

Biparental incubation in the chestnut-vented tit-babbler *Parisoma subcaeruleum*: mates devote equal time, but males keep eggs warmer

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Biparental care in birds is less common during incubation than in other nesting stages. Males share in incubating eggs in a minority of bird species, and male effort is generally thought to be lower than females when sharing does occur. However, male assistance and incubation efficacy is poorly studied in such species. We examined sex differences in incubation effort in 12 pairs of a species with biparental incubation, the chestnut-vented tit-babbler *Parisoma subcaeruleum*. Males and females did not differ in the amount of time spent incubating during the day, time of day spent incubating, nor in their ability to rewarm eggs. Yet, males consistently maintained eggs at higher temperatures than their female partners, despite the absence of a brood patch.

Biparental care is rare in most animal taxa, yet common in birds (Lack 1968, Cockburn 2006). The relative degree of involvement and parental roles of males versus females often differ among pairs within species and among species exhibiting biparental care (Clutton-Brock 1991). Mating system and sex differences in the costs and benefits of providing care are thought to influence how males and females apportion parental care duties and to affect the magnitude of their investment (Trivers 1972, Maynard Smith 1977). Both males and females are assumed to face a trade-off between investment in current offspring and other competing needs such as self-maintenance and future reproductive opportunities (Roff 1992).

Within bird species with biparental care, females are typically involved in all or most parental care duties, generally including nest building, incubating eggs and rearing offspring (Kendeigh 1952, Lack 1968, Clutton-Brock 1991). Males, in contrast, are commonly involved in feeding young but are less frequently involved in incubating the eggs (Silver et al. 1985, Ketterson and Nolan 1994). Thus, most research on paternal care has focused on chick food-provisioning rates, while the relative role of male assistance during

incubation remains poorly known (Whittingham and Dunn 2001).

Males have the potential to positively influence embryo development and success when they participate in incubation. Regulation of egg temperature by incubating parents is vital to both the survival and proper development of avian embryos (Webb 1987, Farmer 2000). Thermal intolerance of embryos to temperatures outside an optimal range can lead to a reduction in hatchability and offspring performance (Lyon and Montgomerie 1985, Webb 1987, Gorman et al. 2005b). Providing heat to eggs and spending more time on the nest can help maintain higher egg temperatures within this optimal range. These higher temperatures can then have positive impacts on hatching success and offspring phenotype (Reid et al. 2002b, Hepp et al. 2006), and even small increases in egg incubation temperature can increase the rate of embryonic development, reducing overall time-dependent mortality due to nest predation (Martin 2002, Hepp et al. 2006). However, incubation is an energetically costly component of parental care (Williams 1996, Reid et al. 2002a), and small birds must spend time off the nest gathering food to supplement their energy

(White and Kinney 1974). Thus, males can potentially help maintain optimal egg temperatures by sharing time on the nest with females and reducing time that developing embryos are exposed to cool temperatures.

Males maintained eggs at cooler temperatures and spent less time on the nest compared with females in four passerine species (Kleindorfer et al. 1995, Reid et al. 2002b, Bartlett et al. 2005). Male incubation may only minimize detrimental effects of inclement weather in such species (Smith and Montgomerie 1992). However, males exhibit equal or higher nest attentiveness (time spent on the nest) relative to females in some species (Miller and Bock 1972, Greenberg and Gradwohl 1983, Morton et al. 1998, Cresswell et al. 2003). Males might exhibit increased egg-warming abilities in species where males invest an equal or greater amount of time on the nest relative to females, but egg-warming abilities of males versus females are unexplored in such species.

We addressed this issue in a population of chestnut-vented tit-babblers *Parisoma subcaeruleum*, a small, socially monogamous passerine of southern Africa. The species is monomorphic, both males and females participate in nest building, incubation, and rearing nestlings and fledglings (Maclean 1993), but only females develop brood patches (Auer pers. obs.). Early observations suggested that males contributed equally to incubation with regards to time spent on the nest (Martin unpubl. data) and, thus, provided a good test of sexual differences in efficacy of heating eggs. We, therefore, measured sex differences in nest attentiveness and egg temperatures experienced by developing embryos during incubation among 12 pairs of this species.

Methods

Study site and species

We studied chestnut-vented tit-babblers at Koeberg Nature Reserve (33° 41'S, 18° 27'E), Western Cape Province, South Africa from August to November of 2000–2004 (Nalwanga et al. 2004, Martin et al. 2006), but examined sex differences in incubation behavior from September to October of 2004. The reserve area covers 3000 ha of low-lying coastal plain, is characterized by a Mediterranean climate, and is dominated by dwarf (<3 m tall) shrubland habitat (Low and Rebelo 1996, Nalwanga et al. 2004). Chestnut-vented tit-babblers typically nest from 0.8–1.2 m high in shrubs ranging from 1–2 m tall (Nalwanga et al. 2004). Nests were located during the building phase and were found primarily through parental behaviour, e.g. adults making frequent trips to the nest site with material. Nests were then monitored daily in the late morning or early

afternoon to check nest contents and determine when laying and incubation were initiated.

Nest attentiveness

We measured nest attentiveness as the percent of time that a bird spent incubating during video observations for 6–7 h during the morning and 2–3 d after the last egg was laid. Twelve nests, each from a different pair, were filmed. All video sessions started at 0.5 h before sunrise to minimize potential effects of time of day (Martin and Ghalambor 1999, Martin 2002). Nests were filmed during the morning and into early afternoon in order to assess parental incubation abilities under the more challenging lower ambient temperatures associated with this time period. Hourly ambient air temperatures (mean \pm standard error) at the site during September, 2004 ranged from $11.9 \pm 0.4^\circ\text{C}$ at 6 am to $17.4 \pm 0.5^\circ\text{C}$ at 2 pm and during October, 2004 ranged from $13.3 \pm 0.4^\circ\text{C}$ at 6 am to $18.1 \pm 0.5^\circ\text{C}$ at 2 pm. Ambient air temperature was recorded by a HOBO Stowaway XTI datalogger secured for the entire season in the shade and at the base of a randomly selected shrub at the site. Thus, nest attentiveness and incubation abilities were monitored at times during the day when ambient air temperatures were well below the average temperature of 32°C required to sustain embryonic development in passerines (Webb 1987).

Nests were filmed using small handheld camcorders that were mounted on a tripod 2–4 m from the nest. Camcorders were covered with camouflage sleeves, and tripods were concealed within the surrounding vegetation. Nest attentiveness of each sex for each nest was later scored in the laboratory. Six different nests were also filmed from dusk until nightfall to determine which sex incubated at night. Nighttime incubation was filmed a total of 10 times; two nests were filmed on three different evenings and the remaining four nests were filmed only once. We assumed that the adult sitting on the nest at nightfall remained there throughout the night.

Males and females are monomorphic and thus were sexed by presence/absence of a brood patch during capture and color-banding of birds during incubation, and by a distinct sex-specific combination of behaviours that were matched to known-sex color-banded birds. In particular, we identified males of each pair by their singing, counter-singing, chasing intruders during territorial disputes, and engaging in aerial display flights as typical of males in the family Sylviidae (Cramp 1992). Additionally, all individuals identified as males through behavioural observations lacked brood patches when captured during incubation ($n = 5$), whereas brood patches were present in all captured individuals identified as females ($n = 4$) by

previous behavioural observations. This 100% concurrence between our behavioral determination of sex identification and presence/absence of brood patches in the hand suggest that we accurately identified sex for our study. A total of 18 of the 24 birds at our 12 nests were banded: nine were captured at the nest during incubation and the rest were captured during the nonbreeding season. At least one member of all 12 pairs was banded such that it was always easy to keep track of male versus female individuals at each nest.

Egg incubation temperature

We measured egg temperatures in the same 12 nests that were concurrently being filmed to determine egg incubation temperatures of males versus females. On the afternoon prior to filming, we inserted a temperature thermister through a small punctured hole in the blunt end of the egg and to where it was positioned in the center of the egg. The hole was then sealed with glue, thereby fixing the thermister and wire in place. The wire was threaded through the nest <6 mm above the nest bottom. This permitted the egg to lie on its side and also allowed the incubating parent to turn the egg. The wire protruding out the bottom of the nest was wound around the substrate trunk and connected to a HOBO Stowaway XTI datalogger (Onset Computer Corporation) placed at the base of the nest substrate. Temperatures were recorded every 12 s on the subsequent day while the nest was being filmed such that concurrent video footage could be used to match the sex of the incubating bird to the recorded egg temperatures.

Statistics

We used a randomized block design with nest pair as the blocking variable in all analyses since measures of parental care of one sex are not independent from contributions made by the other sex. We tested for sex differences in nest attentiveness and whether or not one sex incubated more during the colder, early hours (6–10 am) or the warmer, later hours of the morning (10 am–2 pm) using an ANOVA approach with nest pair as a random, blocking variable and sex and time of day as fixed factors. We tested for sex differences in mean egg incubation temperatures and mean egg rewarming rates using an ANCOVA approach. As in the previous analysis, nest pair was used as a random, blocking variable, sex was included as a fixed factor, and starting temperature as a covariate. Egg rewarming rates were calculated from the mean egg temperature increase during the first five minutes of each on-bout. Data were analyzed using SPSS version 12.0 (2003). All mean values are reported with their standard errors.

Results

Nest attentiveness

Mean nest attentiveness across the 12 nests was $95.8 \pm 1.1\%$ and ranged from 85–100%. The distribution of nest attentiveness was not significantly different from normal (Shapiro-Wilk $W = 0.95$, $P = 0.7$). Nest attentiveness ranged from 31–61% in males and from 31–64% in females. Male nest attentiveness did not differ from females (ANOVA sex: $F_{1,11} = 1.34$, $P = 0.27$; pair: $F_{11,11} = 0.08$, $P = 1.0$), and averaged $45.1 \pm 2.6\%$ and $47.9 \pm 1.8\%$, respectively. On-bouts were longer in the late compared to early morning for both males and females (Fig. 1), but males did not differ from females in on-bout duration; i.e., one sex did not incubate more, earlier or later, on average than the other sex (ANOVA time: $F_{1,34} = 5.36$, $P = 0.027$; pair: $F_{11,34} = 2.61$, $P = 0.016$; sex: $F_{1,34} = 0.61$, $P = 0.44$; sex \times time $F_{1,11} = 0.02$, $P = 0.9$). Male nighttime incubation was observed only one time and at a nest that was filmed for only a single night; the female incubated during the night at all other nests ($n = 5$) and nights ($n = 9$) filmed.

Egg incubation temperatures

Mean egg incubation temperatures ranged from 34.5 – 37.2°C in males and 34.6 – 37.0°C in females and averaged $36.0 \pm 0.02^\circ\text{C}$ and $35.7 \pm 0.02^\circ\text{C}$, respectively. Mean egg incubation temperatures of males were significantly higher than those of their female partners, and these sex differences were not influenced by the egg temperature at which each sex started incubating (ANCOVA sex: $F_{1,11} = 5.32$, $P = 0.042$; pair: $F_{10,11} = 2.66$, $P = 0.067$; starting temperature:

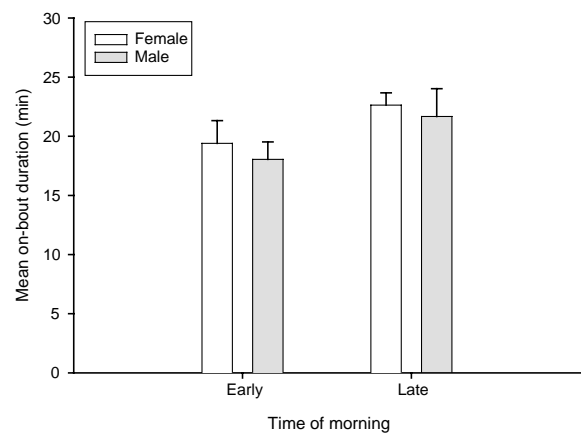


Fig. 1. Chestnut-vented tit-babbler male and female mean on-bout duration in the early (6–10 a.m.) and late (10 a.m.–2 p.m.) morning ($n = 12$ pairs).

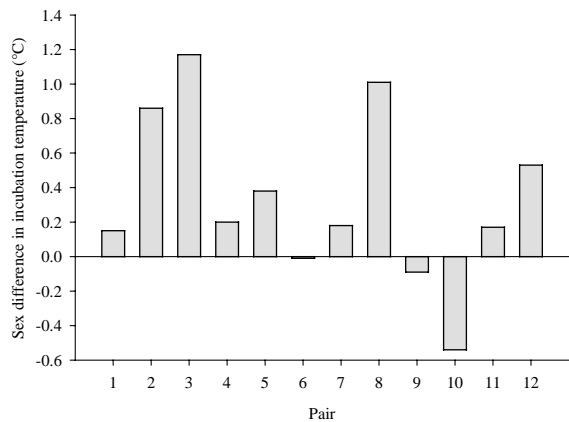


Fig. 2. Sex differences (male minus female) in daytime egg incubation temperatures ($^{\circ}\text{C}$) of 12 pairs of chestnut-vented tit-babbler.

$F_{1,10} = 0.49$, $P = 0.5$; Fig. 2). In one outlier pair (Pair 10; Fig. 2), mean male egg incubation temperature were significantly lower than those of the female; in this particular case, two unusually long off-bouts (3 and 7 min compared to the mean off bout duration of 0.7 ± 0.1 min across other pairs), caused abnormally cold eggs at the start of each of two on-bouts by the male, potentially explaining this contrasting nest. The mean magnitude of difference in male and female incubation temperatures was $0.3 \pm 0.1^{\circ}\text{C}$. Egg rewarming rates were $0.06 \pm 0.01^{\circ}\text{C}/\text{min}$ and $0.04 \pm 0.01^{\circ}\text{C}/\text{min}$ in males and females, respectively. Mean egg rewarming rates were the same across males and females and were not influenced by starting temperatures (ANCOVA sex: $F_{1,10} = 0.14$, $P = 0.72$; pair: $F_{11,10} = 1.11$, $P = 0.44$; starting temperature: $F_{1,10} = 0.002$, $P = 0.96$).

Discussion

Previous studies of sex differences in incubation effort found that lower daytime nest attentiveness in males was accompanied by lower egg incubation abilities relative to females, while male nest attentiveness in other species was equal to or even greater than that of females. Here, we found that equal sharing of daytime nest attentiveness was accompanied by greater egg incubation abilities in males relative to females; daytime nest attentiveness did not differ between males and females, and males incubated eggs at a higher, rather than lower, temperature than their female partners. Moreover, sex differences in egg incubation temperature were not due to one sex incubating more during warmer or colder times of the day. To the best of our knowledge, our results are the first to demonstrate significantly higher egg incubation temperatures in males relative to females.

Males not only rivaled their female mates in their daytime nest attentiveness but also had higher egg incubation temperatures. However, it is unclear if these sex differences in incubation effort are representative of the entire 24 h period in general. For example, we have no reason to suspect that sex-specific incubation patterns might change during the unsampled latter part of daylight hours, but differences might alter our conclusions summarized here. In addition, females appeared to be more involved in nighttime incubation, but this pattern needs to be viewed with caution given our small sample size. Nonetheless, our study clearly shows that males can rival females in time and temperature invested in incubating eggs throughout a substantial portion of daylight hours that might otherwise be spent engaging in self-maintenance activities.

However, males lacked a brood patch, which raises the question of how they can maintain eggs at a higher mean temperature relative to their female mates. Males of many species that share incubation lack a well-developed brood patch (Bailey 1952, Drent 1975) and their ability to regulate egg temperatures within the optimal range is generally thought to be less than females. However, equal or potentially higher incubation temperatures in males relative to females have been reported in at least one species where males lack a brood patch (Ball 1983). Brood patch formation can be costly (Haftorn and Reinertsen 1985, Brummermann and Reinertsen 1991), so the selective advantage of a brood patch remains unclear. Bailey (1952) suggested that brood patches might be beneficial during times of thermal stress such as during the night. Indeed, nighttime incubation appears to be performed solely or primarily by the female in species where males lack a brood patch and contribute to incubation during the daytime (Ball 1983, this study). Finally, if we assume that heat transfer is more effective with a brood patch, then males potentially have to expend substantially more effort than females to maintain similar or greater temperatures in the cold ambient conditions of our study site. Clearly, further investigation is needed to better understand the relationship between variation in brood patch formation, parental incubation effort and thermal efficacy of incubation effort for developing embryos.

Nest attentiveness has been the focal parameter in many studies of sex differences in incubation investment (Schwagmeyer et al. 1999, Gorman et al. 2005a, Kopisch et al. 2005, Martin et al. 2006). Time devoted to incubation represents a significant commitment as it detracts from time otherwise spent foraging and engaging in self-maintenance activities (White and Kinney 1974). While time may serve as a good proxy for energetic expenditure in some cases, results from our study suggest that it may not serve as a true indicator of

differences in male and female parental effort when males and females incubate eggs at different temperatures. This discrepancy in nest attentiveness versus incubation temperature highlights the need to look at multiple aspects of incubation behaviour when examining sex differences in parental effort.

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