce the time available for foraging; and parents may reduce this time by shifting to foraging sites closer to the nest (frequently containing prey of smaller size; Whittingham &

Robertson 1993; Naef-Daenzer et al. 2000), or switching to smaller prey items to reduce handling time (Houston 1985). Concurrently, increased provisioning rates may reduce selectivity in prey type (Tinbergen 1981; Lifjeld 1988); however, we observed no change in prey types between treatments. In antshrikes, prey distribution may be such that parents are unable to increase food load. Antshrike males (which initially had a higher food load) reduced their food load between the control and begging treatments more than females. This finding supports a constraint on foraging. Overall, when offspring beg more, parents work harder to increase provisioning rates, offspring work harder to beg more, and both parents and offspring increase risks to themselves. Yet these costs are apparently not offset by an increase in benefits (more food is not brought to the nest) owing to the foraging constraint on parents. This constraint may be one factor limiting the evolution of runaway begging.

Allocation of food to particular nestlings

When faced with hungry nestlings, adults are predicted to switch to feeding the nestling with the greatest marginal fitness returns or with a greater reproductive value to parents (Smith & Fretwell 1974; Winkler 1987; Godfray 1991, 1995). During the begging treatment, male and female antshrikes switched to preferentially feed the closest nestling. Parents may have switched to the closer nestling as a mechanism for reducing the amount of time between arrival to the nest and feeding of a nestling, and they may have chosen to feed the nestling that was able to occupy the closer position (Ryden & Bengtsson 1980; McRae et al. 1993; Kilner 1995). In some species, the closer nestling is able to outcompete its siblings because it is larger or has a greater need for food (and is willing to expend more effort to occupy the position) (Kacelnik et al. 1995; Kolliker et al. 1998; Whittingham et al. 2003). In these cases, parents use the outcome of sibling competition to determine which nestling to feed (Kilner 2002; Whittingham et al. 2003). The offspring in our study did not appear to change their behaviour between treatments; however, the parents' behaviour changed during the begging treatment to favour the closer nestling. Antshrike parents primarily fed from two quadrants on the nest rim (in 89% of feedings), giving nestlings the opportunity to monopolize these positions. Ability to obtain the better position was not a result of relative sibling size. Differences in competitive ability based on size are unlikely because of the small size difference between siblings (mean ± SE percentage difference in body mass 2–3 days before fledging: 7.2±0.6%, *N*=78 broods). Further experimentation is required to determine whether the closer nestling in antshrike nests has a greater need for food (and thus is more motivated to fight for this spot) or is the dominant sibling (due to factors other than size).

Parents did not preferentially feed larger or smaller nestlings, possibly because small differences between nestlings in body mass do not lead to differences in reproductive value. Alternatively, both parents may not have switched to prefer the same-sized nestling because this may affect brood division. Brood division begins when offspring are close to fledging and the associations formed between a parent and an individual offspring in the nestling period are often maintained throughout the postfledging period (Tarwater & Brawn 2008). Parent antshrikes appeared to have the same feeding preferences (favouring the highest-begging nestling in both treatments and the closest nestling under elevated begging); however, male and female parents also had preferences for offspring of different sizes (in both treatments): we observed males feeding larger nestlings and females feeding smaller ones. These results seem counter to one another and one potential explanation is that offspring may beg differently depending upon the parent. Differential begging may occur if offspring play a role in brood division, which appears to be true after fledging (Tarwater & Brawn 2008). Parents may also have multiple decision rules about which nestlings to feed (Kilner 1995; Leonard et al. 2003). For example, under elevated begging, parents used a combination of cues: allocating food towards the highest-begging nestlings, the closest nestlings, and nestlings of a particular size. Parental provisioning decisions may depend upon an integration of nestling behaviours. For example, when nestlings are begging at the same height, or the closest nestling is not begging, females may then favour the smaller nestling, and males the larger one. Using multiple cues and differential feeding by parents may result in equitable feeding for offspring (Kolliker et al. 1998; Kilner 2002).

Influence of predation threat on magnitude of response

Nest predation is predicted to influence the magnitude of parental response to begging (Zahavi 1977; Price 1998). To our knowledge, only three studies have compared ecological factors as possible reasons for different parental responses to begging (Burford et al. 1998; Clark & Lee 1998; Price 1998). The magnitude of parental response in our study population of antshrikes (78% increase) was greater than that found by Burford et al. (1998) (37% increase) and Clark & Lee (1998) (no increase) for red-winged blackbirds, *Agelaius phoeniceus*, and similar to that found by Price (1998) (approximately doubled) for yellow-headed blackbirds, *Xanthocephalus xanthocephalus*. In these three studies, nest predation was approximately the same (34–40%). Price (1998) attributed the high level of parental response (compared to the other two studies) to studying a species that is single-brooded, has higher nest predation (40%) and higher starvation risk (all three factors are predicted to increase response). In slaty antshrikes, except for the high risk of nest predation (78.8% in this study), other factors are predicted to lead to a low response. Threat of starvation appears low (C. E. Tarwater, unpublished data), and many breeding pairs attempt second nests after a first successful brood (Tarwater & Brawn 2008). Yet, antshrikes appear to be on the upper end of the range in responses. This suggests that high nest predation may have a disproportionate effect on the magnitude of response to begging. Comparative studies using the same methodologies in different environments are essential to examine how these ecological factors interact to influence parental response to begging.

In conclusion, although slaty antshrike parents increased feeding rates in response to begging, greater begging did not increase the amount of food given to offspring. This study stresses the importance of measuring food load because of the implications for the costs and benefits of begging. Our study is among the few demonstrating a change in food allocation to favour the closer nestling under increased begging. In addition to a high magnitude of response to begging, antshrike parents appeared to use a different strategy (which as far as we know has not been tested in other species) that may be in response to a high predation environment. Parents reduced the time between arrival to the nest and feeding of nestlings, potentially reducing begging sounds and thus predation risk. Our results suggest that environmental conditions (predation and prey location/type) influence parental response to offspring begging and that parents use multiple cues to decide how to allocate food within the brood.

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FIGURES AND TABLES

Table 5.1 Relative percentages of the four prey types most frequently brought to nests by antshrike parents during the begging and control treatments

	Treatment	
Prey type	Control	Begging
Katydids	16.7	36.4
Caterpillars	25.0	18.2
Spiders	26.2	15.9
Beetles	4.2	13.6

Other prey types made up less than 5% of prey items delivered.

Table 5.2 Percentage of feeding visits by antshrike parents to the nestling that was heaviest, highest in the nest begging and closest to the feeding parent during each treatment compared to an expected value of 50% (based on random allocation of feeding offspring in broods of two)

	Beg treatment				Control treatment			
Preferred offspring	%Feeding visits	*t*	*df*	*P*	%Feeding visits	*T*	*df*	*P*
Heaviest	47.6	0.515	6	0.63	50.9	0.097	6	0.93
Highest	64.5	3.27	10	**0.01**	69.3	3.69	8	**0.001**
Closest	62.3	2.19	10	**0.053**	49.9	-0.01	10	1.0

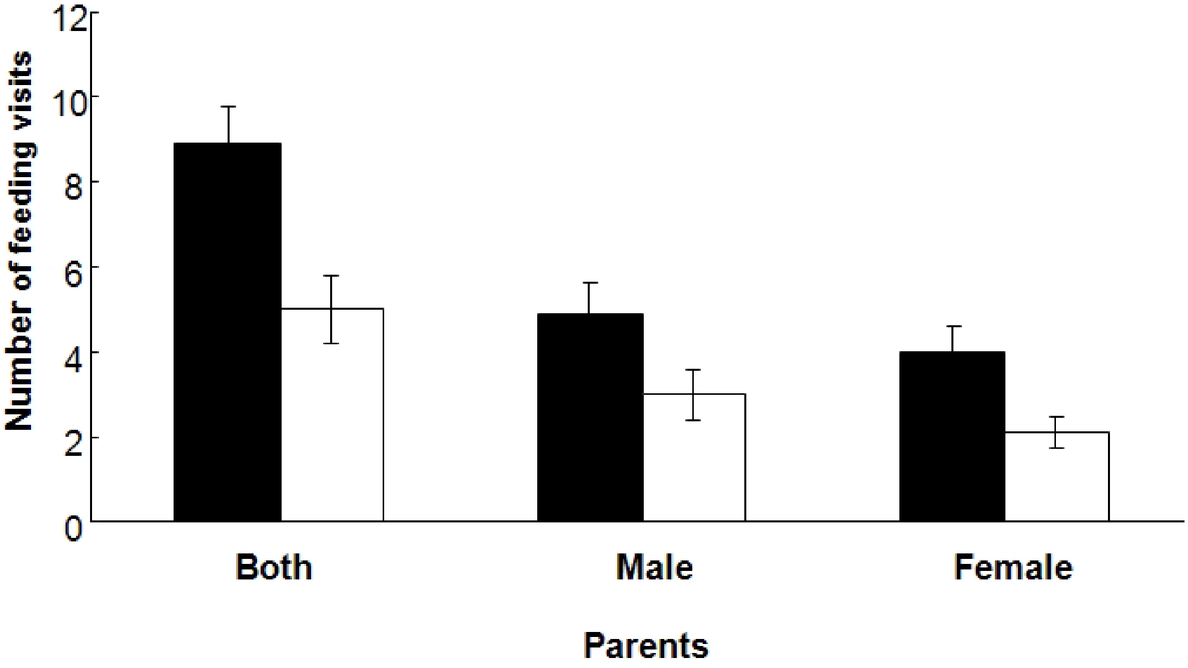

Figure 5.1 Mean ± SE number of parental feeding visits by male and female antshrikes, separately and combined, to 11 nests during the begging (black bars) and control (open bars) treatments.

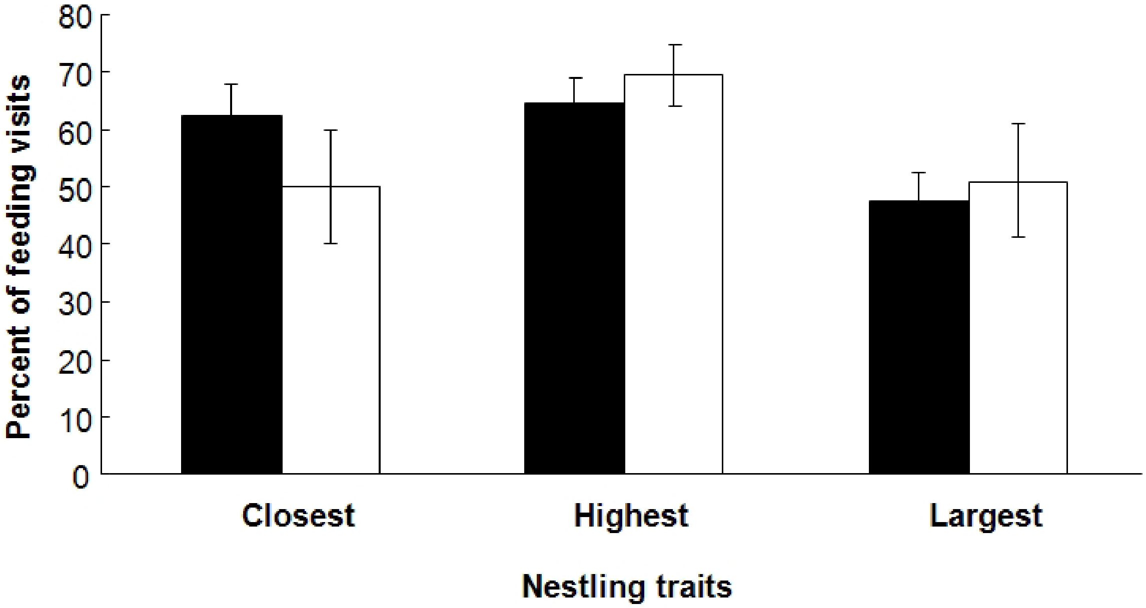

Figure 5.2 Mean ± SE percentage of feeding visits (out of the total number of feeding visits) to the nestling that was closest to the feeding parent (*N*=11), highest begging (*N*=11) and largest (*N*=7) in the nest during the begging treatment (black bars) and the control treatment (open bars).

CURRICULUM VITAE

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EDUCATION

Ph.D. **University of Illinois at Urbana-Champaign** (UIUC), 2010
Program in Ecology, Evolution, and Conservation Biology (PEEC), Advisor: Jeff Brawn. Title: The pre-reproductive period in a tropical bird: parental care, dispersal, survival, and avian life histories

M.S. **University of Illinois at Urbana-Champaign**, 2006
Department of Natural Resources and Environmental Sciences, Advisor: Jeff Brawn. Title: Brood division and inflexible behavior in a neotropical passerine

B.S. **University of California at Davis**, 1999
Department of Wildlife, Fish, and Conservation Biology, with wildlife emphasis. Advisor: John Eadie

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PUBLICATIONS

IN PRINT/IN PRESS

Tarwater C.E., and J.D. Brawn. 2010. The post-fledging period in a tropical bird: patterns of parental care and survival. Journal of Avian Biology. *In press*.

Tarwater C.E., and J.D. Brawn. 2010. Family living in a neotropical bird; variation in timing of dispersal and higher survival for delayed dispersers. Animal Behaviour. *In press.*

Brawn J.D., G. Angehr, N. Davros, W.D. Robinson, J. Styrsky, and **C.E. Tarwater**. 2010. Sources of variation in the nesting success of understory tropical birds. Journal of Avian Biology. *In press.*

D.W. Robinson, M. Hau, K.C. Klasing, M. Wikelski, J.D. Brawn, S.H. Austin, **C.E. Tarwater**, and R. E. Ricklefs. 2010. Diversification of life histories in New World birds. Auk 121:1-10.

Tarwater C.E., J.P. Kelley, and J.D. Brawn. 2009. Parental response to elevated begging in a high predation, tropical environment. Animal Behaviour 78:1239-1245.

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Tarwater C.E. 2008. Predators at nests of the Western Slaty Antshrike. Wilson Journal of Ornithology 120:620-624.

AWARDS & FELLOWSHIPS

2009-2010	Scott Dissertation Completion Fellowship, UIUC	$20,000 (+ tuition waiver)
2009, 06, 05	Graduate College Conference Travel Grants (3 awarded), UIUC	$1050

2009, 2006	Incomplete List of Teachers Ranked as Excellent by their Students (2 awarded), UIUC	
2008	Clark Summer Research Grant	$3000
2008	Conference travel grant, American Ornithologists' Union	$250
2007	Ernst Mayr Fellowship, Smithsonian Tropical Research Institute (awarded to the best short-term fellowship candidate of the year)	$3880
2007	Animal Behavior Society Student Research Grants	$1000
2007	Joseph Grinnell Student Research Award, Cooper Ornithological Society	$1000
2007	Louis Agassiz Fuertes Award, Wilson Journal of Ornithology	$2500
2007, 2006	PEEC Summer Research Grant (2 awarded), UIUC	$2000
2006	Alexander Wilson Prize for Best Student Presentation, North American Ornithologists' Conference	$300
2006	PEEC Travel Grants (2 awarded), UIUC	$300
2002-2004	Jonathan Baldwin Turner Fellowship (for M.S.), UIUC	$15,000/year (+ tuition waiver)
1999	Graduated Highest Honors, University of California at Davis	
1998	Elected to Phi Kappa Phi at UC Davis	

TEACHING EXPERIENCE

University of Illinois at Urbana-Champaign

2009	Organismal and Evolutionary Biology, IB 105: 3 discussions (20 students/ discussion).
2006	Ecology, IB 203: 2 field labs (16 students/ lab).
2003	Environmental Sciences, IB 105: Lecture T.A. Presented one lecture.

University of California at Davis

1999	Ornithology: Undergraduate T.A. 1 lab (30 students/ lab).
1996	Introductory Biology: Undergraduate T.A. 1 lab (25 students/ lab).

OUTREACH

2010, 2008	Three 2nd grade classes at elementary school in South Lake Tahoe Unified School District, South Lake Tahoe, CA; lectured for 45 minutes to 60 students on tropical forests, predators of birds and nests, and parental care.
2009	Panama field course with Michigan State University; lectured to students, conducted song experiment in field, analyzed data, and discussed conclusions over 2 day period.
2009	Field course for one high school class in Panama City, Panama; captured birds using mist-nets and lectured on communication in birds for 2 hour period.
2003-2008	I had 16 assistants help with my research, including eleven females and five long-term assistants from Panama.

PRESENTATIONS AT PROFESSIONAL MEETINGS

PAPERS

2010	**Tarwater C.E.**, and J.D. Brawn. Pre-reproductive survival and the factors influencing survival in a tropical passerine bird. American Ornithologists' Union Conference, San Diego, CA.

2009 **Tarwater C.E**., and J.D. Brawn. High juvenile survival and delayed age at maturity in a tropical bird. American Ornithologists' Union Conference, Philadelphia, PA.

2009 Kelley J.P., and **C.E. Tarwater**. Song as an indicator of age in tropical suboscine birds: implications towards studies of demography, sexual selection, and parental care. American Ornithologists' Union Conference, Philadelphia, PA.

2008 **Tarwater C.E**., and J.D. Brawn. Patterns and consequences of natal dispersal in a neotropical passerine: the western slaty antshrike. American Ornithologists' Union Conference, Portland, OR.

2007 **Tarwater C.E**. Life history implications of the post-fledging period in a neotropical passerine. Smithsonian Tropical Research Institute Graduate Student Symposium, Panama City, Panama.

2006 **Tarwater C.E**., and J.D. Brawn. Life history implications of the post-fledging period in a neotropical passerine. North American Ornithological Conference, Veracruz, Mexico.

2006 **Tarwater C.E**., and J.D. Brawn. Ecology of lowland forest birds: results of long- and short-term studies. Smithsonian Tropical Research Institute Symposium, Panama City, Panama.

2006 **Tarwater C.E**. Brood division and stereotyped behavior in a neotropical passerine. University of Illinois Graduate Student Symposium, Urbana, IL.

2005 **Tarwater C.E.** Brood division in a neotropical passerine. University of Illinois, Program in Ecology, Evolution, and Conservation Biology Seminar Series, Urbana, IL.

2004 **Tarwater C.E.** Brood division in a neotropical passerine: the Western Slaty Antshrike. University of Illinois, Department of Natural Resources and Environmental Sciences Graduate Student Symposium, Urbana, IL.

POSTERS

2005 **Tarwater C.E**., and J.D. Brawn. Brood division during the nestling and post-fledging periods in a neotropical passerine. American Ornithologists' Union Conference, Santa Barbara, CA.

PROFESSIONAL ACTIVITIES

Invited Reviewer for: Ecology, Wilson Journal of Ornithology, American Naturalist

Service: Student representative on entrance committee for PEEC, Judge for Graduate Students in Ecology and Evolutionary Biology Symposium, Master's field advisor for Panamanian student, Ph.D. co-advisor for Panamanian student

Member: American Ornithologists' Union (2004-present), Animal Behavior Society (2004-present), Wilson Ornithological Society (2004-present), Ecological Society of America (2004-present)

PROFESSIONAL EXPERIENCE

2001-2002 **Wildlife Technician**, **U.S. Geological Survey, Biological Resources Division**, Vallejo, CA. How the feeding preferences of diving ducks influence heavy metal contamination and the role of the introduced Asian clam. Migration of shorebirds and white-fronted geese.

2001	**Project Leader**, **Sloat Consulting**, Fall River, CA. Surveys of the declining Northern Goshawk.
2001	**Faculty Research Assistant, Cooperative Wildlife and Fisheries Research Unit, Oregon State University**, Corvallis, OR. The effects of dams on migration and stress of Chinook salmon and steelhead.
2000	**Volunteer Assistant, Bookmark Biosphere Reserve**, Renmark, Australia. The effects of invasive species on native species diversity and abundance.
1999	**Research Assistant, Department of Wildlife, Fish, and Conservation Biology, UC Davis**, Davis, CA. Nesting success, movement, and demography of the declining American wood ducks.
1999	**Field Assistant, Department of Land, Air, and Water Resources, UC Davis**, Davis, CA. Testing what irrigation practices yield the most return and increase water efficiency.
1998	**Laboratory Research Assistant, Department of Wildlife, Fish, and Conservation Biology, UC Davis**, Davis, CA. Investigate whether changes in the vegetation due to management practices of Suisun Marsh has lead to a decline in waterfowl populations.
1998	**Volunteer Field Assistant**, **Department of Wildlife, Fish, and Conservation Biology, UC Davis**, Davis, CA. Pre-survey of the abundance and diversity of small mammals to investigate the changes in small mammal populations with different forest management treatments.