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The Condor 101:854–859

GENETIC MONOGAMY IN LONG-EARED OWLS[1]

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Abstract. We used DNA fingerprinting to study genetic parentage in socially monogamous Long-eared Owls (*Asio otus*). We detected no extra-pair fertilizations (EPFs) in 59 nestlings from 12 nests. One of these nests was solitary, but the other 11 had from one to five pairs of owls nesting simultaneously within 30 to 250 m. Thus, despite the presumably high potential

[1] Received 5 May 1999. Accepted 26 July 1999.

for extra-pair matings, the Long-eared Owls that we studied were genetically monogamous. In addition, based on low band sharing among adults, we found no evidence that nesting aggregations were composed of close relatives. Genetic monogamy appears to be the rule for socially monogamous raptors. We suggest that the high rate of male parental effort in raptors selects against EPFs because females that engage in extra-pair activities risk losing parental investment by males whose confidence in paternity is reduced owing to the behavior of their mates.

Key words: Asio otus, *DNA fingerprinting, genetic monogamy, Long-eared Owl.*

Studies of mating systems based on genetic markers have shown that copulations outside the pair bond are common in many bird species (Westneat et al. 1990). Indeed, genetic monogamy seems to be the exception rather than the rule in socially monogamous passerines (Gowaty 1996). Among socially monogamous non-passerines, however, extra-pair fertilizations (EPFs) are less common. A recent review showed that EPFs have occurred in 86% (42/49 species) of passerines that have been studied but in only 48% (11/23 species) of non-passerines (Westneat and Sherman 1997). On both empirical and theoretical grounds, the occurrence of EPFs in birds is influenced by the density and synchrony of breeding pairs (Stutchbury and Morton 1995, Johnson and Burley 1998). In addition, the amount of parental care provided by males may be positively correlated with their certainty of paternity (Møller and Birkhead 1993).

Because Long-eared Owls (*Asio otus*) sometimes nest close to one another (Marks et al. 1994), they represent an important test case for the hypothesis that genetic parentage is associated with breeding density. Male parental effort is extremely high in all species of owls because males provide nearly all of the food to the female and nestlings from courtship until at least mid-way through the brood-rearing period (Marks et al. 1999), although they do not incubate or brood. Thus, one might expect owls to be genetically monogamous independent of proximate factors that could influence mating systems (breeding density and breeding synchrony).

Investigators have used DNA fingerprinting to assess relatedness and genetic parentage in three previous studies of owls. Galeotti et al. (1997) compared genetic similarity within and between communal winter roosts of Long-eared Owls and concluded that roosts were not composed of close relatives. Lawless et al. (1997) found no evidence of EPFs in Eastern Screech-Owls (*Otus asio*), which are highly territorial and nest solitarily. In contrast, Johnson (1997b) reported a low level of EPFs (2 of 31 nestlings) in a colony of Burrowing Owls (*Athene cunicularia*), which nest below ground and do not defend large nesting territories. Like the Burrowing Owls in Johnson's (1997b) study, most of the Long-eared Owls that we studied nested in groups. If breeding density influences opportunities for extra-pair copulations, then EPFs would be most likely to occur in Long-eared Owls that nest close to each other. By focusing primarily on nesting aggregations, we provide a stringent test of the hypothesis that EPFs occur in Long-eared Owls. We also use band sharing coefficients from adults to determine whether nesting aggregations are composed of close relatives.

METHODS

STUDY AREA AND FIELD METHODS

The study areas were in Lake and Ravalli Counties, western Montana, in isolated groves of quaking aspens (*Populus tremuloides*), black hawthorns (*Crataegus douglasii*), and willows (*Salix* sp.). The Paul Smith study area (Lake County) had six Long-eared Owl nests in 1997 and five in 1998. The Victor study area (Ravalli County) was 150 km south of Paul Smith and had four nests in 1998. The Airport study area was 14 km east of Paul Smith and had one nest in 1997 and two close-nesting pairs in 1998.

We captured adults at night in mist nets placed in natural flight paths to the nest or set in front of flightless young that had recently left the nest. Thus, we were reasonably certain that these owls were the social parents at the nests where they were captured. We determined the sex of captured adults based on presence or absence of an incubation patch. Adults were banded with U.S. Fish and Wildlife Service metal leg bands. Young were banded at three to four weeks of age, just before or shortly after they left the nest.

BLOOD SAMPLING AND DNA FINGERPRINTING

To determine whether nesting density is associated with EPFs in Long-eared Owls, we conducted parental-exclusion analyses using multilocus DNA fingerprinting. This permitted us to evaluate background levels of genetic variation in the population of Long-eared Owls in western Montana and to perform paternity-exclusion analysis for 59 nestlings from 12 nests during two years of study. Blood samples (100 μL) were taken from the brachial vein of adults and nestlings at the time of banding. Samples were placed in Queen's lysis buffer (Seutin et al. 1991) in the field and then transferred to the lab, where they were frozen at −20°C. We digested 5 to 10 μg of nuclear DNA with HaeIII and evaluated the quality and concentration of DNA in the restriction digests on a 1% agarose test gel stained with ethidium bromide. Samples containing 5 μg of digested DNA in Ficoll loading buffer were loaded on 27–30 cm agarose gels (1%) and run alongside a 1-kb ladder at 40 V for three days. The social parents were run in lanes adjacent to their offspring (Fig. 1). In addition, we ran sets of breeding adults (n = 22 dyads) to obtain the background level of band sharing within the population. DNA in the gel was denatured in 0.5 M NaOH/1.5 M NaCl and transferred in fresh denaturing solution to a charged nylon filter (Zetaprobe). Filters were UV-crosslinked and hybridized overnight at 63–65°C in DEPC-treated 1X SSC, 1% SDS, 1% Blotto, and then washed at 65°C in 0.75–1XSSC and 0.1% SDS until the low molecular weight end of the filter measured 1,000–3,000 cpm with a Geiger counter. We scored autorads as described by Birkhead et al. (1990), including all bands above 4 kb, unless they were blurred or could not be distinguished from bands produced by fragments of similar mobility. Means are presented ± SD.

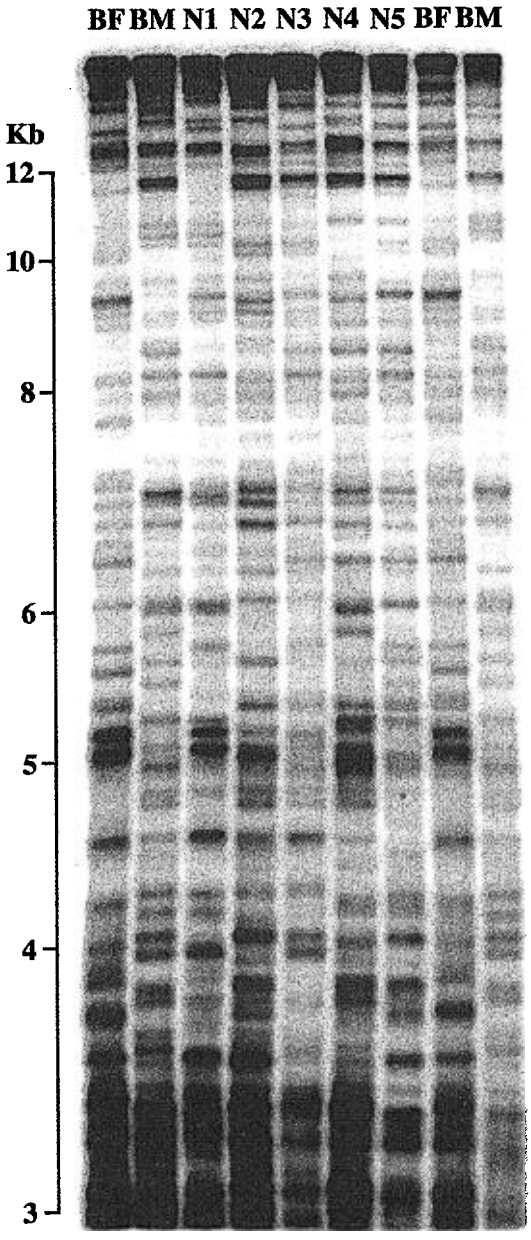

FIGURE 1. DNA fingerprint of a Long-eared Owl family. Filter was probed with Jeffreys' probe 33.15 (Jeffreys et al. 1985). BM = breeder male, BF = breeder female, N = nestlings.

RESULTS

NEAREST-NEIGHBOR DISTANCE

Eighteen Long-eared Owl nests occurred in our study areas in 1997 and 1998, but owing to nesting failures and other complications, we caught the adult males at only 12 nests for which we obtained blood samples from all young that left the nest. Four of the 12 nests were at Paul Smith in 1997 (mean nearest-neighbor distance = 88.8 ± 33.8 m, range = 63–140 m, $n = 6$ nests total, including those with and without fingerprinting data), two were at Paul Smith in 1998 ($\bar{x}$ = 105.2 ± 93.8 m, range = 51–245 m, $n = 4$), one was a solitary nest at Airport in 1997, two were at Airport in 1998 (nests 46 m apart), and three were at Victor in 1998 ($\bar{x}$ = 86.8 ± 66.3 m, range = 32–166 m, n = 4). All of the nests within each of the three study areas were active simultaneously (within each nesting group, all owls were present during the fertile period of each female). Thus, except for the solitary pair at Airport in 1997, each pair for which we had fingerprinting data had from one (Airport in 1998) to five (Paul Smith in 1997) other nesting pairs within close proximity (32 to 245 m) at the time the nest was initiated. Consequently, the potential for extra-pair fertilizations within nesting aggregations was high.

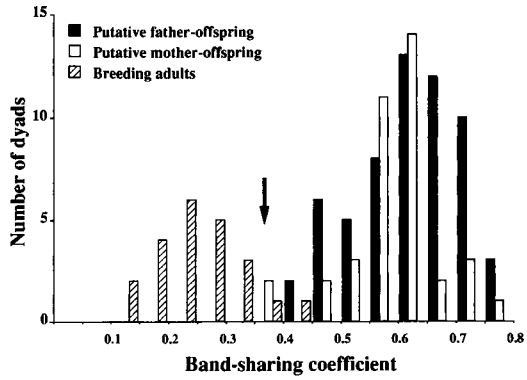

FIGURE 2. Distribution of band sharing coefficients between putative parents and offspring compared with band sharing between presumably unrelated dyads of breeders in the population. Arrow approximates the exclusion threshold.

MULTILOCUS DNA FINGERPRINTING AND PARENTAL EXCLUSION

The mean band sharing coefficient for dyads of adults that were run no more than two lanes apart (0.25 ± 0.08) was lower than those for dyads of breeder females and nestlings (0.60 ± 0.08) and breeder males and nestlings (0.62 ± 0.09) (Mann-Whitney U-tests, $Z > 6.3$, $P < 0.001$ for both comparisons; Fig. 2). Parent-offspring band sharing coefficients did not differ significantly between breeder males and females (Mann-Whitney U-test, $Z = 1.50$, $P = 0.13$). Assuming that bands segregate independently and that the other parent is correctly assigned, the probability of false inclusion of a sire or dam that is unrelated to the true breeder is $I' = x^m$, where x is the mean band sharing coefficient for 22 dyads of breeding adults run no more than two lanes apart, and m is the mean number of paternal- or maternal-specific bands in the offspring (Bruford et al. 1992; Table 1). The mean number of paternal-specific bands was slightly higher than the mean number of maternal-specific bands, but the probability of false inclusion was low for both sexes (5.8×10^{-6} for sires and 4.6×10^{-5} for dams; Table 1).

TABLE 1. DNA fingerprinting results for 59 Long-eared Owl nestlings from 12 different nests in western Montana, 1997 and 1998. Means are presented ± SD.

Variable	Value	Sample size
No. of bands scored	21.5 ± 9.2	59 nestlings
Band sharing among breeders, observed (x)	0.25 ± 0.08	22 dyads
No. of paternal-specific bands in nestlings	8.7 ± 4.6	38 nestlings
No. of maternal-specific bands in nestlings	7.2 ± 3.5	38 nestlings
Observed sibling band sharing	0.60 ± 0.10	54 dyads
Expected sibling band sharing (s)[a]	0.62	
Probability of false inclusion of an unrelated male	5.8×10^{-6}	
Probability of false inclusion of an unrelated female	4.6×10^{-5}	
Mutation rate	1.8×10^{-3}	
Allelic frequency (q)[b]	0.134	
Heterozygosity (h)[c]	0.928	

[a] Where $s = [(4 + 5q - q^2)/4(2 - q)]$ (case i; Jeffreys et al. 1985).
[b] Where $x = 2q - q^2$ (Jeffreys et al. 1985).
[c] Where $h = 2(1 - q)/(2 - q)$.

We calculated sibling band sharing to be 0.60 ± 0.10, based on a subset of 54 sibling dyads. Exclusion analysis was based on band sharing and the number of bands in the offspring that could not be attributed to either of its putative parents (unattributable bands). This resulted in the following parental-exclusion criteria: (1) we did not exclude a breeder from genetic parentage unless an offspring had more than two unattributable bands or the band sharing coefficient was below 0.343 (observed band sharing for full sibs minus 2.57 SD; Table 1). Fewer than 0.5% of first-order relatives are expected to have band sharing coefficients below this threshold. (2) In 21 cases (n = 4 nests) where we had blood from the male breeder only, we used father-offspring band sharing below 0.343 as the basis for exclusion.

Using these exclusion criteria, we inferred parentage for all 59 Long-eared Owl nestlings from 12 pairs in 1997 and 1998. We observed one unattributable band in each of three offspring for which we had blood from both parents, but in these cases parent-offspring band sharing exceeded 0.49. We attributed these three bands to mutation and used this information to calculate the mutation rate for minisatellite alleles (Table 1). In no case was parent-offspring band sharing below 0.343. The mean father-offspring band sharing for nestlings whose mother was not captured was 0.61 ± 0.10 (range = 0.43–0.78, n = 21 nestlings), which did not differ from the mean for males whose mate also was run (0.62 ± 0.08, range = 0.40–0.75, n = 38 nestlings) (Mann-Whitney U-test, Z = 0.26, P = 0.79). Our exclusion criteria assigned all 59 offspring to their putative fathers and all 38 offspring for which we had maternal blood to their putative mothers. Thus, we found no evidence for EPFs. If we assume that all 59 of the fertilizations were independent, then the binomial probability is 0.05 that the true frequency of extra-pair paternity in this population is 6%.

DISCUSSION

Nesting groups were common in our study areas during both years, but most Long-eared Owls nest solitarily, with nearest-neighbor distances exceeding 1 km (Marks et al. 1994). Even when nesting synchronously in close proximity to conspecifics, however, the Long-eared Owls that we studied were genetically and socially monogamous. We determined parentage for 56 nestlings from 11 grouped nests in three areas and for three nestlings from one solitary nest, and all were sired by their putative fathers. This suggests that the pattern of genetic monogamy that we observed holds in Long-eared Owls regardless of nest dispersion. We recognize that because we had only one solitary nest, we have not provided a complete test of the influence of breeding density on the frequency of EPFs. However, our conclusion that breeding density does not influence the likelihood of EPFs in Long-eared Owls is based on the assumption that because EPFs were absent in close-nesting owls, they would be highly unlikely to occur in solitary pairs.

Mean band sharing in Long-eared Owls at two communal winter roosts in Italy was 0.18 within roosts and 0.14 between roosts (Galeotti et al. 1997). Based on these data, Galeotti et al. (1997) concluded that communal roosts were not made up of close relatives. Mean band sharing among breeding adults in Montana was higher (0.25) than band sharing measured by Galeotti et al. Nonetheless, compared with mean band sharing among siblings (0.60), our results suggest that nesting aggregations of Long-eared Owls in Montana are not composed of close relatives.

Male raptors provide most of the food during incubation and brood rearing (Snyder and Wiley 1976). Indeed, male owls probably provide more parental care in terms of food provisioning than do males of any other birds besides hornbills (Kemp 1995). To the extent that females have some control over EPFs (Gowaty 1997, Stutchbury and Neudorf 1998), one might expect low rates of EPFs in species in which a large amount of parental care by males is essential. In agreement with this notion, rates of EPFs are low (0 to 3% of young) in the handful of socially monogamous raptors that have been studied (Table 2). Included among these species are Eleonora's Falcon (*Falco eleonorae*) and Lesser Kestrel (*F. naumanni*), both of which nest in dense colonies but nonetheless tend to be genetically monogamous (Swatschek et al. 1993, Negro et al. 1996).

TABLE 2. Reported frequency of extra-pair fertilizations (EPF) in socially monogamous raptors (Falconiformes and Strigiformes) based on DNA fingerprinting analysis.

Species	% EPF	Reference
Eurasian Kestrel (*Falco tinnunculus*)	2	Korpimäki et al. 1996
Lesser Kestrel (*Falco naumanni*)	3	Negro et al. 1996
Merlin (*Falco columbarius*)	0	Warkentin et al. 1994
Eleonora's Falcon (*Falco eleonorae*)	0	Swatschek et al. 1993
Eastern Screech-Owl (*Otus asio*)	0	Lawless et al. 1997
Burrowing Owl (*Athene cunicularia*)	6	Johnson 1997b
Long-eared Owl (*Asio otus*)	0	This study

The highest rate of EPFs reported for a raptor, 6.4%, was for a Burrowing Owl population in California (Johnson 1997b). These owls potentially were not socially monogamous (two nests were attended by three adults), and brood movements among burrows complicated the assessment of social relationships between parents and young. Moreover, some Burrowing Owl populations appear to be highly structured and to exhibit relatively high levels of inbreeding (Johnson 1997a, Millsap and Bear 1997), indicating that the mating system in this species may be fundamentally different from that in most other species of owls.

On balance, genetic monogamy seems to be the rule among socially monogamous birds of prey, although relatively few species have been studied. We suggest that the high rate of male parental effort in raptors selects against EPFs because females that engage in extra-pair activities risk losing parental investment by males whose confidence in paternity has been reduced owing to the behavior of their mates (Whittingham et al. 1992, Korpimäki et al. 1996). Because male owls provide such a large amount of parental effort, we predict that most species of owls will prove to be genetically monogamous. Additional studies of genetic parentage in birds of prey will be required to evaluate the relationship between parental investment and EPFs more thoroughly. In this regard, parentage studies of raptors in which males exhibit relatively low rates of parental care would be especially valuable.

We thank K. Kraaijeveld and F. Smit-Kraaijeveld for helping with the DNA fingerprinting, A. Perkins, C. Olson, L. Clough, T. Dial, and B. Petty for helping to catch owls, P. and D. Smith and the Confederated Salish and Kootenai tribes for granting access to their lands, and T. Lubjuhn and three anonymous referees for commenting on the manuscript. JSM was supported by a grant from the University of Montana Research and Creativity Committee.

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The Condor 101:859–862

BROWN THRASHER NEST REUSE: A TIME SAVING RESOURCE, PROTECTION FROM SEARCH-STRATEGY PREDATORS, OR CUES FOR NEST-SITE SELECTION?[1]

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Abstract. We examined the potential functions of old nests in a population of Brown Thrashers (*Toxostoma rufum*) nesting on the Konza Prairie Research Natural Area in northeastern Kansas. We determined whether thrashers reuse nests constructed in previous years, and tested predictions of the hypothesis that old nests function to reduce the risk of nest predation by saturating the cues used by search-strategy predators. We also manipulated old-nest densities to test the hypothesis that old nests are used as indirect cues for nest-site selection. Thrashers were found to reuse nests, albeit at low rates (4% of nests monitored). We found no significant relationships between the density of old nests and the success of active nests, and experimentally removing nests did not influence nest-site selection. These results suggest that old nests may only benefit thrashers in this population as a resource to reduce the time spent in nest construction.

Key words: Brown Thrasher, nest-reuse, nest-site selection, old nests, Toxostoma rufum.

Considerable variation exists in the longevity of open cup nests built by passerines. Some nests deteriorate during, and shortly after, a nesting attempt (Skutch 1976, Briskie and Sealy 1988), whereas others may last for several years (Watts 1987). The accumulation of old nests on the territories of breeding birds has led to the supposition that they may provide an adaptive function. Three hypotheses proposed for the function of old nests include: (1) old nests may be reused and thus, provide a savings in time and energy to parents, (2) the accumulation of old nests may provide protection from search-strategy predators (Watts 1987), and (3) old nests may function as an indirect cue for nest-site selection (Erckmann et al. 1990). These hypotheses are not mutually exclusive and may act in concert, depending on the species and the local environment in which it breeds. Despite the potential adaptive function of old nests, these hypotheses have been largely untested. The reuse of nests constructed in previous years has been well documented for cavity breeders (Nilsson 1984, Brawn and Balda 1988), and species that place their nests on ledges (Skutch 1976). However, few open nesting passerines have been found to reuse old nests (Clark and Mason 1985) and only recently has

[1] Received 12 January 1999. Accepted 22 June 1999.

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