Ecological, social, and genetic contingency of extrapair behavior in a socially monogamous bird

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Extrapair mating strategies are common among socially monogamous birds, but vary widely across ecological and social contexts in which breeding occurs. This variation is thought to reflect a compromise between the direct costs of mates' extrapair behavior and indirect benefits of extrapair fertilizations (EPF) to offspring fitness. However, in most free-living populations, the complete spatial and temporal distribution of mating attempts, genetic characteristics of available mates, and their relative contribution to EPF strategies are difficult to assess. Here we examined prevalence of EPF in relation to breeding density, synchrony, and genetic variability of available mates in a wild population of house finches *Carpodacus mexicanus* where all breeding attempts are known and all offspring are genotyped. We found that 15% of 59 nests contained extra-pair offspring and 9% of 212 offspring were sired by extra-pair males. We show experimentally that paired males and females avoided EPF displays in the presence of their social partners, revealing direct selection against EPF behavior. However, at the population level, the occurrence of EPF did not vary with nests dispersion, initiation date, synchrony, or with distance between the nests of extrapair partners. Instead, the occurrence of EPF closely covaried with genetic relatedness of a pool of available mates and offspring of genetically dissimilar mating tended to be resistant to a novel pathogen. These results corroborate findings that, in this population, strong fitness benefits of EPF are specific to each individual, thus highlighting the ecological, social, and genetic contingency of costs and benefits of an individual's extrapair behaviors.

Extrapair mating strategies are widespread in birds (reviewed in Westneat and Stewart 2003), and their occurrence and prevalence vary extensively across species, populations, and individuals (Petrie and Kempenaers 1998, Griffith et al. 2002). In socially monogamous species, where the direct benefits of extrapair fertilizations (EPF) are assumed to be rare, variation in extrapair behavior is thought to reflect a balance between costs of mates' extrapair behavior and genetic benefits of EPF to offspring fitness (Hamilton 1990, Birkhead and Møller 1996, Gowaty 1996a, Gowaty and Buschhaus 1998, Jennions and Petrie 2000). For example, in temperate biparental birds, constraints on initial mate choice imposed by strong selection for early breeding can favor rapid social pairing with a genetically suboptimal male, followed by a subsequent adjustment of social mate choice with EPF (e.g., Spottiswoode and

Møller 2004). At the same time, the degree to which genetically suboptimal initial pairing can be improved by EPF depends on the genetic variation between available and selected mates (Hosken and Blanckenhorn 1999, Kupper et al. 2004, Johanessen 2005). Thus, an assessment of the relative strength of direct selection against extrapair behaviors and indirect genetic benefits for both social and extrapair mates is crucially important for understanding the variability in EPF (Webster et al. 1995, Hosken and Blanckenhorn 1999, Shellman-Reeve and Reeve 2000, Whittingham and Dunn 2005). Indeed, recent analyses suggested that directional selection against extrapair behavior is stronger and more consistent than indirect selection favoring extrapair behavior (Arnqvist and Kirkpatrick 2005), and that the relative importance of direct and indirect fitness benefits of EPF can vary with female condition

and context of breeding (Gowaty 1996a, Gowaty and Buschhaus 1998, Møller and Jennions 2001).

Temporal and spatial distribution of extrapair mating opportunities can strongly affect the intensity of sexual selection (Shuster and Wade 2003). In particular, breeding synchrony and nest density are thought to be important determinants of variation in EPF because of their effect on costs of mate search and assessment (Westneat et al. 1990). When higher breeding synchrony and nest density lower these costs, they can enable greater frequency of EPFs (Birkhead and Møller 1992, Westneat and Sherman 1997). The high costs of females' search and assessment of extrapair mates is thought to favor clustering of nesting territories and more synchronous breeding in some birds (Wagner 1993, Gowaty 1996a). At the same time, higher breeding synchrony and nest density can limit the effectiveness of mate guarding and thus increases the opportunity for males to seek EPF without penalty of paternity loss in their own nest (Birkhead and Biggins 1987, Stutchbury and Morton 1995, Thusius et al. 2001, Václav and Hoi 2002, Mota and Hoi-Leitner 2003, Arlt et al. 2004).

With apparently large differences in direct costs and benefits of EPF between males and females, but similar genetic benefits (Arnqvist and Kirkpatrick 2005), the persistence of extrapair behaviors in females is poorly understood (Jennions and Petrie 2000, Hasselquist and Sherman 2001, Westneat and Stewart 2003). One proposed hypothesis is that females mating with extrapair males that have more compatible or complementary genes than the female's social partner can override the costs of extrapair behaviors. Indeed, some studies document female choice of complementary extrapair partners (e.g., Double and Cockburn 2000, Johnsen et al. 2000), although the context-dependency of such choice has been examined in only a few studies (Gowaty 1996, 1999, Johnsen et al. 2000, Schmoll et al. 2005, Oh and Badyaev 2006). Alternatively, females' acceptance of EPFs might be a mechanism for lowering the high physical costs of resistance to extrapair males, a behavioral or physiological constraint imposed by concurrent within-pair matings, or insurance against social male's infertility (Westneat et al. 1990, Birkhead and Møller 1992, Lifjeld et al. 1993, Westneat and Stewart 2003). To fully explore the costs and benefits of extrapair behavior in both sexes, we need a study system where the complete spatial and temporal distribution of mating opportunities, as well as the genetic characteristics of available mates, can be assessed, which is rarely possible in free-living populations.

Here we examined prevalence of EPF in relation to breeding density, synchrony, and genetic variability of available mates in a wild population of house finches *Carpodacus mexicanus* where all breeding attempts are

known and most adults and all offspring are genotyped. We first show that both males and females avoid displaying to extrapair partners in the presence of their social mates, suggesting that direct negative selection on extrapair displays might be strong in this population. We then examine the prevalence of EPF in relation to breeding synchrony and nest density and find that EPFs do not vary with these factors. Instead, we report evidence for preference for genetically unrelated extrapair partners, apparently driven by strong fitness benefits of heterozygosity in this population. We discuss the implications of these results for understanding the variability in extrapair behaviors across reproductive contexts.

Methods

Study system

We studied a resident population of house finches in northwestern Montana (USA), near the northwestern edge of the species range. House finches started breeding in this population in late 1970s, and the study site has been maintained since 1994 (for details of the study site and field protocol see Badyaev and Martin 2000, for history of this population see Badyaev 2005). The study site is a cluster of buildings and two sets of 74 identical ornamental shrubs planted 4m apart along two linear arrays (46 and 28 bushes each) in an open grassland. Finches used these 2–3 m high ornamental shrubs for nesting and several large coniferous trees at the edge of the complex for roosting. Each year from 1995 to 2004, at the onset of the breeding season, all birds in this isolated study population were captured, individually marked, and pair affiliations, behavior, and nesting were monitored continuously (Badyaev et al. 2000). Once finches breed at the study site in their first year, most continue to breed there for the rest of their lives and reside within the study site throughout the year (Badyaev and Duckworth 2003). Dispersing individuals arriving to the population for their first breeding were captured within two days of arrival and individually marked (Badyaev et al. 2001b). To account for the effects of mate familiarity and previous breeding experience in the analyses of offspring survival, we included only newly pairing birds. Temporal changes in the pool of individuals available for mating were measured in relation to adult finches' date of arrival at the study site.

Within the study site, finches often nest in aggregations, but over the course of each breeding season, all 74 bushes typically contain at least one nest. For the purposes of this study, a nest was considered "active" from the time a female of a breeding pair had initiated oogenesis (10 d prior to egg-laying, typically during

middle of the nest building, Young and Badyaev 2004) to the end of egg-laying. We calculated the distance, in 4 m increments, between the focal active nest and other active nests within the study site. When several active nests were located within a single bush, the distance between them was recorded as zero. Breeding synchrony was calculated as the average number of active nests initiated during each calendar week of the breeding season.

Behavioral experiments

Both sexes in this population solicit extrapair copulations. Males actively display to fertile extrapair females when these females are foraging or collecting nest material on the ground, while females typically undertake directional forays to the vicinity of a potential extrapair male's social nest for extrapair displays. We investigated an individual's propensity to display to extrapair mates in relation to their social mate's presence by conducting two tests. In the first test, we captured fertile females at the ovulation stage from a different study population 8 km away, and presented them, one per small cage, to those males at the study population whose social females were at the stage of early egg-laying (first two eggs of a clutch) and were incubating from the first egg, i.e., females that were both confined to their nests and at their most fertile stage. Each social pair with an egg-laying and incubating female was assigned two treatments. First, a cage with an extrapair female was placed on the ground directly under the nesting bush of a focal female (treatment "0 m"), where a focal nesting female can observe a cage directly. Second, a cage with the same extrapair fertile female was placed under a bush on the ground two nesting bushes away, along a linear transect (treatment "15 m"), where no direct visual or acoustic observations by a focal nesting female is possible. Both sites were baited with sunflower seeds and treatments were conducted in varying sequence on the same morning, between 08.00 and 12.00. Extrapair females (n =7 over the course of experiment) were released at their capture site immediately after the experiment. Directionality of cage placement along the transect was determined by the location of and distance to other active nests at the study site. After a social male appeared, we conducted 10 min trials, recording the duration of three categories of behaviors: fight/attack displays, solicitation displays, and all other behaviors apparently neutral in relation to a caged female (e.g., foraging, preening). When non-focal males interacted with a caged female, their behavior was not included and the test was repeated. When the incubating female left the

nest during the trial or attacked the extrapair female, the trial was stopped and repeated later in the day or on the following day when possible. We collected data for 22 paired presentations (n =11 social pairs) in 1997 and 14 paired presentations (n =7 social pairs) in 1998. In 2000–2001, we collected data on a female's propensity to display to extrapair males in relation to the presence of her social male. During intensive behavioral observations that took place daily between 07.00 and 12.00 h, we recorded all within and extrapair behaviors that occurred within the study site. For each observed female-initiated extrapair display, we recorded the identity of the individuals involved, the presence of the female's social male, as well as the female's reproductive stage.

Microsatellite genotyping and paternity analysis

We collected 20 µl of blood from each individual by brachial venipuncture. All adults and offspring were genotyped at 16 highly polymorphic species-specific microsatellite loci (HOFI53, HOFI ACAG07, HOFI ACAG 25, HOFI16, HOFI29, HOFI10, HOFI70, HOFI ACAG01, HOFI30, HOFI39, HOFI19, HOFI35, HOFI69, HOFI ACAG15, HOFI07, HOFI26; Oh and Badyaev 2006). PCR was carried out using fluorescent-labeled primers (Applied Biosystems, USA), and analyzed by capillary electrophoresis in an ABI Prism 3730 DNA analyzer. Discrete microsatellite allele sizes were determined using Genotyper software. Genotypes were analyzed with CERVUS v. 2.0 (Marshall et al. 1998), to calculate expected and observed heterozygosities and to test for departures from Hardy-Weinberg equilibrium (Oh and Badyaev 2006). Parentage was assessed at each nest by comparing genotypes of offspring and attending adults. Paternity for a putative father was excluded if two or more loci did not match. In each of the ten years, the combined exclusion probability was >0.999. Paternity analysis was carried out using the likelihood approach implemented in CERVUS (Marshall et al. 1998; for details of paternity assignment see Oh and Badyaev 2006). Briefly, simulations (reiterated for 10,000 cycles) were performed to obtain critical values of delta (the difference in log-likelihood ratio scores between two most likely candidate sires) for a 95% confidence level. Paternity was assigned to putative father only when the delta value for a 95% confidence level was achieved. If none of the candidate males met this criterion, offspring were considered to have been sired by an unsampled individual (e.g., non-resident 'floater' male). We assigned paternity for 12 out of the 19 extra-pair young identified.

Estimation of pairwise genetic relatedness and genetic diversity

Pairwise estimates of relatedness were calculated for all adults using a method of moments estimator of MER software (Wang 2002). Allele frequencies were calculated separately for each year and standard errors were from bootstrapping over loci (30,000 iterations). Genetic diversity within individuals was calculated as internal relatedness (*IR*, Amos et al. 2001), a maximum likelihood estimator derived from a method proposed by Queller and Goodnight (1989). The average pairwise relatedness of social and extrapair partners was compared with the average relatedness of a pool of potential partners at the time of pairing or fertilization correspondingly (Oh and Badyaev 2006). In the calculation of available mates we report the mean pairwise relatedness values for each female and unpaired males that were present (excluding the male with whom she mated) when that female arrived at the study site (or 1 February for overwintering residents). For each female, we defined a potential extrapair partner as any resident male that was present in the population during ten days preceding the onset of ovulation of the focal female (Young and Badyaev 2004). Complete genotypes of an entire population (i.e., mating females and all available social and extrapair males) were available for 45 female mate selection episodes; average pairwise female relatedness to available, social, and extrapair males was calculated for each female separately as least-squared means with year as a covariate.

Novel pathogen resistance

Mycopslasmal conjunctivitis is a highly contagious and contact-transmitted bacterial infection caused by a novel strain of *Mycoplasma gallisepticum* that since its emergence in 1994 had reached epidemic proportions in the house finches of eastern North America (Fischer et al. 1997). In April 2002, in this study population, we discovered the first case of this infection in western North America (Duckworth et al. 2003). To test for an association between individual genetic diversity and disease resistance, we compared genetic diversity of 18 local offspring that developed symptoms and tested positive for *M. gallisepticum* with PCR (Duckworth et al. 2003) after contact with infected individuals with 48 local offspring that were observed in close contact with at least one infected individual (e.g., on communal feeders or at nests), but never developed mycoplasmosis.

Statistical analyses

We used logistic regression (PROC PROBIT, SAS 1998) to calculate maximum likelihood estimates of the logistic regression parameters of distance, synchrony, and mate relatedness on probability of EPF occurrence. Probability of EPF was fitted with a spline curve (Schluter 1988). For EPF frequency across each trait distribution, we used the method of cross-validation and the algorithm provided in Schluter (1989) to select the smoothing parameter with the maximum predictive power. This was done by excluding, with replacement, all individuals in turn for different values of the parameter. Multiple comparisons of means were conducted with t (LSD) multiple range tests ($\alpha = 0.05$).

Results

Nine percent of nestlings (19/212) were extrapair offspring and 15% of nests (9/59) contained nestlings that were sired by an extrapair male. There was no brood parasitism in any nests. One nest contained two nestlings sired by two different extra-pair males and another single nest contained all extra-pair young. Occurrence of extrapair young did not vary with nest density, and nests with extrapair young were not closer to nests of extrapair sires than to the other active nests (Fig. 1A and 2AC, both t's < 0.50, P > 0.37). Nests with extrapair young were more common in the middle of breeding season (Fig. 2B), but this was largely due to a greater number of active nests in the study population (Fig. 1B and 2C, t $= -1.56$, P $= 0.06$). Occurrence of extrapair young in the nest increased when females were, on average, more related to all males present during fertile period, but did not vary with average relatedness of individual males to available females (Fig. 3A, B). Extrapair partners were more genetically dissimilar than social partners (Fig. 3C). Offspring that had tested positive for mycoplasmal conjunctivitis tended to be less genetically diverse than individuals that did not develop the disease despite having close contact with at least one infected conspecific (Fig. 3D; higher genetic diversity = low IR, Wilcoxon test, Z $= 1.59$, P $= 0.06$).

Males were more likely to display to an extrapair female placed away from their social female and more likely to attack extrapair female when near their social female. The proportion of time spent fighting versus displaying to extrapair female strongly differed between "0m" vs "15 m" distance treatments (display, Kruskal-Wallis, $\chi^2 = 26.4$, P < 0.001, attack: $\chi^2 = 23.6$, P < 0.001), except for "ignore" group ($\chi^2 = 0.78$, P $= 0.38$). Males mostly attacked or ignored extrapair females at "0m" treatment (display vs. attack, $t_{crit} = -8.62$, P < 0.001, display vs ignore, t $= 1.40$, P $= 0.18$), whereas at "15 m" treatment, males mostly displayed to extrapair females (display vs attack, t $= -9.75$, P < 0.001, display vs ignore, t $= -4.03$,
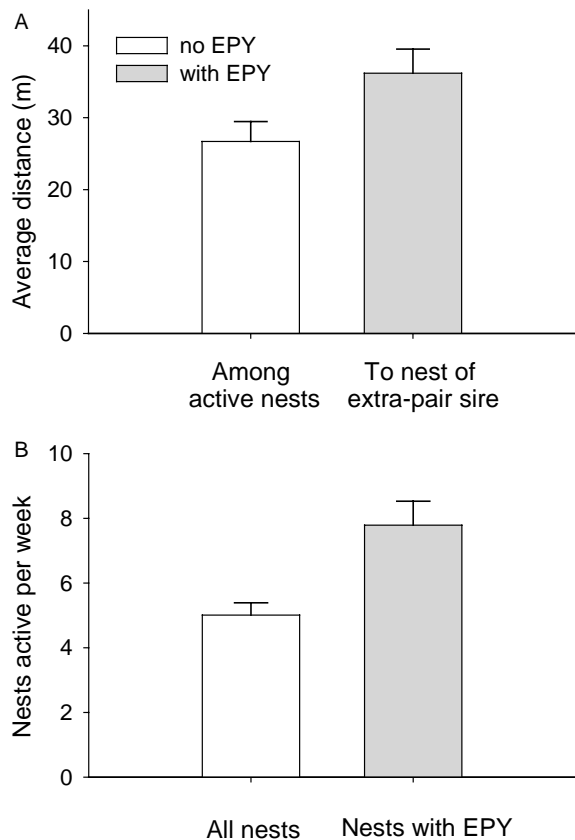
Fig. 1. Extrapair fertilizations in relation to (A) average distance between all active nests without extra-pair young (EPY; open bars) and nests of extrapair partners (filled bars), and (B) number of simultaneously active nests. Shown are means ± SE.

P = 0.001; Fig. 4A). Females were more likely to display to extrapair males when their social male was absent during prospecting ($\chi^2 = 15.32$, P < 0.001), nest building ($\chi^2 = 3.57$, P = 0.06), and egg-laying periods ($\chi^2 = 9.94$, P = 0.002), but not during nest-lining stage ($\chi^2 = 1.69$, P = 0.19; Fig. 4B).

Discussion

Extrapair behaviors in socially monogamous biparental species occur when they enable individuals to gain additional direct and indirect benefits while overcoming constraints imposed by social mate choice (Fitch and Shugart 1984, Birkhead and Møller 1992, Gowaty 1996a, 1999, Hasselquist and Sherman 2001, Westneat and Stewart 2003). In particular, EPF might be most prevalent when the environmental conditions or a pool of available mates change between the time of social and extrapair matings (Blomqvist et al. 2002, Foerster et al.
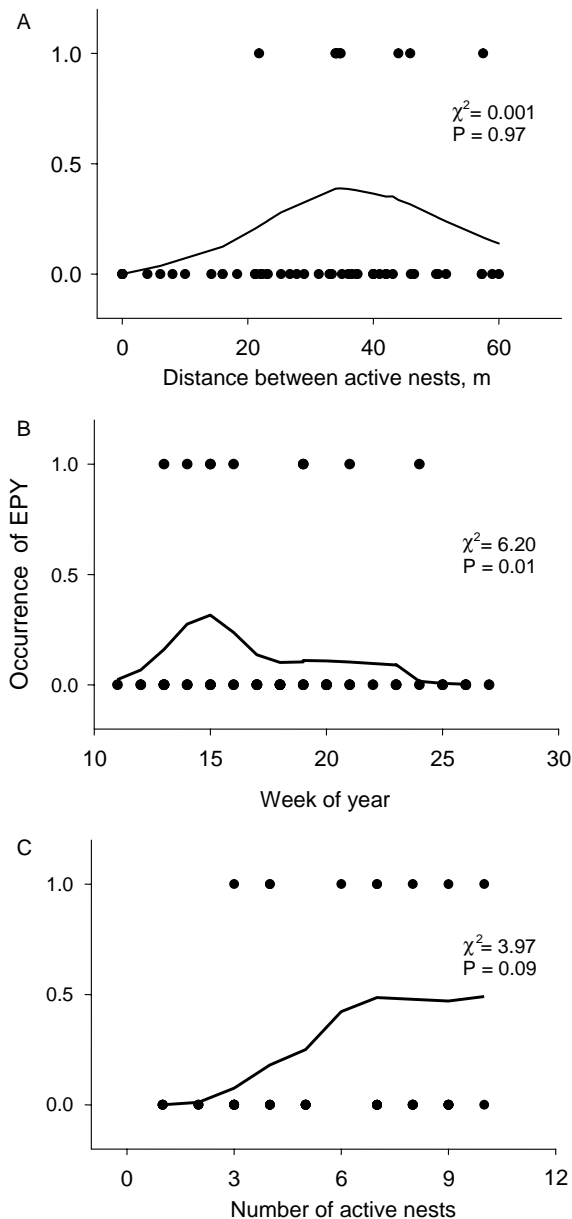

Fig. 2. Occurrence of extrapair young in relation to (A) average distance between active nests, (B) week of the year, and (C) number of simultaneously active nests. Shown are spline curves of EPY probability.

2003, Hansson et al. 2004, Kupper et al. 2004, Schmoll et al. 2005). In socially monogamous biparental birds within-pair reproductive success contributes more to the opportunity for sexual selection than does extra-pair reproductive success (Freeman-Gallant et al. 2005, Whittingham and Dunn 2005). At the same time, the costs and benefits of EPF might differ between males and females; a male's reproductive success often
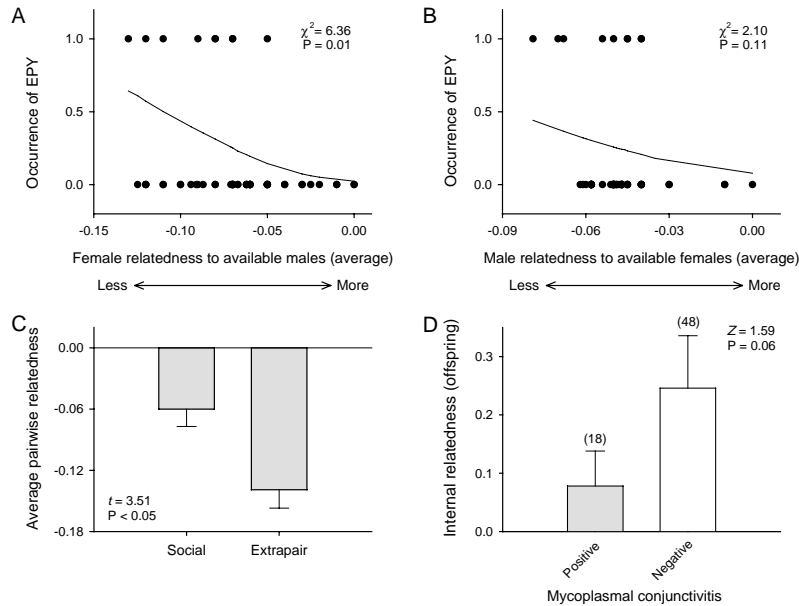
Fig. 3. Extrapair fertilizations in relation to (A) average genetic relatedness of males to all females present within a study site, and (B) average genetic relatedness of females to all males present at the study site. (C) Average pairwise relatedness between social (n = 45 pairs) and extrapair (n = 8 pairs) partners. (D) In offspring that had contact with mycoplasmal conjunctivitis, individuals of higher genetic diversity (i.e., low IR, mean $\pm$ SE) were more resistant to the infection compared to individuals with lower genetic diversity.

increases with additional EPF, especially when accompanied by effective social mate guarding, whereas the indirect genetic benefits of EPF for females might be weak and less variable among individuals (Westneat et al. 1990).

In order to understand how extrapair strategies can evolve, we need to know the extent to which spatial and temporal distribution of available social and extrapair mating opportunities differ among individuals (Shuster and Wade 2003). We found that neither nesting synchrony or density, nor proximity of extrapair partners affected the prevalence of EPF in our study population. At the same time, both sexes solicited extrapair copulations when social mates were absent but avoided these displays in the presence of their social mates. In addition, we found that extrapair mates were consistently more genetically dissimilar compared to social mates, corroborating the findings of strong fitness consequences of offspring heterozygosity in this population (Fig. 3D; Oh and Badyaev 2006). These findings raise several questions. First, given the apparent costs of extrapair behaviors revealed by the mate presentation experiments, why was no concomitant correlation found between such costs and EPF at the population level (i.e., EPF covariation with breeding density and distribution)? Second, the mate presentation experiments and observations show that in this population extrapair solicitations are common.

How to reconcile this observation with the relative rarity of EPF rates? Third, what are the mechanisms for the selection of extrapair mates based on genetic diversity?

Our results suggest that the EPF frequency in this population is determined more by availability of suitable extrapair mates and less by the potential costs of extrapair mate searching or sampling (Fig. 2 and 3). The lack of uniform effects of breeding synchrony and nest dispersion on EPF frequency is concordant with the finding of individual EPF strategies; when extrapair mate choice is based on genetic complementarity, the best mate for one individual may not be the best mate for another. Similarly, whereas the probability of EPF increased with nest density in a blue tit *Parus caeruleus* population, the distance between the nests of extrapair partners or the number of extrapair males did not vary with nest density, suggesting active individual female choice of extrapair partners (Charmantier and Perret 2004). Alternatively, the risk of predation or expense of traveling to sample extrapair mates might be low in this relatively small population. The semi-colonial nesting settlements of house finches and great degree of familiarity between the pairs within each settlement (Badyaev and Hill 2002, this study), might further reduce the effectiveness of mate guarding, especially when females' extrapair displays are conducted during directional forays to locations of specific
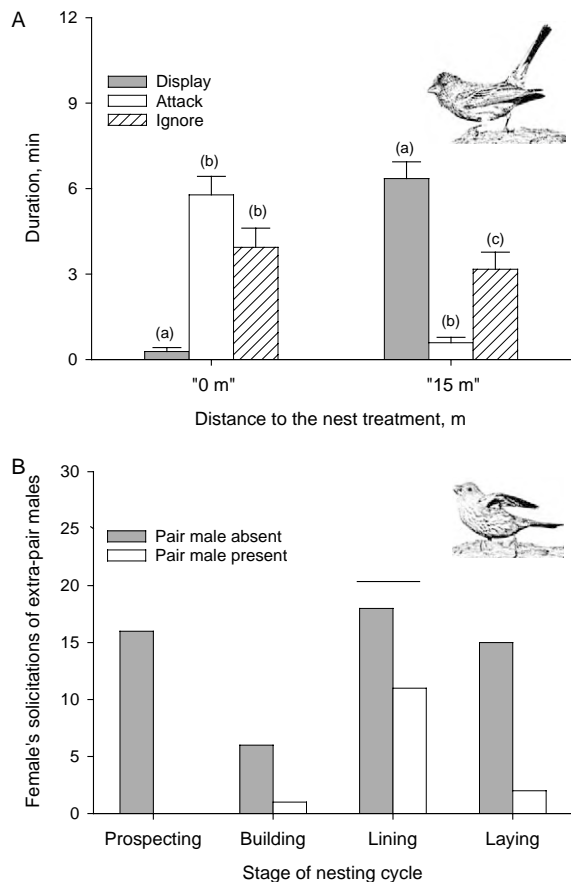
Fig. 4. Distribution of extrapair displays in relation to (A) distance to fertile female (duration of displays in min ±SE), bars with the same letters are not significantly different within treatment, and (B) presence of a social male at different breeding stages, a line shows non-significant differences within a nesting stage.

potential extrapair mates as they are in this population (pers. obs.).

House finches in this population engage in frequent extrapair solicitations and copulations, including during the female's egg-laying period. However, most of these copulations do not result in fertilizations, corroborating finding of comparably low EPF rates from other house finch populations (Hill et al. 1994, Badyaev et al. 2001a). There are several explanations to this pattern. First, in this population, most extrapair displays, and especially female-initiated extrapair copulations involve birds that become social partners in future breeding attempts, such that extrapair displays can be a form of mate sampling (Cezilly and Nager 1995, Slagsvold et al. 2001). Such mate sampling might be especially true for females whose social males do not feed them during nest-building and egg-laying stages; the lack of such provisioning is the best predictor of within-breeding season divorce in this population (Badyaev and Hill 2002). This is similar to other species of cardueline finches, where females are often observed food begging from extrapair males during egg-laying, a display that typically concludes with copulation (Badyaev 1993, Hoi-Leitner et al. 1999). Second, the frequency of within-pair copulations – 6–14 per h during nest building – greatly exceeds the frequency of extrapair fertilizations, which might explain the discordance between frequent behavioral observations of extrapair copulations (Fig. 4B), and rare occurrence of extrapair young (Møller and Birkhead 1993, Birkhead et al. 2004).

Further evidence of weak general costs and constraints on extrapair behavior in this population comes from consistent choice of the least related extrapair partners (Fig. 3C). In several populations of house finches, matings among unrelated partners have strong fitness advantages; offspring of such matings are more heterozygous, and have greater resistance to a novel pathogen (Fig. 3D) and higher survival to recruitment (Hawley et al. 2006a, Oh and Badyaev 2006). In this population, the availability of genetically diverse mates is largely determined by the seasonal patterns of immigration of genetically dissimilar females settling in the study population for their first breeding (Oh and Badyaev 2006). Mating preference for nonlocal and unfamiliar extrapair mates (e.g., Peacock and Smith 1997, Masters et al. 2003) might be especially favored in recently established and introduced house finch populations in North America that underwent bottleneck events and suffered significant inbreeding (Hawley et al. 2006b). At the same time, prevalence of EPF might be limited by strong fitness benefits of biparental provisioning and rare opportunities for EPF with non-local mates; the amount of provisioning by a pair's social male is the main predictor of offspring growth and survival in both nests with and without extrapair young (Badyaev and Hill 2002, Oh and Badyaev 2006).

Our results suggest that EPF in this population are confined to contexts where the benefits of extrapair mating with rare and genetically distinct non-local individuals overcome the potential costs of reduced within-pair paternity. Such contingency of benefits of mate choice of genetic complementarity diminishes the effect of population-wide variation in breeding synchrony and nest dispersion on the evolution of extrapair strategies.

References

Amos, W., Wilmer, J. W., Fullard, K., Burg, T. M., Croxall, J. P., Bloch, D. and Coulson, T. 2001. The influence of parental relatedness on reproductive success. – Proc. R. Soc. B 268: 2021–2027.

Arlt, D., Hansson, B., Bensch, S., von Schantz, T. and Hasselquist, D. 2004. Breeding synchrony does not affect extra-pair paternity in great reed warblers. – Behaviour 141: 863–880.

Arnqvist, G. and Kirkpatrick, M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior. – Am. Nat. 165: S26–S37.

Badyaev, A. V. 1993. Breeding biology of gold-fronted serin in subalpine of Pamir-Alai Mountains. – Biol. Sci. 93: 89–99.

Badyaev, A. V. 2005. Maternal inheritance and rapid evolution of sexual size dimorphism: passive effects or active strategies? – Am. Nat. 166: S17–S30.

Badyaev, A. V. and Duckworth, R. A. 2003. Context-dependent sexual advertisement: plasticity in development of sexual ornamentation throughout the lifetime of a passerine bird. – J. Evol. Biol. 16: 1065–1076.

Badyaev, A. V. and Hill, G. E. 2002. Parental care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. – Behav. Ecol. 13: 591–597.

Badyaev, A. V. and Martin, T. E. 2000. Sexual dimorphism in relation to current selection in the house finch. – Evolution 54: 987–997.

Badyaev, A. V., Hill, G. E., Dunn, P. O. and Glen, J. C. 2001a. Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. – Am. Nat. 158: 221–235.

Badyaev, A. V., Hill, G. E., Stoehr, A. M., Nolan, P. M. and McGraw, K. J. 2000. The evolution of sexual dimorphism in the house finch: II. Population divergence in relation to local selection. – Evolution 54: 2134–2144.

Badyaev, A. V., Whittingham, L. A. and Hill, G. E. 2001b. The evolution of sexual size dimorphism in the house finch: III. Developmental basis. – Evolution 55: 176–189.

Birkhead, T. R. and Biggins, J. D. 1987. Reproductive synchrony and extra-pair copulation in birds. – Ethology 74: 320–334.

Birkhead, T. R. and Møller, A. P. 1992. Sperm competition in birds. Evolutionary causes and consequences. – Academic Press, San Diego.

Birkhead, T. R. and Møller, A. P. 1996. Monogamy and sperm competition in birds. – In: Black, J. M. and Hulme, M. (eds). Partnership in birds: the study of monogamy. Oxford University Press, pp. 323–343.

Birkhead, T. R., Chaline, N., Biggins, J. D., Burke, T. and Pizzari, T. 2004. Nontransitivity of paternity in a bird. – Evolution 58: 416–420.

Blomqvist, D., Andersson, M., Kupper, C., Cuthill, I., Kis, J., Lanctot, R. B., Sandercock, B. K., Szekely, T., Wallander, J. and Kempenaers, B. 2002. Genetic similarity between mates and extra-pair parentage in three species of shore-birds. – Nature 419: 613–615.

Cezilly, F. and Nager, R. G. 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. – Proc. R. Soc. B 262: 7–12.

Charmantier, A. and Perret, P. 2004. Manipulation of nest-box density affects extra-pair paternity in a population of blue tits (*Parus caeruleus*). – Behav. Ecol. Sociobiol. 56: 360–365.

Double, M. and Cockburn, A. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. – Proc. R. Soc. B 267: 465–470.

Duckworth, R. A., Badyaev, A. V., Farmer, K. L., Hill, G. E. and Roberts, S. R. 2003. First case of mycoplasmosis in the native range of the house finch (*Carpodacus mexicanus*). – Auk 120: 528–530.

Fischer, J. R., Stallknecht, D. E., Luttrell, M. P., Dhondt, A. A. and Converse, K. A. 1997. Mycoplasmal conjunctivitis in wild songbirds: the spread of a new contagious disease in a mobile host population. – Emerg. Infect. Dis. 3: 69–72.

Fitch, M. A. and Shugart, G. W. 1984. Requirements for a mixed reproductive strategy in avian species. – Am. Nat. 124: 116–126.

Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J. T. and Kempenaers, B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. – Nature 425: 714–717.

Freeman-Gallant, C. R., Wheelwright, N. T., Meiklejohn, K. E., States, S. L. and Sollecito, S. V. 2005. Little effect of extrapair paternity on the opportunity for sexual selection in Savannah sparrows (*Passerculus sandwichensis*). – Evolution 59: 422–430.

Gowaty, P. A. 1996a. Battles of the sexes and origins of monogamy. – In: Black, J. M. (ed.). Partnerships in birds. Oxford University Press, pp. 21–52.

Gowaty, P. A. 1996b. Multiple matings by females select for males that stay: another hypothesis for social monogamy in passerine birds. – Anim. Behav. 51: 482–484.

Gowaty, P. A. 1999. Manipulation and resistance: differential male fitness via exploitation of variation among females. – In: Adams, N. and Slotow, R. (eds). Proc. 22 Int. Ornithol. Congr. – University of Natal, pp. 2639–2656.

Gowaty, P. A. and Buschhaus, N. 1998. Ultimate causation of aggressive and forced copulation in birds: Female resistance, the CODE hypothesis, and social monogamy. – Am. Zool. 38: 207–225.

Griffith, S. C., Owens, I. P. F. and Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. – Mol. Ecol. 11: 2195–2212.

Hamilton, W. D. 1990. Mate choice near or far. – Am. Zool. 30: 341–352.

Hansson, B., Hasselquist, D. and Bensch, S. 2004. Do female great reed warblers seek extra-pair fertilizations to avoid inbreeding. – Proc. R. Soc. B (Suppl) 271: S290–S292.

Hasselquist, D. and Sherman, P. W. 2001. Social mating system and extrapair fertilization in passerine birds. – Behav. Ecol. 12: 457–466.

Hawley, D. M., Hanley, D., Dhondt, A. A. and Lovette, I. J. 2006a. Molecular evidence for a founder effect in invasive house finch (*Carpodacus mexicanus*) populations experiencing an emergent disease epidemic. – Mol. Ecol. 15: 263–275.

Hawley, D. M., Sydenstricker, K. V., Kollias, G. V. and Dhondt, A. A. 2006b. Genetic diversity predicts pathogen resistance and cell-mediated immunocompetence in house finches. – Biol. Lett. 1: 326–329.

Hill, G. E., Montgomerie, R., Roeder, C. and Boag, P. 1994. Sexual selection and cuckoldry in a monogamous songbird: implications for sexual selection theory. – Behav. Ecol. Sociobiol. 35: 193–199.

Hoi-Leitner, M., Hoi, H., Romero-Pujante, M. and Valera, F. 1999. Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the 'constrained female hypothesis'. – Proc. R. Soc. B 266: 1021–1026.

Hosken, D. J. and Blanckenhorn, W. U. 1999. Female multiple mating, inbreeding avoidance, and fitness: it is not only the magnitude of costs and benefits that counts. – Behav. Ecol. 10: 462–464.

Jennions, M. D. and Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. – Biol. Rev. 75: 21–64.

Johanessen, L. E., Slagsvold, T., Hansen, B. T. and Lifjeld, J. T. 2005. Manipulation of male quality in wild tits: effects on paternity loss. – Behav. Ecol. 16: 747–754.

Johnsen, A., Andersen, V., Sunding, C. and Lifjeld, J. T. 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. – Nature 406: 296–299.

Kupper, C., Kis, J., Kosztolanyi, A., Szekely, T., Cuthill, I. C. and Blomqvist, D. 2004. Genetic mating system and timing of extra-pair fertilizations in the Kentish plover. – Behav. Ecol. Sociobiol. 57: 32–39.

Lifjeld, J. T., Dunn, P. O., Robertson, R. J. and Boag, P. T. 1993. Extra-pair paternity in monogamous tree swallows. – Anim. Behav. 45: 213–229.

Marshall, T. C., Slate, J., Kruuk, L. E. B. and Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. – Molec. Ecol. 7: 639–655.

Masters, B. S., Hicks, B. G., Johnson, L. S. and Erb, L. A. 2003. Genotype and extra-pair paternity in the house wren: a rare-male effect? – Proc. R. Soc. B 270: 1393–1397.

Møller, A. P. and Birkhead, T. R. 1993. Cuckoldry and sociality: a comparative study of birds. – Am. Nat. 142: 118–140.

Møller, A. P. and Jennions, M. D. 2001. How important are direct fitness benefits of sexual selection? – Naturwiss. 88: 401–415.

Mota, P. G. and Hoi-Leitner, M. 2003. Intense extrapair behaviour in a semicolonial passerine does not result in extrapair fertilizations. – Anim. Behav. 66: 1019–1026.

Oh, K. P. and Badyaev, A. V. 2006. Adaptive genetic complementarity coexists with selection for elaborate sexual traits in mate choice of a passerine bird. – Proc. R. Soc. B 273: 1913–1919.

Peacock, M. M. and Smith, A. T. 1997. Nonrandom mating in pikas *Ochotona princeps*: Evidence for inbreeding between individuals of intermediate relatedness. – Mol. Ecol. 6: 801–811.

Petrie, M. and Kempenaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. – Trends Ecol. Evol. 13: 52–58.

Queller, D. C. and Goodnight, K. F. 1989. Estimating relatedness using genetic markers. – Evolution 43: 258–275.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. – Evolution 42: 849–861.

Schluter, D. 1989. Introduction to GLMS. http://www.zoology.ubc.ca/ ∼ schluter/splines.html.

Schmoll, T., Dietrich, V., Winkel, W., Epplen, J. T., Schurr, F. and Lubjuhn, T. 2005. Paternal genetic effects on offspring fitness are context dependent within the extrapair mating system of a socially monogamous passerine. – Evolution 59: 645–657.

Shellman-Reeve, J. S. and Reeve, H. K. 2000. Extra-pair paternity as the result of reproductive transactions between paired mates. – Proc. R. Soc. B 267: 2543–2546.

Shuster, S. M. and Wade, M. J. 2003. Mating systems and strategies. – Princeton University Press.

Slagsvold, T., Johnsen, A., Lampe, H. and Lifjeld, J. T. 2001. Do female pied flycatchers seek extrapair copulations with familiar males? A test of the incomplete knowledge hypothesis. – Behav. Ecol. 12: 412–418.

Spottiswoode, C. and Møller, A. P. 2004. Extrapair paternity, migration, and breeding synchrony in birds. – Behav. Ecol. 15: 41–57.

Stutchbury, B. J. and Morton, E. S. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. – Behaviour 132: 675–690.

Thusius, K. J., Dunn, P. O., Peterson, K. A. and Whittingham, L. A. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. – Behav. Ecol. 12: 633–639.

Václav, R. and Hoi, H. 2002. Importance of colony size and breeding synchrony on behaviour, reproductive success and paternity in house sparrows *Passer domesticus*. – Folia Zool. 51: 35–48.

Wagner, R. H. 1993. The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. – J. Theor. Biol. 163: 333–346.

Wang, J. 2002. An estimator for pairwise relatedness using molecular markers. – Genetics 160: 1203–1215.

Webster, M. S., Pruett-Jones, S., Westneat, D. F. and Arnold, S. J. 1995. Measuring the effects of pairing success, extrapair copulations and mate quality on the opportunity for sexual selection. – Evolution 49: 1147–1157.

Westneat, D. F. and Sherman, P. W. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. – Behav. Ecol. Sociobiol. 41: 205–215.

Westneat, D. F., Sherman, P. W. and Morton, M. L. 1990. The ecology and evolution of extra-pair copulations in birds. – Curr. Ornithol. 7: 331–369.

Westneat, D. F. and Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. – Annu. Rev. Ecol. Syst. 34: 365–396.

Whittingham, L. A. and Dunn, P. O. 2005. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. – Behav. Ecol. 16: 138–144.

Young, R. L. and Badyaev, A. V. 2004. Evolution of sex-biased maternal effects in birds: I. Sex-specific resource allocation among simultaneously maturing follicles. – J. Evol. Biol. 17: 1355–1366.