

Male songbirds provide indirect parental care by guarding females during incubation

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Across many taxa, guarding of fertile mates is a widespread tactic that enhances paternity assurance. However, guarding of mates can also occur during the nonfertile period, and the fitness benefits of this behavior are unclear. Male songbirds, for example, sometimes guard nonfertile females during foraging recesses from incubation. We hypothesized that guarding postreproductive mates may have important, but unrecognized, benefits by enhancing female foraging efficiency, thereby increasing time spent incubating eggs. We tested the hypothesis in 2 songbird species by examining female behavior during natural and experimentally induced absences of males. Male absence caused increased vigilance in foraging females that decreased their efficiency and resulted in less time spent incubating eggs. Male guarding of nonfertile females can thus provide a previously unrecognized form of indirect parental care. *Key words*: foraging, gray-headed juncos, mate guarding, parental care, red-faced warblers. [*Behav Ecol* 20:1034–1038 (2009)]

The close association of animal social pairs during the breeding season is ubiquitous and often explained as a mechanism to protect paternity (Møller and Birkhead 1989; Birkhead and Møller 1992; Alcock 1994; Shine 2003). Guarding of fertile females by males can protect their paternity and increase mating success in taxa as diverse as insects (Alcock 1994), fish (Reavis and Barlow 1998), reptiles (Shine 2003), mammals (Møller and Birkhead 1989), and birds (Birkhead and Møller 1992). Mate guarding may also continue after insemination, and most hypotheses of this behavior assume that females are still fertile and paternity is at risk (Alcock 1994). However, guarding of mates persists into nonfertile periods in some species (Barber et al. 1998). The benefit, if any, of guarding nonfertile mates is unknown.

The question of why males guard nonfertile mates is particularly pertinent for avian species. Males of some species guard their female partner while she forages during recesses from incubation (McDonald and Greenberg 1991; Gilbert 1994; Barber et al. 1998), a period when females are both not fertile and incapable of sperm storage (Briskie 1994). Guarding of these nonfertile females by males is surprising given current theory. Indeed, when females are nonfertile and have embryos, guarding clearly does not serve a paternity function. One novel and, as yet, untested alternative explanation for this behavior is that guarding may improve female foraging efficiency (Artiss and Martin 1995; Barber et al. 1998) to thereby enhance incubation performance. In other words, guarding may provide an unrecognized form of indirect parental care by males.

Incubation is energetically expensive for small birds that necessitates breaks from incubation to forage for energy replenishment (Lack 1940; Williams 1998). Males do not incubate in most species (Lack 1940; White and Kinney 1974), but males of species with nests that are relatively safe from predation (e.g., cavity nests) provide indirect parental care by

delivering food to incubating females (White and Kinney 1974; Carey 1980; Lyon and Montgomerie 1985). Such energy delivery enables females to spend more time on the nest, enhancing fitness through improved survival and faster developmental rates of avian embryos (White and Kinney 1974; Carey 1980; Lyon and Montgomerie 1985, Martin et al. 2007). However, male visits to the nest can increase the likelihood of nest predation, thereby constraining supplemental feeding of females by their male mates in species with higher predation risk (Martin and Ghalambor 1999). We hypothesized that male guarding of females during foraging bouts in the incubation period is a subtle, and previously overlooked, strategy to enhance energy acquisition by female mates. If guarding allows females to forage more efficiently, this may indirectly enhance male fitness because it allows females to increase attendance of eggs without increasing nest predation risk.

To avoid predators, birds must be vigilant while foraging (Lima and Dill 1990). The presence of other birds can allow individual vigilance to decrease and foraging efficiency to increase (Lima et al. 1999). Guarding by males may provide such vigilance, permitting females to decrease vigilance, forage more rapidly, and increase prey attack rates. In turn, increased foraging efficiency could increase time spent incubating by females (nest attentiveness). We tested the influence of male guarding on female foraging efficiency and nest attentiveness in 2 species of ground nesting passerines at high elevation sites in Arizona, where adult predators such as bird-eating raptors (e.g., sharp-shinned hawk *Accipiter striatus*, Cooper's hawk *Accipiter cooperii*) are common. Furthermore, if males are focused on predator vigilance when guarding females, we would predict a decline in male foraging efficiency in the presence of females. We also examined the potential costs to males by measuring their foraging efficiency in the presence and absence of females.

Gray-headed juncos (*Junco hyemalis caniceps*) and red-faced warblers (*Cardellina rubrifrons*) rarely feed their mates (Martin and Ghalambor 1999), only females incubate (Martin and Barber 1995; Nolan et al. 2002), and males commonly guard females during incubation recesses, although males are absent for some recesses (Barber et al. 1998). We observed female foraging and incubation behaviors when males were

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present and during natural and experimentally induced male absences.

MATERIALS AND METHODS

Study area and study species

The study area was located on the Mogollon Rim in central Arizona at approximately 2600 m elevation and consisted of a series of snowmelt drainages (Martin 1998). Data were collected from May–June 2000, 2001, and 2007 for red-faced warblers and May–June 2007 for gray-headed juncos. We located nests, collected foraging data, and performed temporary removals of males of 2 passerine species. Red-faced warblers are small (ca. 9 g) ground nesting birds that forage in the mid and upper canopy (Martin and Barber 1995). Gray-headed juncos are larger (ca. 24 g) than red-faced warblers and also nest in open-cup nests on the ground but forage primarily on the ground (Nolan et al. 2002). Males of both species are often in close proximity of their mates during foraging incubation recesses. For example, Barber et al. (1998) followed 15 pairs of red-faced warblers during incubation recesses in 2 consecutive years. Overall, the mean distance between pairs was 9 m in 1 year and 15 m in the other. Under natural circumstances, we found gray-headed junco males were present for all but 1 of the 43 female “foraging sequences” we recorded (see below for definition). Some birds in our study were not banded (gray-headed juncos: 4 of 13 females; red-faced warblers: all unbanded), but individual identification was confirmed by following females away from their nests for observations. We determined breeding stage based on nest content and parental behavior.

Foraging observations and incubation patterns

Foraging behavior observations were conducted between 0600 and 1430 during incubation. The incubation period began when the final egg in a clutch was laid and females spent the majority of their time on the nest. Incubation continued until the eggs hatched or the nest was predated. Males were considered present during female incubation recesses when they were less than 10 m from the female. While following a bird, its foraging maneuvers were dictated into a portable tape recorder and later transcribed using a digital stopwatch. Incubation patterns in 2000 and 2001 were determined using video cameras (for details, see Martin et al. 2007). Incubation patterns in 2007 were recorded by placing a temperature data logger (Hartman and Oring 2006) in the nest. These devices recorded the temperature every 2 min, and we determined off-bout duration from these temperature data. Video cameras and temperature data loggers provided similar data on incubation patterns (Martin et al. 2007) and were combined for all red-faced warbler incubation analysis. We recorded the duration of each on- and off-bout throughout the observation periods. Incubation schedules were documented between 0600 and 1430 to correspond with the foraging observations.

Removals

Males were temporarily removed during incubation (gray-headed juncos: $n = 10$; red-faced warblers: $n = 8$). Removals occurred throughout the incubation period, ranging from the second day of incubation until the day before hatch. Birds were captured between 0600 and 0730 h using mist nets and playbacks of recorded songs. Individuals were placed in a cage and given mealworms and water ad libitum. Individuals were removed for up to 7 h and released back onto their territories at the end of the experiment. Males resumed normal activities after release.

Analyses

Foraging data were averaged over multiple observations for each individual, so that each individual was represented once for each treatment (male present or male absent). Foraging sequences were >30 s (Robinson and Holmes 1982; mean number of sequences = 5.6 ± 0.4 standard error of mean [SEM], mean sequence duration = 3.4 ± 0.7 min). The foraging variables of interest differed between the 2 focal species. For gray-headed juncos, the response (foraging) variables of interest were collected for females and included: 1) the number of movements per minute, 2) the number of foraging attacks per minute, and 3) the number of alert postures per minute. For red-faced warblers, the response variables of interest were collected on males and females and included: 1) the number of movements per minute, 2) the number of foraging attacks per minute, and 3) the percentage of flight maneuvers. We tested the significance of male presence on female foraging behaviors using 2 approaches because of different data structures. Experimental foraging data were available for all red-faced warblers in a matched-pairs format. We therefore used matched-pairs *t*-tests for these analyses. Several ($n = 3$) gray-headed junco nests were predated during the study, and therefore, matched-pairs data did not exist for all nests. Thus, for gray-headed juncos, we tested the significance of male presence on female foraging using a mixed-model approach to accommodate individual identity as a random factor into the estimation of model parameters.

Incubation patterns were studied at 7 nests from 7 unique pairs of each species. The effects of male presence on female incubation behavior were all analyzed in a matched-pairs format. We recorded mean incubation on- and off-bout lengths. Incubation patterns at each nest were measured under both treatments (male present or absent). To analyze effect of males on the total amount of time females spent incubating, we standardized incubation time to a 6 h period. We chose to standardize over a 6 h period for direct comparison with video data on incubation patterns that were typically collected over a 6 h period (Martin et al. 2007). This time frame included the hours of greatest daily activity for both species. Control and experimental observations were performed on consecutive days. The order of the control and experimental observations was randomized across nests. Data were presented as mean (\pm SEM) and all analyses were conducted in SAS ver. 9.1.

RESULTS AND DISCUSSION

When males were experimentally absent, female gray-headed juncos dramatically increased their number of alert postures per minute (generalized linear mixed model [GLMM], $F_{1,8,3} = 23.48$, $P = 0.001$, $n = 13$ females; Figure 1A), where vigilance was measured as the number of upright alert postures per unit time. We had limited vigilance data for red-faced warblers ($n = 3$ individuals), but the pattern was similar with increased female vigilance during experimental male absence (female alert postures per minute: male present = 1.2 ± 0.7 , male absent = 7.4 ± 0.4). In addition, during experimental removals red-faced warbler females significantly decreased the frequency of foraging maneuvers that involved flight, a behavior that increases conspicuousness to avian predators (matched-pairs *t*-test, $t_7 = -3.61$, $P_{1-tailed} = 0.004$; Figure 1B). This pattern of decreased foraging maneuvers that involved flight was the same for female red-faced warblers when we compared natural male absences with male presence (*t*-test, $t_{18} = -2.77$, $P_{1-tailed} = 0.006$). Thus, females of both species showed increased behaviors consistent with vigilance and aversion to risky behavior in the absence of males, which can affect female foraging efficiency.

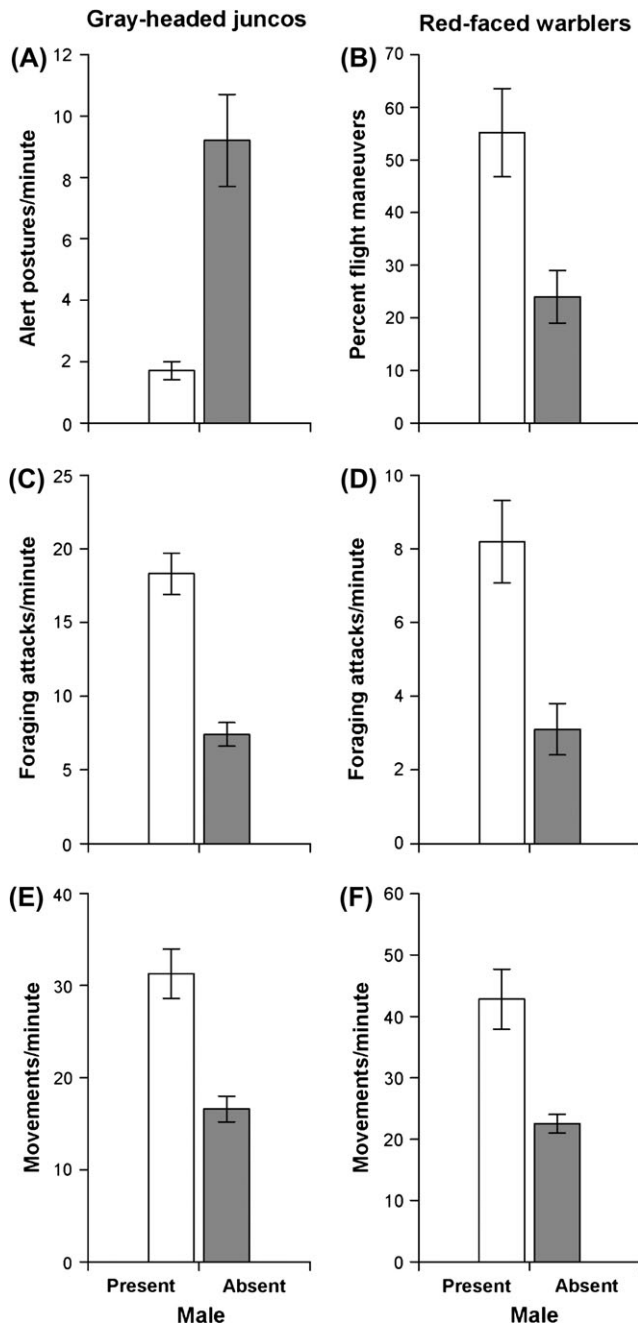


Figure 1

Female foraging behavior in presence and absence of their male partner for gray-headed juncos and red-faced warblers. (A) Gray-headed junco mean number of alert postures per minute, (B) red-faced warbler percentage of movements that involved flight, (C–D) mean number of movements per minute, and (E–F) mean number of foraging attacks per minute. Male absence significantly affected risk aversion behavior in both species. (A) Male absence increased the number of gray-headed junco female alert postures per minute and (B) reduced the overall percentage of female red-faced warbler flight maneuvers. When males were absent, (C) female movement rate decreased in gray-headed juncos and (D) red-faced warblers. Female foraging rate also decreased in both species. The means \pm SEM (error bars) are shown. Percent data (B) were arcsine transformed prior to analysis.

When males were removed, females of both species also decreased foraging attack rates (gray-headed juncos: GLMM, $F_{1,18} = 45.69$, $P < 0.001$, $n = 13$ females, Figure 1C; red-faced

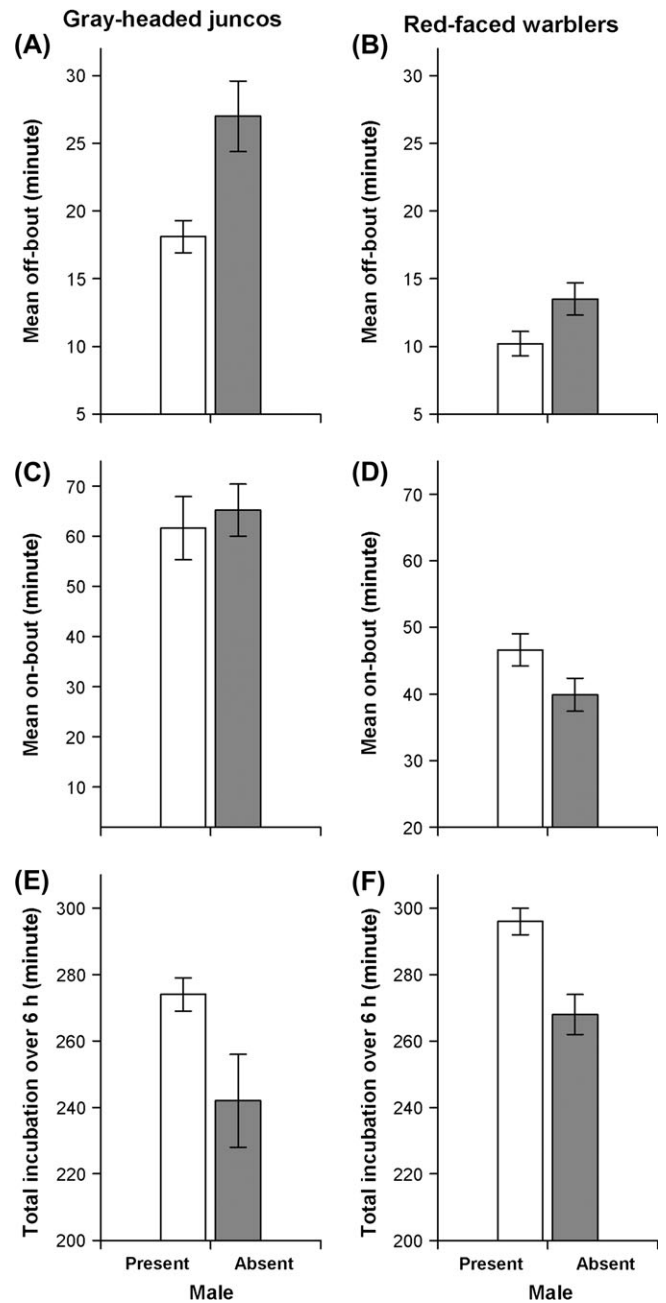


Figure 2

Incubation behavior of females in the presence and absence of males. Male absence was associated with longer female foraging bouts off the nest (i.e., recesses) in both (A) gray-headed juncos and (B) red-faced warblers. (C) Male absence did not affect duration that females spent on the nest during an incubation bout (i.e., on-bout duration) in gray-headed juncos. (D) However, for red-faced warblers female on-bout duration decreased when males were absent. We standardized the total time (minute) a female spent on the nest incubating to a 6 h period in order to examine the overall effect of male absence on female incubation. Male absence resulted in females spending less time on the nest in both species. The means \pm SEM (error bars) are shown for 7 nests for each species.

warblers: matched-pairs t -test, $t_7 = -6.22$, $P_{1-tailed} < 0.001$, Figure 1D) and moved substantially more slowly (gray-headed juncos: GLMM, $F_{1,11.1} = 26.51$, $P < 0.001$, $n = 13$ females, Figure 1E; red-faced warblers: matched-pairs t -test, $t_7 = -4.82$, $P_{1-tailed} < 0.001$, Figure 1F). Again, for female

red-faced warblers, the pattern of decreased foraging attack rates and movements per minute was similar when males were naturally absent (foraging attack rates per minute: t -test, $t_{18} = -7.48$, $P_{1\text{-tailed}} < 0.001$; movements per minute: t -test, $t_{18} = -4.46$, $P_{1\text{-tailed}} < 0.001$). Thus, energy acquisition appeared to be compromised by male absence, which could then influence energy available for incubation. Consistent with this interpretation, altered female foraging behavior during male absences corresponded with reductions in the time females spent incubating eggs. Incubation analyses were all paired within each nest. Both species increased duration of foraging recesses from incubation (i.e., off-bout durations) when males were absent (gray-headed juncos [matched-pairs t -test within nests]: $t_6 = -2.56$, $P = 0.043$; red-faced warblers: $t_6 = -4.12$, $P = 0.006$; Figure 2A–B). Duration of time that females spent on the nest for each incubation bout (i.e., on-bout durations) did not change in response to male absence in gray-headed juncos (matched-pairs t -test within nests, $t_6 = -0.61$, $P = 0.563$; Figure 2C) but was reduced for red-faced warbler females ($t_6 = 2.89$, $P = 0.028$; Figure 2D). Together, these behavioral changes yielded a substantial overall decrease in the amount of time females spent on the nest in a standardized 6 h period (gray-headed juncos: $t_6 = 2.98$, $P = 0.025$, red-faced warblers: $t_6 = 5.79$, $P = 0.001$; Figure 2E–F). Thus, males clearly provided benefits to offspring when guarding foraging females by increasing female nest attentiveness.

Given the benefits of increased incubation to multiple fitness-related traits (White and Kinney 1974; Carey 1980; Lyon and Montgomerie 1985, Martin et al. 2007), we might wonder why all species with female-only incubation do not show strong guarding of mates? One possibility is costs to males of guarding females. Mate guarding may be energetically costly (Komdeur 2001) and may compromise male foraging efficiency. We examined foraging behavior of male red-faced warblers while attending foraging females versus foraging alone while the female was incubating. Males had lower foraging efficiency when guarding females including decreased number of movements (matched-pairs t -test within pairs, $t_6 = -11.43$, $P < 0.001$; Figure 3A) and foraging attacks ($t_6 = -10.96$, $P < 0.001$; Figure 3B) per minute. Males also avoided risky behavior while following females and engaged in 66% fewer flight maneuvers ($t_6 = -9.44$, $P < 0.001$; Figure 3C). Thus, males may incur significant foraging costs when guarding their mates.

Species constrained from feeding their mates by nest predation risk (Martin and Ghilambor 1999) may enhance incubation of eggs through the close proximity of males during female foraging recesses. Suboptimal incubation conditions can lengthen incubation period, increase risk of predation,

and depress survival and quality of embryos (White and Kinney 1974; Carey 1980; Lyon and Montgomerie 1985, Martin et al. 2007) that may affect offspring fecundity later in life (Gorman and Nager 2004). Thus, male vigilance during the nonfertile period can indirectly benefit offspring fitness in multiple ways and, thereby, represents an indirect form of parental care. Male parental care is rare in animals, with birds being notable exceptions. Yet, even in birds, attention has focused on male feeding of nestlings. Our study suggests that male contributions to indirect parental care during incubation may be much more common than currently recognized. We recommend broader consideration of indirect male contributions when considering measurements of parental care investment.

Trade-offs between parental effort and additional mating effort have long been of interest to biologists (Trivers 1972; Magrath and Komdeur 2003). However, male guarding of females during incubation is a component of male investment that has not been recognized in the literature on avian mate choice (Andersson 1994). Our understanding of sexual selection and mating systems requires accurate quantification of male investment, but until now the importance of male guarding as an indirect form of parental care has been ignored. Indeed, extrapair copulations (EPCs) are common in both gray-headed juncos and red-faced warblers (Martin and Barber 1995; Nolan et al. 2002), and males may sacrifice EPC opportunities (mating effort), whereas they are guarding mates during the incubation period (parental effort). This trade-off between mating and parental effort may ultimately be mediated by variation in nest predation risk in that higher predation risk may result in greater mating effort. Recognition and quantification of the guarding of mates during the nonfertile period, and the indirect parental care it provides for avian species constrained from feeding at the nest, may be critical to understanding sexual selection and the trade-offs between mating and parental effort that are currently underappreciated.

Our research also challenges a commonly used definition of mate guarding. Fundamentally, mate guarding involves the close proximity of social pairs combined with male following of female-initiated movements. However, the term “mate guarding” is often used synonymously with paternity assurance because of the extensive literature on the importance of mate guarding for paternity assurance in many taxa (e.g., Alcock 1994). Furthermore, mate guarding is considered widely in terms of the fertilization benefits that result from guarding mates (Alcock 1998). Others have suggested that male vigilance can improve female foraging efficiency (Artiss and Martin 1995; Barber et al. 1998), however, our research

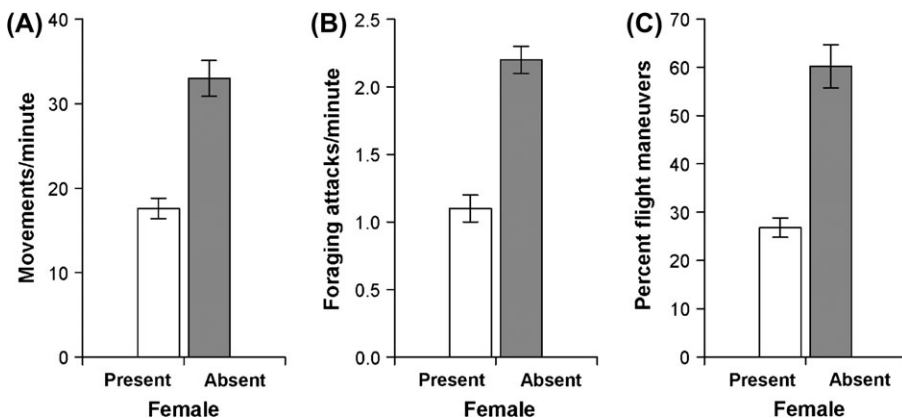


Figure 3
Foraging behavior of male red-faced warblers when females were present and absent. (A) Males moved at lower rates per minute when females were present. (B) Males also demonstrated lower foraging attack rates in female presence. (C) Overall, female presence had a negative effect on the percentage of flight maneuvers of males. The means \pm SEM (error bars) are shown for 7 pairs. Percent data (C) were arcsine transformed prior to analysis.

experimentally tested this hypothesis during the nonfertile period. We showed that male guarding during the nonfertile period can potentially convey fitness benefits to the male outside of the fertilization benefits conferred by guarding during the fertile period. Thus, we propose a reconsideration of the commonly accepted definition of mate guarding to more generally include consideration of all potential fitness benefits—those realized through both paternity assurance and indirect parental care.

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