

Social and ecological factors affecting paternity allocation in American robins with overlapping broods

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Abstract Factors that affect extra-pair mating in birds are likely to vary across the breeding season. Changing densities of active nests may alter the opportunities for extra-pair mating, and parental duties may alter a male's opportunity to guard his mate from extra-pair mating. The latter affects species with multiple broods, where males care for fledglings from first nests while females initiate second nests. We studied a population of multi-brooded American robins (*Turdus migratorius*) to assess how seasonal changes in nesting density and changes in mate-guarding opportunity influenced paternity patterns over successive breeding attempts. Extra-pair paternity (EPP) occurred in 71.9% of broods and accounted for 48.1% of young. High nesting densities in the study population may explain the high overall rate of EPP, but seasonal variation in breeding density did not explain patterns of EPP among nests. Contrary to the predictions of the mate-guarding hypothe-

sis, EPP did not increase in the second nests that followed successful first nests, and the percentage of extra-pair young in second nests did not decline as the overlap between successive nests increased. The fact that EPP was actually lower when the interval between clutches was shorter suggests that the sooner the males can assume sole care of first broods and allow their mates to renest (indicative of superior paternal quality), the more paternity they realize in the next nest. These results suggest that mate-guarding opportunity does not influence paternity in this population of American robins and that female robins may allocate paternity based on their assessment of male parental performance at first nests.

Keywords Extra-pair paternity · Mate guarding · *Turdus migratorius* · Interclutch interval · Breeding density

Introduction

Molecular genetic studies have demonstrated that nearly 90% of bird species engage in extra-pair copulations, despite social monogamy being the norm (Griffith et al. 2002). Among taxa, there is extensive variation in levels of extra-pair paternity (EPP) (from <1 to 76%; Griffith et al. 2002), and identifying the factors responsible for this variation is central to our understanding of mating systems, sexual selection, and life-history strategies (Gowaty 1996; Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003). Griffith et al. (2002) and Bennett and Owens (2002) have proposed a hierarchy of explanatory factors based on taxonomic level such that at lower levels (i.e., among species, populations, and individuals), variation in extra-pair mating can be attributed to social, ecological, and genetic factors related to the opportunities and trade-offs

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associated with mixed reproductive strategies such as mate guarding (Westneat and Stewart 2003), breeding synchrony (Birkhead and Biggins 1987; Møller and Ninni 1998), breeding density (Westneat and Sherman 1997), and genetic variability (Petrie et al. 1998). In this study, we consider how paternity allocation in American robins (*Turdus migratorius*) is affected by the conflict between paternal care and mate guarding resulting from having overlapping broods, and by seasonal effects such as changes in breeding density that occur over successive broods.

Extra-pair fertilizations can increase a male's reproductive success but infidelity by his mate can reduce the male's success (Gibbs et al. 1990; Whittingham and Dunn 2005). Thus, when extra-pair mating is common, males should evolve paternity assurance behaviors to prevent their mates from seeking extra-pair copulations (Van Rhijn 1991; Fishman et al. 2003). Mate guarding (the close association of a male with his social mate during her fertile period) can influence levels of EPP (Westneat and Stewart 2003). Because females can benefit from extra-pair fertilizations (Foerster et al. 2003; Hansson et al. 2004), however, they should resist or avoid mate guarding if possible, suggesting the relationship between mate guarding and paternity may be complex (Kokko and Morrell 2005).

Mate guarding and its consequences for paternity have been examined in a variety of species using correlational (e.g., Blomqvist et al. 2002; Johnsen and Lifjeld 2003; reviewed in Westneat and Stewart 2003) and experimental approaches (e.g., Dickinson 1997; Komdeur et al. 1999; Brylawski and Whittingham 2004). Most studies have examined species that are single-brooded, or for simplicity, only one brood of a multi-brooded species. However, multi-brooded species have enormous potential for understanding extra-pair mating. Successive broods involving the same pair of birds in the same breeding season provide natural variation in mate-guarding opportunities among broods (Weatherhead and McRae 1990), while minimizing effects of age or mate identity typically encountered when following the same individuals across years (Dietrich et al. 2004). When broods overlap, males often care for fledglings from first nesting attempts, allowing females to begin a new attempt (Edwards 1985). Males are thus forced to trade-off caring for young with guarding their mates when they are fertilizable (Weatherhead and McRae 1990). Unlike when initiating first broods, females initiating second broods should be unconstrained in their potential to obtain extra-pair copulations. Only when first broods fail will extra-pair-mating opportunities for females be similar for first and second broods. Furthermore, the degree to which broods overlap (the interclutch interval [ICI]) can affect mate-guarding opportunities, and thus EPP, because males should be able to invest increasingly in mate-

guarding activities as offspring reach independence and parental duties decline. Although EPP has been examined in multi-brooded species (e.g., Stutchbury et al. 1994; Freeman-Gallant 1996; Lubjuhn et al. 2001), the focus has been on determining how seasonal changes in breeding synchrony (Conrad et al. 1998), male pairing status (Freeman-Gallant 1997), and parental care (Dixon et al. 1994) affect paternity allocation among broods. We examine paternity patterns in American robins to test the hypothesis that changes in mate-guarding opportunity through the breeding season influence patterns of EPP among broods (Weatherhead and McRae 1990).

Breeding density is also likely to vary across successive broods and can also affect extra-pair mating (Westneat and Sherman 1997). As breeding density increases, the likelihood of encountering potential extra-pair mates increases, suggesting that the incidence of EPP should increase. If a male's extra-pair-mating opportunities increase with breeding density, however, so too will his risk of being cuckolded, so a male might exert more effort guarding his mate, thereby reducing EPP. Because breeding density could potentially interact with the opportunities for mate guarding and extra-pair mating in successive broods, we also consider the effects of breeding density on the incidence of EPP. By examining both factors (overlapping broods and breeding density) simultaneously, we can gain insight into the relative importance of each factor in producing the paternity patterns we observe (e.g., Johnsen and Lifjeld 2003; Dietrich et al. 2004; Stewart et al. 2006).

American robins regularly produce multiple, overlapping broods within a single breeding season and pairs remain together for the entire breeding season (Young 1955; Weatherhead and McRae 1990). In a New York population, males display typical mate-guarding behavior (Gowaty and Plissner 1987). Males attended their mates more closely and were more likely to follow them during their fertilizable period (during nest building and egg laying) than during their nonfertilizable period (during incubation). In this study, we first address the incidence of EPP in multiple broods of American robins. Although the majority of passerines examined to date exhibit some level of EPP, extra-pair mating has not been examined in American robins. Second, we attempt to identify the factors associated with variation in EPP among and within individuals. We expect higher incidence of EPP in nests where male mate-guarding opportunity is compromised. That should occur when breeding densities are higher and in second nests that follow successful first nests. In addition, the greater the overlap between a successful first nest and a second nest, the more a male's mate-guarding ability should be compromised. Thus, we expect that EPP in second nests that follow successful first nests should increase as the ICI decreases.

Materials and methods

Study species

American robins are medium-sized (~80 g) passerines that breed throughout most of North America. Pairs mate for the season, but individuals rarely remate with the same partner in subsequent years (Young 1955; Weatherhead and McRae 1990). Females build the nest and incubate the eggs, but both parents provision the young and defend the nest. Once the young have fledged, both parents continue to provide care but males gradually take over caring for the fledglings until they reach independence at approximately 21 days of age (Weatherhead and McRae 1990). The shift to male-only care coincides with females beginning another nesting attempt, resulting in overlapping broods. Males are therefore unable to simultaneously provide care for young and mate guard during the female's fertile period for the second nesting attempt. This problem is exacerbated by the fledglings becoming more widely dispersed at the same time that males assume exclusive care (Weatherhead and McRae 1990). When first broods fail, however, opportunity for mate guarding by males should be unconstrained when those pairs initiate second nests.

Study population and field methods

We studied American robins breeding in 4 ha of a mixed species coniferous tree farm located near Urbana, Illinois (40°02'N, 88°10'W) during the 2003 and 2004 breeding seasons (lasting from mid-April to mid-July in Illinois). Adult birds were captured in mist nets, sexed by the presence of a brood patch (female) or cloacal protuberance (male), and fitted with a US Fish and Wildlife Service aluminum band and three unique color bands. Blood samples were collected from adults (75–100 μ L) by brachial venipuncture and stored in Queen's lysis buffer (Seutin et al. 1991) at 4°C.

Nests were located by systematically searching all trees on the site every third day. Once located, nests were monitored every day to determine clutch size, the ultimate fate of the nest, and the number of young fledged. Adults were unambiguously assigned to nests by direct observation of defense behavior and by their presence in video recordings of nestling provisioning collected for other behavioral analyses. Pairs were followed the entire season over multiple nesting attempts, and the ICI (time from fledging of the first brood to clutch initiation of the second brood) was determined. To examine paternity in each attempt, blood samples (50–75 μ L) were collected from nestlings at 7 days post-hatch and stored in the same manner as samples from adults.

Breeding density

For each nest, we calculated an index of breeding density at two spatial scales—populationwide and local. Population breeding density was calculated as the maximum number of active nests within the study area during the fertile period of the focal female. For this study, we defined the fertile period as the time from 5 days before clutch-initiation through the completion of egg laying. Because previous studies have suggested extra-pair copulations occur regularly with neighbors (Gibbs et al. 1990; Chuang et al. 1999; Mennill et al. 2004), we also calculated breeding density at the local scale. Local breeding density was defined as the maximum number of active nests within 50 m of the focal nest during the focal female's fertile period. We chose a distance of 50 m because it produced substantial variation in our measure of local densities (see “Results”).

Mate-guarding opportunity

In pairs that attempt multiple broods, previous nesting success and ICI could also influence patterns of EPP by affecting the mate-guarding opportunity of the male. We classified double-brooded pairs as either ‘unsuccessful’, if the first nesting attempt failed (i.e., males had the opportunity to mate guard at second nests), or ‘successful’, if at least one offspring fledged from the first nest (i.e., where the male's opportunity to mate guard at second nests was constrained). We verified that mate-guarding opportunity was compromised in successful pairs by determining whether the ICI was less than 21 days (the time it takes for American robin fledglings to reach independence; Weatherhead and McRae 1990). In one case, a pair successfully fledged offspring in their first nest, but did not attempt to reneest until 43 days later. Because the mate-guarding opportunity of this male would not have been compromised at the second nest, we excluded this pair from analyses. We were unable to quantify mate-guarding behavior directly in this population because the habitat consisted of closely spaced coniferous trees, preventing us from remaining close enough to keep the birds in sight without altering their behavior.

Parentage analysis

DNA was extracted, and polymerase chain reaction (PCR) was used to amplify three microsatellite loci previously identified in Swainson's thrushes (*Catharus ustulatus*; Cu μ 05, Cu μ 28, and Cu μ 32; Gibbs et al. 1999). Each PCR contained 30 ng genomic DNA, 5 pmol fluorescently labeled forward primer, 5 pmol unlabeled reverse primer, 2 mM MgCl₂, 1 mM dNTPs, 10 mM Tris-HCl (pH 8.3),

50 mM KCl, and 1 U *Taq* polymerase. Each PCR thermal cycle consisted of an initial denaturation step of 95°C for 5 min, then 35 cycles of 95°C for 1 min, 54°C for 1 min, and 74°C for 1 min 30 s, and finished with a final extension step at 74°C for 10 min. All PCR products were run on a 2% agarose gel to verify amplification and then run on a capillary electrophoresis ABI Prism 3730xl Analyzer with a size standard. To assign genotypes to each individual, allele sizes were determined using GeneMapper™ 3.7 software (Applied Biosystems). The number of alleles per locus ranged from 18 to 34, observed heterozygosities were 0.73 to 0.92, and the combined exclusion probability over all three loci was 0.996.

In the only other parentage study of American robins to date, Gowaty and Davies (1986) reported that 9.5% of young (4:42) were excluded from the putative mother and were considered the result of intraspecific brood parasitism. Although interesting, this result was not based on DNA methods for genotyping individuals, but rather on protein polymorphisms determined by electrophoresis, and used an exclusion method for assigning genetic maternity. In addition, sample sizes were small, and although intraspecific brood parasitism has been documented in at least 66 species of Passeriformes (Yom-Tov 2001), occurrence is predominantly associated with colonially nesting species and those where nest sites are limited. To evaluate whether intraspecific brood parasitism occurred in our population, we assessed genetic maternity for all offspring before conducting paternity analyses.

To assign genetic parentage to offspring, we used the program Cervus 2.0 (Marshall et al. 1998). Through a simulation module, Cervus incorporates the occurrence of null alleles and mutations as well as incomplete sampling into likelihood calculations to decrease the probability of false exclusions. Input parameters used in the simulation module included: (1) the number of simulated offspring (defaulted to 10,000), (2) the number of candidate parents (estimated from field observations), (3) the proportion of candidate parents sampled (estimated from field data), (4) the proportion of loci typed (calculated in the allele frequency module), and (5) the proportion of loci mistyped (calculated from known parent–offspring genotype mismatches in the allele frequency module). For all our parentage assignments, we used an 80% confidence level to conservatively estimate the level of extra-pair parentage.

To account for incomplete sampling of males in our population, we performed paternity assignments in a two-stage process of paternal exclusions and EPP assignments. First, for nests in which both parents and all young were genotyped, we were able to evaluate directly whether the social father was the genetic father. For the simulation module in this analysis, the number of candidate parents was set to two (i.e., the social father and an extra-pair sire).

The proportion of candidate parents sampled was set to 0.99 to account for incomplete sampling of individuals in the population, and the proportion of loci mistyped was 0.065. Second, for nests where the social father was not sampled, we attempted to assign genetic paternity to those offspring from the pool of sampled males in the entire population. If an offspring was assigned to a sampled male, we considered that offspring to be an extra-pair. Because we were unable to sample all of the males in the population, these estimates of EPP are conservative, because a non-assignment could result from either a nestling being sired by the unsampled social father (i.e., within-pair paternity) or being sired by some other unsampled male in the population (i.e., EPP). For this analysis, the number of candidate parents was increased to 40 to represent the estimated total number of reproductively active males in the population. The proportion of candidate parents sampled was decreased to 0.95 to account for the greater level of incomplete sampling of potential sires in the entire population, and we lowered the proportion of loci mistyped to 0.02 to decrease the probability of a false assignment.

Based on the results of the two-step parentage analyses, we created two data sets. The restricted set consisted of all broods in which social fathers were sampled and those in which social fathers were not sampled, but extra-pair sires were identified from the pool of sampled males. The full data set contained all broods in the population, including those in which the social father was not sampled and no extra-pair sire was identified. Although sample sizes are larger within the full data set, the estimate of EPP will be conservative because some cases of EPP are likely to have been undetected. Results from both the restricted and full data sets are presented to provide a realistic range of actual EPP within the population.

Statistical methods

Basic statistics and regressions were performed using SPSS (v. 11.5 2002). We used nonparametric tests to analyze patterns of paternity because data were not distributed normally. Multilevel generalized linear models (MLGLM) were used to examine the effect of socioecological factors (i.e., nest order, clutch initiation date, previous nesting success, ICI, and density) on the proportion of extra-pair young (EPY) using a binomial error structure and a logit link function (ML Win v. 2.02; Rasbash et al. 2005). The number of offspring in the brood was used as the binomial denominator. We used a two-level hierarchical structure with the identity of the pair at the highest (second) level and broods within pairs at the lowest (first) level. Using MLGLM allowed us to take advantage of all available data while accounting for variation across pairs in the number of broods (1–2) and the number of offspring produced per

brood (1–4; see Bouwman and Komdeur 2006). The model was run using iterative generalized least squares, and we evaluated the significance of each predictor variable in the model by testing for a significant change in deviance score with and without the variable, using a χ^2 approximation. We present the Wald test statistic, which also follows a χ^2 distribution, and corresponding significance values for each variable in the model and for each excluded variable before elimination.

In 2003 and 2004, five females and one male bred in both years but all individuals switched breeding partners between years. Therefore, we treated each pair as an independent observation. However, to avoid potential pseudoreplication, we repeated our analyses by randomly selecting 1 year of data from pairs where one member of the pair bred in both years. We therefore ran two models—one including data from all pairs breeding in either year and one including data from all pairs breeding in either year, randomly excluding 1 year of data from pairs in which one member of the pair bred in both years. Because the latter approach never qualitatively altered the results, we only present results from the former approach. Means are expressed ± 1 SE, and we assumed significance if $p < 0.05$.

Results

Patterns of paternity

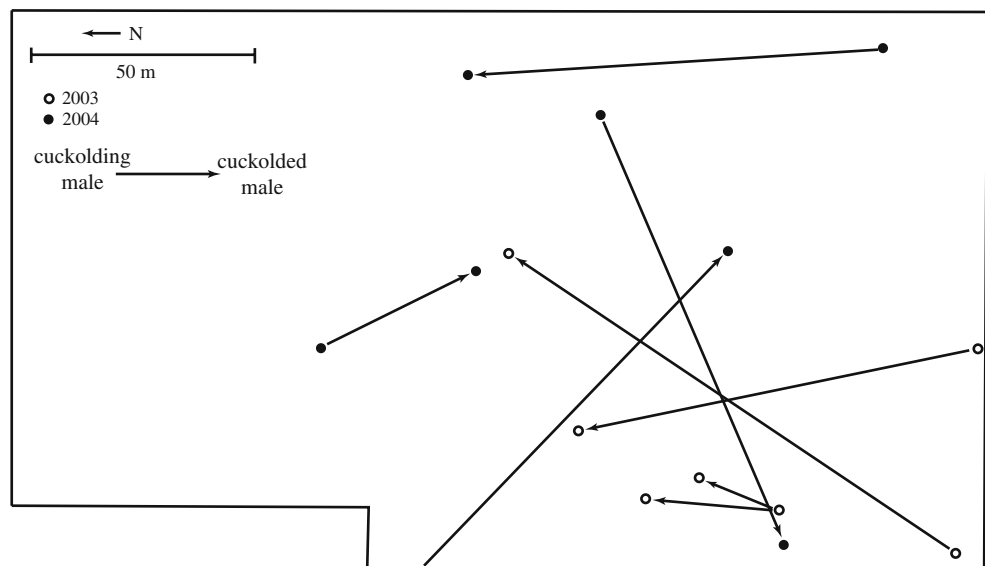
Over both years, we genotyped 212 young from 74 broods (34 in 2003 and 40 in 2004). We unambiguously assigned genetic maternity to the putative mother of all 212 offspring, and thus detected no cases of intraspecific brood

parasitism. In broods with both parents sampled, we excluded the social father for 68 of 148 (45.9%) nestlings in 34 of 52 (65.4%) nests. For the remaining 22 broods in which the social father was unsampled, we assigned an extra-pair sire from the pool of sampled males for 22 of 64 (34.4%) offspring from 12 (54.5%) broods. Thus, our restricted data set consisted of 64 broods (52+12), and our full data set consisted of all 74 broods.

Across both data sets, between 62.2 (46:74) and 71.9% (46:64) of broods contained at least one EPY, 42.5 (90:212) to 48.1% (90:187) of young were sired by an extra-pair male, and the percentage of EPY/brood ranged from 41.1 ± 4.5 to $47.5 \pm 4.7\%$. Using the restricted data set, the percent of broods with EPY, the percent of EPY, and the percentage EPY/brood were higher in 2003 than in 2004, but the differences were not significant ($\chi^2 = 0.24$, $p = 0.62$, $n = 64$; $\chi^2 = 3.06$, $p = 0.08$, $n = 187$; *Mann-Whitney U test*; $Z = -1.30$, $p = 0.20$, $n = 64$, respectively). The results were similar using the full data set (% broods, $\chi^2 = 0.004$, $p = 0.95$, $n = 74$; % EPY, $\chi^2 = 1.92$, $p = 0.17$, $n = 212$; % EPY/brood, $Z = -0.92$, $p = 0.36$, $n = 74$). Thus, for the analysis of socioecological factors and EPP we pooled data across years.

Examining the restricted data set, extra-pair mating was not correlated with the number of eggs laid (*Sperman's rho*; $r_s = -0.09$, $p = 0.48$, $n = 60$), or the number of young fledged ($r_s = 0.01$, $p = 0.95$, $n = 61$). Results were similar for the full data set (number of eggs, $r_s = -0.01$, $p = 0.92$, $n = 69$; number of young, $r_s = 0.08$, $p = 0.54$, $n = 70$). Of the 12 extra-pair sires we identified, eight nested simultaneously with the nesting attempt in which they sired young. Cuckolding males nested on average 74.3 ± 13.9 m from the nest where they sired EPY (range 18–120 m; Fig. 1), although the mean nearest neighbor distance was only 20.2 ± 1.2 m.

Fig. 1 Map of EPP in American robins breeding near Urbana, Illinois in 2003 and 2004. *Open and closed circles* represent nests from 2003 and 2004, respectively. The *origin of the arrow* shows the nest location of the cuckolding male, and the *arrowhead* shows the nest location where he sired an EPY. Average distance between nests of cuckolding and cuckolded males was 74.3 ± 13.9 m (range 18–120 m)



Breeding density

Site-wide breeding density was significantly lower in 2003 (51.6 ± 2.7 pairs, range 11–70) than in 2004 (84.0 ± 5.0 pairs, range 17–124; t test, $t = -5.47$, $df = 71$, $p < 0.0001$). In both years, site-wide density increased as the breeding season progressed (*quadratic regression*; 2003, $R^2 = 0.90$, $F = 128.0$, $df = 30$, $p < 0.0001$; 2004, $R^2 = 0.88$, $F = 113.2$, $df = 32$, $p < 0.0001$; Fig. 2a,b) and was highest shortly after pairs began initiating second nesting attempts (peak density [date]; 2003, 65 pairs [4 June]; 2004, 106 pairs [28 May]). Local breeding densities did not differ between years (4.4 ± 0.3 and 5.4 ± 0.7 pairs in 2003 and 2004, respectively, range 0–22; $t = -1.28$, $df = 71$, $p = 0.21$). There was no relationship between local density and clutch initiation date in 2003 (*quadratic regression*; $R^2 = 0.10$, $F = 1.59$, $df = 30$, $p = 0.22$), but local density increased significantly during the course of the breeding season in 2004 ($R^2 = 0.28$, $F = 6.2$, $df = 32$, $p = 0.005$; Fig. 2c,d).

Socioecological factors and paternity allocation

First nest failures were due to nestling starvation ($n = 2$), depredation ($n = 2$), or environmental causes ($n = 1$). There were no significant differences between successful and unsuccessful pairs in terms of the number of eggs laid (3.6 ± 0.14 eggs vs. 3.6 ± 0.24 eggs; t test, *unequal variances*, $t = -0.04$, $df = 7.01$, $p = 0.97$) or in clutch initiation

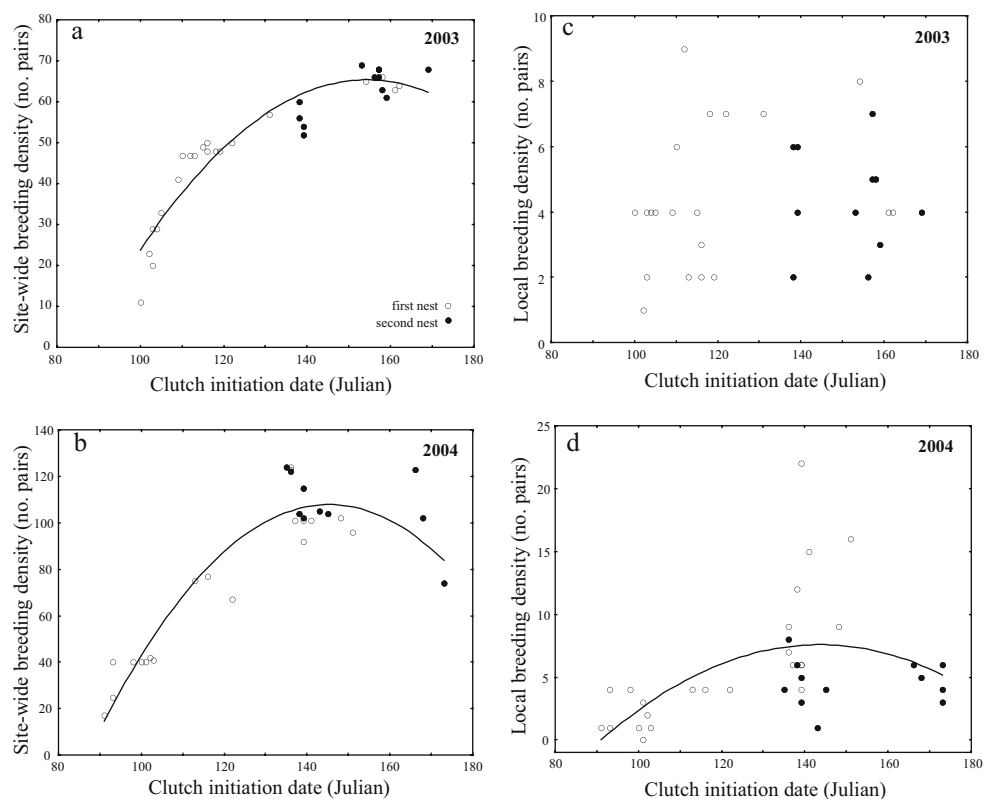
Table 1 MLGLM of EPP in relation to several social and ecological factors in American robins

Variables	Wald	<i>p</i>
Nest order	-1.97	0.16
Clutch initiation date	0.92	0.34
Previous nesting success	3.72	0.05
Interclutch interval (ICI)	4.48	0.03
Local density	-0.06	0.81
Site-wide density	-1.96	0.16
Final model	7.47	0.02

Direction of the parameter estimate, Wald test statistic and their significance are given for each variable before elimination from the model. Variables included in the final model are bolded.

date (2 June ± 3 days vs. 23 May ± 6 days, $t = -0.76$, $df = 6.5$, $p = 0.47$) for second broods. Of the variables we tested, previous nesting success and ICI were significant predictors of the level of EPP (*deviance* = 64.4, $df = 2$, $p < 0.0001$; Table 1). EPP in second nests was significantly higher after a successful first nest than after an unsuccessful first nest (45.6 ± 8.9 vs. $6.6 \pm 6.6\%$; *Wald statistic*, $W = 3.72$, $p = 0.05$). The significant effect of previous nesting success appears to support the hypothesis that constrained mate-guarding opportunity influences the level of EPP in second nests. Were that the case, however, we would have expected EPP to remain constant from first to second nests of unsuccessful pairs, but to increase substantially in second nests of successful pairs. In fact, EPP decreased sharply from first to

Fig. 2 Relationships between breeding densities and season progression in American robins during 2003 and 2004. *Open and closed circles* represent first and second nesting attempts, respectively. Site-wide breeding density (a and b) is a measure of the number of actively breeding pairs on the entire site during the focal female's fertile period. Local breeding density (c and d) measures the number of actively breeding pairs within 50 m of the focal nest during the focal female's fertile period. Site-wide breeding density was an increasing quadratic function of clutch initiation date in both years (2003, $R^2 = 0.90$, $p < 0.0001$; 2004, $R^2 = 0.88$, $p < 0.0001$). The same was true for local breeding density in 2004 ($R^2 = 0.28$, $p = 0.005$), but not in 2003 ($R^2 = 0.10$, $p = 0.22$)



second nests of unsuccessful pairs (33.3 vs. 6.6%) and was similar in the first and second nests of successful pairs (39.5% vs. 45.6%). Thus, despite the overall influence of the fate of first nests supporting the mate-guarding hypothesis, the individual patterns of EPP are not consistent with the hypothesis.

ICI was also a significant predictor of EPP in second nests but in the opposite direction from that predicted ($W=4.48$, $p=0.03$). ICI was positively, rather than negatively, related to level of EPP in second broods (Fig. 3). There was no relationship between EPP and nest order ($W=1.97$, $p=0.16$) or clutch initiation date ($W=0.92$, $p=0.34$). We also found no relationship between our two measures of breeding density and EPP (local density, $W=0.06$, $p=0.81$; site-wide density, $W=1.96$, $p=0.16$).

Discussion

Consistent with many other socially monogamous birds, the American robins we studied regularly engaged in extra-pair mating. The extent of EPP we found is among the highest documented in avian species to date. Because population density is generally associated positively with frequencies of extra-pair fertilizations among populations (Westneat and Sherman 1997), high breeding densities in our population may have contributed to overall high levels of EPP. The maximum number of breeding pairs per hectare was 30.5 and 49.5 in 2003 and 2004, respectively, between two and six times higher than that reported for American robins in more natural habitats (Howell 1942; Young 1951; Pitts 1984).

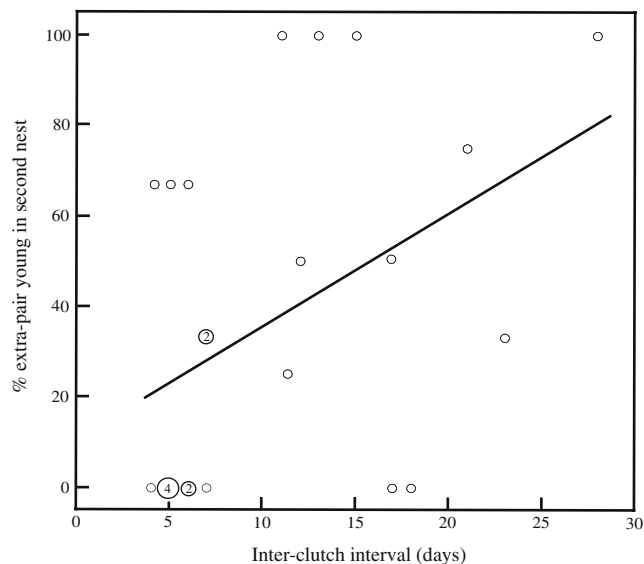


Fig. 3 Relationship between ICI and the percentage of EPY in the second nests of American robins. The analysis was conducted using a generalized linear model, but a linear regression line is included to show the trend. ICI was a significant predictor of the percentage of EPY in second nests ($W=4.48$, $p=0.03$). Enlarged circles with numbers indicate the number of overlapping data points

If high breeding density contributed to the high incidence of EPP in our population, variation in breeding density on our study site did not affect the occurrence of EPP among nests. However, we also did not find that extra-pair sires were more likely to be near neighbors, contrary to what has been found in other studies (e.g., Gibbs et al. 1990; Kempenaers et al. 1992; Charmantier and Perret 2004). Although American robins have been described as territorial (Sallabanks and James 1999), we witnessed few aggressive interactions in our population and regularly observed birds using common feeding grounds. Furthermore, breeding American robins do not respond to conspecific playbacks or decoys (Weatherhead, personal observation), suggesting an absence of territoriality. Territoriality can inhibit extra-pair copulation attempts (e.g., Sherman and Morton 1988), reducing the likelihood of finding an extra-pair mate at low nesting densities (Charmantier and Perret 2004). Lack of territoriality presumably allows American robins much greater ease of movement, thereby creating extra-pair-mating opportunities involving individuals whose nests are not necessarily close to one another. Therefore, breeding density could be important in determining the overall opportunity for individuals in this population to engage in extra-pair mating, whereas local breeding density has no effect. Ultimately, we need to know more about the movements of males and females associated with extra-pair mating to assess these kinds of hypotheses (Westneat and Stewart 2003).

Because male American robins provide postfledging parental care and successive broods overlap, Weatherhead and McRae (1990) hypothesized that a successful first nest should increase the probability of EPP in the second nests if a male's ability to mate guard is compromised by his parental obligations. Our overall results appeared to support this hypothesis—EPP was higher in the second nests that followed successful first nests than in those that followed unsuccessful first nests. However, that difference did not result from EPP increasing in second nests that followed successful first nests (i.e., when mate-guarding opportunity would have been diminished), but from EPP decreasing in second nests that followed unsuccessful first nests. The first implication of these patterns is that our results do not support the mate-guarding hypothesis. In particular, the failure of EPP to increase substantially in the second nests that followed successful first nests is not consistent with that hypothesis. The second implication of our results is that we must explain the unanticipated decline in EPP in the second nests that followed unsuccessful first nests. EPP could have declined because opportunities for extra-pair mating declined, which seems unlikely given that EPP remained high in the second nests that followed successful first nests. Alternatively, American robins whose first nests failed could have reduced

extra-pair-mating effort, or the males could have increased mate guarding. It is not apparent why either would have happened. Because nest failure was rare, and thus the sample of second nests that followed nest failure was small, the most parsimonious explanation may be that this result is a statistical artifact.

The corollary of the mate-guarding hypothesis that we tested was that EPP should decrease as the overlap between successive brood (i.e., ICI) decreased. We assumed that as fledglings approach independence males should be able to provide less care to young and invest more in mate guarding. As with our central test of the mate-guarding hypothesis (above), this result indicates that mate-guarding opportunity appeared to have little effect on rates of EPP. The fact that EPP actually increased when the opportunity for mate guarding was highest suggests that the overlap between nests affected extra-pair-mating behavior in some other way. One possibility is that the interval between clutches is determined in part by the quality of paternal care at the previous nest. Females mated to males that are good providers may be able to initiate their next clutch more quickly because their mates can assume sole care of the first brood sooner. In turn, females may allocate more paternity to mates that are good parents (Weatherhead and McRae 1990; Wagner 1992). Support for this hypothesis comes from savannah sparrows, *Passerculus sandwichensis*, (Freeman-Gallant 1996, 1997), where more male parental care in first nests resulted in greater female fidelity in second nests.

There are several reasons that may explain why we did not find support for the mate-guarding hypothesis. First, short-term trade-offs may allow males to guard their mates and to provide care to fledglings simultaneously. Møller (1991) found that mate-guarding intensity and frequency of extra-pair copulations in swallows (*Hirundo rustica*), did not differ between broods, despite brood overlap. Marthinsen et al. (2005) found that mate guarding by male reed buntings (*Emberiza schoeniclus*) was positively related to within-pair paternity, but that males also sired EPY on days when they were guarding. Similarly, male red-winged blackbirds (*Agelaius phoeniceus*) achieve extra-pair fertilizations even during their mate's fertilizable period (Weatherhead 1997; Westneat and Gray 1998). These results suggest that although males cannot strictly mate guard and pursue extra-pair copulations simultaneously, they may make optimal short-term trade-offs among multiple activities enhancing their reproductive success both with their own mate and elsewhere. Short-term trade-offs have been documented in hooded warblers (*Wilsonia citrinia*; Stutchbury 1998) and in European starlings (*Sturnus vulgaris*), where diurnal patterns of mate-guarding intensity support the idea that males guard their females when their paternity is most at risk (Pinxten and Eens 1997). However, if "targeted" mate guarding is as effective as

continuous mate guarding, it begs the question of why males spend so much time mate guarding when they have conflicting time commitments.

The widespread occurrence of both mate guarding and EPP clearly indicates that the former must have only limited effects on the latter. Mate guarding is less likely to be effective if females actively seek extra-pair matings, as has been documented for many species (Double and Cockburn 2000; Lifjeld and Robertson 1992; reviewed in Westneat and Stewart 2003). If females can circumvent male mate guarding, patterns of paternity will be based on female decisions of whether to seek extra-pair copulations and the criteria on which they base those decisions. Among species for which male parental care is critical for offspring survival, females should select mates at least in part based on parental care abilities.

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