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Extrapair Paternity and Intraspecific Brood Parasitism in Eastern Bluebirds Revealed by DNA Fingerprinting

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Traditionally, mating systems have been classified on the basis of observed social relationships between males and females, but parentage of offspring may not reflect observed social bonds. Copulations between nonmates (extrapair copulations) are common in many monogamous birds (reviewed in Ford 1983, McKinney et al. 1984, Westneat et al. 1990), and recent genetic studies have shown that extrapair copulations can lead to extrapair fertilizations (e.g. Westneat 1987, Sherman and Morton 1988, Bollinger and Gavin 1991). In some monogamous species there is no evidence of extrapair paternity (e.g. Willow Warblers, *Phylloscopus sibilatrix*; Gyllensten et al. 1990), but in others as many as 40% of nestlings may be fathered by extrapair males (Tree Swallows, *Tachycineta bicolor*; Lifjeld et al. 1993).

Several factors are thought to influence the likelihood of extrapair copulations and extrapair paternity in birds. A high density of breeding individuals promotes extrapair copulations in colonial species (Møller 1985), and can also affect extrapair paternity in dispersed species (Gowaty and Bridges 1991a). Low breeding synchrony should encourage extrapair copulations by enabling mated males to guard their mates while they are fertile, and to pursue copulations with other females when their mates are not fertile (Birkhead and Biggins 1987, Westneat et al. 1990). In several species, younger males suffer more extrapair paternity than older males (Westneat 1987, Morton et al. 1990, Gowaty and Bridges 1991b).

Male birds protect their paternity primarily through mate guarding or frequent copulations with their mate (Birkhead and Lessells 1988). Males guard their mates through constant surveillance (Mumme et al. 1983,

Birkhead et al. 1987) and close following (Møller 1987, Birkhead and Lessells 1988) of females during the females' fertile periods.

Eastern Bluebirds (*Sialia sialis*) are secondary cavity nesters, which readily breed in nest boxes. They are socially monogamous, with extensive biparental care (Pinkowski 1978, Meek 1991). Male Eastern Bluebirds guard their mates (Gowaty et al. 1989, Meek and Robertson 1994), and allozyme electrophoresis has detected extrapair paternity in populations in South Carolina (Gowaty and Karlin 1984) and Arkansas (Karlin et al. 1990). Eastern Bluebirds and Tree Swallows compete aggressively for nest cavities in areas where the two species co-occur (Hersey 1933, Kuerzi 1941, Rustad 1972), and Meek and Robertson (1993) found evidence of a trade-off between mate guarding and territory defense in an Ontario population of Eastern Bluebirds. Competition between Eastern Bluebirds and Tree Swallows is more intense on bluebird territories containing multiple nest boxes than territories with a single nest box, with the consequence that male Eastern Bluebirds on multiple-box territories guard their mates significantly less than males on single-box territories (Meek and Robertson 1994).

We assessed the level of extrapair paternity in an Ontario population of Eastern Bluebirds. We examined the relationship between mate guarding and paternity by looking at the correlation between mate guarding and paternity for individual males, and by comparing paternity on territories with one nest box with territories having multiple nest boxes. We also assessed whether male or female age, first or second brood, or the breeding stage of the nearest neighbor was associated with extrapair paternity in our study.

Methods.—We studied a population of Eastern Bluebirds nesting in boxes in the vicinity of Chaffeys Locks, Ontario, Canada (44°34'N, 76°19'W) in the summers

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of 1989 to 1991. Each year 20 to 30 pairs of bluebirds breed in our study area and about 20% return the next year (Meek 1991). We caught and color-banded adults during late incubation or just after hatching, because disturbance earlier in the nest cycle can cause nest desertion (Gowaty and Bridges 1991a). All bluebird nests were monitored regularly to determine date of clutch initiation (first egg), clutch size, hatch date, brood size, fledging date, and fledging success. We checked nests daily between 1300 and 1500 EST from territory establishment until incubation, and every two days from hatching until the young were 12 days old. We measured mate guarding by males in 1989. Focal pairs were observed between 0600 and 1100 because egg laying (and fertilization of the next egg) occurs in the morning for most birds (Birkhead et al. 1987). For each pair of birds we made at least two 30 min focal-pair watches during the fertile period, three days prior to the first egg through the day that the penultimate egg was laid (Birkhead 1979). We recorded behavior of bluebirds continuously, noting all movements of bluebirds and the distance between male and female (nearest 0.5 m). We calculated the proportion of time males and females spent together on the territory and the frequency with which males and females followed (i.e. flew at least 10 m in same direction within 30 s) movements initiated by their mates. Further details of methods for collecting the mate guarding data are described in Meek and Robertson (1994).

For the parentage investigation reported here, we analyzed DNA data from 21 broods. All putative parents fed the young, and males made approximately 50% of feeding trips to nestlings (Meek 1991). Ten broods were from territories containing a single nest box, and 11 broods were from territories containing multiple nest boxes. We determined the breeding stage of nearest neighbors from data collected during regular nest checks. Natural cavities are occasionally used by Eastern Bluebirds in our study area. These cavities are not accessible, but we estimate that three pairs breed in natural cavities each year. Some captured adults could be aged as second year (SY) or after second year (ASY) by the color and shape of the tenth-primary coverts (Pitts 1985); others could only be aged as after hatch year. We banded nestlings when they reached 8 to 12 days of age. We collected 75 to 200 μl of blood from adults and nestlings by jugular venipuncture (1989 and 1990) or by puncture of the brachial (adults) or metatarsal (nestlings) veins (1991).

Blood was stored in 50 μl Tris-NaCl-EDTA buffer at $-20°C$ (1989, 1990 samples) or in 100 μl of "Queen's" lysis buffer at 4°C (1991 samples; Seutin et al. 1991). DNA was extracted from blood samples following the procedures of Seutin et al. (1991), except that extractions were done by hand, and DNA was precipitated with isopropanol. DNA was cut with *Alu* I and hybridized with the minisatellite probes 33.15 (Jeffreys et al. 1985) and *per* (Shin et al. 1985). Electrophoresis,

Southern blotting, and prehybridization followed Smith et al. (1991), except that we used 5 μg of DNA per sample, and Immobilon (Millipore) transfer membranes. Transfer membranes were hybridized, washed, and autoradiographed following Smith et al. (1991), except that the membranes were washed in 2× SSC, 0.1% SDS. In 16 cases broods from neighboring territories were run on the same fingerprint gel, usually with at least one additional neighboring male.

We assessed parentage of nestlings by comparing DNA fragments (bands) of nestlings and their putative parents on the autoradiographs. Bands were scored in the 2 to 24 kilobase (kb) region by marking all bands on acetate sheets, using different colored markers for maternally and paternally derived bands. Bands were considered identical if their centers were less than 1 mm apart and they did not differ greatly in density. We used a combination of two methods to determine whether a nestling was produced by its putative parents. First, we examined nestlings for bands not present in either putative parent (novel fragments; see Westneat 1990). Second, we calculated the degree of band sharing between putative parents and offspring to determine which parent was excluded (Westneat 1990). Band sharing (D) was calculated as

$$D = 2\,(n_{AB})/(n_A + n_B), \qquad (1)$$

where n_{AB} is the number of bands shared by birds A and B, and n_A and n_B are the number of bands in birds A and B, respectively (Wetton et al. 1987). This coefficient varies from 0 (no bands shared) to 1 (all bands shared) and, on average, parents and genetically related offspring should share more than 50% of their bands. Both *per* and Jeffreys 33.15 probes produced DNA fingerprints similar to those described for other bird species. The two probes produced different numbers of novel fragments and different band-sharing coefficients between individuals, but both resulted in identical exclusions of mismatched offspring from all autoradiographs. For simplicity, we report only the results obtained from blots probed with Jeffreys 33.15, since these produced clearer autoradiographs.

Results.—The use of band-sharing coefficients to analyze parentage assumes that bands are inherited independently of each other. We analyzed the DNA fingerprints of a male and his nine offspring (from two broods with two different females), and a female and her 12 offspring (from three broods with three different males) to see how bands were distributed in a large sibship. Nestlings in this analysis had zero (17/21) or one (4/21) novel fragments, and there was nothing to suggest that they were not truly descended from the putative parents. For each nestling, paternal or maternal bands were scored as either present (=1) or absent (=0), and Pearson correlation coefficients were calculated for all pairwise combinations of the bands. There were 19 clearly resolved paternal bands, none of which was homozygous (found in all nine

nestlings). There were no allelic pairs of bands ($r = -1$) and no linked pairs of bands ($r = 1$). The mean transmission frequency of the 19 paternal bands was $0.538 \pm$ SE of 0.050, which is close to the expected value of 0.5. There were 22 clearly resolved maternal bands, one of which was homozygous. Again, there were no allelic pairs of bands or linked pairs of bands. The mean transmission frequency of the 22 maternal bands was 0.532 ± 0.039, which is close to the expected value of 0.5. On the whole, bands were transmitted independently.

We estimated the background level of band sharing between unrelated birds in our population by calculating band-sharing coefficients for 47 pairs of presumably unrelated adults run within three lanes of each other on a gel. Average band sharing was 0.160 ± 0.008, ranging from 0.044 to 0.286 (Fig. 1). The number of detectable bands in the 2 to 24 kb range averaged 20.98 ± 0.26 ($n = 133$) for all fingerprints analyzed.

In our sample, 56 of 83 (67.5%) nestlings had fingerprints in which all bands were present in one or both putative parents. Eighteen nestlings (21.6%) had one or two novel fragments, and high band-sharing coefficients with both parents. Nestlings having zero to two novel fragments had average band-sharing coefficients of 0.552 ± 0.009 (range 0.38 to 0.76) with the putative father, and 0.572 ± 0.010 (range 0.40 to 0.77) with the putative mother. For nestlings with zero to two novel fragments, the distribution of band-sharing coefficients between nestlings and putative parents was distinct and did not overlap with the distribution of band-sharing coefficients between putatively unrelated adults (Fig. 1). Nine nestlings (10.8%) had four or more novel fragments and low band-sharing coefficients with at least one parent. Of these, seven nestlings (8.4%) from five nests (24%) had high band sharing with the putative mother, and low band sharing with the putative father. Band-sharing coefficients between these seven offspring and the putative father ($D = 0.238 \pm 0.022$, range 0.10 to 0.33) were distinct, and did not overlap with the band-sharing coefficients of nestlings having only zero to two novel fragments. Thus, we concluded that these seven nestlings were all fathered by extrapair males.
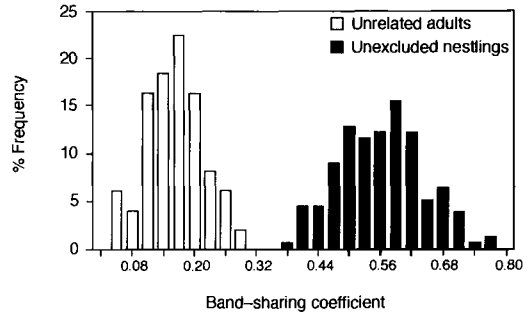

Fig. 1.   Frequency distributions of proportions of bands shared (D) between putatively unrelated adults (open bars), and all comparisons between each unexcluded nestling (those having zero to two novel fragments) and their putative parents (solid bars).

Two nestlings (2.4%) from two broods (9.5%) had many (≥ 10) novel fragments and low band-sharing coefficients (<0.30) with both putative parents. We concluded that these offspring were the result of intraspecific brood parasitism.

In all five nests with extrapair paternity, either one or two nestlings did not match the putative father, and a single extrapair male was responsible for all mismatched nestlings in a brood (Table 1). We were able to identify one male that probably fathered both extrapair young in a neighboring nest 300 m away (nest KT1; Table 1). This neighboring male was run on the same fingerprint gel, next to the putative father (the resident male). All nine mismatched bands in one nestling and seven of eight in the other nestling were explained by this male. The neighboring male explained all nonmaternal bands and all but two nonmaternal bands in the extrapair young. Band-sharing coefficients between this neighboring male and the two mismatched nestlings were each 0.490. When the female at KT1 was fertile, the neighboring male's mate was incubating her eggs.

We found no evidence of a relationship between mate guarding and extrapair paternity. Males on territories with multiple nest boxes guard their mates less strongly than males on single-box territories (Meek

TABLE 1.   Paternity of Eastern Bluebird nestlings in nests containing extrapair young. D_m and D_f denote band-sharing coefficients between nestlings and putative male and female parents, respectively.

Nest	Nestlings related to male			Nestlings unrelated to male			No extrapair males
	n	D_m	D_f	n	D_m	D_f	
KT1	2	0.58–0.63	0.61–0.62	2	0.26–0.33	0.56–0.65	1[a]
BM1	2	0.52–0.54	0.42–0.63	2	0.21–0.30	0.52–0.59	1[b]
BGC7	1	0.52	0.59	1	0.10	0.50	1
LS3	3	0.56–0.60	0.38–0.53	1	0.27	0.59	1
BS4	4	0.63–0.70	0.44–0.51	1	0.24	0.53	1

[a] Indicated from fingerprint profile of neighbor.
[b] Indicated from sharing of novel fragments between illegitimate siblings.

and Robertson 1994). Extrapair nestlings were found in 2 of 11 (18%) broods from multiple-box territories, and 3 of 10 broods from single-box territories (30%; $G_{adj} = 0.365$, $P > 0.1$). Mate guarding varied widely among individual males (range 10 to 98%), but there was no significant relationship between the proportion of time males spent with their fertile mates and the proportion of nestlings fathered (Spearman ρ [corrected] $= -0.228$, $n = 8$, $P = 0.546$). Males with low mate-guarding scores were not more likely to have extrapair young in their nests.

Both SY and ASY males had extrapair young in their nests, and male or female age did not appear to affect the likelihood of extrapair paternity. We found that 29% (2/7) of SY males and 30% (3/10) of ASY males had extrapair young in their nests ($G_{adj} = 0.011$, $P > 0.1$). Also, 20% (1/5) of SY females and 33% (3/9) of ASY females produced extrapair young ($G_{adj} = 0.253$, $P > 0.1$). Extrapair fertilizations and intraspecific brood parasitism occurred throughout the breeding season. Extrapair young occurred in 20% (3/15) of first broods and 33% (2/6) of second broods ($G_{adj} = 0.355$, $P > 0.10$). One of the two cases of egg dumping occurred in a first-brood nest, the other in a second-brood nest. Breeding synchrony may affect the opportunity for extrapair matings, because there should be a trade-off for males between mate guarding and seeking extrapair copulations. When resident females were fertile, those having nonfertile female neighbors were more likely to produce extrapair young (4 of 9) than those having fertile neighbors (1 of 12), although this trend was not significant ($G_{adj} = 3.427$, $0.05 < P < 0.1$), possibly due to small sample size.

Discussion.—DNA fingerprinting of Eastern Bluebirds revealed that in an Ontario population 7 of 83 (8.4%) nestlings resulted from extrapair matings, and 5 of 21 (24%) nests contained at least one extrapair nestling. Extrapair matings are an important part of the mating system of Eastern Bluebirds and have been documented for a number of socially monogamous birds (Birkhead and Møller 1992). We also found two cases of intraspecific brood parasitism, which accounted for 2.4% of nestlings and 9.5% of nests. Unlike Gowaty and Bridges (1991a), we have never observed cases of two eggs appearing in one day or skips in the laying sequence in our population, and we did not expect to discover intraspecific brood parasitism. Both intraspecific brood parasitism and extrapair paternity have been detected by electrophoresis in a South Carolina population of Eastern Bluebirds (Gowaty and Karlin 1984, Gowaty and Bridges 1991a, b). In South Carolina the number of extrapair nestlings varies in relation to nearest-neighbor distance, ranging from 8% when neighbors are 1 km apart to 44% when neighbors average 70 m apart (Gowaty and Bridges 1991a). Our figure of 8.4% extrapair nestlings, with nearest-neighbor distances averaging around 400 m, fits this general pattern. Because extrapair young increased with increasing density of neighbors, Go-

waty and Bridges (1991a) concluded that neighboring males were responsible for the extrapair fertilizations. Our one identified extrapair male, a neighbor at a nest 300 m away, is consistent with this hypothesis.

Opportunities for extrapair copulations should be reduced by males guarding fertilizable mates (Westneat et al. 1990). Few investigations to date have examined the influence of mate guarding on the frequency of extrapair paternity, but studies so far have found no relationship (Morton et al. 1990), a negative relationship (Gowaty and Bridges 1991b, Kempenaers et al. 1992) and a positive relationship (Burke et al. 1989) between mate guarding and paternity. We found no correlation between mate guarding and paternity for individual males, and extrapair paternity occurred at a similar rate on territories with multiple nest boxes, where mate guarding is low, and on territories with a single nest box, where mate guarding is stronger. We found no evidence of an association between mate guarding and paternity in our population, although there may have been a relationship that was not detected by our small sample sizes. Males may not reduce mate guarding to the extent that it results in loss of paternity (Meek and Robertson 1994). Additionally, if female Eastern Bluebirds seek extrapair copulations off their territories as Gowaty and Bridges (1991b) suggested, mate guarding by males may have little influence on paternity unless males are able to remain with their mates close to 100% of the time when the females are fertilizable.

In other species, paternity varies among individuals in a number of ways. Males are more likely to have extrapair young in their nests if they are less attractive (Kempenaers et al. 1992), less experienced (Bollinger and Gavin 1991), or younger (Westneat 1987, Morton et al. 1990, Gowaty and Bridges 1991b) than other males. We found no evidence that extrapair paternity was related to male age; similar proportions of SY and ASY males had extrapair young in their nests. Gowaty and Bridges (1991b) found that SY male Eastern Bluebirds were more likely to have extrapair young in their nests. Within our study area, the likelihood of extrapair paternity may have been associated with the presence of a nonfertile neighbor (a neighboring male that was not mate guarding). This tendency for breeding synchrony to influence extrapair paternity suggests that in our population males may face trade-offs between mate guarding and seeking extrapair copulations, as well as between mate guarding and territory defense (Meek and Robertson 1994). The behavior of individual males will depend on how they balance these competing demands.

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Impact of Interspecific Aggression and Herbivory by Mute Swans on Native Waterfowl and Aquatic Vegetation in New England

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One of the greatest threats to American avifauna is the establishment of free-ranging exotic avian populations (Temple 1992). Despite evidence of substantial harm caused by exotic birds, most exotic species are so poorly studied that many of their alleged environmental impacts remain largely undocumented (Temple 1992). One such exotic species is the Mute Swan (*Cygnus olor*), a Eurasian species that has been introduced several times into North America, beginning in the late 1800s (Allin et al. 1987). By the 1970s, free-ranging populations existed in Michigan, Minnesota, Wisconsin, Wyoming, British Columbia, Ontario, and in Atlantic coastal states from Maryland to Massachusetts (Allin 1981). In the Atlantic Flyway, free-ranging populations increased from 200 birds in 1955 to 5,300 in 1987 (Allin et al. 1987).

Some biologists are concerned that the increasing population of free-ranging Mute Swans may have an adverse impact on native waterfowl, owing to the swan's aggressive nature (Reese 1975, Williams 1989). Swans sometimes attack other waterfowl, causing injury or death (Stone and Marsters 1970, Willey and Halla 1972, Allin et al. 1987). Furthermore, aggressive swans may displace other waterfowl (Willey and Halla 1972). An additional concern is that the foraging behavior of swans may adversely affect aquatic plant biomass, reducing the food available for other waterfowl. Currently, data are insufficient to judge whether these concerns are real or whether swan populations should be controlled. At present, Mute Swans are protected in some states and unprotected in others; in still others, government employees attempt to control swan populations by shaking eggs and removing adults (Allin et al. 1987). In this study, we examined interspecific aggression by free-ranging adult Mute Swans with breeding territories in freshwater ponds and the impact of their herbivory on aquatic vegetation.

Methods.—Territorial pairs of free-ranging Mute Swans were observed at 15 freshwater ponds (2 to 30 ha) in New Haven County, Connecticut from 1982 to 1987. These ponds represented all freshwater sites in the study area known to have nesting pairs of free-ranging Mute Swans in 1982. Observations were limited to freshwater sites because these were the main areas where Mute Swans came into contact with native waterfowl.

Data on the impact of interspecific aggression were collected on both members of a swan pair simultaneously; data for males and females were analyzed separately. Sex of pair members was determined by the larger body size and larger fleshy knob on the forehead of males (Bellrose 1980). Pairs were observed year-round for 30-min periods, randomly selected among daylight hours. Observations were made from shore, usually from a car to minimize disturbance of