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REVIEW

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Density and extra-pair fertilizations in birds: a comparative analysis

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Abstract Møller and Birkhead (1992, 1993) reported that extra-pair copulations (EPCs) occur more frequently in colonial than dispersed nesting birds. We comprehensively reviewed published data to investigate how breeding density affects extra-pair fertilizations (EPFs). Within species EPFs appeared to increase with density: two of three studies on colonial breeders and six of eight on dispersed nesters showed increases in EPFs with increasing density. However, comparisons among species ($n = 72$) revealed no evidence that EPF frequencies correlated with (1) nesting dispersion, (2) local breeding density, or (3) breeding synchrony, even when each of these variables in turn was held constant and phylogenetic relationships were taken into account via contrast analyses. Methodological and biological reasons for the disparity between observational studies of EPCs and molecular genetic analyses of EPFs are discussed.

Key words Extra-pair fertilizations · Breeding density · Dispersion · Synchrony · Contrast analyses

Introduction

Density affects behavior because as spatial proximity increases, so does the likelihood of direct interactions, both cooperative and competitive. Interactions between the sexes (e.g., copulations, inter-sexual aggression) in particular are sensitive to variations in spatial proximity among members of the limiting sex, usually females (e.g., Crook 1964; Jarman 1974; Parker 1983; Crowley et al. 1991; Davies 1991). For example, field observations and experiments have demonstrated effects of density on female resistance in insects (e.g., Arnqvist 1992a, b; Shelly and Bailey 1992; Rowe 1992; Krupa and Sih 1993), patterns of amplexus in toads (Kagarise Sherman 1980; Sullivan 1982; Arak 1983), territorial versus group-spawning in fishes (Warner and Hoffman 1980; Kodric-Brown 1988), and patterns of social bonds in birds (Davies 1992; Höglund and Alatalo 1995). Local density also can influence costs of parental care (e.g., time spent foraging) and costs and benefits of defending a territory, which can affect aspects of mating behavior (e.g., Brown 1969; Trivers 1972; Emlen and Oring 1977; Davies 1991).

Extra-pair copulations (EPCs) are mating behaviors that would seem especially sensitive to density. EPCs are common in birds (e.g., Westneat et al. 1990; Birkhead and Møller 1992) and they often lead to extra-pair fertilizations (EPFs; e.g., Birkhead and Møller 1992; Westneat and Webster 1994), frequently with neighboring males (e.g., Gibbs et al. 1990; Westneat 1993; Stutchbury et al. 1994; Hasselquist et al. 1995b). The revelation that social and genetic monogamy often are not synonymous has both spurred a revolution in thinking about avian mating systems and created a need for new hypotheses about patterns of avian mating behavior that take extra-pair activities into account.

An important first step is to clarify how the dispersion of individuals affects such activities. This issue has not been addressed theoretically, and existing data yield inconsistent conclusions. On the one hand, several workers (e.g., Hoogland and Sherman 1976; Birkhead 1978; Wrege and Emlen 1987; Møller 1991; Morton et al. 1990) have suggested that EPCs should increase with increasing density. Indeed, increases in local breeding density were associated with higher EPC frequencies in common guillemots (*Uria aalge*; Hatchwell 1988), yellow-billed magpies (*Pica nutalli*; Birkhead et al. 1992), barn swallows (*Hirundo rustica*; Møller 1991), and cliff swallows (*Hirundo pyrrhonota*; Brown and Brown 1996),

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but not in white ibises (*Eudocimus albus*; Frederick 1987). Birkhead et al. (1987) and Møller and Birkhead (1992, 1993) amassed information on individual species, which they classified as (1) colonial or dispersed nesters, (2) showing no mate-guarding or some mate-guarding, and (3) breeding monogamously, polygynously, or in cooperative groups. They found that EPCs were more frequent in colonial than dispersed nesting species. They interpreted this as being due either to increased proximity of individuals or lower intensity of mate-guarding in colonial species.

On the other hand, genetic analyses have revealed high frequencies of EPFs in many dispersed-nesting birds, indeed often exceeding rates of EPCs observed or EPFs inferred in colonial species (e.g., Westneat and Webster 1994). At one extreme, the fairy wrens *Malurus splendens* and *M. cyaneus* have the highest frequencies of EPFs yet documented ($>65\%$ of chicks, Brooker et al. 1990; and 76% of chicks and 95% of broods, Mulder et al. 1994, respectively). Both wrens are cooperative breeders with highly dispersed nests, and nearly all EPFs are due to copulations with males outside the alloparental group.

This paper investigates how dispersion affects the genetic mating system. In particular, do colonially nesting birds and those breeding at high densities exhibit higher rates of EPFs than species that breed solitarily and at low densities? To find out, we compiled all available information on EPFs in bird populations, and on their density and dispersion patterns. We discovered that data on EPCs and EPFs do not yield congruent conclusions about density effects, and we explore some of the factors that may have created this intriguing disparity.

Methods

We assessed the effects of density in two ways. First, we reviewed studies that either explicitly examined density effects within a species or population, or pairs of studies conducted on populations of the same species that differed in density. We analyzed these data with simple pairwise comparisons (e.g., Møller and Birkhead 1992) in a meta-analysis to test for an effect of density within species. Second, we compared EPF frequencies among species that differed in density, and used phylogenetic contrasts to study relationships between EPF frequencies and density.

Before we began, we defined some key terms that would determine what information we needed to gather. First, we viewed a *pair-bond* as an extended social and sexual association between a male and a female, lasting for days to months or more, considerably longer than it takes to copulate. An *extra-pair copulation* is a mating between a female and a male other than her pair-bonded mate (Westneat et al. 1990); such a copulation might result in an *extra-pair fertilization*. This definition excludes copulations/fertilizations (1) in species that have no pair bonds (e.g., many lek breeders), and (2) between females and males that have extensive social associations, such as males in polyandrous social groups (e.g., dunnocks, *Prunella modularis*; Burke et al. 1989).

We defined *population density* as the number of individuals breeding per unit area of all habitat used by the population (i.e., for nesting, foraging, etc.). Often, however, information on population density was not available, particularly for species that nest close together and forage over a wide and generally unknown area (e.g., swallows, many seabirds). Thus for our analyses, we considered both *local breeding density*, which refers to the number of individuals breeding per unit area of suitable nesting habitat (i.e., excluding habitat areas not used for nesting) and *breeding dispersion*, which refers to clustering of nests within the habitat used for nesting or foraging by the population. For local breeding density we used the average distance between the center of a territory and the center of the nearest neighbor's territory (nearest neighbor distance, NND). For dispersion, we assigned each species as being either *colonial* (i.e., a very clumped breeding dispersion) or *dispersed* (spread out through the available habitat).

NNDs were based on information presented by authors either in the focal paper or in correspondence, or that were provided in another publication on the same population. Assignments of breeding dispersion were based on the researchers' own characterization of the species or on the descriptions of Lack (1968). After making our decisions, we compared our categorizations with those of Møller and Birkhead (1992). For the 21 species that we and they analyzed, there was only one disagreement. Whereas Møller and Birkhead categorized red-winged blackbirds as colonial, we believe they are more appropriately regarded as dispersed nesters, at least in eastern North America where breeding territories are spread throughout suitable habitat and individuals spend $>95\%$ of their time on those territories (Westneat 1993).

We compiled data on EPFs and density from original sources that we located by searching the major behavioral and ornithological journals, the BIOSIS database, and by contacting laboratories that are engaged in paternity analyses. We tabulated the results of every study we could find that (1) sampled ≥ 20 chicks from unmanipulated populations, and (2) presented an unambiguous estimate of the proportion of chicks sired through EPFs. Thus we omitted several allozyme studies that only estimated the proportion of broods with mixed paternity (e.g., Evarts and Williams 1987) or that did not specify whether mismatched chicks resulted from EPFs or intra-specific brood parasitism (e.g., Petter et al. 1990; Price et al. 1989; McKitrick 1990). We also omitted studies of manipulated populations (e.g., barn swallows with manipulated tail feathers: Smith et al. 1991; dark-eyed juncos, *Junco hyemalis*, with testosterone implants: Ketterson and Nolan 1992).

In total, 88 studies on 72 bird species fulfilled our criteria (Fig. 1). Among these, paternity was inferred using several techniques: DNA fingerprinting [$n = 65$ studies using multi-locus probes (Jeffreys et al. 1985) and $n = 3$ using single locus probes], protein electrophoresis ($n = 9$), plumage markers ($n = 1$), and asymmetries in heritabilities of tarsus lengths between female and (putative) male parents and chicks ($n = 10$). Studies of paternity using heritabilities have been severely criticized (e.g., Lifjeld and Slagsvold 1989; Dhondt 1991; Gebhardt-Henrich and Nager 1991; Hasselquist et al. 1995a) and defended (e.g., Alatalo et al. 1989). To be safe, we analyzed the EPF data including and excluding heritability studies.

For ten species, EPF frequency data have been collected on more than one population. In all non-phylogenetic analyses, we

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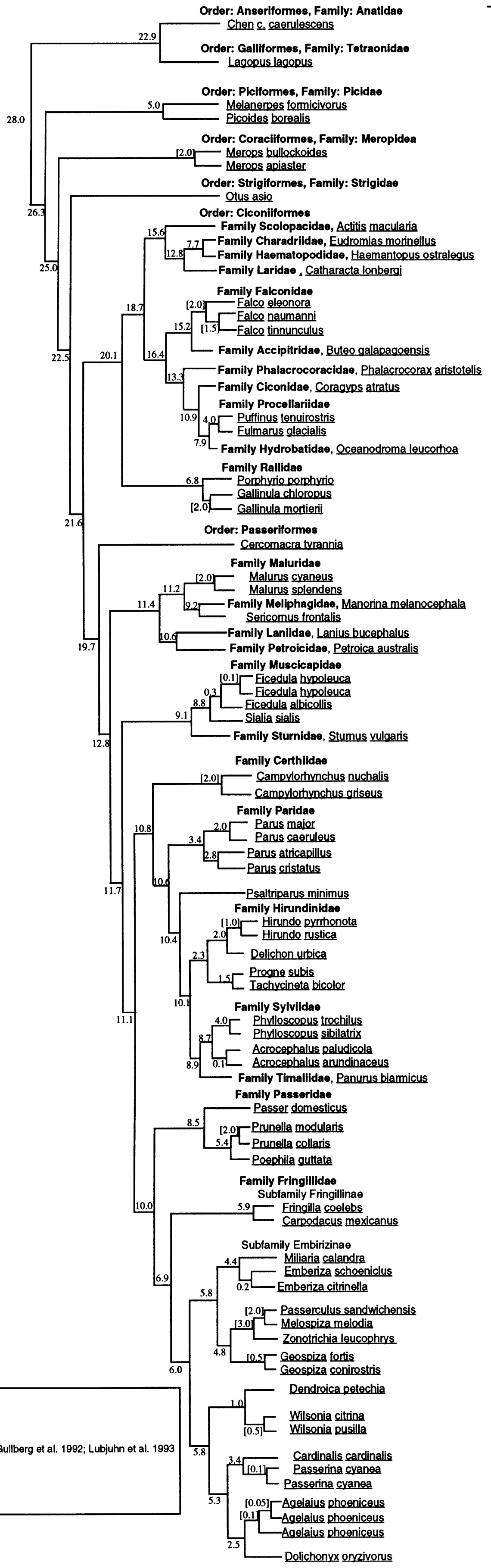
Fig. 1 Phylogenetic relationships, dispersion (*D* dispersed nesting, *C* colonial nesting), average nearest neighbor distance (NND), and estimated proportion of offspring sired through extra-pair fertilizations (EPFs) for 72 species of birds. Values at nodes indicate relative divergence. The values without brackets are mean delta $T_{50}H$ from Sibley and Ahlquist (1990), from Sheldon et al. (1992) for the Paridae, and from Sheldon and Winkler (1993) for the Hirundidae. For nodes within genera and species not shown in the above references, we arbitrarily picked values shown in brackets (congeneric species = 2.0 and populations within a species = 1.0, except when lower nodes constrained the values, e.g., within the genus *Falco*). Average NNDs were collected either from the authors of the paper, or calculated from territory sizes as twice the radius of a circular territory of average size. *Superscripts* indicate additional references, not used in the analysis (see text), that reported EPFs using a different technique or in a different population for which no data on average neighbor distances were available

PHYLOGENY



Taxon	Dispersion	Ave. nearest neighbor (m)	%EPFs	References
Order: Anseriformes, Family: Anatidae				
Chen c. caerulescens	C	36	2	Lank et al. 1989
Order: Galliformes, Family: Tetraonidae				
Lagopus lagopus	D	541	9	Freeland et al. 1995
Order: Piciformes, Family: Picidae				
Melanerpes formicivorus	D	350	2	Mumme et al. 1985
Picoides borealis	D		0	Haig et al. 1994
Order: Coraciiformes, Family: Meropidea				
Merops bullockoides	C	0.2	2	Wrege & Emlen 1987
Merops apiaster	C		0	Jones et al. 1991
Order: Strigiformes, Family: Strigidae				
Otus asio	D	423	0	Lawless et al. 1997
Order: Ciconiiformes				
Family Scolopacidae, Actitis macularia	D	40	10	Oring et al. 1992
Family Charadriidae, Eudromias morinellus	D		5	Owens et al. 1995
Family Haematopodidae, Haemantopus ostralegus	D	45	2	Heg et al. 1993
Family Laridae , Catharacta lonbergi	C	264	0	Millar et al. 1994
Family Falconidae				
Falco eleonora	C		0	Swatschek et al. 1993
Falco naumanni	C		3	Negro et al. 1996
Falco tinnunculus	D	683	2	Korpimäki et al. 1996
Family Accipitridae, Buteo galapagoensis	D		0	Faaborg et al. 1995
Family Phalacrocoracidae, Phalacrocorax aristotelis	C		18	Graves et al. 1992
Family Ciconidae, Coragyps atratus	D	1860	0	Decker et al. 1993
Family Procellariidae				
Puffinus tenuirostris	C	2	18	Austin et al. 1993
Fulmarus glacialis	C	2.5	0	Hunter et al. 1992
Family Hydrobatidae, Oceanodroma leucorhoa	C	0.5	0	Mauck et al. 1995
Family Rallidae				
Porphyrio porphyrio	D		0	Jamieson et al. 1994
Gallinula chloropus	D		0	Mcrae and Burke 1996
Gallinula mortierii	D	113	0	Gibbs et al 1994
Order: Passeriformes				
Cercomacra tyrannia	D	75	0	Fleischer et al. 1997
Family Maluridae				
Malurus cyaneus	D	110	76	Mulder et al. 1994
Malurus splendens	D	400	65	Brooker et al. 1990
Family Meliphagidae, Manorina melanocephala	D		6	Poldmaa et al. 1996
Sericornus frontalis	D	100	12	Whittingham et al. 1997
Family Laniidae, Lanius bucephalus	D	200	10	Yamagishi et al. 1992
Family Petroicidae, Petroica australis	D		0	Ardern et al. 1997
Family Muscicapidae				
Ficedula hypoleuca	D	80	4	Lifjeld et. al. 1991[a]
Ficedula hypoleuca		65	24	Gelter & Tegelstrom 1992
Ficedula albicollis	D		21	Alatalo et al. 1984,1989 [b]
Sialia sialis	D	371	19	Gowaty & Bridges 1991a
Family Sturnidae, Sturnus vulgaris	C	13	5	Pinxten et al. 1993 [c]
Family Certhiidae				
Campylorhynchus nuchalis	D	230	1	Rabenold et al. 1990
Campylorhynchus griseus	D	250	2	Haydock et al. 1996
Family Paridae				
Parus major	D	50	14	Blakey 1994[d]
Parus caeruleus	D	75	10	Kempenaers et al. 1992[e]
Parus atricapillus	D		17	Otter et al. 1994
Parus cristatus	D		12	Lens et al. 1997
Psaltriparus minimus	D		0	Bruce et al. 1996
Family Hirundinidae				
Hirundo pyrrhonota	C	0.3	2	Brown & Brown 1988
Hirundo rustica	C	40	24	Møller 1987
Delichon urbica	C	0.3	23	Whittingham & Lifjeld 1995[f]
Progne subis	C	1	19	Morton et al. 1990; Dale 1995
Tachycineta bicolor	C	34	44	Lifjeld et al. 1993
Family Sylviidae				
Phylloscopus trochilus	D	101	0	Gyllensten et al. 1990
Phylloscopus sibilatrix	D		0	Gyllensten et al. 1990
Acrocephalus paludicola	D		36	Schulze-Hagen et al. 1993
Acrocephalus arundinaceus	D	200	3	Hasselquist et al. 1995b
Family Timaliidae, Panurus biarmicus	C		14	Hoi and Hoi-Leitner 1997
Family Passeridae				
Passer domesticus	C	18	14	Wetton & Parkin 1991
Prunella modularis	D	56	1	Burke et al. 1989
Prunella collaris	D	370	0	Hartley et al. 1995
Poephila guttata	C	2	2	Birkhead et al. 1990
Family Fringillidae				
Subfamily Fringillinae				
Fringilla coelebs	D		17	Sheldon & Burke 1994
Carpodacus mexicanus	D	10	8	Hill et al. 1994
Subfamily Embirizinae				
Miliaria calandra	D		4	Hartley et al. 1993
Emberiza schoeniclus	D		55	Dixon et al. 1994
Emberiza citrinella	D		37	Sundberg and Dixon 1996
Passerculus sandwichensis	D		23	Freeman-Gallant 1996
Melospiza melodia	D		9	Smith & Zack 1979
Zonotrichia leucophrys	D	160	36	Sherman & Morton 1988
Geospiza fortis	D		0	Boag & Grant 1978
Geospiza conirostris	D		21	Grant & Grant 1989
Dendroica petechia	D	55	37	Yezerinac et al. 1995
Wilsonia citrina	D	120	29	Stutchbury et al. 1994
Wilsonia pusilla	D	61	32	Bereson et al. in press
Cardinalis cardinalis	D	227	13	Ritchison et al. 1994
Passerina cyanea		180	37	Westneat 1987a[g]
Passerina cyanea	D	116	35	Westneat 1990
Agelaius phoeniceus	D	75	24	Westneat 1993
Agelaius phoeniceus		44	30	Gibbs et al. 1990
Agelaius phoeniceus		12	35	Gray 1996
Dolichonyx oryzivorus	D	80	15	Bollinger & Gavin 1991

[a] Alatalo et al. 1984, 1989
[b] Meek et al. 1994
[c] Smith and von Schantz 1993
[d] Alatalo et al. 1984; Dhondt 1991; Gullberg et al. 1992; Lubjuhn et al. 1993
[e] Dhondt 1991; Gullberg et al. 1992
[f] Riley et al. 1995
[g] Payne & Payne 1989

included only data from the study that presented information on average NNDs; if there was more than one of these, we included just the one with the largest sample size. In phylogenetic contrast analyses of how dispersion affects EPFs, we included only the EPF frequency from the study with the largest sample of nestlings. In phylogenetic contrast analyses of how mean NNDs affect EPFs, we included studies on different populations of three species (*Ficedula hypoleuca*, *Passerina cyanea*, and *Agelaius phoeniceus*: Fig. 1) for which we obtained data on average NNDs. We assumed that separate populations are genetically distinct and could potentially have diverged in EPF frequencies.

Various authors (e.g., Felsenstein 1985; Harvey and Pagel 1991; Brooks and McLennan 1991) have argued that related species should not be regarded as independent data points in statistical analyses, especially when they share one of the attributes of interest (e.g., type of nesting dispersion; Fig. 1). Interestingly, however, Ricklefs and Starck (1996) recently reported that phylogenetic corrections made little difference in the outcome of comparative analyses of avian physiological and morphological traits. These results led the authors to suggest that the need for phylogenetic corrections may have been overstated.

Nonetheless, to be safe, we analyzed EPF data using the independent contrasts procedure of Felsenstein (1985) and Harvey and Pagel (1991). Phylogenetic relationships among most species could be estimated based on Sibley and Ahlquist (1990), except for species in five families. For the Paridae we adopted the phylogeny of Sheldon et al. (1992) and Slikas et al. (1996), for the Hirundinidae we relied on Sheldon and Winkler (1993), we used the AOU checklist (American Ornithologists' Union 1983) to resolve the location of *Passerina cyanea* and the Geospizine finches within the Embirizinae, and we used Christidis and Boles (1994) combined with Sibley and Ahlquist (1990) to determine the locations of *Gallinula* (*Tribonyx*) *mortierii* and *Petroica australis*.

Species were assigned a dummy variable for breeding dispersion (colonial = 0, dispersed = 1), and contrasts were calculated by the differences between dyad species at each node using the Phenotypic Diversity Analysis Program 3.0 (Garland et al. 1993). Relationships between contrast values and the standard deviation in branch lengths, calculated with several different methods of transforming branch lengths, were tested for internal biases in the data (a relationship between the absolute value of the contrast and the standard deviation of branch length; Garland et al. 1992). The associations between standardized contrasts of NNDs or dispersion and EPFs were tested with (1) linear regression, using parametric statistical analyses in SYSTAT, or (2) a randomization test (Manly 1991).

Results

Among the 72 species studied to date (Fig. 1), EPFs have been documented in 53 (74%), with considerable variation in EPF frequency among them (Fig. 2). The distribution (Fig. 2) resembles a Poisson: 34 species have EPF rates of ≤ 0.05 whereas only 4 species have EPF rates of ≥ 0.40. The mean frequency for the entire sample is 0.13 ± 0.16 (SD) and the median is 0.07. Among the 53 species in which some EPFs occur, the mean frequency is 0.18 ± 0.17. It is apparent from Fig. 2 that EPFs occur more commonly among passerine species (42/49 = 86%) than among non-passerines (10/23 = 45%), at higher average frequencies [0.18 ± 0.17 (SD) vs. 0.03 ± 0.05], and with a larger range (0.0–0.76 vs. 0.0–0.18). EPFs have been documented in species from every passerine family studied, but no evidence of EPFs has yet been discovered in several non-passerine families (e.g., Rallidae, Hydrobatidae).

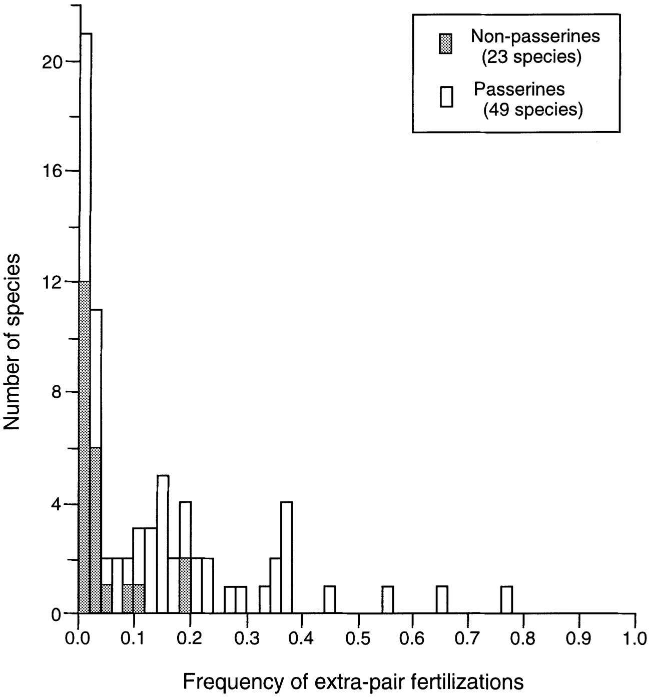


Fig. 2 Distribution of the frequencies of extra-pair fertilizations among 72 bird species. Passerine birds are shown in *open bars*, non-passerines in *stippled bars*

Effect of density within species

Genetic studies on 11 species have either directly compared rates of EPFs between areas differing in local nesting density or have reported frequencies of EPFs and density in two or more populations that could be compared (Table 1). Eight studies found that EPFs were greater in areas or years of higher density; in six of these the relationship with density was significant. If each species is considered as an independent test of the intraspecific effect of density, the one-tailed probability is 0.11 that 8 of 11 comparisons would fall in a particular direction given the null expectation of equal likelihood. For the eight studies of dispersed nesters alone, the probability is 0.14 that six or more would show a positive effect of density. These analyses are conservative because they do not incorporate the magnitude of any density effect, but unfortunately we cannot take that into account because among the studies (Table 1) density was measured differently (nearest neighbor distance, number of neighbors, number of breeding groups per unit of area) and units of comparison also differed (individual breeding groups within populations, or average differences between populations).

Effect of density between species

Among 46 dispersed and colonial species there was no correlation between NNDs and frequencies of EPFs (Kendall's $\tau = -0.07$, $P = 0.50$). Omitting black

Table 1 Intra-specific comparisons of associations between density and extra-pair fertilizations

Species	Technique used[a]	Direction of density effect and significance	Dispersion	Reference
Bearded tit (*Panurus biarmicus*)	DNA	+(P < 0.05)	Colonial and solitary	Hoi and Hoi-Leitner 1997
Bobolink (*Dolichonyx oryzivorus*)	proteins	−(NS)	Dispersed	Bollinger and Gavin 1991
Eastern bluebird (*Sialia sialis*)	proteins	+(P < 0.05)[b]	Dispersed	Gowaty and Bridges 1991b
Eurasian kestrel (*Falco tinnunculus*)	DNA	+(P < 0.05)	Dispersed	Korpimäki et al. 1996
Great reed warbler (*Acrocephalus arundinaceus*)	DNA	+(P < 0.05)	Dispersed	Hasselquist et al. 1995b
Hooded warbler (*Wilsonia citrina*)	DNA	−(NS)	Dispersed	Tarof et al. in press
House finch (*Carpodacus mexicanus*)	DNA	+(P < 0.05)	Colonial	Hill et al. 1994
Pied flycatcher (*Ficedula hypoleuca*)	DNA	+(not tested)	Dispersed	Lifjeld et al. 1991; Gelter and Tegelström 1992
Red-winged blackbird (*Agelaius phoeniceus*)	DNA	+(P < 0.05)[c]	Dispersed	Gibbs et al. 1990; Westneat 1993; Gray 1996
Tree swallow (*Tachycineta bicolor*)	DNA	−(NS)	Colonial	Dunn et al. 1994
Yellowhammer (*Emberiza citrinella*)	DNA	+(NS)	Dispersed	Sundberg and Dixon 1996

[a] *Proteins* protein electrophoresis, *DNA* single or multi-locus DNA fingerprinting

[b] Experimentally manipulated density, but frequent intra-specific brood parasitism included in result leaving effect on EPFs unclear

[c] Significance tested between marshes within one locale (Gibbs et al. 1990), trend (not tested) also present among studies in different locales

vultures (*Coragyps atratus*), which have an extreme NND (1860 m), further reduces the statistical significance (Kendall's $\tau = -0.03$, $P = 0.76$, $n = 45$; Fig. 3). Local breeding density differed significantly between the colonial ($\bar{x} = 30 \pm 69$ m, $n = 14$) and dispersed nesters ($\bar{x} = 227 \pm 335$ m, $n = 32$, Mann-Whitney $U = 31.5$, $P < 0.0001$) in our sample, so we analyzed the relationship with EPFs separately for each dispersion. In neither was the correlation significantly different from zero [colonial: $\tau = 0.05$, $P = 0.82$; dispersed: $\tau = -0.11$, $P = 0.38$ (omitting black vultures)].

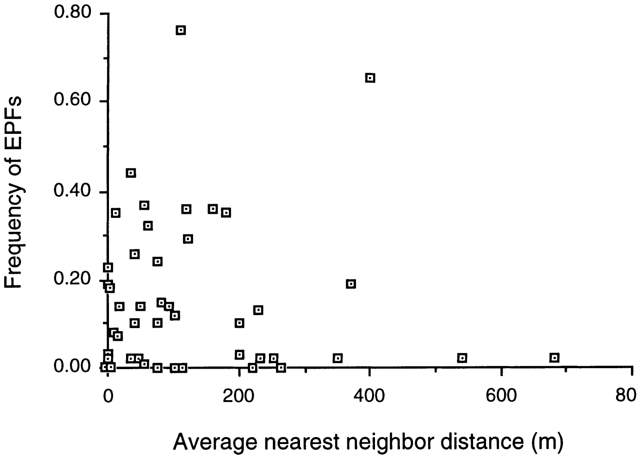


Fig. 3 Correlation between average nearest neighbor distance and proportion of chicks sired through EPFs in 45 bird species. Black vultures are omitted from this figure because they are an extreme outlier: their EPF rate is 0 and their mean inter-nest distance is 1860 m (Decker et al. 1993, P. Parker, personal communication)

Among 52 dispersed nesting species 14% ± 18% (SD) of chicks were sired through EPFs, and among 20 colonially nesting species 10% ± 12% of chicks were sired through EPFs (Fig. 4A). This difference is not statistically significant (Mann-Whitney $U = 488.5$, $P = 0.60$). Reanalysis of the data with red-winged blackbirds reassigned as colonial breeders (Møller and Birkhead 1993) does not alter the conclusion.

Cooperatively breeding species introduce special complexities. Some authors (e.g., Birkhead and Møller 1992) consider within-group matings between individuals other than social mates to be EPCs, while others (e.g., Westneat et al. 1990) do not, because females have long-term associations with males in their own group (e.g., in striped-backed wrens, *Campylorhynchus nuchalis*; Rabenold et al. 1990). In our initial analysis (Fig. 4A) we followed Westneat et al. (1990) and counted as EPFs only fertilizations resulting from matings between members of different groups. We repeated the analysis (Fig. 4B), this time excluding cooperative breeders because, at the least, helpers could complicate the dynamics of how density affects interactions between breeding females and extra-group males. For this analysis we also excluded the ten studies on sexual asymmetries in tarsus heritabilities; this removed only five species for which there were no data on EPF frequencies based on another genetic technique. This more conservative analysis again revealed no significant difference in EPF frequencies between dispersed nesters (15% ± 15%[SO], $n = 35$)

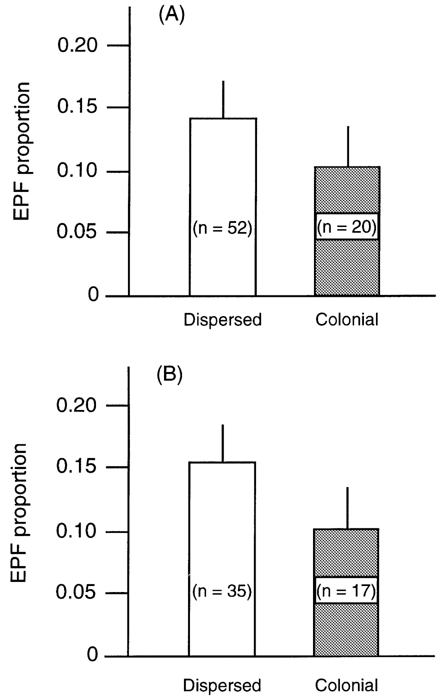


Fig. 4 Average proportions (±SE) of chicks sired through EPFs for dispersed versus colonial nesting species; **A** all studies included, **B** excluding studies employing asymmetries between the sexes in heritabilities and those on cooperative breeders

and colonial nesters (10% ± 12%, $n = 17$; Mann-Whitney U = 256, $P = 0.41$).

The foregoing analyses treat species as independent data points. To deal with potential lack of independence of closely related species we conducted phylogenetic contrasts analyses (Felsenstein 1985). We found no relationships between EPF frequencies and either NNDs or dispersion, regardless of what transformation of branch lengths we used. We first inferred branch lengths from genetic distances (Fig. 1). Neither the categorical measures of dispersion ($r = 0.044$, $n = 64$, $P = 0.26$) nor NNDs ($r = 0.025$, $n = 45$, $P = 0.43$) were associated with EPFs in tests of 20,000 r values generated by repeatedly drawing new pairs of independent and dependent contrast values at random from the original dataset.

However, there was a significant negative correlation between the standard deviation of branch lengths (square root of the sum of branch lengths for each contrast) and contrasts of arcsine transformations of EPF frequencies ($r^2 = 0.21$, $t = -4.4$, $P < 0.01$, $df = 73$). This means that variation in EPF frequencies between closely related species matched or exceeded that between more distantly related species. The resulting bias in EPF contrasts along the phylogenetic tree violates the assumption that contrasts are independent (e.g., Garland et al. 1992). This bias disappeared when we used constant branch lengths (Garland et al. 1993) instead of the lengths shown in Fig. 1. Contrasts of transformed EPF values using constant branch lengths were not correlated either with the categorical measures of dispersion ($r^2 = 0.005$, $t = 0.61$, $df = 74$, $P > 0.4$) or NNDs ($r^2 = 0.005$, $t = 0.46$, $df = 47$, $P > 0.5$). Moreover, neither variable was significant in a multivariate analysis using both coloniality (std. coeff. = −0.021, $t = 0.13$, $P = 0.90$) and NNDs (std. coeff. = −0.06, $t = 0.34$, $P = 0.73$; $df = 48$) as independent variables.

Species that breed in dense aggregations often nest synchronously (e.g., Hoogland and Sherman 1976; Wittenberger and Hunt 1985; Burger and Gochfeld 1991; Brown and Brown 1996). Synchrony is a potentially confounding variable, but there is disagreement over whether synchrony increases (Stutchbury and Morton 1995) or decreases (Birkhead and Biggins 1987; Westneat et al. 1990) frequencies of EPCs and EPFs. No comparative analysis of how extra-pair activities are affected by density or synchrony has incorporated the other factor. We therefore performed a multivariate analysis on contrasts in arcsine transformed EPF frequencies, using contrasts in both NNDs (data in Fig. 1) and breeding synchrony (data from Stutchbury and Morton 1995) as independent variables, and the branch lengths given in Fig. 1 (tests for bias in EPF contrasts along the phylogenetic tree revealed no significant trends, P values all exceeded 0.05). Contrasts in EPF frequencies were not associated with either NNDs (std. coeff. = 0.37, $t = 1.27$, $P = 0.23$) or synchrony (std. coeff. = 0.34, $t = 1.16$, $P = 0.27$).

Discussion

Results presented here suggest an intriguing mix of effects of density on extra-pair fertilizations. Our review of 11 intraspecific studies revealed positive relationships between density and frequencies of EPFs. A statistical test of the data was not significant, but few species have been surveyed and our conservative analysis did not take into account that six of the studies found significant positive effects of density. The generally positive relationship between density and EPFs within species seems to be similar to the relationship between density and EPCs reported by Møller and Birkhead (1992), although our analyses suggest that effects of density on extra-pair activity within a species may be contingent on other factors (see below).

Møller and Birkhead (1993) reported that EPCs occurred more commonly in colonial than dispersed-nesting birds. By contrast, we found no significant effects of dispersion or local breeding density on EPFs among species (Figs. 1–3). The differences between our results and Møller and Birkhead's, and between the intra- and interspecific analyses reported here, are puzzling. One might suppose that patterns of fertilizations would reflect patterns of copulations (e.g., Birkhead and Møller 1992; but see Eberhard 1996). Clearly, however, rates of EPCs and EPFs are not necessarily synonymous. We suggest that there are several possible methodological and biological explanations for the discrepancies.

First, effects of density on EPFs may somehow have been obscured in our comparative analyses. Frequencies of EPFs themselves are likely to be accurate because most studies that we included are based on multi-locus fingerprinting techniques which detect nearly all EPFs that occur. However, there is controversy over avian phylogenies, particularly relationships at the generic and species levels (e.g., Sibley and Ahlquist 1990; Lanyon 1992; Mindell 1992; Harshman 1994). Resolution of these disagreements and adjustments to branch lengths as new information becomes available could conceivably modify our conclusions. Nevertheless, the general results that (1) no correlation exists between NNDs and EPFs (Fig. 2), and (2) dispersed nesters have slightly higher EPF rates than colonial nesters (Fig. 3) do not rely on phylogenetic methods. Furthermore, the basic phylogeny we used (Fig. 1) is the same one Møller and Birkhead (1993) used in their phylogenetic contrast analyses. This implies that our different results relate to something else.

A second possibility is that observational data on EPCs are systematically biased. For example, intra- and extra-pair copulations may be more easily detected in colonial than dispersed nesters. Because breeding colonies often occur in open habitats, observers can watch many pairs simultaneously and see numerous copulations involving many different individuals. When EPCs occur on the colony and in the open, they are as observable as within-pair copulations. By contrast, intra- and extra-pair copulations in dispersed nesters are much harder to observe, due to visually occluded habitats and the difficulty of watching more than one focal female at a time. This is probably why the data set of Møller and Birkhead (1993) includes reports of high numbers of observed copulations for many colonial nesters, but numerous studies of dispersed nesters that recorded few or no copulations.

In a few well-studied dispersed nesters, many matings have been observed. However, quantifying the relative frequencies of intra- and extra-pair copulations is still difficult because different behaviors are associated with each type of mating. For example, male indigo buntings (Westneat 1987b) and red-winged blackbirds (Westneat 1992) assault extra-pair females. This behavior is more conspicuous than copulations between social mates, but often females flee considerable distances or dive into vegetation when they are attacked. This reduces opportunities to observe successful EPCs if they occur. Alternatively, female black-capped chickadees (*Parus atricapillus*; Smith 1988) and blue tits (*Parus caeruleus*; Kempenaers et al. 1992) seek out extra-pair males by flying surreptitiously to their territory, often at times of day when observations are difficult (e.g., at dawn), and then engage in EPCs that are less conspicuous than within-pair copulations. Taken together, these observational biases magnify the variance in EPC rates among dispersed nesters, creating a skewed distribution toward species with few or no EPCs, and reducing the reliability with which we can infer the proportion of copulations that are EPCs.

The third and perhaps most intriguing possibility is that density actually affects EPCs and EPFs differently. Furthermore, density might interact with other variables in ways that mask its effects in comparative studies, and could in some cases influence its effects within a species. In order to be successful, EPFs require insemination and fertilization – two additional steps beyond encountering and attempting a copulation with an extra-pair male. Within a species, increasing density ought to increase rates of encounters, but might have less effect on the probabilities of both insemination and fertilization. For example, although extra-pair encounters might increase with increasing density, at higher densities social mates are forced into greater proximity, which should make it easier for males to see and repel intruders, to control female movements, or to witness an EPC and perform a compensatory within-pair copulation. Alternatively, increasing density may severely impair a male's abilities to successfully guard his social mate, because either there are too many males to chase away, high density occurs when nests are clustered at sites distant from other resources important to males, or habitat complexity allows females more opportunity to escape from male surveillance and increasing density makes it more valuable for them to do so. Males that cannot guard their mate might shift their behavior from guarding to copulating repeatedly with her (Birkhead and Møller 1992). This, in turn, may reduce the chance that successful EPCs actually fertilize an egg as density increases, depending on how females respond to frequent male overtures. Finally, the fitness benefits and abilities of females to control copulations and subsequent fertilizations (e.g., Lifjeld and Robertson 1992; Birkhead et al. 1993) and the importance of cryptic female choice (Eberhard 1996) also may vary with ecology (e.g., Westneat et al. 1990); increasing density may have little or no effect on the rates of EPCs and EPFs when females often pursue EPCs (e.g., Dunn et al. 1994), although increasing proximity could affect the payoffs to females for pursuit.

These complications are magnified when comparing between species. Other ecological factors, such as the openness of the habitat and the constraints on female choice of social mates could have major effects on frequencies of extra-pair behaviors that obfuscate effects of density. For example, species that nest in clusters (high local breeding density) often live in open habitats, whereas dispersed nesters live in visually-occluded areas. If the success of mate-guarding and the transmission of cues about the reproductive status of males or females in nearby areas is affected by both proximity and by the openness of the habitat, increasing density might have an effect within a habitat (i.e. within a species). However, comparisons between species might overlook effects of density because the exact relationship between density and EPFs is confounded by effects of habitat differences. The impact of breeding synchrony also could depend on habitat differences and on factors influencing the relative roles of males versus females in pursuing EPCs (e.g., Birkhead and Biggins 1987; Stutchbury and Morton 1995). Unfortunately, clear criteria for assessing critical features of habitat openness that affect EPFs have yet to be developed, and little information on habitat complexity is available for most of the species included in our analyses.

Our results offer no support for either the hypothesis of Wagner (1993) that high-density nesting is promoted by females because it enhances their opportunities for obtaining EPFs, nor for that of Stutchbury and Morton (1995) that greater nesting synchrony should increase EPF frequencies. However, regarding the latter analysis, it should be noted that the sample size was only 14 species (13 contrasts), so the power of our statistical test was undoubtedly low.

Thus our analyses suggest the need for careful reconsideration of exactly how population parameters such as density and synchrony might influence specific behaviors in the sequence of events that leads to fertilizations under particular circumstances. The general assumption that increased proximity increases either the number of extra-pair males encountered per fertilizable female or the frequency of encountering fertilizable females per extra-pair male (e.g., Birkhead and Møller 1992), although intuitively appealing, may be complicated by the ways individuals space themselves, how female movement patterns affect encounters with extra-pair males, by the structure of the habitat, and the timing of breeding relative to others in the population. At present, however, there is little theory explicitly formulated to explore the influences of population level characteristics on specific mating strategies such as extra-pair matings. Many potentially interesting relationships are likely to be hidden in this mix of interacting factors, a prospect that invites additional theoretical and empirical exploration.

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Note added in proof The passerine birds, a relatively recently evolved clade, show wide variation in breeding dispersion, breeding density, and EPFs. However, restricting our analyses to just the passerines did not affect our results; there was no association between contrasts of arcsine transformed EPF frequencies and either contrasts in dispersion ($r^2 = 0.01$, $t = -0.22$, $df = 51$, $P > 0.75$) or NNDs ($r^2 = 0.03$, $t = -1.1$, $df = 34$, $P > 0.5$). Use of constant branch lengths did not change these results.

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