

Effects of breeding density and plumage coloration on mate guarding and cuckoldry in blue grosbeaks (*Passerina caerulea*)

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Abstract: For species in which females mate outside of the pair bond, selection should favor male mate-guarding behaviors that minimize investment in genetically unrelated offspring. Mate guarding may impose costs by diverting time and energy from activities such as foraging and seeking extra-pair copulations, so males should adjust their mate-guarding behavior according to the risk of cuckoldry. In this study, we investigated cuckoldry and mate guarding in the blue grosbeak (*Passerina caerulea* L., 1758), a socially monogamous, territorial songbird. Fifty-three percent of nestlings were extra-pair, and 70% of nests had at least one extra-pair fertilization. Males with dull plumage coloration were more likely to be cuckolded than males with more brightly colored plumage, but duller males did not guard their mates more. Instead, males appeared to adjust mate-guarding behavior according to the attractiveness of neighbors. Males with more brightly colored neighbors guarded their mates more intensely than males with fewer colorful neighbors. These observations suggest that in the blue grosbeak, mate guarding is a context-dependent strategy that is adjusted according to the density and ornamentation of neighboring males.

Résumé : Chez les espèces dont les femelles s'accouplent en dehors du lien de couple, la sélection devrait favoriser chez les mâles des comportements de surveillance du partenaire qui minimisent l'investissement dans les rejetons non apparentés génétiquement. La surveillance du partenaire peut imposer des coûts en détournant temps et énergie d'activités telles que la recherche de nourriture et la poursuite de copulations hors-couple; les mâles doivent donc ajuster leur comportement de surveillance du partenaire en fonction de leur risque d'être cocufiés. Notre étude examine l'infidélité et la surveillance des partenaires chez le guiraca bleu (*Passerina caerulea* L., 1758), un oiseau chanteur territorial et socialement monogame. Cinquante-trois pour cent des petits au nid sont d'origine hors-couple et 70 % des nids contiennent au moins un petit issu d'une fertilisation hors-couple. Les mâles au plumage de coloration terne ont plus de chances d'être trompés que les mâles au plumage plus brillamment coloré; toutefois, les mâles plus ternes ne surveillent pas plus leurs partenaires. Au contraire, les mâles semblent ajuster le comportement de surveillance de leur partenaire au pouvoir d'attraction de leurs voisins. Les mâles dont les voisins sont plus brillamment colorés gardent leur partenaire avec plus de soins que ceux qui ont moins de voisins bien colorés. Ces observations indiquent que la surveillance du partenaire chez le guiraca bleu est une stratégie qui varie selon le contexte et qui s'ajuste en fonction de la densité et de l'ornementation des mâles avoisinants.

[Traduit par la Rédaction]

Introduction

Extra-pair mating is a common behavior in birds, including species with biparental care (for reviews see Gowaty 1985; Westneat et al. 1990; Petrie and Kempenaers 1998). Investing in offspring sired by other males imposes an important fitness cost on males (Trivers 1972; Westneat and Sherman 1990), and the risk of cuckoldry has led to the evolution of cuckoldry-avoidance behaviors. The two most com-

mon such behaviors are frequent copulation and maintenance of close proximity to social mates (i.e., mate guarding; Birkhead and Møller 1992). Variation in both the sexual attractiveness of a male and the distribution or density of neighboring males and their phenotypes likely plays an important role in determining a male's risk of cuckoldry and hence may shape the evolution of paternity-assurance behaviors (Andersson 1994; Bennett and Owens 2002). Effects from these factors are likely to be local, as females of most

Received 2 March 2005. Accepted 3 August 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 16 September 2005.

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songbird species engage in extra-pair copulatory behavior primarily with males from neighboring territories (Møller 1989; Gibbs et al. 1990; Kempenaers et al. 1992; Westneat 1993; Hasselquist et al. 1995; Weatherhead et al. 1996; Komdeur et al. 1999; Webster et al. 2001, but also see Double and Cockburn 2000 and Westneat and Mays 2005).

Comparative studies of the effects of local breeding density or male plumage coloration on extra-pair paternity have generally found positive associations between rates of extra-pair paternity and both local breeding density and male coloration (Westneat and Sherman 1997; Møller and Ninni 1998). However, population-level studies of some songbird species have not found such relationships (Hill et al. 1994; Weatherhead and Boag 1995; Cordero et al. 1999; Westneat and Mays 2005). Behaviors thought to function in guarding paternity in male birds have been less well studied, but single studies have found relationships between mate guarding and plumage coloration (Johnsen et al. 1998a) and between mate guarding and neighbor density (Komdeur 2001). No study has simultaneously considered the effects of male coloration and neighbor density on cuckoldry and mate-guarding behavior.

In this study we examined patterns of cuckoldry and mate-guarding behavior in relation to male coloration and neighborhood context in blue grosbeaks (*Passerina caerulea* L., 1758). Blue grosbeaks maintain all-purpose breeding territories, are socially monogamous (Keyser and Hill 2000), and engage in extra-pair copulations and fertilizations (this study). They are sexually dichromatic, with females being drab brown and males having brilliant blue coloration over most of their plumage. Structurally based blue/UV male plumage coloration in blue grosbeaks has been shown to be an honest signal of male quality (Keyser and Hill 1999). Our goal was to assess patterns of cuckoldry and mate guarding in relation to both male plumage ornamentation and local breeding density. Following the results of Møller and Ninni (1998), we predicted that dull male grosbeaks would be cuckolded more often than bright males.

For our predictions of mate-guarding behavior, we considered the results of several recent papers (reviewed in Badyaev and Qvarnstrom 2002) suggesting that sexually selected behaviors may be expressed in a context-dependent manner. We wanted to determine whether mate guarding is expressed relative to the local competitive context; i.e., whether males adjusted their mate-guarding behavior to their perceived risk of cuckoldry. If mate guarding is adjusted to the local competitive arena, then males surrounded by other males brighter than themselves should mate-guard more intensely. On the other hand, if expression of this trait is not dependent on local context, then duller males should always mate-guard more than brighter males, regardless of the surrounding density of bright males.

Materials and methods

Field procedures

We studied blue grosbeaks from May through August in 1997 and 1998 in Lee County, Alabama (see Keyser and Hill 2000 for a more detailed description of the study area). Most resident male and female blue grosbeaks were captured and marked with unique combinations of colored leg bands and

aluminum US Fish and Wildlife Service bands. We collected feathers for plumage-color measurements. In this study, we used a single blueness color score that was a composite of percent blue, peak wavelength, and intensity as a color rank for each male. See Keyser and Hill (1999) for a description of color variable measurements and justification for blueness score. We monitored nests every other day, recording the dates on which chicks hatched and fledged as well as when nests were abandoned or lost to predators. Blood was collected from chicks by puncture of the brachial vein (approximately 50–100 μ L) and stored in 500 μ L of Queen's lysis buffer (Seutin et al. 1991). All treatment of live animals in the field was approved by the Auburn University Care and Use Committee (PRN No. 9809-R-1025) and conducted under banding permits from the US Fish and Wildlife Service.

We defined the territory for each breeding pair using song perches or points of aggressive interaction between males. These male behaviors were mapped daily, with a minimum of 6 weeks of observation per male. We plotted these points on an aerial photograph and determined territory boundaries using the minimum convex polygon method.

In 1998, we recorded the mate-guarding behavior of each male while his mate was fertile. We defined the fertile period as the period from initial pairing to the penultimate egg for the first nest of the season, and from nest abandonment or chick fledging date to the next penultimate egg for all subsequent nests (Birkhead and Møller 1992; Ballentine et al. 2003).

As a measure of mate-guarding intensity, we recorded proximity between males and females every 2 min during 20-min observations. We designated two categories of proximity between pair mates: (1) 0–5 m and (2) beyond 5 m. We used the mean number of 2-min observations during which a male was within 5 m of his mate as the measure of mate guarding. We used this male-to-female distance as our measure of mate guarding because it was positively correlated with the percentage of mate-following events made by the male ($r^2 = 0.67$, $P = 0.001$, $n = 14$) and had been used in previous studies of mate guarding (Komdeur 2001).

Paternity analysis

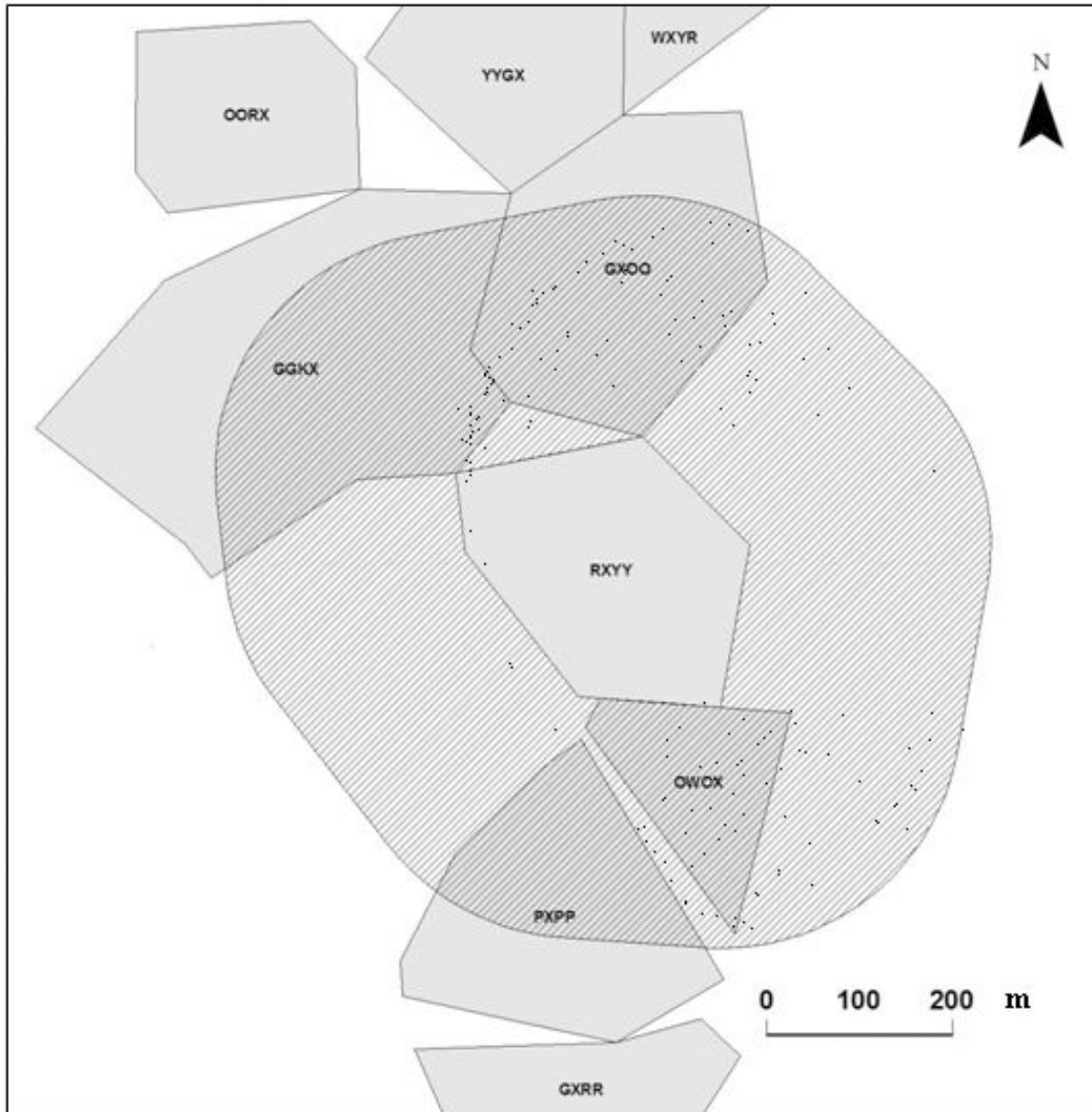
Genomic DNA was extracted from blood using a standard phenol–chloroform separation. We used three primers developed to amplify microsatellite loci in other species to amplify homologous sites in blue grosbeaks (ASE18 and ASE56, Richardson et al. 2000; LOX1, Piertney et al. 1998). Details of polymerase chain reaction (PCR) conditions are available on request. 32 P-labeled primers were used during PCR, and products were visualized by polyacrylamide gel electrophoresis followed by autoradiography. Genotypes were scored directly from the autoradiographs by H.L.M.

Two-parent detection probabilities were estimated by entering genotypes for presumably unrelated adults into CERVUS (Marshall et al. 1998). Across all three loci the two-parent probability of detecting unrelated offspring was 0.96.

Territory analysis

We created territory maps in ArcGIS® (Environmental Systems Research Institute, Inc. 2004) by digitizing the territory maps, originally plotted on aerial photographs, onto a georeferenced digital image of the study site that we ob-

Fig. 1. An example of a male blue grosbeak (*Passerina caerulea*) territory (shaded) and its buffer zone (hatched). For each territory, the total number of neighboring territories with all or part of their area falling within the buffer zone was calculated. In this example, focal male RXYY has four neighbors.



tained from the Alabama Water Quality Authority. Georeferencing was done using road intersections as common reference points for the two maps.

After creating these maps, we calculated the area of each territory in ArcGIS. To identify neighboring territories, we created buffer zones around each territory (Fig. 1). We defined neighbors for a focal territory as those males occupying a territory within a distance equal to the diameter of the average territory in our study population. We calculated mean territory diameter by converting all territory areas into circles, calculating the diameter of each, and calculating the mean diameter. We then created buffer zones around each male territory equal to the mean territory diameter (258.94 m). We could thus identify neighbors for each territorial male as the conspecifics with territories in the buffer zone for his territory. For each male we then calculated the number of neighboring males that had higher blueness scores for their breast and rump feathers.

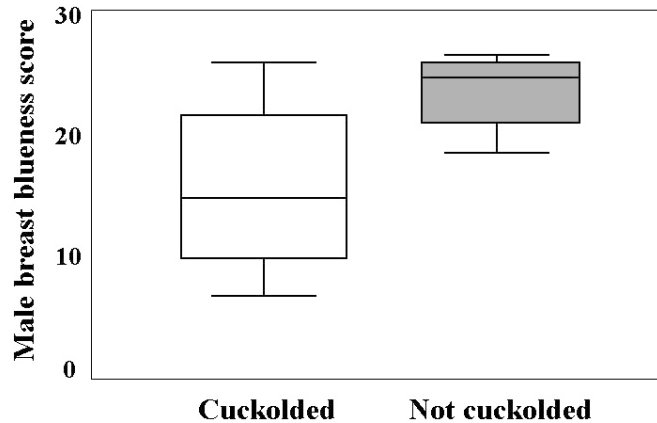
Data analysis

We used the following variables in our statistical analyses: breast plumage blueness score, rump plumage blueness score, number of neighbors, number of neighbors with higher breast color score, and number of neighbors with higher rump color score. All variables were normally distributed (Kolmogorov–Smirnov, all $P > 0.065$). We used a forward logistic regression to test whether these variables predicted cuckoldry. A male was considered to have been cuckolded if he had at least one extra-pair offspring in his nest. Similarly, we used a forward multiple linear regression to determine whether any of these variables predicted the intensity of mate-guarding behavior.

Results

We found and monitored 36 nests in the territories of 18 males in 1997 and 55 nests in territories of 23 males in

Fig. 2. Mean plumage coloration of male blue grosbeaks in relation to whether their nests contained extra-pair offspring. Cuckolded males had duller breasts, on average, than males that were not cuckolded ($P = 0.008$, $n = 19$). Boxplots show the mean, interquartile range, and extreme data points within three standard deviations of the mean.



1998. Predation rates were high, and the high ratio of nests monitored to males studied can be attributed to both the laying of replacement clutches following depredation and double brooding by females. Forty-six percent of blue grosbeak nests were lost to predators before we could sample nestlings. We were therefore able to establish paternity for only 25 nestlings from nests of 12 males in 1997 and 37 nestlings from nests of 11 males in 1998. For 3 males that had nests in both years, we chose one nest at random to include in our analyses. Also, one male was excluded from our analyses because no plumage color data were available for his only neighbor, so that totals of 8 males from 1997 and 11 males from 1998 were used for the statistical paternity analysis.

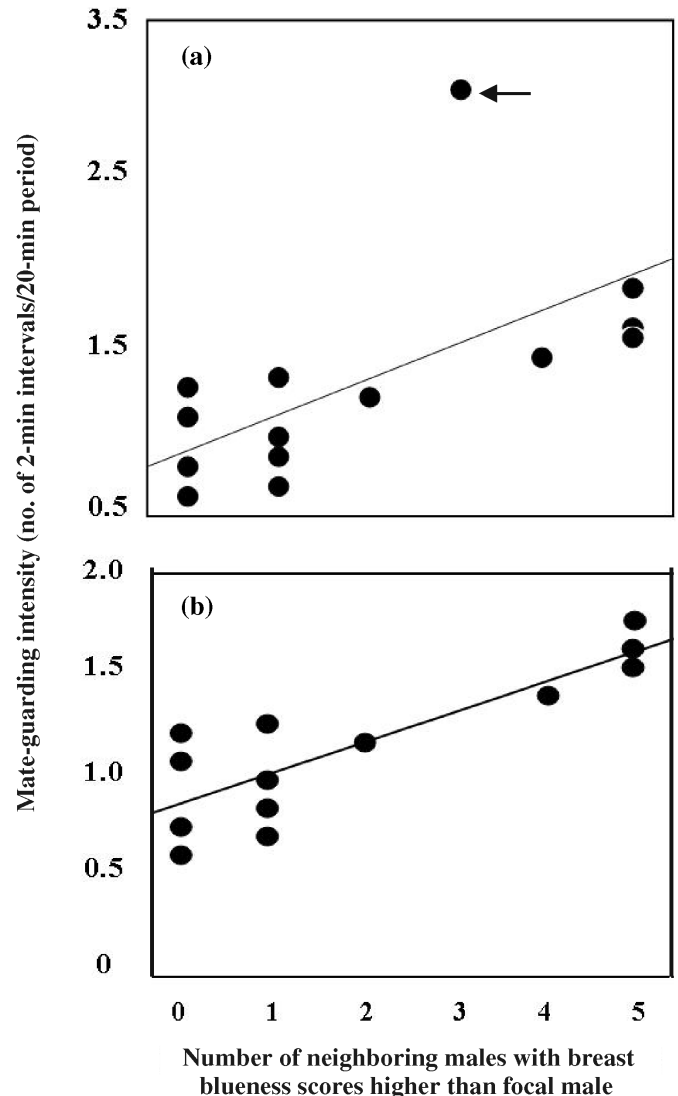
Twenty-nine of 55 (52.7%) nestlings were sired by an extra-pair male. Fourteen of 20 (70%) broods had at least one extra-pair offspring. Of the 9 males whose nestlings were tested in 1997, 7 (77.8%) had at least one extra-pair offspring. In 1998, 7 of 11 (63.6%) males had extra-pair offspring in their nests.

The blueness of male breast feathers significantly predicted whether or not a male would be cuckolded (forward logistic regression; $P = 0.008$; $n = 19$): bluer males were cuckolded less often than duller males (Fig. 2). The number of neighbors with a breast plumage color score higher than that of the focal male was the only significant predictor of mate-guarding intensity (forward multiple linear regression; $P = 0.018$, $n = 14$, $R^2 = 0.386$; Fig. 3). Thus, the magnitude of local competition experienced by a male, as determined by the density of more brightly colored neighbors, determined how intensely he guarded his mate.

Discussion

Our results reveal two potentially important interactions between cuckoldry, mate guarding, male plumage coloration, and local competition in the blue grosbeak. First, males that were not cuckolded had brighter plumage than males that were cuckolded. This result suggests that drabber males are at a greater risk of being cuckolded than brighter males. Second, while male mate guarding did not vary with focal male

Fig. 3. (a) Relationship between mate guarding and the number of male neighbors with bluer plumage coloration in blue grosbeaks ($P = 0.018$, $n = 14$). Mate guarding is represented by the number of 2-min observations for which a male was within 5 m of his social mate. (b) Relationship between mate guarding and the number of male neighbors with bluer plumage coloration in blue grosbeaks with outlier (indicated by an arrow in panel a) removed ($P < 0.0001$, $n = 13$).



plumage color, males that had a greater number of neighbors with plumage brighter than their own guarded their mates more intensely than males in less competitive contexts. This result suggests that the local competitive context, rather than the population-level context, influences mate-guarding strategies among male blue grosbeaks.

Several previous studies of songbirds have shown that less ornamented males within a population are cuckolded more often than more highly ornamented males (for review see Møller and Ninni 1998). Thus, ornamental coloration appears to function in both social and extra-pair mate choice. A previous experimental aviary study of mate choice in blue grosbeaks found that females do not prefer males with brighter plumage coloration (Ballentine and Hill 2003). This

mate-choice study, however, tested female choice of social mates. Evidence to date suggests that when choosing social mates, female blue grosbeaks settle based on the quality of a territory and accept the male that defends it. Thus, it is not surprising that females showed no preference for bluer males when choosing social mates.

Male blue grosbeaks with brighter plumage coloration have territories that are larger, with higher food abundance, than those of drabber males (Keyser and Hill 1999). Possession of these high-quality territories may create extra-pair opportunities for bluer males. Females may forage on these resource-rich territories and then engage in extra-pair copulations with the territory owner. Gray (1997) reported such an increase in extra-pair activity during foraging forays of red-winged blackbirds (*Agelaius phoeniceus* L., 1766). Alternatively, bluer males could be preferred as extra-pair mates because they have high-quality genes that could confer fitness advantages to offspring (Andersson 1994). Blue/UV plumage coloration in male blue grosbeaks correlates with male condition (Keyser and Hill 1999), but whether blueness is associated with good genes remains untested. Finally, females mated to drabber males may be more likely to engage in extra-pair copulations for the purposes of fertility assurance, as less ornamented males may have lower functional fertility (Sheldon 1994).

Unlike many researchers (for review see Westneat and Sherman 1997), we did not find a relationship between cuckoldry and neighbor density, which suggests that patterns of extra-pair paternity in the blue grosbeak are not influenced by encounter rate alone. Rather, our results suggest that a cascade of events leads to an extra-pair copulation. Females may more frequently encounter males with whom they can engage in extra-pair copulations in more densely packed neighborhoods, but whether or not a male is cuckolded may depend on factors such as the relative attractiveness of potential extra-pair mates, mate-guarding effort, and whether or not a potential extra-pair sire himself will forego his own mate-guarding activities to pursue extra-pair copulations. Each of these factors will mediate the effect of territory density on the distribution of matings in the population.

Our results suggest that relative variation in male plumage ornamentation mediates the effect of territory density on the risk of cuckoldry and male mate guarding. There are at least three possible mechanisms by which the local neighborhood could influence male mate-guarding behavior. First, males may directly assess the attractiveness of neighboring males at the onset of breeding and use this assessment to adjust mate-guarding behavior throughout the breeding season. Second, males may adjust their mate-guarding behavior in response to female behavior. For instance, if females engage in more forays when they are surrounded by more brightly colored males, males could detect movements of females on and off the territory. It is likely that the movement of females off the territory would be perceived as a cuckoldry risk, especially during periods of female fertility. Finally, males may adjust their mate-guarding behavior in response to the behavior of neighboring males. For instance, more ornamented males may be more aggressive and participate in more territorial intrusions than drabber males. Again, it is likely that territorial intrusions, especially during periods of female fertility, are likely to be perceived as a threat to pa-

ternity (Oldendorf et al. 2004). Although we do not have data on the rates of territorial intrusions or extra-territorial forays by females, we have shown here that cuckoldry is widespread, meaning that either females are leaving their territories or males are intruding, or both. Radiotelemetry observations of other passerine birds have demonstrated that both males and females participate in extra-territorial intrusions to varying degrees in different species (Neudorf et al. 1997; Johnsen et al. 1998b; Double and Cockburn 2000; Mays and Ritchison 2004); therefore, it is likely that male blue grosbeaks adjust their mate-guarding effort in accordance with both extra-territorial forays of their mates and intrusions by neighboring males. It is important to note that these mechanisms are not mutually exclusive or exhaustive explanations for changes in mate-guarding behavior.

While our data do not allow us to identify the specific cue that males use to adjust their mate-guarding intensity, they do suggest an interesting concept: that the composition of neighborhoods around a male's territory affects his behavior. These results are in accordance with those of Greene et al. (2000), who found that male lazuli buntings (*Passerina amoena* (Say, 1823)) adjusted their territory settlement patterns according to their perceived risk of cuckoldry in local competitive contexts. We suggest that future research is needed to understand the demographic and behavioral circumstances under which males maximize their fitness either by basing their territory settlement decisions on their perceived risk of cuckoldry, as in lazuli buntings, or by first settling into territories and then adjusting their mate-guarding behavior according to their perceived risk of cuckoldry, as appears to be the case in blue grosbeaks.

Acknowledgements

This manuscript was improved by comments from G.E.H.'s laboratory staff and two anonymous reviewers. Research was supported by an Alabama Space Grant Consortium fellowship to L.K.E., the Department of Biological Sciences at Auburn University, and the Alabama Agricultural Experiment Station. Molecular paternity analyses were supported by National Science Foundation Grants to G.E.H. (IBN 0235778, DEB 0077804).

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