



Incubation delays territory defence by male blue-headed vireos, *Vireo solitarius*

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Animals often face trade-offs during reproduction between activities such as parental care and territory defence. In species that are socially monogamous, males and females are faced with the additional problem of coordinating their respective contributions to such activities. Here, we examined male incubation behaviour in a passerine that shows genetic monogamy and in which males incubate extensively. Male incubation is rare in North American passerines and little is known about how males defend their territories during the incubation stage and whether females compensate for lower male incubation during territorial intrusions. Blue-headed vireo males contribute 50% of incubation time during the day. We performed playbacks to simulate intrusions to males while they were on the nest and off the nest during the incubation period. On average, males took 18 min to arrive at the playback location while on the nest incubating, but took less than 2 min when not incubating. In addition, only 44% of the males sang while on the nest, whereas all males sang in response to the playback when off the nest. This result suggests that males probably delay territory defence until females return to the nest to avoid exposing the nest to predators. Females returned to the nest to relieve their mates from incubation duties sooner during experimental intrusions than during control periods, which also allowed males to pursue intruders sooner. Genetic monogamy may underlie this apparent cooperation and the sex-role convergence exemplified in this species.

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Male parental care is most common in birds but is also found in some species of fish and mammals. The large variation in the type and extent of male parental care within species is thought to arise from intersexual conflict (Clutton-Brock 1991). Sexual conflict occurs when the male invests in activities other than parental care to maximize his fitness at the expense of the eggs or young, reducing the fitness of his mate. The most common source of sexual conflict involves species in which males can obtain fertilizations outside a pair bond. Males that are cuckolded and detect a low relatedness to their offspring may decrease parental care. In bluegill sunfish, *Lepomis macrochirus*, where males provide all parental care, there

is sexual conflict because parental males who are cuckolded decrease their defence of the nest, which increases risk of predation to the female's eggs and fry (Neff 2003). In species with an extrapair mating system, males can also increase their reproductive success by investing time and energy in pursuing extrapair fertilizations, which could conflict with parental care duties (reviewed in Whittingham & Dunn 2001). Male Australian fairy martins, *Hirundo ariel*, decrease their participation in incubation when there are more fertile females in the breeding colony (Magrath & Elgar 1997). Male European starlings, *Sturnus vulgaris*, that invest more in attracting additional mates contribute less parental care at the incubation stage (Komdeur et al. 2002). In birds, trade-offs between parental and mating effort within a species have been observed mainly at the incubation stage rather than the nestling-feeding period (reviewed in Magrath & Komdeur 2003). Pursuing extrapair matings may not necessarily be time costly and trade-offs may be less at the nestling stage

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(Pitcher & Stutchbury 2000). To date, many studies have focused on the sexual conflict resulting from male pursuit of alternative mating tactics and investment in parental care (Qvarnstrom 1997; Raouf et al. 1997; Whittingham & Dunn 2001; Royle et al. 2002; Schwagmeyer et al. 2002; Magrath & Komdeur 2003; Barlow 2005; Draganovic et al. 2005).

In contrast, much less is known about the potential for cooperation between pair members in species in which the males do not invest in alternative mating strategies. In species that are socially and genetically monogamous, the costs and benefits of parental care are predicted to be similar for both sexes; in such species, parental care duties may be shared equally and cooperation is more likely to evolve (DeWoody et al. 2000; Schwagmeyer et al. 2002). In the monogamous convict cichlid, *Archocentrus nigrofasciatus*, both males and females care for the young and parents coordinate their activities to the immediate needs of the offspring. Typically, the parents share tasks, but when faced with intruders, the male takes over territory defence and the female cares for the offspring (Itzkowitz et al. 2002). In the spotted tilapia, *Tilapia mariae*, males take over care of the embryos while the female is foraging (Annett et al. 1999). Male and female cooperation with parental duties results in higher survivorship of the embryos and of fry to independence because the time the nest is unattended is reduced (Annett et al. 1999).

The question of how parents coordinate their activities during intrusions in truly monogamous species is little studied. In the monogamous convict cichlid, the male typically responds to intruders; however, if the intruder is larger than the defending male, the female may defend the territory and the male increases his care of the young even though he does not fully compensate for lower female attendance (Itzkowitz et al. 2005). In North American passerine birds, males typically sing, patrol and defend territories from conspecific intruders and few species show extensive male incubation. In species in which males extensively contribute to incubation, it is not known how males resolve the conflict of dealing with intruders. Do males leave the eggs to defend territories and do females compensate for their mates' lower nest attendance during intrusions?

Here, we examined how male blue-headed vireos resolve the conflict between territory defence and incubation duties. In this species, males contribute an average of 49% of daytime incubation and male effort remains constant throughout the 14-day incubation period (Morton et al. 1998). In addition, males are solely responsible for the acquisition and defence of territories. Large territories are an important prereproductive investment for males because males having the largest territories attract mates earlier than those acquiring smaller ones (Morton et al. 1998). Maintaining large territories is also important because nest predation is high and re-nesting attempts are often far, over 100 m, from the failed nest (I. Chiver, unpublished data). Males defend territories by singing and patrolling their territories; song duels at borders as well as fighting are often observed throughout the breeding season (James 1978). While incubating, males are unable to patrol or to engage intruders directly. They ordinarily

do not leave the nest until their mates approach and, following soft vocalizations, they exchange quickly in a coordinated fashion. Males occasionally sing from the nest (James 1998) but because of the large size of territories, singing from the nest probably cannot take the place of patrolling.

There is extensive variation in male incubation effort, ranging from 14.5% to 100%. Greater male incubation effort results in higher nest survival during the incubation period (Morton et al. 1998). Females compensate for low male incubation effort by increasing their own time on the nest, and together, the pair members keep the eggs covered for 96% of the time during the incubation period. It is not known whether male variation in incubation effort is a result of conflict with territory defence.

In this study, we used playbacks to simulate intrusions to (1) document the response of males to intruders while on the nest incubating versus off the nest during the incubation stage of nesting, (2) determine whether male blue-headed vireos sing from the nest in response to intruders and (3) determine whether females return to the nest sooner during intrusions, allowing their mates to leave their nest.

MATERIALS AND METHODS

The study was conducted in a 150-ha continuous mixed forest in northwestern Pennsylvania, U.S.A. The forest supports approximately 25 pairs of blue-headed vireos each year. Playback experiments were conducted in 2003 and 2004. Each year, at the beginning of the breeding season, the adults were colour banded for individual recognition as they returned to breed in mid-April and early May. We monitored territory sizes by observing singing males and territory disputes with neighbours.

To determine how male vireos respond to territorial intrusions during the incubation stage, playback experiments ($N = 9$) were conducted in a paired design: when males were on the nest and off the nest. Playback experiments were conducted within 3 days of incubation commencement, between 0800 and 1400 hours. During the incubation stage, pair members switch at the nest approximately every 30 min, and in the present study, there was no difference in the time of day for playbacks while the male was on the nest and off the nest (paired sample t test: $t_{16} = 0.17$, $P = 0.87$).

A standard playback tape, 3-min long, consisted of a natural song series that contained 21 different song types recorded from a local conspecific male that was no longer present at the study site. The song was recorded in 1996, through a Sennheiser MKH 104 omnidirectional microphone mounted in a 44-cm diameter parabolic reflector, using a Nagra III tape recorder with a recording speed of 38.1 cm/s. This high-quality recording was copied from the Nagra to a Sony ProII cassette recorder onto a 60-min Sony Type II High Bias cassette tape. Songs were played back through an SME-AFS amplified field speaker driven by a Sony ProII cassette tape recorder.

In this species, each male sings 6–22 different song types, one following another at the rate of 20–30 songs/min,

forming a first-order Markov chain wherein individual song types are delivered in a stereotyped sequence (e.g. A-B-C-D-A-B-C-D, etc., Martindale 1980; James 1981). Within a population, males share most songs but each bird has a slightly different repertoire of additional songs (reviewed in Morton et al. 2006).

During playback experiments, the speaker was placed at a standard distance of 50 m from the nest and within the male's territory. The amplitude was set at 100 dB SPL at 1 m measured with a General Radio sound and vibration analyser. Each male was presented with two playbacks: one while off the nest (control) and the other while incubating for 2 min following a nest exchange, to ensure that all males were at the beginning of an incubation bout. The order of the playbacks (control versus experiment) was randomly assigned for each male. The playback was repeated every 10 min until the male arrived within 5 m of the playback location. The time (min) from the start of the playback experiment until the male arrived within 5 m of the playback site constituted the response time.

Next, we examined whether females returned to the nest sooner and whether males sang on the nest more frequently during playbacks compared to control conditions (without any playbacks). In addition to the nine pairs where playbacks were performed in a paired design, we performed playbacks to seven additional pairs during male incubation bouts only. For males, singing on the nest was noted. Female return time to the nest during playback conditions was calculated as the time (min) she spent off the nest between incubation bouts.

To determine the birds' behaviour during control conditions, we monitored the birds' incubation and singing behaviour at the nest using video cameras. In addition to the nine pairs monitored for male response time to playbacks, 13 pairs were videotaped for a total of 77 h (average 3.5 h/nest). The incubation time and the time it took to return to the nest between incubation bouts ('return time') were recorded for each sex. During control conditions, female return time to the nest was calculated as the average time (min) she spent off the nest between incubation bouts. For males, we noted song on the nest. To determine whether males are more likely to sing on the nest during playback conditions, we compared male responses during playback experiments to one randomly selected incubation bout during control conditions. In addition, we compared average song rate (number of songs/min) for males during playback and control conditions.

Statistical Analysis

Analyses were conducted using SPSS 14.0 (SPSS, Chicago, Illinois, U.S.A., 2005). We used parametric tests because all data were normally distributed (Shapiro–Wilk tests: $P > 0.1$) except where noted. Tests are two tailed.

RESULTS

Males took significantly longer to respond to the playback when they were on the nest incubating (average

time: 18.2 min) than when they were off the nest (<2 min) (paired samples t test: $t_8 = 7.0$, $P < 0.001$; Fig. 1). Once off the nest, all males sang in response to the playback and searched for the intruder near the playback station.

While on the nest incubating, 3 of 16 males left the nest during playback before their mates returned. All others waited to be relieved by their mates. Variation in male response time was not related to incubation effort (average response time during the day: 56%; range 45–67%, Pearson correlation coefficient: $r_7 = -0.28$, $P = 0.45$).

Males were more likely to sing while on the nest during playback than during control conditions. During playbacks, 44% of the males sang in response to the simulated intruder (7 of 16; five males sang only during the 3-min playback, while the other two sang following the playback as well), whereas during control conditions, only 18% of males sang on the nest (4 of 22 males; Fisher's exact test: $P = 0.16$, $N = 41$). During control conditions, three of the four males that did sing on the nest, appeared to do so in response to neighbours' song. Taking into account all observations of male incubation, average song rate of males that sang on the nest during playback was significantly higher (0.85 songs/min, $N = 7$) than the song rate of males that sang on the nest during control conditions (0.19 songs/min, $N = 16$) (independent samples t test: $t_{21} = -4.46$, $P = 0.003$).

To determine whether females returned to the nest sooner during simulated intrusions than during control periods, we compared their mean return times to the nest during both conditions. Average return time of females to the nest was significantly less during playback (16.4 min) than during control periods (27.7 min) (independent samples t test: $t_{24} = 4.8$, $P < 0.009$; Fig. 2a). We also compared return times of nine females both during playback and during control conditions to allow a within-female pairwise test. Individual females also showed a significant tendency to return to their nest sooner during playback than during control periods (18.0 min versus 27.7 min, respectively; paired samples t test: $t_8 = 3.2$, $P = 0.011$; Fig. 2b).

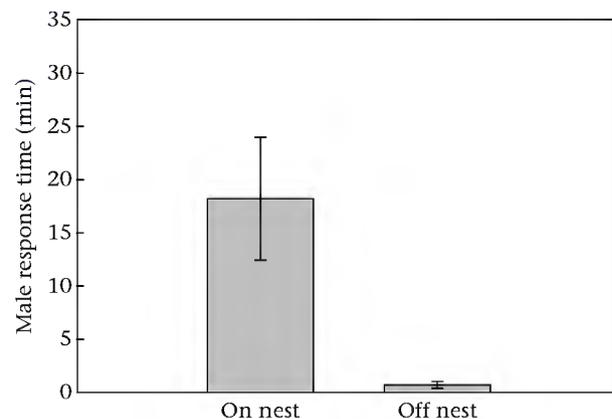


Figure 1. Mean response time (with 95% confidence intervals) of male blue-headed vireos ($N = 9$) to playbacks while off the nest versus on the nest during the incubation stage. Response time was defined as approach and song within 5 m of the playback station.

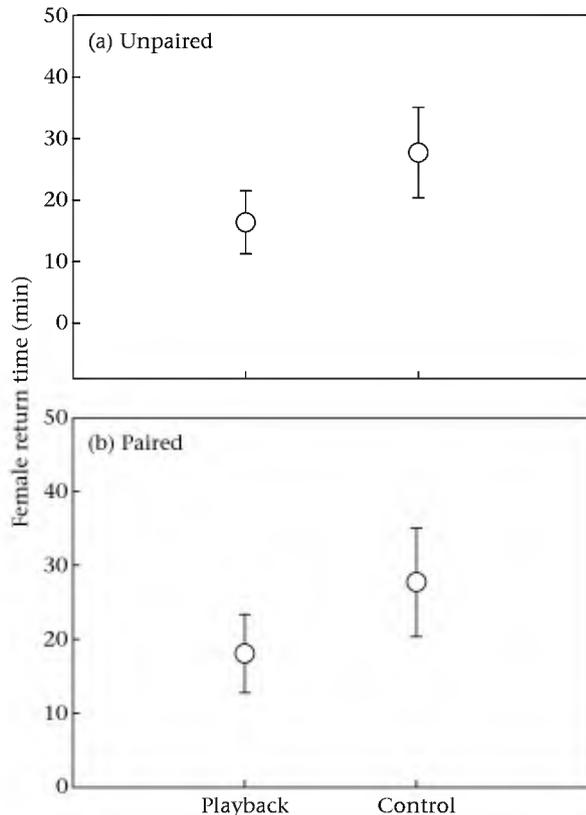


Figure 2. Mean female return time (with 95% confidence intervals) to the nest during natural versus playback conditions. (a) Unpaired test: females observed during no-playback ($N = 22$) and playback conditions ($N = 16$). (b) Paired test: females observed during both no-playback and playback conditions ($N = 9$).

DISCUSSION

During simulated intrusions, most blue-headed vireo males waited until their mates relieved them before leaving the nest to investigate the playback. Thus, males choose to remain on the nest and provide parental care rather than departing and confronting an intruder. Males may stay on the nest to reduce predation risk to eggs, because nests at which males spend more time incubating have higher survivorship to the hatchling stage (Morton et al. 1998). Our study is the first to show that male incubation in a passerine species is favoured over territory defence, possibly as a result of predation pressure.

This trade-off is found in other species. In the monogamous convict cichlid, paired males spend more time patrolling their territory than they do guarding the nest; however, when their mates are removed, males spend more time guarding the nest, suggesting that defence of the young is more important than guarding against intruders (Itzkowitz et al. 2001). In the moustached warbler, *Acrocephalus melanopogon*, male incubation effort increases with increased risk of predation (Kleindorfer & Hoi 1997). In the Seychelles warbler, *Acrocephalus sechellensis*, males guard their nest intensively on islands where predators are present and, when predation risk is increased, males increase the time that they spend guarding the nest (Komdeur & Kats 1999).

Males in the present study showed variation in their response to playbacks while they were on the nest incubating; however, this was not related to male incubation effort over the season. Most males (16 of 19) waited for their mates to return before leaving to search for the intruder, so female return time may dictate when males leave the nest. Female condition or foraging efficiency may affect when a female returns to the nest to allow the male to respond to intruders. In the Antarctic petrel, *Thalassoica antarctica*, females in poorer condition take longer foraging trips, forcing their mates to remain at the nest for longer periods (Tveraa et al. 1997). In the pied flycatcher, *Ficedula hypoleuca*, when females received extra food, they spent more time on the nest and less time foraging (Smith et al. 1989). Male response to intruders during the incubation stage may therefore depend both on the female's ability to return to the nest and the costs to the female of reducing foraging trips.

Three of 19 males left the nest before their mates returned to take over incubation duties, and two of these males sang on the nest before departing and flying to the playback location. In another study, male singing and territorial aggression in blue-headed vireos was inversely related to the amount of parental care during incubation as well as all other nest stages (Van Roo 2004). Of the three males that left the nest before their mates returned, one male contributed 45% of incubation duties, so for this male, incubation effort appeared to be lower than that of other males that did not leave the nest early. When considering all males in the study, male response to the playback was not related to incubation effort. Hyman et al. (2004) found that male age and previous interactions with neighbours in song sparrows, *Melospiza melodia*, affected response strength to playbacks of conspecifics. Experienced males approached the playback location and spent more time singing in response to the playback. In our study, 17 of the 19 male subjects were at least 2 years of age or older, so male age was probably not a factor. Male aggressiveness may be influenced by interactions within the neighbourhood, such that some males may respond more strongly because they have been recently challenged by neighbouring males (Wingfield et al. 1987). Although hormone profiles of male blue-headed vireos vary (Van Roo et al. 2003), it is not clear why and how individual variation affects male aggressive behaviour.

Given that males chose to remain on the nest during simulated intrusions, one way to defend the territory while on the nest incubating is to sing from the nest. Males that sang from the nest sang at a significantly higher song rate during playback than they did when singing from the nest during control conditions. Singing by itself has been shown to be effective in repelling conspecific males in the short term (Krebs 1977; Falls 1987). However, when songs of nonconspecific males were played back on territories of nonincubating males, all males sang in response to the playback and approached the playback station within 2 min. Males in this species often sing along their territory boundaries, and a response from one of their neighbours results in border song duels (where males are within 15 m of each other) and

sometimes fights. In addition, singing on the nest may attract predators. Willow flycatchers, *Empidonax traillii*, that vocalized more were more likely to be parasitized by brown-headed cowbirds, *Molothrus ater* (Uyehara & Narins 1995). Singing on the nest, therefore, may be ineffective and sometimes costly, and males that do sing on the nest may be making the best of a bad situation.

In other taxa with biparental care, the male or the female is able to assume either territory defence or care of the offspring (Storey et al. 1994; Itzkowitz et al. 2001). In blue-headed vireos, as in most temperate zone passerines, only the males sing and defend territories. So, we wanted to determine whether females return to the nest earlier during intrusions, freeing their mates to defend the territory. Female breaks from incubation were indeed shorter during playbacks than during control conditions (Fig. 2). On average, females spent 35% less time foraging during playbacks than during control conditions (18 min versus 28 min). In this way, females may cooperate with their mates in defending their territories more efficiently. Males, once relieved, flew directly to the playback site, in some cases, several minutes after playback had ceased, which is consistent with their ability to range and remember locations of intruders after intruders have stopped singing (Morton et al. 2006). These results suggest that incubating males could respond to intruders even more rapidly if they were relieved by their mates sooner.

Pair members in blue-headed vireos share nesting duties extensively, much more than is usual for temperate zone songbirds. Males devote as much effort as females to nest building, daytime incubation and feeding nestlings (James 1998). Pair members jointly defend against nest predators, such as blue jays, *Cyanocitta cristata*, which are attacked in coordinated dives, with each pair member coming from opposite directions nearly simultaneously (Morton et al. 1998). Morton et al. (1998) suggested that genetic monogamy underlies the extensive male contribution to reproduction. In the present study, we found that females appear to cooperate with their mates by relieving males from incubation earlier during territorial intrusions. Variable intensity in incubation by females may be an indirect form of territorial defence that should be looked for in other bird species with egalitarian sex roles during reproduction.

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