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SEX-SPECIFIC INVESTMENT IN INCUBATION AND THE REPRODUCTIVE  
BIOLOGY OF TWO TROPICAL ANTBIRD SPECIES

by

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B.S., The University of Montana, 2005

Presented in partial fulfillment of the  
requirements for the degree of

Master of Science

The University of Montana

May 2008

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Date

Sex-specific investment in incubation and the reproductive biology of two tropical  
antbird species

Chair: Thomas E. Martin

Paternal care has been neglected in behavioral studies because it is rare among most animals. Birds express wide variation in male care across a broad life-history gradient, but such variation among species remains poorly explored. At the same time, contributions of male assistance with incubation have been largely overlooked with the assumption that incubation is a time of low parental energy expenditure. We compared male versus female biparental incubation effort between two tropical antbird species in the northern Andes of Venezuela. We found that males and females apportion reproductive effort differently between these two species, but that male contributions of time and incubation effort were generally greater than for north temperate species which exhibit different life-history strategies. Males spent an equal or greater amount of time incubating, yet maintained lower egg temperatures than females during different age-specific stages of the incubation period. Despite sex differences in incubation temperatures, males rewarmed cold clutches at similar rates to females suggesting similar sex-specific physiological incubation abilities. For the first time in a nidicolous species, we found that temperatures experienced by developing embryos increased with age of eggs independent of male and female time spent on the nest. Our results suggest that males may benefit embryo development by minimizing time eggs experience cold temperatures during female absences, and concurrently benefit female physiological condition for future nesting efforts. Lastly, we report standardized measures of reproductive traits in these two endemic tropical species in hope of improving data collection efforts outside of North America. Standardized measures of reproductive traits are essential for improving our understanding of reproductive biology and avian life-history evolution among different regions of the world. The Tropical Andes are among one of the most species-rich areas in the world and represent an area of critical conservation concern. Yet, for many endemic taxa inhabiting this region even basic descriptions of reproductive traits are entirely absent. This study extends the range of variation in reproductive strategies among a broader range of species among geographical regions.

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## **CHAPTER 1**

**SEX-SPECIFIC INVESTMENT IN BIPARENTAL INCUBATION: COMPARISONS**

**BETWEEN TWO TROPICAL ANTBIRD SPECIES**

## **Abstract**

Paternal care has been neglected in behavioral studies because it is rare among most animals. Birds express wide variation in male care across a broad life-history gradient, but such variation among species remains poorly explored. Previous studies have primarily focused on male contributions to chick-provisioning with only four studies examining male assistance during incubation, all of which in north temperate species which differ in their life-history strategies from the majority of species of the world. We compared male versus female incubation effort between two tropical antbird species. We found that males and females apportion reproductive effort differently between these two species, but that male contributions of time and effort were generally greater than for north temperate species. Males spent an equal or greater amount of time incubating, yet maintained lower egg temperatures than females during parts of the incubation period. Nonetheless, males rewarmed cold clutches at similar rates to females suggesting similar physiological incubation abilities. Interestingly, males and females in both species increased the temperature at which they incubated eggs independent of time spent on the nest as embryos approached hatching. These results suggest males may benefit embryo development by minimizing time eggs experience cold temperatures during female absences, and concurrently benefit female physiological condition for future nesting efforts. This study extends the range of variation in paternal care strategies among a broader range of species among geographical regions of the world.



## **Introduction**

Parental behaviors that increase offspring survival are favored in the evolution of parental care strategies, which vary extensively among taxa (Clutton-Brock 1991). The relative degree of male versus female involvement in parental care presumably stems from balancing offspring care against other means of enhancing fitness (Trivers 1972, Maynard Smith 1977, Roff 1992). Yet, parental roles of males have received much less attention than for females because male care is rare or entirely absent in most animal taxa (Clutton-Brock 1991). As a result, the full range of variation in the type and magnitude of male care strategies exhibited among species remains unclear.

Birds comprise an excellent group in which to investigate sex-specific investment and hence the relative degree of male versus female involvement in parental care. More than 95% of all bird species exhibit biparental care (Lack 1968; Cockburn 2006), with both male and female partners typically providing substantial levels of parental effort. Nevertheless, even within birds, considerable variation remains unexplored in the type and magnitude of male allocations to reproduction.

Within birds exhibiting biparental care, males commonly feed young but are less frequently involved in incubating eggs (Silver et al. 1985; Ketterson and Nolan 1994). Previous studies of male care have thus largely focused on the nestling stage. Indeed, male assistance in feeding young results in clear fitness benefits for offspring (Martin 1987; Bart and Tornes 1989). However, male assistance during the incubation stage remains largely unknown (Ketterson and Nolan 1994; Whittingham and Dunn 2001)

Incubation is an energetically costly form of parental care that can convey large fitness consequences to both adults and offspring (Bryan and Bryant 1999; Reid et al.

2000; Reid et al. 2002b; Visser and Lessels 2001). Incubating parents must resolve a trade-off between time and energy necessary for warming eggs versus time off the nest to forage and replenish energy stores (White and Kinney 1974; Haftorn 1988). Extended parental absences result in low egg temperatures that reduce hatching success, offspring quality and negatively influence the duration of incubation (Lyon and Montgomerie 1985; Webb 1987; Martin 2002; Hepp et al. 2006; Olson et al. 2006; Martin et al. 2007). Thus, males that share incubation duties with females (biparental incubation) have the potential to minimize time eggs experience cold temperatures during female absences and simultaneously benefit female physiological condition for future breeding efforts. Yet, increased male assistance during this stage may yield negative consequences for embryos and reproductive success (Kleindorfer et al. 1995; Bartlett et al. 2005).

The few studies that have examined sex-specific roles during biparental incubation found males did indeed increase minimum temperatures experienced by eggs during female absences in four north temperate species, yet males in these species spent less time on the nest and maintained eggs at substantially colder temperatures than females (Kleindorfer et al. 1995, Reid et al. 2002a, Bartlett et al. 2005) In contrast, males incubated eggs at higher temperatures and spent equal amounts of time on the nest compared with females in the only study a southern hemisphere passerine (Auer et al. 2007). Tropical and southern hemisphere species exhibit life history strategies that differ from north temperate species (Moreau 1944, Yom-Tov 1987, Yom-Tov et al. 1994, Martin 1996, Martin et al. 2000b, Martin 2004) and, therefore, might be expected to differ in the relative roles of males versus females in species exhibiting biparental incubation. Furthermore, tropical birds are unique in that entire taxonomic families (e.g.

Eurylaimidae, Furnariidae, Dendrocolaptidae, Formicariidae, and Thamnophilidae) may exhibit biparental incubation (Skutch 1949, 1969, 1996; Willis 1967, 1972; Zimmer and Isler 2003), but the degree to which males versus females divide reproductive time and energy in representatives of such families is unstudied and remains a critical gap in our knowledge of the full range of variation in biparentalpaternal care strategies (Kunkel 1974; Martin 2004).

In this study, we examined sex differences in incubation effort between two tropical Thamnophilidae (typical antbirds) species that are ecologically similar (i.e. overlapping territories and breeding seasons, foraging repertoires and nest site placement). Thamnophilidae is a large clade of more than 190 species endemic to the Neotropics, and all species reported thus far exhibit biparental incubation (Skutch 1996). We addressed four questions with respect to sex-specific parental effort and incubation effectiveness in these species: 1) Do males and females share nest attentiveness (% of daytime spent on the nest) equally? 2) Do temperatures experienced by developing embryos differ between male and female parents? 3) Do these two related and ecologically similar species exhibit similar patterns of male and female parental effort? and 4) Does male and female parental effort change with age of the embryo?

## **Methods**

### *Study Area and Species*

We examined sex differences in incubation behavior in the Slaty Antwren (*Myrmotherula schisticolor*) and the Plain Antvireo (*Dysithamnus mentalis*) in a tropical cloud forest in the northern Andes of Venezuela (9° N). The study area consisted of

primarily mature and some secondary vegetation with a mean annual precipitation of over 2000mm (for further description see Martin et al. 2006; Fierro-Calderón and Martin 2007).

Incubating parents regulate heat delivered to eggs by adjusting metabolic rates and shunting blood flow to brood patches (Drent 1975; Haftorn and Reinertesen 1982). Mist-netting (2003-2007) showed that sexes did not differ within species in brood patch size or adult mass (Chapter 2). Plain Antvireos ( $15.4 \pm 0.22\text{g}$ ,  $n = 44$ ) were larger than Slaty Antwrens ( $9.8 \pm 13\text{g}$ ,  $n = 89$ ) but they had similar incubation periods ( $16.0 \pm 0.80$  d,  $n = 6$  versus  $15.7 \pm 0.89$  d,  $n = 12$ ; respectively). Sexes in both species are dimorphic in plumage, which allowed accurate behavioral determinations of sex-specific parental behavior.

We searched 10 study plots (~ 600 ha) divided along an elevational gradient (1350-2000m) for Slaty Antwren and Plain Antvireo nests during breeding seasons (March to July) from 2002 to 2007. Nests were located by parental behavior and systematically searching territories of breeding pairs (Martin et al. 2006, 2007). Nests were monitored daily during both late morning and early afternoon to determine initiation of incubation (day last egg was laid). We videotaped nests during incubation for the first six to eight hours of the day, beginning within 0.5 h of sunrise (Martin et al. 2007). Nests were filmed using small camcorders covered with camouflage sleeves and concealed within the surrounding vegetation > 5m from all nests. Filmed nests were sampled across the incubation period to examine any variation with age of embryos. Three Slaty Antwren nests were filmed from dusk to nightfall (early incubation:  $n = 1$ ; late incubation:  $n = 2$ ) in 2006 and ocular night-time (after 7pm) observations were made on 2 Plain Antvireo

nests (early incubation: n = 1; late incubation: n = 1) in 2007 to determine which sex incubated at night.

### *Measurements of Sex-specific Parental Effort*

We calculated three measures of male versus female parental effort and incubation temperatures from filmed nests: 1) daytime nest attentiveness, 2) incubation temperatures experienced by developing embryos during parental on-bouts, and 3) rate of rewarming cold eggs after extended nest absences. A total of 51 nests found between 2002 and 2007 were used in measurements of male and female nest attentiveness (Slaty Antwren: n = 32; Plain Antvireo: n = 19). Sex differences in incubation temperatures and re-warming rates were examined for 19 of the total nests found in 2006 and 2007 (Slaty Antwren: n = 9; Plain Antvireo: n = 10). Nest attentiveness was calculated as the percent of time for the first 6-8 hours of the day each sex spent on the nest (Martin et al. 2007). Incubation temperatures experienced by developing embryos were measured by inserting thermistors inside one egg per clutch on either the first or second day of incubation (Weathers and Sullivan 1989; Martin et al. 2007). Thermistors were connected to a HOBO Stowaway XTI datalogger (Onset; Bourne, MA) that recorded egg temperatures every 12s until hatch or fail day. Nests containing probed eggs were filmed starting the day after thermistors were inserted to avoid disrupting normal behavioral activities (Martin et al. 2007). Temperature data from concurrently filmed nests were used to quantify on-bout egg temperatures for each sex. We measured the rate that males versus females rewarmed cold clutches by calculating the rate of change in egg temperature every 12 seconds for the first 3 minutes for the on-bout following the first recess of the

morning (6-8am). We used the first 3 minutes as our sample duration to ensure rewarming rates would not be biased by potential sex differences at which parents maintain egg temperatures during on-bouts. We used the first on-bout of the morning because preliminary temperature profiles revealed that egg temperatures during these protracted recesses often drop to or near ambient temperature in these and other tropical species (see Fig. 1) (Martin et al. 2007). Reheating eggs is an energetically expensive component of care (Drent 1975; Haftorn and Reinertesen 1982; Biebach 1986). Thus, rate at which parents rewarm cold eggs indicates both effort and physiological ability to heat developing embryos.

#### *Environmental Parameters*

Daily ambient air temperature is commonly assumed to influence avian incubation behavior (Drent 1975; White and Kinney 1974; Haftorn 1988). Daytime ambient air temperatures (mean  $\pm$  SE °C) experienced by our plots differed among altitudes in 2006 and 2007 (low:  $19.0 \pm 0.005$ ; mid:  $17.4 \pm 0.005$ ; high:  $16.5 \pm 0.004$ ). Thus, ambient air temperature was recorded every 12-48s (HOBO Stowaway XTI, Onset; Bourne, MA) when nests were filmed and nests were divided between low (1350m), mid (1675m), and high (2000m) elevations to examine the possible influence of ambient temperature on sex-specific parental effort. Films were scored in the laboratory for male and female on-off bout durations, male and female on-bout egg temperatures and mean ambient air temperatures during on-bouts.

## *Data Analysis*

We used a hierarchical general linear mixed model (GLMM; SPSS V12.0) approach to examine differences between male and female parental effort (i.e. nest attentiveness, on-bout egg temperatures, and egg rewarming rates). In all analyses, we included sex as a blocking factor and nest pair as a subject variable with correlated random effects to correct for repeated sampling of individuals. We investigated sex-specific differences and temporal changes in nest attentiveness and egg temperatures during incubation by separating the incubation stage into three age categories: early (days 1-5), middle (days 6-10) and late (day 11-hatch). We analyzed sex-specific nest attentiveness using incubation age (early, middle, late) as a covariate. For sex-specific on-bout egg temperatures, we used egg temperature at the start of each bout, bout duration length and incubation age as covariates. We were interested in the relative effort of male versus female partners in mean on-bout egg temperatures rather than phenotypic differences among pairs that may arise from age or other conditions. Accordingly, we corrected for this variance before analysis by subtracting individual on-bout egg temperatures from mean on-bout egg temperatures of all bouts for each nest sampled. This transformation allowed for standardized comparisons of sex-specific trait differences (Lande & Arnold 1983) in on-bout egg temperatures across nests. When temporal changes in parental effort were significant, we used least-significant difference tests (LSD) to conduct *post hoc* tests. In all analyses we tested for potential influences of on-bout ambient air temperature and elevation on sex-specific parental effort. On-bout ambient air temperature and elevation did not significantly influence measurements of parental effort, thus filmed nests were pooled for subsequent analyses. Proportional data

were arcsine transformed prior to analysis and results are presented as means and with associated standard errors (SE).

## **Results**

### *Nest Attentiveness*

Females incubated at night in both species (Slaty Antwren:  $n = 3$ ; Plain Antvireo:  $n = 2$ ). Nest attentiveness did not differ between male and female Slaty Antwrens and increased similarly in both sexes with incubation age (Fig. 2a; sex:  $F_{1,113} = 0.3$ ,  $P = 0.60$ ; age:  $F_{1,130} = 14.6$ ,  $P < 0.001$ ; sex  $\times$  age:  $F_{1,113} = 1.0$ ,  $P = 0.36$ ). Total parental nest attentiveness (males + females) was similar (LSD,  $P = 0.27$ ) during late and middle incubation, but was less (LSD,  $P < 0.01$ ) in early incubation (Fig. 2a). Plain Antvireo males exhibited greater nest attentiveness than females (Fig. 2b; sex:  $F_{1,29} = 11.7$ ,  $P < 0.01$ ; age:  $F_{1,43} = 3.0$ ,  $P = 0.06$ ; sex  $\times$  age:  $F_{1,29} = 3.6$ ,  $P = 0.04$ ). However, the interaction indicated males and females increase nest attentiveness differently with incubation age. Indeed, male Plain Antvireo nest attentiveness was greater than females during late incubation (Fig. 2b; LSD,  $P < 0.01$ ), but male and female nest attentiveness did not differ during either early or middle age categories (LSD,  $P > 0.25$ ; both periods). Only male nest attentiveness increased with incubation age in the Plain Antvireo. Plain Antvireo male attentiveness during early incubation was similar to the middle period (LSD,  $P = 0.48$ ) but male nest attentiveness during late incubation was greater than both early and middle periods (Fig 2b; LSD,  $P < 0.04$ ; both comparisons). Plain Antvireo female nest attentiveness did not increase among age categories (Fig 2b; LSD,  $P > 0.29$ ; all comparisons).



### *Incubation Temperatures*

Slaty Antwren females maintained eggs at marginally higher temperatures than males during on-bouts (sex:  $F_{1,136} = 3.0$ ,  $P = 0.08$ ; age:  $F_{1,143} = 8.8$ ,  $P < 0.001$ ; sex  $\times$  age:  $F_{1,142} = 2.2$ ,  $P = 0.10$ ;  $T_{\text{egg}}$  start of bout:  $F_{1,100} = 91.8$ ,  $P < 0.001$ ; on-bout duration:  $F_{1,138} = 6.5$ ,  $P < 0.01$ ). Plain Antvireo females incubated eggs at appreciably higher temperatures than males (sex:  $F_{1,59} = 4.3$ ,  $P = 0.01$ ; age:  $F_{1,68} = 4.3$ ,  $P = 0.02$ ; sex  $\times$  age:  $F_{1,67} = 2.9$ ,  $P = 0.06$ ;  $T_{\text{egg}}$  start of bout:  $F_{1,62} = 52.9$ ,  $P < 0.001$ ; on-bout duration:  $F_{1,67} = 11.5$ ,  $P < 0.01$ ). The marginal interaction between sex and age in both species indicated males and females maintain eggs temperatures differently with incubation age. Slaty Antwren females maintained egg temperatures marginally higher than males only during late incubation (Fig 2c; LSD,  $P = 0.08$ ) whereas Plain Antvireo females maintained higher egg temperatures than males only during early incubation (Fig. 2d; LSD,  $P < 0.01$ ).

Temperatures experienced by developing embryos increased with age when both males and females incubated in Slaty Antwrens and Plain Antvireos (Fig. 2c, d). Moreover, increases in egg temperatures were independent of differences between egg temperatures at the start of on-bouts and the duration of parental on-bouts (see results above). Slaty Antwren males increased the amount of heat they delivered to eggs between early and late incubation (Fig. 2c; LSD,  $P = 0.08$ ); male on-bout egg temperatures did not differ between middle and late age categories (LSD,  $P = 0.42$ ). Slaty Antwren females consistently increased the amount of heat they delivered to eggs between early, middle and late incubation (Fig. 2c; LSD,  $P < 0.03$ ; all comparisons). Plain Antvireo males also increased the amount of heat delivered to eggs between early and late incubation (Fig. 2d; LSD,  $P = 0.04$ ) but did not differ between middle and late age categories (LSD,  $P = 0.21$ ).

Female Plain Antvireos also increased incubation egg temperatures from early to late incubation (Fig. 2d; LSD,  $P = 0.02$ ), but did not differ between the early and middle period (LSD,  $P = 0.41$ ).

### *Egg Rewarming Rates*

Egg temperatures following the first recess of the day and at the start of first daily on-bouts (6-8am) ranged from 17.6 to 23.9°C ( $n = 17$ ) in Slaty Antwren and 14.9 to 25.1°C ( $n = 11$ ) in Plain Antvireo nests. Egg rewarming rates did not differ between males and females in the Slaty Antwren (Fig. 4a; sex:  $F_{1,235} = 0.1$ ,  $P = 0.75$ ; time:  $F_{14,229} = 71$ ,  $P < 0.001$ ;  $T_{\text{egg}}$  start of first bout:  $F_{1,232} = 1.0$ ,  $P = 0.31$ ; age:  $F_{1,236} = 1.1$ ,  $P = 0.29$ ). Rewarming rates were also similar between sexes in the Plain Antvireo (Fig. 4b; sex:  $F_{1,142} = 1.8$ ,  $P = 0.28$ ; time:  $F_{14,136} = 52.3$ ,  $P < 0.001$ ;  $T_{\text{egg}}$  start of first bout:  $F_{1,80} = 38.5$ ,  $P < 0.000$ ; age:  $F_{1,84} = 32.0$ ,  $P < 0.001$ ).

## **Discussion**

Studies of male and female roles in biparental incubation are rare and have focused on north temperate species. Tropical birds are unique in that entire taxonomic families may exhibit biparental incubation, but the degree to which sexes divide reproductive effort in these species has been unstudied. We found that males and females apportion measures of parental effort differently between two related and ecologically similar tropical species that exhibit biparental incubation.

Nest attentiveness represents a significant commitment of parental effort as it detracts from time otherwise spent foraging, engaging in self-maintenance activities,

territory defense and seeking extra-pair fertilization opportunities (White and Kinney 1974, Westneat and Sargent 1996). Here, we found sexes were similar in their daytime nest attentiveness in Slaty Antwrens, but males invested greater time than females in Plain Antvireos (Fig. 2b). While we did not observe males incubating during nighttime hours in either species these observations need to be viewed with caution given our small sample size. Nonetheless, our results clearly demonstrate males spend equal or even greater amounts of time incubating than females for a substantial portion of the day.

Time spent on the nest may not, however, serve as a complete indicator of energetic expenditure if males and females incubate eggs at different temperatures (Auer et al. 2007). Reheating and maintaining egg temperatures is energetically costly to parents (Biebach 1986; Bryan and Bryant 1999; Reid et al. 2000; Visser and Lessels 2001) and studies of field metabolic rates using doubly labeled water have shown that energy expenditure during incubation is as high or higher than during the nestling period (reviewed in Williams 1996). Here, we found males and females were equally capable of rewarming cold eggs in both the Slaty Antwren and the Plain Antvireo (Fig. 3a, b). This result was not surprising given that males and females were similar in size, developed similar brood patches in both species (Chapter 2) and incubating birds sense and adjust egg temperatures by increasing both metabolic heat production and blood flow to the brood patch (Haftorn and Reinertesen 1982). Yet, despite being physiologically similar in their ability of rewarming cold eggs, we found that males maintained cooler egg temperatures than females during on-bouts in both species and sex differences were greater in the Plain Antvireo where males spent more time incubating (Fig. 2c, d). Cooler egg temperatures can result in longer incubation periods such that greater male help may

negatively influence embryonic development (Kleindorfer et al. 1995). Yet, egg temperature differences between males and females in these two species were small and the presence of males during female absences did increase overall egg temperatures. For example, egg temperatures during protracted first off-bouts of the morning (see Fig. 1) often fell to or near ambient temperature, yet males and females did not allow egg temperatures to fall to such lows in subsequent off-bouts later in the day.

Additionally, we found males and females adjusted their magnitude of parental time and energy expenditure as the incubation period progressed, highlighting the utility of measuring multiple aspects of parental effort in studies of biparental care and offspring development. We found both species increased the amount of time spent incubating as the embryos aged, but sexes differed within species in these age-related changes. Yet, in both species males consistently spent more time incubating as eggs approached hatch day (Fig. 3a, b) thus minimizing the time eggs were exposed to cooler temperatures during female absences. At the same time, increased attentiveness by males may also improve female physiological condition through increases in female time availability for foraging and self-maintenance during this costly stage of reproduction.

Equally as interesting as age-related changes in parental nest attentiveness, we found that males and females in both species physiologically increased the amount of heat delivered to developing embryos as eggs approached hatching (Fig. 3c, d). While increased time spent incubating increases overall egg temperatures, our results clearly show egg temperatures experienced during parental on-bouts were not influenced by either the duration of on-bouts or temperatures of eggs at the start of on-bouts. Moreover, increased egg temperatures were not due to thermoregulation of aging embryos as probed

eggs do not develop. This result indicates that in addition increased nest attentiveness with age; males and females enhance embryonic development through increased metabolic heat transfer to eggs as clutches approach hatching. Alternatively, parents in these species may delay full brood patch development until later in the incubation period. Regardless of the physiological mechanisms, increases in egg temperatures convey clear fitness benefits to offspring (Lyon and Montgomerie 1985; Webb 1987; Martin 2002; Hepp et al. 2006; Olson et al. 2006; Martin et al. 2007) and to our knowledge this result is the first to demonstrate that parents in nidicolous birds increase temperatures experienced by developing embryos independent of parental time spent on the nest. Summed together, the multiple components of biparental effort revealed here now afford comparisons of variation in sex-specific patterns of parental time and energy among broader geographic regions.

Tropical and southern hemisphere species exhibit life-history strategies that generally differ from north temperate species (Moreau 1944, Yom-Tov 1987, Yom-Tov et al. 1994, Martin 1996, Martin et al. 2000b, Martin 2004) and patterns of sex-specific effort in biparental incubation appear to be no exception. For example, in the southern hemisphere, male Chestnut vented tit-babblers (*Parisoma subcaeruleum*; Sylviidae) exhibited equal nest attentiveness and even incubated eggs at higher temperatures than females (Auer et al. 2006). In contrast, males in their north temperate relatives (*Acrocephalus spp.*; Sylviidae) incubated less, rewarmed clutches at slower rates and maintained cooler egg temperatures than females (Kleindorfer et al. 1995). Here, we also found patterns of male and female effort in tropical antbirds different than that of north temperate species (Kleindorfer et al. 1995; Reid et al. 2002; Bartlett et al. 2005), yet more

similar to that of the southern hemisphere Chestnut vented tit-babbler: equal and even greater male nest attentiveness and similar egg rewarming rates, although they differed with respect to temperatures at which males incubated. However, reasons for these sex differences in incubation strategies among species, such as the Slaty Antwren and the Plain Antvireo, remain unclear with the full extent of variation largely unknown given the limited attention to male care during incubation in general.

Differences in adult mortality between species may be one explanation for sex differences in incubation strategies among regions of the world. Tropical and southern hemisphere species express low adult mortality and low reproductive effort while north temperate species express the converse. Variation in adult mortality along this ‘slow-fast’ life-history gradient is thought to influence duration of pair bonds because increased adult mortality increases the probability of re-mating (Martin 2004). In contrast, species with low adult mortality often exhibit longer pair bond durations which reduces chances for parents to seek additional mating opportunities to enhance fitness (Kunkel 1974; Sæther 1986; Choudhury 1995). Thus, low adult mortality may favor the evolution of increased male involvement in offspring care because male fitness is higher when remaining with the same female (Emlen and Oring 1972). Indeed, long-term pair bonds are common in many tropical birds, including species of antbirds (Kunkel 1974; Greenberg and Gradwohl 1983; Skutch 1996). Variation in adult mortality among species may then even explain why biparental incubation is so pervasive among tropical versus north temperate families.

In conclusion, our results highlight the importance of understanding the relative role of male versus female parental effort among a broader range of species in

understanding variation in biparental care strategies among geographical regions. We suggest that further investigations of sex-specific parental effort among other species which exhibit biparental incubation will prove fruitful in assessing not only why male care is so extensive in birds, but also in explaining why paternal care strategies differ across taxa.

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## **Figure Legends**

### **Figure 1 | First daily off-bouts are the most protracted parental absences.**

Twenty-four hour egg temperature profiles for Slaty Antwren and Plain Antvireo eggs. Brackets depict longest daily recesses (protracted off-bouts) from nests between 6-8am.

### **Figure 2 | Male and female parental effort changes over the incubation period. Male**

and female differences in nest attentiveness (% daytime on nest) and mean on-bout egg temperatures within and among all three periods of incubation: Early (days 1-5), Middle (days 6-10) and Late (11-hatch) in the Slaty Antwren and the Plain Antvireo. Letters depict significant differences in which the first letter denotes male and female differences within periods and the second letter denotes sex-specific differences among periods. Bars represent EMMs  $\pm$  SE.

### **Figure 3 | Males and females rewarmed cold eggs at similar rates in both species.**

Males and females in both species rewarmed cold eggs at similar rates after the longest daily recesses from the nest (see Fig. 1). Values represent EMMs  $\pm$  SE.

**Figure 1**

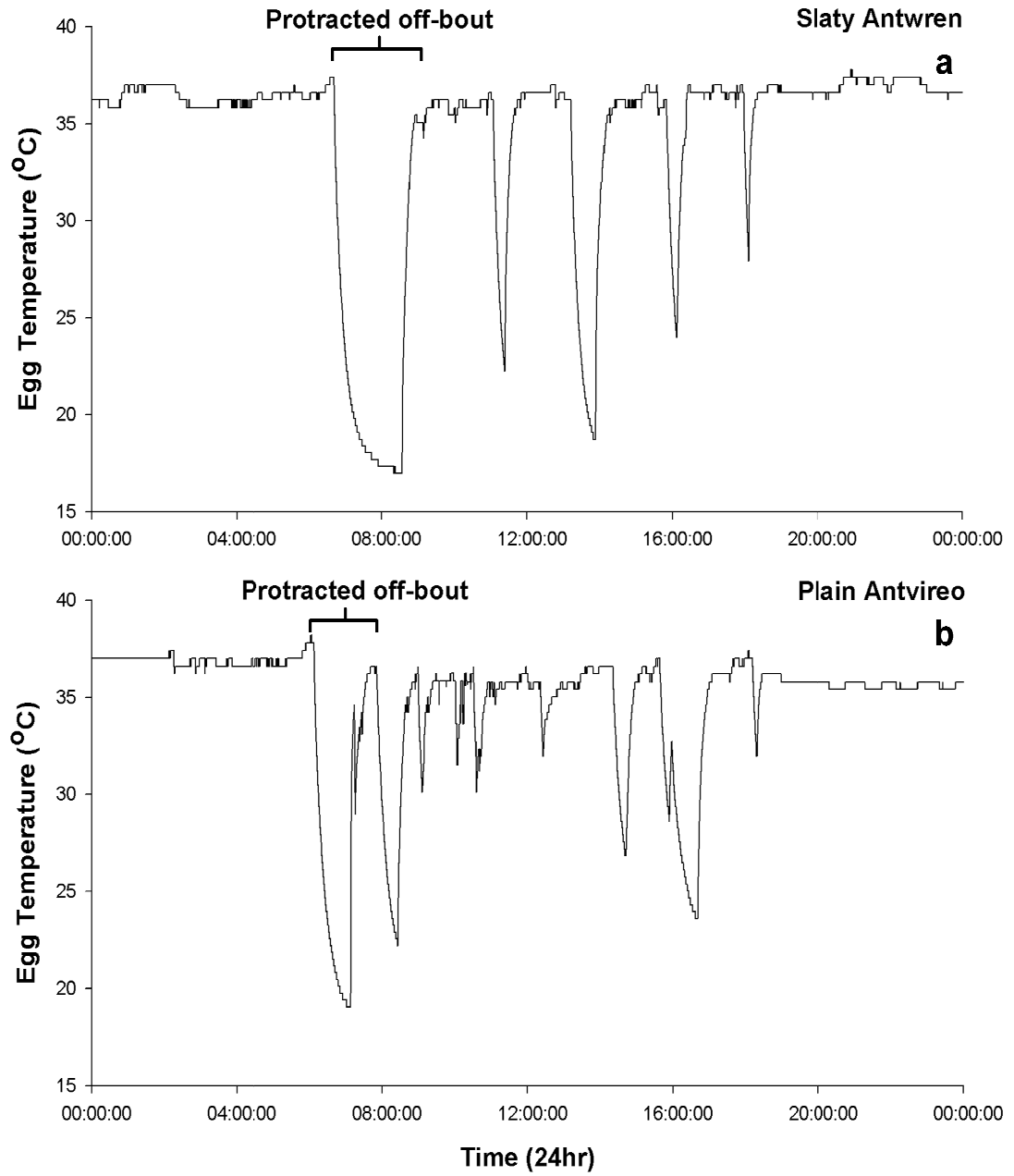




Figure 2

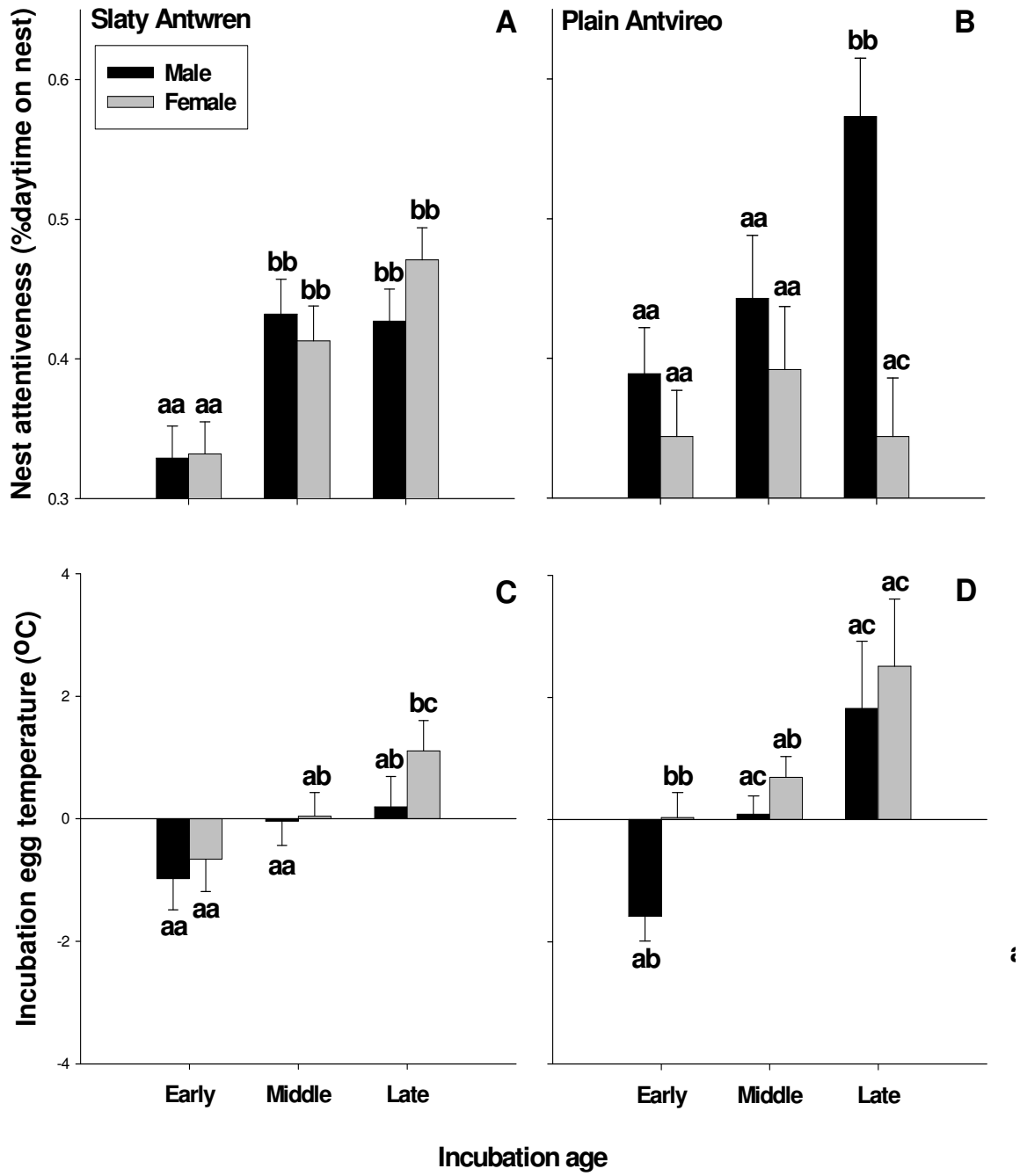
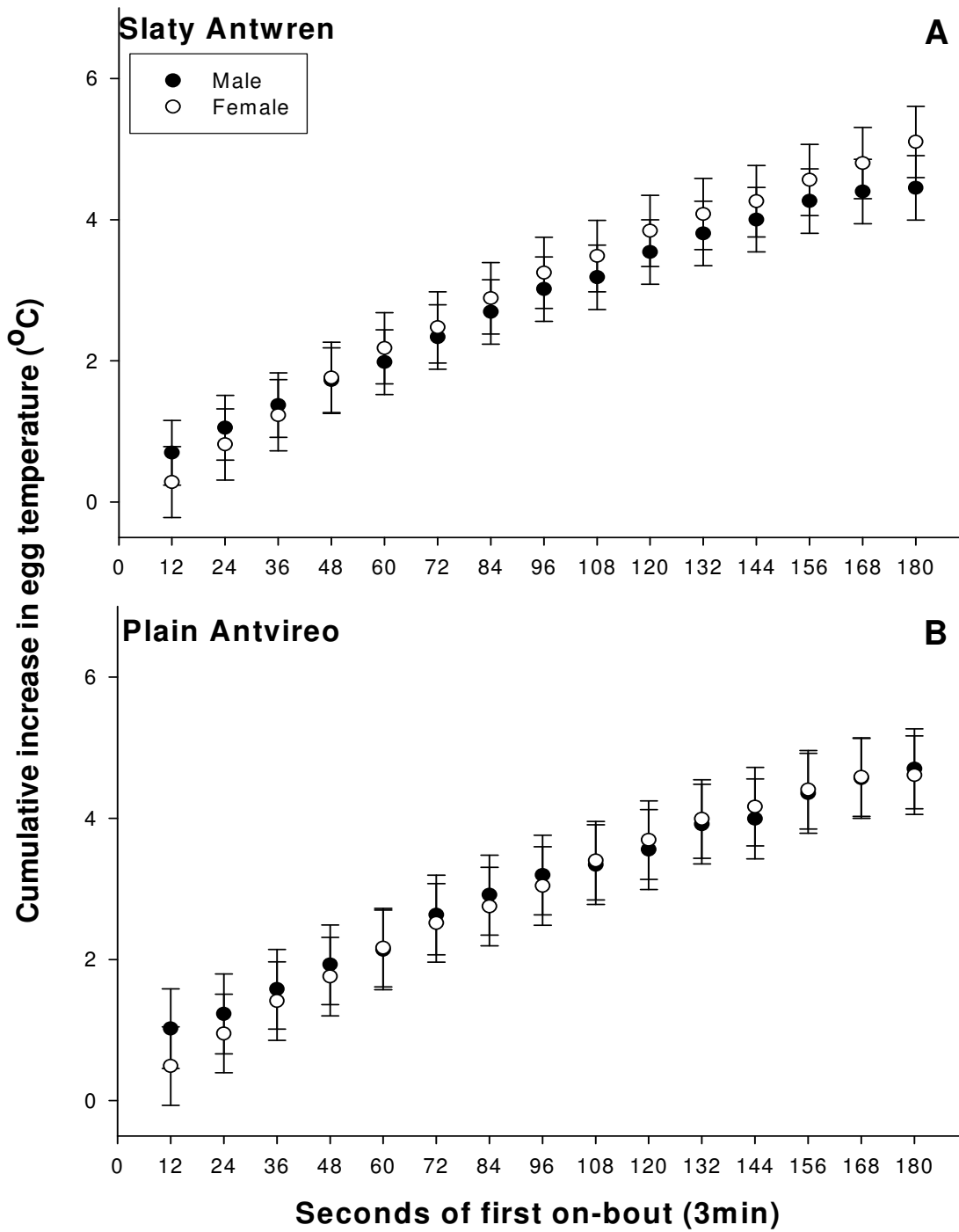


Figure 3



## **CHAPTER 2**

### **REPRODUCTIVE BIOLOGY OF THE SLATY ANTWREN AND THE PLAIN ANTVIREO IN THE NORTHERN ANDES OF VENEZUELA**

## **Abstract**

Tropical regions are of considerable importance in conservation biology, yet even basic descriptions of reproductive traits are entirely absent. Standardized measures of reproductive traits are essential in improving our understanding of reproductive biology and avian life-history evolution at large. Here, we report comprehensive details on the breeding biology and provided standardized measures of reproductive traits among two endemic tropical species: The Slaty Antwren and the Plain Antvireo. We found 138 Slaty Antwren nests and 112 Plain Antvireo nests from 2002-2007 in Yacambú National Park, Venezuela. Clutch size was always two eggs, usually laid every other day for both species. Incubation periods were similar between Slaty Antwrens ( $15.7 \pm 0.89$  d) and Plain Antvireos ( $16.0 \pm 0.80$ d) despite species differences in male versus female nest attentiveness and were longer than or similar to those exhibited by species with female only incubation. Males in both species developed full brood patches and shared equal or greater nest attentiveness as females during incubation, yet males incubated eggs at cooler temperatures during some parts of incubation. Both sexes shared brooding effort equally during the nestling phase, yet sexes differed between species in rates at which they fed nestlings. Growth rates based on nestling mass, tarsus and wing cord were similar between both species and daily nest survival rates decreased across stages (egg-laying, incubation, nestling). This study aims at advancing our knowledge of tropical life-history strategies and improving data collection efforts outside of North America.

## Introduction

Antbirds (Formicariidae and Thamnophilidae) comprise the third largest radiation of birds rivaled only by hummingbirds and tanagers (Skutch 1996). With over 190 species, classified in 43 genera, Thamnophilidae are a monophyletic and diverse family of suboscine passerines that inhabit the Neotropical forests of central and South America (del Hoyo et al. 2003). Most Thamnophilidae are closely associated to understories of mature forest stands and may be affected by increasing forest fragmentation in tropical regions (Willis 1979, Bierregaard et al. 1992, Sieving and Karr 1997). Yet, even basic breeding descriptions such as nest characteristics, clutch size, incubation period and nestling period remain entirely absent for many species in this large family.

Here, we report the first comprehensive study of the reproductive biology of two Thamnophilidae: the Slaty Antwren (*Myrmotherula schisticolor*) and the Plain Antvireo (*Dysithamnus mentalis*). Both species are evaluated as one of Least Concern for conservation (BirdLife International 2004). Nonetheless, we report important components of reproductive effort such as nest attentiveness, percentage of brooding, feeding and growth rates all of which directly impact fitness and thus population persistence. Both species are arboreal undergrowth inhabitants of humid and wet premontane forest from 700 to 2000 m elevation, and also occur along stream sides and forest borders (del Hoyo et al. 2003) and range from Mexico to Bolivia and northern Argentina (Stiles and Skutch 1989; Ridgely and Tudor 1994; Hilty 2003). Despite their widespread distribution and relative abundance, very little is known about the reproductive biology of these two endemic Thamnophilidae other than that both sexes share incubation and brood nestlings (Lill and French 1970; Skutch 1996; Hilty 2003). We conducted our studies in the

northern Andes of Venezuela in a montane tropical cloud forest of primarily mature and some secondary vegetation. The scope of this study aims at furthering our knowledge of the reproductive biology in this large, yet overlooked tropical family.

## **Methods**

We searched for Slaty Antwren and Plain Antvireo nests from March to July, 2002-2007, in Yacambú National Park, in the Lara state of Venezuela (09° 42' N, 69° 42' W). The park, located in northernmost edge of the Andes, covers an area of 14,580 ha and ranges from 500-2200m elevation. Our study area consisted of 10 field sites at 1350-2000 m elevation (~ 600 ha). The rainfall pattern is unimodal with a peak from May to July and an annual mean precipitation of over 2000mm. Nests were located by parental behavior and systematically searching territories of breeding pairs (Martin et al. 2006, 2007). We monitored nests every two to four days, except at stage-changing events (laying, hatching, fledging) when we monitored nests daily or twice daily (Martin and Geupel 1993; Martin 2002). For details on how nest, egg and nestling measurements were performed, and how behavioral data were collected, see Martin et al. (2000, 2006, 2007) and Fierro-Calderón and Martin (2007). Briefly, we weighed eggs and nestlings using an ACCULAB (Elk Grove, Illinois) portable electronic scale with an accuracy of 0.001 g (Martin et al. 2006), and measured nestlings (i.e., tarsus length, wing chord) using Mitutoyo (Kingsport, Tennessee) digital calipers. Growth rates were calculated following Remeš and Martin (2002), and nest predation and survival rates were calculated following Mayfield (1961, 1975; Hensler and Nichols 1981). We used video cameras to measure parental behavior and sex roles for 6-8 hours early in the morning

during incubation and nestling phases. Additionally, we captured breeding adults using passive mist netting or target netting active nests from 2003-2007.

Average 24 hour incubation temperatures experienced by developing embryos were measured by inserting thermistors inside one egg per clutch on either the first or second day of incubation. Thermistors were positioned in the center of eggs through a small hole sealed with glue (Weathers and Sullivan 1989; Martin et al. 2007). The wire was threaded through the nest < 5mm above the nest bottom to allow eggs to be naturally positioned and turned in the nest. The wire was connected to a HOBO Stowaway XTI datalogger (Onset; Bourne, MA) that recorded egg temperatures every 12s until hatch or fail day. We measured ambient temperatures over the same periods using a shaded thermistor and datalogger.

### *Data Analysis*

For all data, means are reported with 1 standard error (SE). Sample sizes reflect numbers of nests or individuals sampled in all cases. We used a hierarchical general linear mixed model (GLMM; SPSS V12.0) approach to examine differences between male and female parental effort during both the incubation and nestling phase (i.e. nest attentiveness, egg incubation temperatures, brooding effort, nestling feeding rates). We investigated sex-specific differences and temporal changes in nest attentiveness during incubation by separating the incubation stage into three age categories: early (days 1-5), middle (days 6-10) and late (day 11-hatch). We analyzed sex-specific nest attentiveness using incubation age (early, middle, late) as a covariate. We tested sex-specific differences in brooding effort and nestling feeding rates using nestling age as a covariate.

We used linear regression to test for temporal changes in parental behavior during the nesting stage (i.e. brooding effort; feeding rates). In analyses of sex-specific differences in parental effort we included sex as a blocking factor and nest pair as a subject variable with correlated random effects to correct for repeated sampling of individuals. When temporal changes in parental effort were significant, we used least-significant difference tests (LSD) to conduct post hoc tests.

## Results

### *Adult morphology*

We captured Slaty Antwrens and Plain Antvireos using passive mist-netting from 2003-2007. Plain Antvireos males ( $15.5 \pm 0.22\text{g}$ ,  $n = 25$ ) and females ( $15.4 \pm 0.22\text{g}$ ,  $n = 19$ ) were larger than Slaty Antwrens males ( $9.7 \pm 0.1\text{g}$ ,  $n = 44$ ) and females ( $9.9 \pm 0.1\text{g}$ ,  $n = 45$ ). Sexes in both species were dimorphic in plumage, which allowed accurate behavioral determinations of sex-specific parental behavior. Males and females developed full brood patches (i.e. de-feathering, vascularization and oedema formation) in both the Slaty Antwren (males: length  $19.2 \pm 1.9 \times$  width  $14.8 \pm 0.9$ ,  $n = 13$ ; females: length  $17.6 \pm 1.3 \times$  width  $15.5 \pm 0.6\text{mm}$ ,  $n = 17$ ) and the Plain Antvireo (males: length  $21.0 \pm 1.9 \times$  width  $16.8 \pm 0.5$ ,  $n = 14$ ; females: length  $21.9 \pm 2.3 \times$  width  $16.5 \pm 0.9\text{mm}$ ,  $n = 11$ ). Length and width (mm) of brood patches did not differ between males and females in Slaty Antwrens (Mann-Whitney U-test: length:  $Z_{13,17} = -0.98$ ,  $P = 0.34$ ; Whitney U-test: width:  $Z_{13,17} = -1.215$ ,  $P = 0.23$ ) or Plain Antvireos (Mann-Whitney U-test: length:  $Z_{14,11} = -0.493$ ,  $P = 0.65$ ; Whitney U-test: width:  $Z_{14,11} = -1.215$ ,  $P = 0.23$ ).



### *Nests and eggs*

We found 138 Slaty Antwren nests and 112 Plain Antvireo nests from 2002-2007. Nests of both species were slung in a Y formed by two horizontal branches, 3-4mm, in saplings between 1-10m in height. Nests were predominantly found concealed under large foliage which shielded nests from heavy rains. Slaty Antwren nests were open cups constructed entirely of black fungal rootlets and were thin-walled enough to allow contents to be seen from below and through the sides. Slaty Antwren nests at lower elevations (~ 1350m) were often lined with fresh ochre colored rootlets 2-3 days prior to laying. Nest height for 52 Slaty Antwren nests ranged 1-4m and averaged  $1.5 \pm 0.09$  m. Size of 164 Slaty Antwren nests averaged  $5.1 \pm 0.05$  mm inner diameter,  $6.8 \pm 0.08$  mm outer diameter,  $4.0 \pm 0.06$  mm inner height and  $5.5 \pm 0.08$  mm outer height.

Plain Antvireo nests also consisted of black fungal rootlets and were slightly larger than Slaty Antwren nests, yet nest cups were more heavily insulated and lightly decorated with moss and incorporating small stems, similar to previous nest descriptions for this genus and species (i.e. Skutch 1969, Lill and French 1970, Wetmore 1972, Willis and Eisenmann 1979, Stiles and Skutch 1989, Skutch 1996, Greeney2002). Nest height for 26 Plain Antvireo nests also ranged 1-4m and averaged  $1.5 \pm 0.12$  m. Size of 156 Plain Antvireo nests averaged  $5.4 \pm 0.06$  mm inner diameter,  $7.5 \pm 0.09$  mm outer diameter,  $4.4 \pm 0.07$  mm inner height and  $6.1 \pm 0.09$  mm outer height.

Slaty Antwren and Plain Antvireo nests were frequently found within 30-60m of each other and pairs of both species foraged in overlapping territories based on color-banded birds (Schwartz personal observation). Slaty Antwren nests were predominantly found in ravine drainages near small ephemeral creeks or on slopes. Plain Antvireo nests

were frequently located in the same or adjacent ravine on a steep slope or bank. At all elevations nests of both species were chiefly concealed in thick foliage.

Males and females in both species were observed participating in nest construction. Females in both species often took several days to lay eggs after nest construction. For example, one Slaty Antwren female took 28 days before laying her first egg after the nest was completed (pre-lay period). We also observed > 30 day pre-lay period in one Plain Antvireo female. Dates of nest initiation (day the first egg was laid) ranged from the 27<sup>th</sup> of February to the 22<sup>th</sup> of June for 107 Slaty Antwren nests across five breeding seasons (2002-2007); the mean initiation date was the 3<sup>rd</sup> of May (Fig. 1). Initiation of the first Plain Antvireo nest occurred nearly a month later ranging from the 18<sup>th</sup> of March to the 21<sup>st</sup> June; the mean initiation date was the 13<sup>th</sup> May for 87 Plain Antvireo nests (Fig. 1). Mean initiation of nests for both species coincided with the beginning of the rainy season. Fifteen females in both species laid eggs every other day while only 2 females in both species laid two eggs in successive days. Two Plain Antvireo pairs and 3 Slaty Antwren pairs initiated nests in the same territories in consecutive years (2006-2007) based on color-banding. Most territories contained multiple old nests from previous seasons suggesting, along with color banded pairs, high site-fidelity between pairs and years.

Clutch size was always two eggs in both the Slaty Antwren (n = 16) and Plain Antvireo (n = 19) when exact lay dates were observed. More than 2 eggs were never observed in nests in either species. Eggs in both species were off-white in color, heavily flecked and blotched with brown, purple and red, similar to previous descriptions for these genera (Skutch 1969, Lill and French 1970, Stiles and Skutch 1989, Skutch 1996,

Greeney 2002). Slaty Antwren and Plain Antvireo egg mass averaged  $1.28 \pm 0.02$  g ( $n = 36$ ) and  $2.22 \pm 0.03$  g ( $n = 29$ ) during early incubation (day 0-3 of incubation), respectively. Therefore, fresh egg mass was approximately 12.9% of the corporal mass of females in Slaty Antwrens and 14.4% of females in Plain Antvireos.

### *Incubation Period*

We calculated nest attentiveness from videos of 32 Slaty Antwren and 19 Plain Antvireo nests. Males and females in both the Slaty Antwren and the Plain Antvireo participated in incubation. The incubation period was similar between the Plain Antvireo than the Slaty Antwren, averaging  $16.0 \pm 0.80$  d ( $n = 6$ ) versus  $15.7 \pm 0.89$  d ( $n = 12$ ), respectively. Total mean daytime nest attentiveness (males + females) was  $77.2 \pm 1.6\%$  and ranged from 25.3 to 99.8% in Slaty Antwrens. Total mean daytime nest attentiveness was  $78.5 \pm 2.2\%$  and ranged from 42.3 to 99.7% in Plain Antvireos. Sex-specific nest attentiveness ranged from 3.8 to 56.1% in Slaty Antwren males and 6.9 to 65.2% in females. Plain Antvireo nest attentiveness ranged from 9.5-69.4% in males and 11.6-47.2% in females. Nest attentiveness did not differ between male and female Slaty Antwrens (Fig. 2a) and attentiveness increased similarly in both sexes with incubation age (sex:  $F_{1,113} = 0.3$ ,  $P = 0.60$ ; age:  $F_{1,130} = 14.6$ ,  $P < 0.001$ ; sex  $\times$  age:  $F_{1,113} = 1.0$ ,  $P = 0.36$ ). Plain Antvireo males exhibited greater nest attentiveness than females (Fig. 2a; sex:  $F_{1,29} = 11.7$ ,  $P < 0.01$ ; age:  $F_{1,43} = 3.0$ ,  $P = 0.06$ ; sex  $\times$  age:  $F_{1,29} = 3.6$ ,  $P = 0.04$ ), however, only male nest attentiveness increased with incubation age Plain Antvireos.

Egg temperature of the Slaty Antwren averaged  $34.5 \pm 0.39$  °C over 24 hour periods from 31 days of sampling across 8 nests (with an overall mean taken from means

of each nest), while the mean temperature for the Plain Antvireo was  $34.3 \pm 0.36$  °C (n = 5 nests, 16 d). Average 24h egg temperatures increased with age of incubation but did not differ between Slaty Antwren (n = 8) and Plain Antvireo (n = 7) nests (species:  $F_{1,53} = 0.755$ ,  $P = 0.389$ ; age:  $F_{1,73} = 136.466$ ,  $P < 0.001$ ; species  $\times$  age:  $F_{1,73} = 0.267$ ,  $P = 0.607$ ). In both species, however, males incubated clutches at lower temperatures than females (Fig. 2b), but only during some parts of the incubation period and sex differences were small (Chapter 1). Daily egg temperatures often fell to quite cold levels, especially during protracted early morning off-bouts (Chapter 1).

### *Nestling Period*

The nestling period in the Slaty Antwren and the Plain Antvireo, was  $10.3 \pm 0.25$  d (n = 6) and  $10.7 \pm 0.36$  d (n = 6), respectively. Nestlings hatched on the same day in both species. At day 0, nestlings were naked with eyes closed but would exhibit begging behavior when we approached nests for measurements. At day 0 Slaty Antwren nestlings weighed  $1.17 \pm 0.06$  g (n = 18) and Plain Antvireo nestlings weighed  $2.29 \pm 0.11$  g (n = 18). Primary feathers achieved pin-break (day the eighth primary feather broke its sheath) approximately 6 to 8 days of age in both the Slaty Antwren and Plain Antvireo averaging  $18.2 \pm 0.64$  mm and  $18.8 \pm 0.41$  mm in length. During pin-break nestlings weighed  $8.52 \pm 0.22$  g (n = 14) and  $12.31 \pm 0.29$  g (n = 16), in the Slaty Antwren and the Plain Antvireo, respectively.

We calculated nestling growth rate (K) from nestling mass, tarsus and wing chord in 96 Slaty Antwren nestlings and 104 Plain Antvireo nestlings (see Fig 3a-f). When Slaty Antwren nestlings left the nest they weighed  $10.89 \pm 0.74$  g (n = 5), with tarsus  $18.5 \pm$

0.5 mm (n = 5) in length, and wing chords 36.0 mm (n = 1) in length. Plain Antvireo nestlings left the nest averaging  $13.12 \pm 0.2$  g (n = 4), with tarsus  $20.3 \pm 0.42$  mm (n = 5) in length, and wing chords  $38.7 \pm 0.7$  mm (n = 5) in length.

Male and females in both species participated in brooding and feeding nestlings. We calculated the average percentage of time that adults spent brooding nestlings (brooding effort) from videos of 19 Slaty Antwren and 10 Plain Antvireo nests. Males and females did not differ in brooding effort in either the Slaty Antwren (Fig. 4a; sex:  $F_{1,22} = 1.234$ ,  $P = 0.279$ ; age:  $F_{1,35} = 13.461$ ,  $P = 0.001$ ) or Plain Antvireo (Fig. 4b; sex:  $F_{1,15} = 0.013$ ,  $P = 0.909$ ; age:  $F_{1,31} = 12.543$ ,  $P = 0.013$ ). Brooding effort declined in Slaty Antwren males and females ( $r = -0.579$ ,  $P = 0.049$ ;  $r = -0.392$ ,  $P = 0.049$ ; respectively) with age of the nestlings (Fig. 4a, b), yet at day 8 (pin-break) females from all 3 nests exhibited brooding effort similar to females at days 2-3 of the nestling stage. Brooding did not significantly decrease in either male or female Plain Antvireos ( $P > 0.2$ ); however we were unable to film nests past day 7 of the nestling stage.

We calculated nestling feeding rates from videos of 17 Slaty Antwren and 9 Plain Antvireo nests. Male and female Slaty Antwrens (sex:  $F_{1,21} = 0.302$ ,  $P = 0.588$ ; age:  $F_{1,32} = 16.599$ ,  $P < 0.001$ ) and Plain Antvireos (sex:  $F_{1,13} = 0.046$ ,  $P = 0.834$ ; age:  $F_{1,18} = 113.596$ ,  $P < 0.001$ ) did not differ in rates (trips/h) at which they feed nestlings and only Plain Antvireo male and females increased their number of feeding visits with nestling age (Fig. 4d;  $r > 0.651$ ,  $P < 0.046$ ).

### *Nest Survival*

Predation was the main cause of nest failure in both species at Yacambú National Park. A total of 66 Slaty Antwren (48 %) and 41 Plain Antvireo nests (37%) failed due to predation. Seven Slaty Antwren (5%) and 6 Plain Antvireo nests (5%) failed due to weather, abandonment or unknown causes. Four, 43 and 18 Slaty Antwren nests and 8, 22 and 11 Plain Antvireo nests were lost to predation during the laying, incubation and nestling period, respectively. Daily predation rates for 112 Slaty Antwren nests were  $0.063 \pm 0.03$ ,  $0.051 \pm 0.008$ ,  $0.043 \pm 0.01$ , and  $0.050 \pm 0.006$  during egg-laying, incubation, nestling and overall, respectively. Daily predation rates for Plain Antvireo nests were  $0.122 \pm 0.04$ ,  $0.031 \pm 0.006$ ,  $0.031 \pm 0.009$ , and  $0.036 \pm 0.006$  during egg-laying, incubation, nestling and overall, respectively. Daily survival rates for Slaty Antwren nests were  $0.938 \pm 0.03$ ,  $0.943 \pm 0.008$ ,  $0.953 \pm 0.01$ , and  $0.945 \pm 0.006$  during egg-laying, incubation, nestling, and overall, respectively. Daily survival rates for Plain Antvireo nests were  $0.863 \pm 0.043$ ,  $0.968 \pm 0.007$ ,  $0.958 \pm 0.011$ , and  $0.959 \pm 0.006$  during egg-laying, incubation, nestling, and overall, respectively.

### **Discussion**

We found nests and eggs similar to previous descriptions for these two species, (Skutch 1969; Lill and French 1970, Wetmore 1972, Willis and Eisenmann 1979; Skutch 1996, Greeney 2002). Nests of both species were often found on steep slopes or banks and within close proximity to ephemeral streams. Nests were concealed under larger vegetation which shielded nests from rain and may serve to reduce predation risk. Despite the appearance of loose construction, nests of both species were found to be surprisingly

sturdy. In fact, most active nests were found by locating old nests that were assumed to be territories from previous years. This observation along with finding individual color-banded pairs nesting in same territories in consecutive years indicates both species have high site and mate fidelity similar to other tropical avifauna (Kunkel 1974; Greenberg and Gradwohl 1983).

Nest site locations observed here were similar to those described for the Bicolored Antvireo (*D. occidentalis*) (Greeney 2002). Greeney (2002) noted Bicolored Antvireo adults visited nests via concealed approaches along slopes below nests. We also observed this behavior in videos of both Slaty Antwren and Plain Antvireo nests with males and females ending turns incubating or brooding by inconspicuously dropping below nests. During foraging trips sexes would often travel together concealed in thick foliage along stream banks or slopes calling back and forth to one another. Interestingly, the Slaty Antwren was almost always observed foraging with Three-striped warblers (*Basileuterus tristriatus*) and sometimes nested within meters of each other (Schwartz personal obsv.). However, we never observed Plain Antvireos in mixed-flock associations though they did share foraging territories and had overlapping breeding seasons with Slaty Antwren neighbors (see Fig 1).

While sexes in both genera have been observed incubating eggs and brooding nestlings (Lill and French 1970; Skutch 1996; Hilty 2003), very little else is known about most species in this large and diverse monophyletic family. Here, we also observed males and females to share duties in building, incubating and brooding nestlings. More interestingly, we found sexes did not differ within species in mass or brood patch development, suggesting that shared roles with reproduction are common among species

in *Thamnophilidae* as suggested by Skutch (1996). Indeed, we found that males spent similar time brooding and provisioning nestlings compared to females, yet species differed in male versus female nest attentiveness during incubation. Sex differences observed during the incubation stage may reflect a trade-off in optimizing reproductive investment between different reproduction stages (i.e. egg production, incubation, and chick-provisioning) in which the relative demands of each stage may differ between species (Heaney and Monaghan 1996). Thus, as compared to Slaty Antwrens, the cost of incubation may be greater for Plain Antvireo females thus requiring greater male assistance during the incubation. Additional male assistance during incubation may allow females to replenish lost energy stores. Interestingly, compared to Slaty Antwren females, Plain Antvireo females increased the rate at which they provisioned nestlings. Increased investment by females during the nestling stage may reflect additional male assistance earlier during incubation.

Despite species differences in male versus female nest attentiveness, incubation periods were surprisingly similar between Slaty Antwrens and Plain Antvireos. Incubation periods reflect embryonic development rates and the rate of embryonic development is of considerable interest because it can have critical fitness consequences (Arendt 1997; Gilbert 2001; West et al. 2003). Males which share incubation duties with females may then enhance development and shorten incubation periods by minimizing time eggs experience cold temperature during female absences (Chapter 1). Yet, Slaty Antwrens, Plain Antvireos and other biparental incubators (i.e. *Formicariidae* and *Furnariidae*), have similar and even longer incubation periods compared to those of several other tropical species at this study site in which only females incubate (see Martin



and Schwabl 2008). Moreover, nest attentiveness in *Thamnophilidae*, *Formicariidae* and *Furnariidae* is on average higher than, and egg temperatures similar to species with uniparental incubation (see Martin and Schwabl 2008). In the case of the Plain Antvireo and Slaty Antwren, protracted incubation periods could result from age-specific parental heat transfer to embryos in which egg temperatures are cooler in early versus late incubation (Chapter 1). However, alternative factors in addition to parental effort may also account for interspecific variation in embryonic developmental rates.

Interspecific variation in maternal deposition of yolk androgens may potentially explain similar embryonic developmental rates between biparental and uniparental incubators in tropical species. Indeed, mothers of tropical species reduce growth-promoting androgen concentrations in yolk, which may slow development rates and enhance offspring quality through physiological trade-offs (Schwabl et. al 2007). Thus, parents may influence the duration of incubation through incubation behavior and through embryo exposure to growth-promoting maternal steroids in the egg (Schwabl et. al 2007). However, the degree to which maternal steroids and sex-specific parental effort influence offspring quality and developmental rates remain to be further investigated in *Thamnophilidae* and other tropical species.

Lastly, the Tropical Andes are among one of the most species-rich areas in the world and represent an area of critical conservation concern (Myers et al. 2000). Yet, for many endemic taxa inhabiting this region even basic descriptions of reproductive traits are entirely absent. Indeed, most avian studies have focused on north temperate species yet the vast majority of bird species live in the tropics and southern hemisphere (Martin 2004). Here, we report standardized measures of reproductive traits in two endemic

tropical species in hope of improving data collection efforts outside of North America. Standardized measures of reproductive traits are essential in improving our understanding of reproductive biology and avian life-history evolution within and among different regions of the world.

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### **Figure Legends**

#### **Figure 1 | Slaty Antwrens and Plain Antvireos have overlapping breeding seasons.**

Distribution of nest initiation dates (date that the first egg is laid in a nest) for the Slaty Antwren and the Plain Antvireo among weekly (7 day) intervals for years 2002-2007.

#### **Figure 2 | Males and females share nest attentiveness and incubate eggs differently in *Thamnophilidae*.**

Sex differences in nest attentiveness (% daytime on nest) and mean on-bout egg temperatures between males and females over the entire incubation stage. Bars represent EMMs  $\pm$  SE.

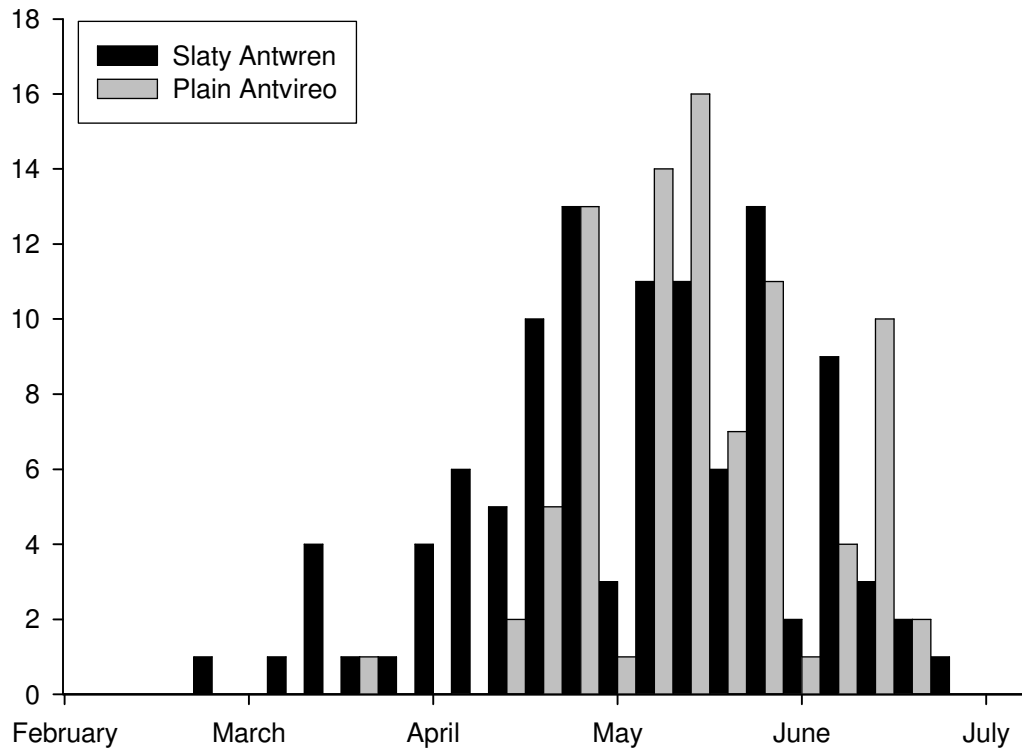
#### **Figure 3 | Nestling growth rates in the Slaty Antwren and Plain Antvireo.**

Relationships of mass, tarsus and wing cord length plotted against age with estimated growth rates (K) and asymptotes (A).

#### **Figure 4 | Brooding effort and chick-provisioning rates during the nestling stage.**

Male and female brooding effort (%daytime brooding nestlings) and rates that males and females visit to feed nestlings plotted against nestling age in the Slaty Antwren and the Plain Antvireo.

**Figure 1**



**Figure 2**



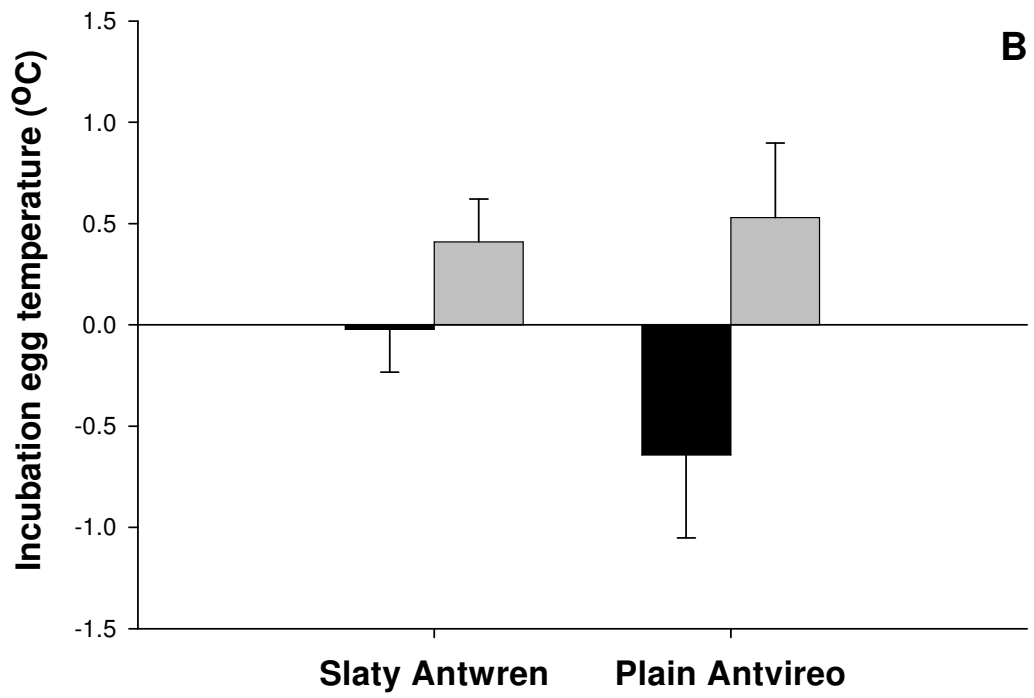
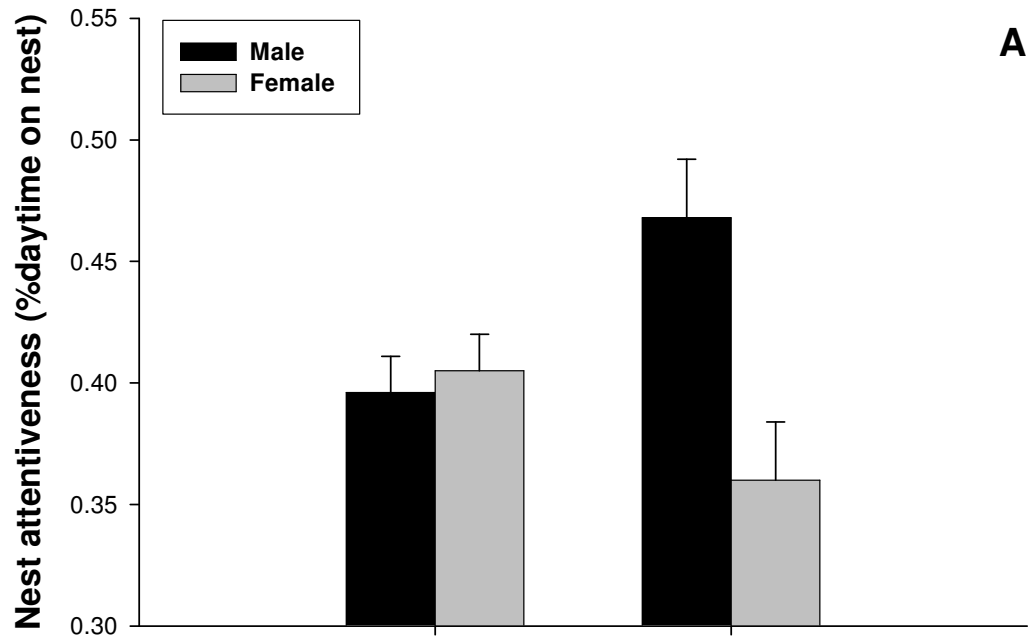
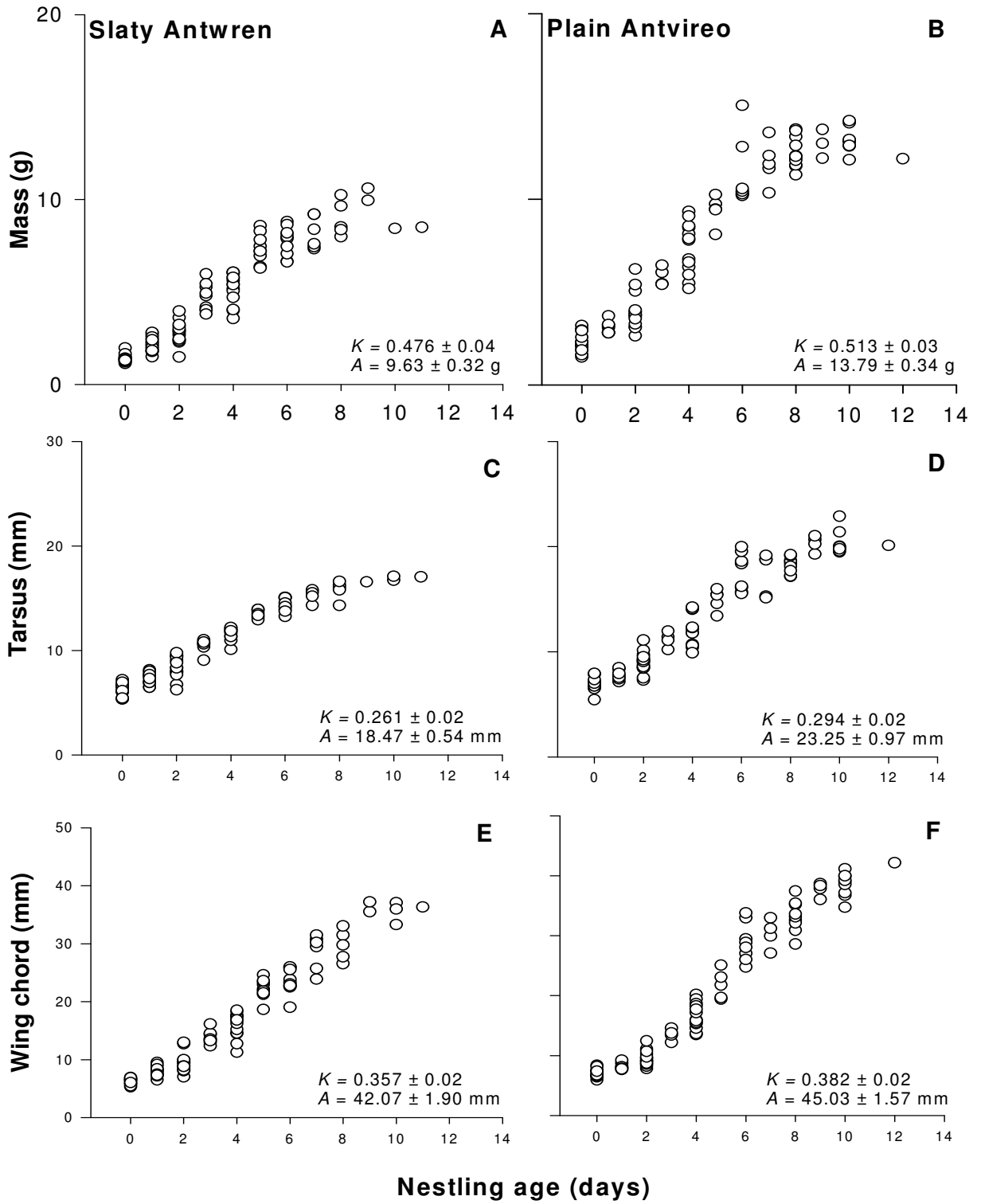


Figure 3



**Figure 4**

