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# THE MATING STRATEGIES OF EASTERN SCREECH-OWLS: A GENETIC ANALYSIS[1]

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*Abstract:* We used genetic analysis to examine the mating strategies of male and female Eastern Screech-Owls (*Otus asio*) in central Kentucky. DNA fingerprinting revealed no evidence of extra-pair fertilizations in 23 broods (80 nestlings). Such results suggest that pursuit of extra-pair copulations by male and female screech-owls may be costly. One possible cost for females is the risk of losing the nest site. Alternatively, pursuit of extra-pair matings by females might be energetically expensive, thereby conflicting with egg production. Male screech-owls provide food for their mate (and young) during much of the breeding season and such feeding probably affects reproductive success. Males pursuing EPCs might have less time for foraging and, as a result, reduced reproductive success.

*Key words: extra-pair fertilizations, extra-pair copulations, Eastern Screech-Owls,* Otus asio, *DNA fingerprinting.*

Recent studies have provided abundant evidence that extra-pair copulations (EPCs) and fertilizations (EPFs) are important components of avian mating systems (reviewed by Birkhead and Møller 1992, Westneat and Webster 1994). However, these studies also reveal that the extent of extra-pair activity varies within populations and among species. Many factors may contribute to such variation. For example, opportunities for EPCs might vary with density (Birkhead and Møller 1992), the degree of breeding synchrony (Birkhead and Biggins 1987, Westneat et al. 1990, Stutchbury and Morton 1995), and features of the habitat (i.e., visually occluded habitats might make mate guarding more difficult; Sherman and Morton 1988). EPCs also might be more common in migratory species than in resident species (Westneat et al. 1990).

Adequately testing these and other hypotheses requires data from a large number of populations and species. Although such data are appearing at an increasing rate, most studies focus on passerines. The objective of the present study was to investigate the mating system of a non-passerine, the Eastern Screech-Owl (*Otus asio*). Specifically, we used genetic analysis (DNA fingerprinting) to examine the

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possibility that male and female Eastern Screech-Owls engage in extra-pair copulations.

Eastern Screech-Owls are socially monogamous and are year-round residents in eastern North America (Gehlbach 1994). Several characteristics of Eastern Screech-Owls led us to believe that females might engage in EPCs. First, females do little hunting during the period prior to and during egg-laying (i.e., their fertile period) because males provide them with prey (Gehlbach 1994); foraging males thus might be unable to guard their mates. In addition, screech-owls occupy visually-occluded habitats (woodlots and woodrows; Sparks et al. 1994) and are nocturnal, conditions which might make extra-territorial movements by either males or females less likely to be detected by social mates. Also, because screech-owls are resident year-round, females might have previous information on the quality of neighboring males, favoring female pursuit of EPCs with such males in a manner similar to that reported for female Black-capped Chickadees (*Parus atricapillus*, Smith 1988) and Blue Tits (*P. caeruleus*, Kempenaers et al. 1992). Thus, we expected to detect extra-pair fertilizations in Eastern Screech-Owls.

## METHODS

We studied the paternity and maternity of Eastern Screech-Owls resident in the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. From mid-March through early June 1994, we checked nest boxes and natural cavities for roosting adult males and incubating or brooding females. Once located, we captured adult males from the roost, banded them, and took a blood sample before placing them back in the roost. When we located females, we checked the reproductive status of their nest. To avoid abandonment, we did not handle females and young until 14 to 21 days post-hatching. Owls (adults and young) were banded with a U.S. Fish and Wildlife Service aluminum band. We also captured 20 owls (18 males and two females) by playing conspecific songs (bounce songs; Ritchison et al. 1988) from a speaker placed below a mist net located near their nest. To enhance response, a mounted screech-owl also was placed near the speaker.

Approximately 200–400 microliters of blood was collected from the brachial vein of each owl using one or more 250 microliter capillary tubes. We transferred the blood sample to vials containing 100 microliters of TNE (10 M Tris-10mM NaCl-2 mM EDTA, pH 8.0) buffer (Quinn and White 1987) and immediately placed them on ice. Samples were stored in a −20°C freezer until analyzed.

Because hatching was never observed, we estimated the age of nestlings based on their size and mass (Gehlbach 1994). We then back-dated to estimate the time of egg-laying and timing of each female's fertile period (we assumed the incubation period lasted 30 days; Gehlbach 1994). We defined the fertile period as lasting from seven days before the first egg of a clutch was laid until the day the penultimate egg was laid, a period similar to that reported in other birds, including some non-passerines (e.g., Birkhead and Møller 1992).

DNA fingerprinting followed standard lab procedures as described in Westneat (1990, 1993). Briefly, about 15 μg of DNA was digested with the enzyme *Hinf*I. We loaded about 6 μg of digested DNA onto 0.8% agarose in TBE (0.089 M Tris, 0.089 M borate, 0.002 M EDTA) and subjected the gel to 1,650 volt-hours (over approximately 48 hours). We transferred the DNA from treated gels (see Westneat et al. 1988) via vacuum blotting onto a nylon membrane (Zetabind, AMF Cuno).

We baked the membranes at 60°C for 2 hr and then washed them in sealable glass tubes (two membranes per tube) in a prehybridization solution (NaPi; Westneat et al. 1988) at 60°C for 24 hr. We hybridized the membranes with radio-labelled DNA probe, either M13 or mouse 2.5 *per*, at 60°C for 24 hr.

We washed all hybridized membranes twice in 2 × SSC and 0.5% SDS at room temperature and once at 60°C. Membranes probed with Mouse 2.5 *per* were washed an additional time in 1 × SSC at 65°C. We placed hybridized membranes on film (Kodak XAR) for 2–7 days. Then we stripped off the labelled probe and reprobed as necessary.

We scored the autoradiographs following procedures outlined in Westneat (1990, 1993). Scoring was not done blindly; nestlings were always run within a few lanes of each social parent. We determined band-sharing between pairs of adults on the same gel, and between parents and putative offspring, and identified any bands not shared with either putative parent (novel bands; Westneat 1990, 1993).

## RESULTS

We located 24 Eastern Screech-Owl nests an average (± SD) of 423 ± 79 m apart (ranging from 304 m to 565 m). Clutches were completed during the period from 15 March through 11 April, and most (67%) were completed during the two-week period from 15 to 28 March. Thus, most female screech-owls in our population (79%) were fertilizable during the period from 1 to 21 March. At the 24 nest sites, we sampled 46 adults and 84 young. The mean brood size per nest was 3.5 ± 1.1, ranging from one to five. We completed genetic analyses on 22 complete families (44 adults and 76 young) and one partial family (adult male plus four young).

DNA fingerprints from both M13 and M2.5 probes revealed considerable variation in fragment patterns among individuals (Table 1). Of 76 young from broods with fingerprints from both putative parents, 53 shared all of their fragments with the combination of the two putative parents (Fig. 1a, b). It is extremely likely that these young were the offspring of both the male and female associated with the nest. The remaining offspring ($n = 23$) had one or two fragments not present in either putative parent. Such novel fragments could come from either mutation or from an adult other than the putative parent being the genetic parent. Assuming mutation rates comparable to other studies (0.001–0.01 per fragment per generation; e.g., Jeffreys et al. 1985b, Burke et al. 1989, Westneat 1990, 1993), then mutation should result in only a few novel fragments, as was observed. In contrast, if an adult other than the putative parent was the genetic parent, then the young should have had a relatively large number of novel fragments. We calculated the expected number of novel fragments as follows: q, the average allele frequency, was found to be 0.18 from the equation $2q - q^2 = 0.32$ (band-sharing between adults; Jeffreys et al. 1985b). An expected band-sharing between parents and offspring was calculated as 0.63 from the equation $(1 + q - q^2)/(2 - q)$ (Jeffreys et al. 1985a). Of the total 51 bands scored per individual (Table 1), 63% would on average be shared with the mother, leaving 19 paternal bands. Because the within-pair male would average 6 bands (0.32) in common with the extra-pair male, we expected 13 novel bands if an extra-pair fertilization had occurred. No nestling had more than 2 novel bands, far below that expectation. Furthermore, band-sharing proportions between these nestlings and their putative parents were all high (Fig. 1a, b), similar to those of nestlings with no novel fragments and well above the distribution of band-sharing values between adults in the population. These data indicate that all 76 offspring were descended from the male and female associated with their nest.

At one additional nest, we were only able to capture the adult male and so were unable to determine the number of novel fragments exhibited by the young. However, these young exhibited a high degree of band-sharing with their putative father (range = 0.53–0.68), suggesting that all were his offspring. Thus, our results indicate that all 80 young screech-owls from 23 nests were the offspring of their putative parents.

## DISCUSSION

Our results suggest that male and female Eastern Screech-Owls rarely if ever engage in mixed mating strategies and are genetically as well as socially monogamous. By contrast, males, and perhaps females, in most other avian species that have been studied often pursue and obtain EPFs (see reviews by Birkhead and Møller 1992, Westneat and Webster 1994). Previous workers have noted the potential benefits of EPFs for both males and females (Westneat et al. 1990, Birkhead and Møller 1992). For males, the primary benefit would be increased mating success; while females might benefit in a number of ways, including fertility insurance and the production of offspring with genetic diversity and increased genetic quality (Birkhead and Møller 1992).

Lack of EPFs in Eastern Screech-Owls despite potential benefits is puzzling. One explanation is that female pursuit of EPCs is costly. One possible cost of pursuit for females is the risk of losing the nest site. An abundance of known nest-site competitors for this species might favor females staying and protecting the cavity throughout the fertilizable period (Belthoff and Ritchison 1990, Gehlbach 1994). Alternatively, pursuit of extra-pair matings might be energetically expensive for females, thereby conflicting with production of eggs.

TABLE 1. Average number of bands scored and average proportion of bands shared with both the M13 and M2.5 *per* probes in nonmate, adult Eastern Screech-Owls.

| | Number of bands scored | | Proportion of bands shared | |
|---|---|---|---|---|
| | M13 | M2.5 | M13 | M2.5 |
| Number of individuals/dyads | 44 | 44 | 32 | 32 |
| Mean | 24.4 | 27 | 0.32 | 0.31 |
| SD | 7.6 | 6.6 | 0.14 | 0.11 |

Even if females do not pursue EPCs, EPFs could occur if females cooperated with male-initiated attempts or were harassed into mating (e.g., Westneat 1992). Because females in this year-round resident

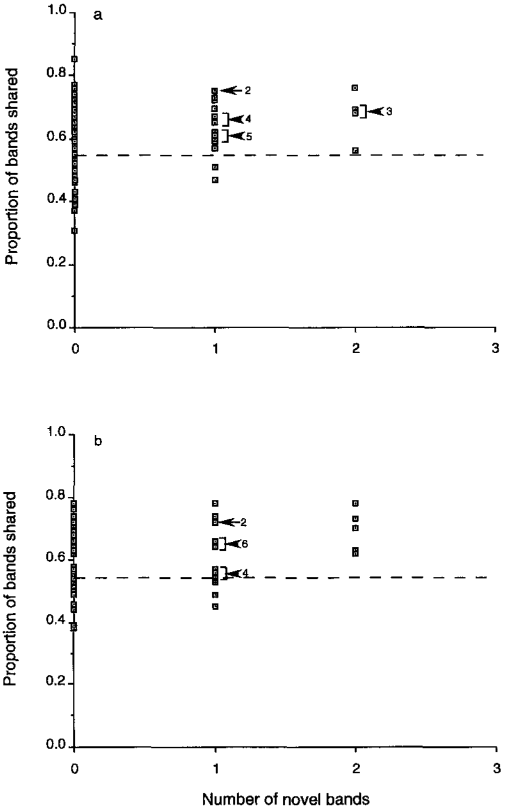

FIGURE 1. Proportion of bands shared by number of novel fragments for 76 screech-owl nestlings. (a) Band-sharing proportions between nestlings and the female at the nest. (b) Band-sharing proportions between nestlings and the male associated with the nest. The horizontal dotted line represents the upper, one-tailed 95% confidence limit for band-sharing between adults in the population. Numbers indicate number of coincident points for nestlings with one or more novel bands.

may have more opportunity to choose a compatible social mate or one of high quality, they may be less willing to cooperate with an extra-pair male than females in a migratory species. An unwilling female in this species is less likely to be harassed into mating because females outweigh males by 30 or more grams (Gehlbach 1994). If so, the unlikely success of EPCs might reduce male investment in pursuing EPCs.

There are several additional reasons why males might not even pursue EPCs at all. First, the high breeding synchrony of screech-owls in central Kentucky means that many male screech-owls must pursue EPCs when their own mate is preparing to lay eggs. However, for several weeks prior to nesting, male raptors, including male screech-owls, provide food for their mates (Snyder and Wiley 1976). Females are completely dependent on their mates for food (Snyder and Wiley 1976, Korpimaki 1991) and this affects female (and hence male) productivity (e.g., Daan et al. 1989, Palokangas 1992), thereby seeming to favor provisioning the current mate rather than searching for possibly uncooperative extra-pair mates. Male feeding also may be important for maintaining the pair before eggs have been laid. A few females do breed asynchronously, but they often are laying replacement clutches much later in the season (Gehlbach 1994, Ritchison, unpubl. data) when most other females are incubating or brooding young nestlings. During these periods, male screech-owls continue to provide most or all of the food for their mate or young. Thus for male Eastern Screech-Owls the substantial costs and poor chances of success might favor little effort at pursuing EPCs.

In conclusion, the patterns of social associations in Eastern Screech-Owls do reflect the patterns of matings. Several important competing demands for both males and females may explain why the costs of EPCs outweigh the benefits, and so EPCs leading to EPFs are rare.

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# CHARACTERISTICS OF NESTING AREAS USED BY SAN CLEMENTE ISLAND SAGE SPARROWS[1]

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*Abstract:* I examined the nest habitat used by Sage Sparrows (*Amphispiza belli clementeae*) on San Clemente Island, one of the California Channel Islands, during March through June 1986. All nests were found in boxthorn shrubs in coastal scrub habitat. The cover of vegetation was greater and more evenly distributed at nest sites than in surrounding habitat. Nests were placed most often on the leeward side of live boxthorn shrubs interspersed by cactus.

*Key words: Sage Sparrow,* Amphispiza belli, *San Clemente, island, habitat, nest.*

Sage Sparrows (*Amphispiza belli*) are widely distributed in western North America, breeding from southern Idaho and eastern Washington south to the Mexican Plateau, including islands off the coast of southern California (Bent 1968). The San Clemente Island (SCI) Sage Sparrow (*A. b. clementeae*) inhabits maritime desert scrub habitat on the west side of SCI, the southern-most of the California Channel Islands (Philbrick and Haller 1977, Willey 1990). The Sage Sparrow was a common island resident but experienced severe declines due to habitat loss caused by livestock (Jorgensen and Ferguson 1984). In 1977 it was listed as "threatened" by the U.S. Fish and Wildlife Service (Greenwault 1977). Previous investigation of Sage Sparrow habitat use has focused on populations in the Great Basin (Rich 1980, Reynolds 1981, Petersen and Best 1985, Winter and Best 1985), and prior to my study, work on the island race was restricted to nesting success (Willey 1990) and taxonomy (Van Rossem 1932, Miller 1968). The purpose of this study was to identify habitat used by Sage Sparrows during the breeding season on SCI using methods developed by Petersen and Best (1985). Vegetation structure, plant composition, and nest placement were measured at nest sites and surrounding habitat to address the following questions: (1) do Sage Sparrows select nest sites that were distinct from the average scrub habitat, and (2) are patterns of nest placement consistent among pairs of Sage Sparrows?

## STUDY AREA AND METHODS

San Clemente Island (143 km$^2$; 33.6 km long; average of 12.8 km wide) is located approximately 110 km northwest of San Diego, California at 118°30′W 33°00′N. Topographically, the island is characterized by steep escarpments on the east, sloping plateaus cut by steep canyons in the central highlands, and marine terraces on the west side. The highest point on the island is approximately 610 m above sea level. The Mediterranean climate features strong westerly winds, dry summers, mild winters, and 270 mm average annual precipitation (Philbrick and Haller 1977). The island's vegetation has been described by Philbrick and Haller (1977). Several exotic animals have been introduced to the island in the early 1900s and the endemic flora was seriously damaged by feral goats and pigs (Jorgensen and Ferguson 1984).

The study area occurred along an 8 km strip of coastal scrub habitat on the two lowest western terraces of the island, located 5 km southwest of Wilson Cove (Willey 1990). Vegetation at the study site was dominated by boxthorn (*Lycium californicum*) shrubs, interspersed with prickly pear cactus (*Opuntia* spp.), cholla cactus (*O. prolifera*), snake cactus (*Bergerocactus emoryi*), and various grasses (*Avena* spp., *Stipa comata,* and *Hordeum jubatum*).

I located nests by observing nest building by adults from early March through June 1986. Habitat structure and composition within the study area were quantified using ten 350-m parallel transects placed in the study area at 500-m intervals. To assess available habitat, I measured vegetation at 80 sample points located every 50 m along the transects. Habitat characteristics also were measured at 31 nests located in the study area. At each sample point and nest site, shrub cover was estimated using line intercept

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