

GENETIC EVIDENCE OF MIXED REPRODUCTIVE STRATEGY IN A MONOGAMOUS BIRD¹

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Abstract. Electrophoresis was used to assess the occurrence of extra-pair copulations and intraspecific brood parasitism in the Field Sparrow, *Spizella pusilla*. Blood samples were taken from 52 nestlings and their putative parents. Results from two polymorphic loci suggested that 19.2% of the nestlings had genotypes inconsistent with at least one putative parent.

Key words: *Spizella pusilla*; extra-pair copulation; electrophoresis; conspecific nest parasitism.

INTRODUCTION

An increasing number of studies detailing avian mating systems have described mixed strategies in apparently monogamous species (Westneat et al. 1987). Extra-pair sexual activities have been reported in over 115 species of apparently monogamous birds spanning 30 families (Gladstone 1979, McKinney et al. 1984). The advent of more detailed behavioral studies and biochemical analyses have revealed that copulations by paired birds with individuals other than their mates is not uncommon in normally monogamous species.

Field observations have shown that males may commonly practice a mixed reproductive strategy, whereby a male will pair with one primary female and contribute to the care of the offspring, and yet take advantage of any opportunities for additional copulations outside the pair-bond (Trivers 1972). Because male passerines lack an intromittant organ, it is assumed that female cooperation is generally required for successful copulation (Van Tienhoven 1983).

Protein electrophoresis has been an effective technique for investigating parentage (e.g., Sherman 1981). Electrophoretic determination of putative and actual genealogical relationships in wild bird species has revealed multiple paternity (Joste et al. 1985, Mumme et al. 1985, Westneat 1987b, Sherman and Morton 1988) and extra-pair copulations and egg dumping (Gowaty and Karlin 1984, Wrege and Emlen 1987). The data generated by such techniques have revealed a com-

plex picture of "monogamy" which includes extra-pair copulations, conspecific nest parasitism, and quasi-nest parasitism ("parasitism by a female who was fertilized by the male attending the parasitized nest"; Wrege and Emlen 1987). Generally, electrophoresis can be used only as a means of parental exclusion (Gowaty 1985, Joste et al. 1985). Multiple parentage may go undetected if the genotype of the genetic parent is similar to the genotype of the putative parent.

The Field Sparrow (*Spizella pusilla*) has been extensively studied (e.g., Walkinshaw 1936, 1939, 1945, 1968; Best 1974a, 1974b, 1974c) and has long been assumed to have a monogamous mating system. Prior to this study, no instances of polygyny had been reported, and only one occurrence of an extra-pair copulation (EPC) observed (Walkinshaw 1968). Additionally, neither intraspecific parasitism or quasi-parasitism has been documented in this species through field observation techniques. Behavioral observations (Petter et al., unpubl.) of color-banded individuals suggested the occurrence of a mixed reproductive strategy in Field Sparrows. Instances of territorial trespassing and attempted extra-pair copulations indicated that a more complex mating system characterized this population of Field Sparrows. The present study was initiated to assess, with electrophoretic data, the incidence of multiple parentage.

METHODS

During the 1986 breeding season (April-July) two study sites were established, a 4.8-ha abandoned orchard/old-field habitat (upper study area) and a 1.6-ha old-field site (lower study area). Both areas were gridded at 10- × 20-m intervals

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for territory mapping and vegetation analysis. Territory boundaries were determined using a modified version of the flush method and monitored throughout the season. Spot mapping and observation of territory defense (Kendeigh 1944) refined territory boundaries. Field Sparrows were captured using mist nets and Potter traps. Adult birds were banded with aluminum USFWS bands and unique color-band combinations for individual identification. Once discovered, nests were checked daily for the appearance of eggs. All eggs were marked allowing us to detect evidence of conspecific nest parasitism (CNP). The first broods captured in 1986 were banded with aluminum bands. However, due to extremely high predation rates (approximately 80%) on the early broods in the study area, subsequent broods were removed as eggs and placed in a humid still-air incubator at 34°C. We determined that the nests were lost to snake predators, mainly *Elaphe obsoleta*. Pairs remained together after a nest was depredated, and the female began construction of a nest shortly thereafter. However, we did observe considerable movement of the males among territories after the loss of a nest (unpubl. data).

Behavioral observations were conducted from April through August. Each area was visited on alternate days and activity patterns of paired individuals were recorded over 15- to 20-min intervals throughout the day using focal female and focal nest techniques. Observation periods were made at varying times of the day. This eliminated a time bias in our data. During 1986, 37 adults were banded and observations made on 15 pairs. Twenty-one nests were sampled. Of these, seven clutches were brought back to the laboratory for incubation. A 65% hatching rate was achieved in the incubated clutches.

Blood samples were obtained by piercing the brachial vein on the underside of the wing and collecting the blood in heparanized capillary tubes. The tubes were placed immediately on ice, and returned to the laboratory within 1-2 hr. Adult Field Sparrows were bled when captured for banding. Nestlings were sampled when they were 5 to 7 days old when hatched in the field, or within 24 hr of hatching when in the incubator. No evidence of fetal-specific allozymes was detected in either polymorphic locus (Romagnano et al. 1989). Thirty-seven adults (23 of which remained in the study areas) and 52 young from 17 nests were sampled over the course of the

TABLE 1. The enzymes, number of presumptive genetic loci, and buffer system used in the survey. Abbreviations for enzyme names follow Harris and Hopkinson (1976). Asterisks indicate polymorphic loci. Buffer A = Tris-citrate pH 6.1, Turner (1983); buffer B = Barbitol pH 8.6, Sigma Chemical.

Enzyme	No. of loci	Buffer
Isocitrate dehydrogenase (ICD)	1	A
Lactate dehydrogenase (LDH)	2	A
Sorbitol dehydrogenase (SORDH)	1	B
Malate dehydrogenase (MDH)	2	A
Phosphohexose isomerase (PHI)	2	A
*Phosphogluconate dehydrogenase (PGD)	1	B
Glycerol phosphate dehydrogenase (GPD)	1	B
Phosphoglucomutase (PGM)	1	A
Fumerate hydratase (FH)	1	A
*Serum cholinesterase	1	B
Acid phosphotase (ACP)	2	A
Leucine aminopeptidase (LAP)	1	B
Mannose phosphate isomerase (MPI)	1	B
Glutamate-oxaloacetate transaminase (GOT)	1	A
Superoxide dimutase (SOD)	1	B
Malic enzyme (ME)	1	A
Albumins	2	B

breeding season. The clutches may be divided into three categories based on the number of putative parents sampled: (1) 12 complete families (both parents sampled) and 33 nestlings; (2) six partial families (only the putative father sampled) and 22 nestlings; and (3) one family with only the putative mother and three nestlings from one nest. An adult was considered the putative parent if the nest occurred within a specific territory (male parent) or the adult was observed on the nest or feeding the young.

Blood samples were separated into serum and cell components by centrifugation at room temperature for 10 min. RBCs and plasma were placed in separate 0.25-ml centrifuge tubes and diluted with 5-15 μ l of buffer (0.1 M Tris, 0.001 M sodium EDTA, 0.1% 2-phenoxyethanol, 0.01% NAD, 0.01% NADP). RBCs were homogenized for approximately 30 sec and recentrifuged. Samples were kept frozen at -90°C until analyzed (no longer than 2 weeks).

Blood cells and plasma were surveyed for genetic variation at 22 enzyme encoding loci (Table 1). Electrophoresis was performed on cellulose acetate (Helena Laboratories). Stain recipes were

TABLE 2. Allele frequencies observed in male (M), female (F), and nestling (N) Field Sparrows in the upper and lower study areas during the 1986 breeding season at the serum cholinesterase and phosphogluconate dehydrogenase loci.

Allele	Allele frequency					
	Upper			Lower		
	M	F	N	M	F	N
Serum cholinesterase						
A	0.09	0	0.10	0.11	0.06	0.13
B	0.55	0.72	0.59	0.33	0.75	0.57
C	0.18	0.21	0.27	0.17	0	0.04
D	0.18	0.07	0.04	0.39	0.13	0.23
E	0	0	0	0	0.06	0.03
Phosphogluconate dehydrogenase						
A	0.56	0.58	0.50	0.72	0.69	0.56
B	0.33	0.34	0.44	0.16	0.12	0.38
C	0.11	0	0	0.06	0.13	0
D	0	0	0	0.06	0	0
E	0	0.08	0.06	0	0.06	0.06

modified from Harris and Hopkinson (1976). Only two loci exhibited genetic variation; serum cholinesterase (E, EC 3.1.1.8) and phosphogluconate dehydrogenase (PGD, EC 1.1.1.44). Putative parents were run alongside nestlings and a reference individual of established genotype was run on each plate.

DATA ANALYSIS

Allele frequencies were calculated for males, females, and nestlings at the two loci. A chi-square value was computed for adults in each area to test for conformation of genotype frequencies to Hardy-Weinberg expectations. Heterogeneity chi-squares were computed for adult allele counts in both study areas, and for adult and nestling counts in each study area.

RESULTS

During approximately 700 observation hours (focal female and focal nest), we witnessed 28 attempted copulations; only one was an EPC, and it did not appear to be successful. We defined attempted copulation as those times when a male mounted a female. Copulations were difficult to observe since they often took place in shrubs or trees. There were no indications of conspecific nest parasitism (i.e., more than one egg laid per day, abnormally large clutches, appearance of new eggs after clutch completion, or late hatching; Yom-Tov 1980).

GENETIC VARIATION IN *SPIZELLA PUSILLA*

Allele frequencies of adults and nestlings sampled during 1986 are listed in Table 2. Adult serum cholinesterase isozymes were consistent with Mendelian expectations in the two study populations of Field Sparrows. With the exception of PGD in the upper area ($\chi^2 = 18.74$, $df = 9$, $P < 0.05$), chi-square tests of observed vs. expected adult allele frequencies were consistent with Hardy-Weinberg expectations (all $P > 0.05$). With the exception of E in the upper area ($\chi^2 = 19.36$), chi-square tests of observed vs. expected frequencies in offspring of both areas were also consistent with Hardy-Weinberg (all $P > 0.05$). A heterogeneity chi-square of adults at both the E and PGD loci demonstrated no significant difference between the two study populations in adult allele frequencies.

PARENTAGE ANALYSIS

Of 52 nestlings sampled, 10 had genotypes inconsistent with one or both putative parents (Table 3). Five of 17 broods sampled at the serum cholinesterase locus showed evidence of genotype mismatch (13% of nestlings sampled). Five of 13 clutches sampled at the PGD locus showed evidence of genotype mismatch (14.7% of nestlings sampled). The electrophoretic evidence suggests that in at least two instances (pair 1 and pair 9) the putative female parent could be ex-

TABLE 3. Electrophoretic phenotypes of all putative parents (males—M, females—F), and their offspring (listed below parents) at the serum cholinesterase (E) and phosphogluconate dehydrogenase (PGD) loci. Offspring were underlined where inconsistencies were detected. The parent(s) whose genotype was not consistent with that of the nonkin offspring is listed. — refers to individuals whose genotype could not be reliably scored.

Pair number	Sex	Color band	Clutch number	E	PGD	Possible excluded parent
Upper area 1986						
1	M	BW		AB	AB	
	F	PG		BB	AE	
			1	BB, BB, BB, BB	BE, BE, AB, AB	
			2	BB, BB, BB, <u>BC</u>	AE, AA, AB, —	either
		3	AB, BB, BB	AA, AA, <u>BB</u>	female	
		4	AB, AB	AA, <u>BB</u>	female	
2	M	WP		BD	AB	
	F	no data				
			1	CD, BB, BC, BB	BB, BB, BB, AB	
			2	<u>CC, CC, CC</u> , BB	AB, AA, AB, BB	male/both
3	M	GG		CC	AA	
	F	OO		BC	—	
				CC, BC, CC, BC	AB, —, AA, AB	
4	M	OG		BB	AB	
	F	GW		CD	AA	
				BC, BD, BC, BC	—, —, —, —	
5	M	OY		BB	AA	
	F	WY		BC	AA	
				BC, BC	AA, AA	
6	M	YY		AB	—	
	F	no data				
				AB, AC, AB, <u>CC</u>	—, —, —, —	male/both
Lower area 1986						
7	M	PG		BD	AA	
	F	WW		BE	AE	
				BB, DE, BB	AA, AE, AA	
8	M	GB		BD	AA	
	F	YG		AB	AA	
				BB	—	
9	M	PO		AD	AA	
	F	BB		BB	AA	
			1	AB, <u>BB</u>	AA, <u>BB</u>	male/both
			2	BD, <u>BD</u>	<u>BB</u> , <u>AA</u>	both
10	M	no data				
	F	GP		BD	AB	
				DD, BC, DD	AB, —, —	
11	M	PB		AD	AA	
	F	GP		BD	AB	
				<u>BB</u> , AB	<u>BB</u> , —	male
12	M	BY		BD	BD	
	F	no data				
				AB, AD, BD, AB	—, —, —, —	

cluded as the actual genetic parent. Data from pairs 2, 6, and 11 suggest situations in which the male parent can be excluded from paternal consideration. Genotypes from clutch 2 of pair 1 suggested that either parent could be excluded. Two cases were observed where both sexes could be excluded from parentage (pair 9, clutches 1 and 2), and represent instances of egg dumping.

DISCUSSION

The analysis of paternity in this population suggests that a species, previously defined as monogamous, may be practicing a mixed reproductive strategy. Extra-pair copulations have been reported in an increasing number of socially monogamous species (Gladstone 1979, Ford 1983, McKinney et al. 1984). The majority of studies have used observations of copulations (Mineau and Cooke 1979, Fujioka and Yamagishi 1981, Werschkul 1982, Roskaff 1983) and mate guarding (Beecher and Beecher 1979, Power et al. 1981, Frederick 1987) to infer that EPCs with paired females have been successful. However, behavioral observations are not necessarily indicative of the occurrence of EPCs or of their actual frequency of success (Gowaty 1985; Westneat 1987a, 1987b). Similarly, intraspecific parasitism or quasi-parasitism may either not be detected through observation, or may be underestimated (Wrege and Emlen 1987).

Electrophoretic analysis, on the other hand, indicated that both male and female Field Sparrows practice a mixed reproductive strategy. Our mismatch data show one nestling with an ambiguous exclusion (i.e., one allele in the nestling could not be explained by reference to either allele in either putative parent); two nestlings that unambiguously excluded the putative mother; two nestlings that unambiguously excluded the putative father; two nestlings that unambiguously excluded both putative parents. At a minimum estimate, two females cared for one or more nestlings that were not her own; one pair raised a nestling that was not their own in two separate broods; and at least four males cared for unrelated offspring. In the last case, however, we lacked the genotype of the putative mother and therefore the social pathway to exclusion (either EPC or CNP) remains ambiguous. While our data show evidence for EPC, the weight of the observations suggests CNP (P. Gowaty, pers. comm.). We found that approximately 18% of the young surveyed were excluded from one or both putative parents. This figure is similar to

that found for Indigo Buntings (*Passerina cyanea*, 14.4%; Westneat 1987b) and White-crowned Sparrows (*Zonotrichia leucophrys*, 14%; Sherman and Morton 1988).

Conspecific nest parasitism may be a nesting behavior employed by unmated, young females, females which had recently lost their nest, and mated females which are presently laying eggs in their own nest (Yom-Tov 1980). Furthermore, the rate of CNP may be determined by limited availability of nest sites and high rates of nest predation. In the Field Sparrow, nest predation rates can be high. Females whose partial clutches had been depredated might attempt to lay their remaining eggs in other nests. Observations of the nesting phenology of our population of Field Sparrows indicate nesting asynchrony (Petter, unpubl. data). Nests within each locality were in various stages of development. In addition, the stability of the territories throughout the breeding season suggests that nest sites are limiting (Petter et al., unpubl.). It should be expected that older females, because of their experience, would be less likely to lose a nest to predators, hence need not exploit a CNP reproductive habit.

Among passerines, the detection of offspring with electrophoretic phenotypes inconsistent with the putative mother, yet compatible with the putative father, has been observed in Eastern Bluebirds (*Sialia sialis*, Gowaty and Karlin 1984) and White-fronted Bee-Eaters (*Merops bullockoides*, Wrege and Emlen 1987). Gowaty and Karlin (1984) were unable to directly discern if paternity was attributable to the resident male or some other male. Consequently, no conclusions could be drawn concerning the mode of parasitism (i.e., egg dumping or quasi-parasitism). In passerines, evidence indicates that female EPCs may be a common occurrence among paired breeding females (Gowaty and Karlin 1984; Moller 1985; Westneat 1987a, 1987b; Wrege and Emlen 1987; this study). However, the observation of multiple paternity is not sufficient evidence that females are opting to practice a mixed reproductive strategy.

A correlate of male EPCs is asynchronous breeding (Emlen and Oring 1977, Westneat 1987a). Asynchronous breeding provides more opportunities for EPCs, since fertile females would be present for a longer time period. Field Sparrows are a multiple-brooded asynchronous breeding species. Consequently, fertile females should be present throughout the breeding season. Additionally, nesting losses due to predation

are often very high in this species (>75%; Best 1977a; this study), creating an increased rate of female availability.

The degree of male parental assistance required, particularly during incubation, may be a major factor in determining the manner in which males acquire additional mates (Ford 1983) (i.e., polygyny of EPCs). In the Field Sparrow, incubation is by females alone. Although males occasionally feed the female on the nest (Best 1974a), his contributions during the incubation period are not substantial. Females incubate for approximately 11 days, during which time the male is essentially free to pursue EPCs. Once incubation begins, the female is no longer fertile (Brown 1967). Consequently, the male need not remain close by to protect his gametic investment from other males. In order for a male to practice a mixed reproductive strategy, he needs first to have the opportunity to copulate with additional females, but must also have confidence of paternity in the offspring in his own nest (Trivers 1972). Therefore, males pursuing EPCs should be adapted to do so while their mates are incubating (Westneat 1988, Westneat et al. 1987). In this study, the one instance of an observed EPC occurred while the female was incubating (Petter, pers. observ.).

Male Field Sparrows provide parental care at a rate approximately equal to that of females (Best 1977b), indicating that male reproductive success is enhanced through parental contributions. If male contributions are indispensable, it might be less advantageous for males to attempt to acquire additional mates which they would assist in caring for young, than to seek EPCs. In this way, the male would reap the benefits of increased reproductive success, without the responsibility (or cost) of additional parental duties.

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