

Extra-pair paternity in Seaside Sparrows

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ABSTRACT. Seaside Sparrows (*Ammodramus maritimus*) nest at varying population densities, and breeding pairs may occupy either large, all-purpose activity spaces or small nesting territories, foraging in undefended areas separate from the nest site. We determined the prevalence of extra-pair paternity in a large, socially monogamous population of Seaside Sparrows nesting in small, overlapping territories. We used six microsatellite DNA markers and a likelihood-based approach to paternity assignment. Five of 47 chicks (11%) in three of 18 broods (17%) in this population were sired by extra-pair males. Although this is the first study of the genetic mating system in the genus *Ammodramus*, the rate of extra-pair paternity we observed is lower than in most other New World emberizines. As the first measurement of extra-pair paternity in Seaside Sparrows, this study provides a baseline for comparative studies of how extra-pair paternity is influenced by the wide variation in nesting density and territoriality found in Seaside Sparrows. These results, from a socially monogamous sparrow may also provide a context for studies of unusual mating systems in other salt-marsh nesting birds.

SINOPSIS. Extra-paternidad en *Ammodramus maritimus*

El gorrion litoral (*Ammodramus maritimus*) anida en una amplia variedad de densidad poblacional, y las parejas pueden ocupar, ya sea amplios espacios para todo uso o territorios pequeños para anidar, en donde el forrajeo se lleva a cabo en áreas separadas en donde no se defiende el territorio. Determinamos la preponderancia de paternidad con individuos que no fueran su pareja, en una población grande y monógama que anidaron en territorios pequeños que solapaban. Utilizamos seis marcadores microsatélites de ADN para determinar la paternidad. Cinco de 47 polluelos (11%) y tres de 18 camadas (17%) de la población tuvieron como padre otro individuo que no formaba parte de la pareja. Aunque este es el primer estudio genético del sistema de apareamiento en el género *Ammodramus*, la tasa de extra-paternidad observada es menor que en la mayoría de los Emberizidos del nuevo mundo. Este estudio, aunque primero en su clase, provee una base comparativa de como la extra-paternidad puede ser influida por la amplia variación en densidad y tipos de territorios encontrados en este gorrion litoral. Los resultados de este trabajo, con una especie considerada monógama, pueden además proveer un nuevo contexto para el estudio de apareamiento poco usual en otras aves que anidan en marjales salados.

Key words: *Ammodramus maritimus*, extra-pair paternity, grouped territory, mating system, microsatellite

Ever since biochemical methods of assessing relatedness in birds became feasible (Gowaty and Karlin 1984; Westneat 1987), it has been apparent that mating systems of birds, especially passerines, are more complex than the prevalence of social monogamy (Lack 1968) would suggest. Some level of extra-pair paternity (EPP) turns out to be the rule rather than the exception in socially monogamous passerines. The prevalence of EPP varies across avian species from 0% to 76% of offspring, with an average across all passerines of about 15% (Griffith et al. 2002). Variation has also been found between different populations of the same species. Variation in EPP has been explained by correlation with breeding synchrony (Stutchbury 1998a, b; Saino et al. 1999; cf.

Weatherhead 1997; Weatherhead and Yezerinac 1998), by correlation with breeding density within species but not across species (Westneat and Sherman 1997), and by correlation with other behavioral, ecological, and genetic factors (Møller and Ninni 1998; Petrie et al. 1998). However, no single coherent explanation has emerged to explain variations in EPP. Although biochemical data on paternity are available for more than 130 avian species (Griffith et al. 2002), data are still unavailable for the other 98% of avian species. Comparative studies gain power from increased taxonomic coverage (Harvey and Pagel 1991) and exploration of a variety of taxa may reveal patterns that are idiosyncratic to (or easy to measure in) particular groups. For example, much of the convincing evidence for female choice for “good genes” has come from studies of the Paridae (Kempnaers et al. 1992; Otter et al. 1998).

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Sparrows in the genus *Ammodramus* inhabit grasslands and marshes and occur at varying population densities and dispersion patterns. Social mating systems range in the genus from monogamy with biparental care to scramble-competition polygyny with no paternal care of young and no pair-bond between adults (Post and Greenlaw 1982), yet patterns of fertilization have not been investigated in any member of this genus. Seaside Sparrows (*Ammodramus maritimus*) are socially monogamous. Despite extensive research throughout the range of the species, all pairings in Seaside Sparrows thus far studied have been socially monogamous: 83 at Oak Beach, New York, and 61 at Cedar Keys, Florida (Greenlaw and Post 1985). The New York and Florida studies also documented no natural cases of mate-switching within the breeding season. When males were experimentally removed, adjacent males expanded their territories to include those of the widowed females, but the males did not aid in feeding the young. Nesting density varies greatly within and among populations of Seaside Sparrows. Male activity spaces may vary 10-fold in size [range of territory sizes 212–2374 m² in one population ($N = 27$ territories) and 598–3598 m² in a second population ($N = 14$ territories), Greenlaw and Post 1985]. Some populations can be classified as occupying grouped territories (Lack 1968), in which both sexes occupy small, often overlapping nesting territories, and feed in communal areas some distance from the nest (Post 1974). Resources vary greatly between adjacent territories, and females often leave the males' territories for distant feeding trips (Post and Greenlaw 1994).

High nesting density combined with off-territory feeding would seem to offer female Seaside Sparrows abundant opportunities to copulate with more than one male. The birds most closely related to Seaside Sparrows whose rate of EPP has been measured have upwards of 20% of chicks sired by extra-pair males. If the opportunity provided by frequent off-territory commuting to feeding areas plays a key role in rates of extra-pair copulation, one would predict that Seaside Sparrows would have higher EPP than their close relatives who, like most temperate songbirds, feed primarily on all-purpose breeding territories.

METHODS

Study site and population. We studied behavior and paternity in a resident population of Seaside Sparrows at Penny's Creek, Johns Island, South Carolina (32° 46'N, 79° 59'W). The 10-ha study site is a high (irregularly flooded) salt marsh on the Stono River, 13 km from the Atlantic Ocean. Vegetative cover consists of a mixture of patches of needle-rush (*Juncus roemerianus*, 40% coverage), medium height cord-grass (*Spartina alterniflora*, 30%), salt-grass (*Distichlis spicata*, 10%), and areas of sparse, short vegetation, primarily glasswort (*Salicornia europea*), sea-lavender (*Limonium carolinianum*) and the dwarf form of *Spartina alterniflora* (15%). The marsh is dissected by several heavily eroded narrow dikes (5%), covered by a low growth of marsh-elder (*Iva frutescens*), groundsel-tree (*Baccharis halimifolia*), sea-ox-eye (*Borrichia frutescens*), and red cedar (*Juniperus virginiana*). The study area was marked with numbered stakes placed at 25-m intervals. Markers that protruded above the vegetation were fitted with wire prongs to prevent predators using them as perches (Post 1981).

This population has been studied since 1998. By 2001, 187 adults, constituting at least 95% of the breeding birds, had been mist-netted and fitted with unique combinations of color bands. The site was visited almost daily from mid-April to mid-June each year. The activity spaces of all males were mapped by an observer who moved along the grid lines and recorded the locations of males in relation to the nearest marker. Seaside Sparrows in this area have a modal clutch size of three eggs (Post and Greenlaw 1994). Nests in this population are placed low in marsh vegetation and are difficult to find. Renesting is common after depredation or flooding, and pairs occasionally successfully raise two broods. Nests were found by flushing females or by mapping females' locations on repeated visits. Nests were visited at least every third day. As rice rats (*Oryzomys palustris*) were common, nests that contained eggs or young less than 5 d old were protected with metal baffles (Post and Greenlaw 1989). The population from which the samples were drawn included approximately 60 pairs in both 2000 and 2001 within 8 ha. We obtained blood samples from mother, father, and chicks from approximately 13% of resident pairs in 2000 and

Table 1. Microsatellite primers used to assess paternity in Seaside Sparrows.

Name	Species of origin	Alleles	Power ^a	Reference
As μ 15	<i>Ammodramus savannarum</i>	10	0.62	(Bulgin et al. 2003)
As μ 18	<i>Ammodramus savannarum</i>	15	0.77	(Bulgin et al. 2003)
Esc μ 01	<i>Emberiza schoeniclus</i>	6	0.43	(Hanotte et al. 1994)
Esc μ 06	<i>Emberiza schoeniclus</i>	12	0.71	(Hanotte et al. 1994)
GF05	<i>Geospiza fortis</i>	7	0.36	(Petren 1998)
GF12	<i>Geospiza fortis</i>	5	0.35	(Petren 1998)

^a Power in this population to exclude a random non-related male as father when mother's genotype is known (Weir 1996).

25% in 2001. Sample sizes were small because many nests were lost to floods and predators. Fifteen nests were found in 2000, but only seven broods were available for sampling. In 2001, 37 nests were found, 15 were available, and 14 sampled.

Sample collection. Between January 2000 and August 2001, adult sparrows were mist-netted, bled (40 μ l by brachial venipuncture), and released. In the summers of 2000 and 2001, we obtained 40 μ l blood by brachial venipuncture from 55 chicks (at approximately 7 d of age) from 21 nests. Samples were preserved in lysis buffer (0.1 M Tris, 0.1 M EDTA, 0.01 M NaCl, 0.5% SDS, pH 8.0), and stored at 4°C. For three nests, we were unable to obtain a blood sample from the father, leaving a total of 18 nests (47 chicks) for which the entire family was bled. Parents were assigned to nests by observing which birds delivered food to nestlings (both male and female Seaside Sparrows provision the young). At each nest at least two independent observers verified the parents' identity. When we were not able to determine the parents' identity from a distance, we erected a blind 10–12 m from the nest and continued watching until the identity of both parents had been confirmed.

Genotyping. We purified DNA from the blood-buffer mixture by a standard phenol-chloroform protocol (Sambrook et al. 1989). The DNA was ethanol precipitated and dried, then resuspended in TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 7.0). We confirmed the presence of DNA of high molecular weight in all samples by agarose electrophoresis, and standardized DNA concentration at 17 ng/ μ l. We amplified alleles from six polymorphic microsatellite loci (Table 1). Given complete genotypes of mother, chick, and putative father,

we calculated the combined paternity exclusion power (Weir 1996) of these six loci in our population as 0.9938. PCR was carried out with dye-labeled primers in 10 μ l volumes containing 50 ng DNA, 2 pmol each primer, 0.2 mM each dNTP, 0.3 units of *Taq* DNA polymerase and 50 mM KCl, 10 mM Tris-HCl (pH 9.0) and 0.1% Triton X-100. MgCl₂ was added to a concentration of 2.5 mM when amplifying each locus except for Esc μ 06 (3.0 mM) and GF05 (2.0 mM). Thermal cycling consisted of 35 cycles (Esc μ 01, As μ 15, As μ 18, GF05) or 32 cycles (Esc μ 06, GF12) of 1 min at 94°C, 1 min at 48°C, and 1 min at 72°C. Each PCR was concluded with a 40-min hold at 72°C. Products were electrophoresed through an ABI 310 genetic analyzer (Applied Biosystems, Inc., Foster City, CA.). Alleles were sized by comparison to concurrently run dye-labeled DNA size standards. Repeated runs of the same bird demonstrated that allele sizing was consistent within \pm 0.8 base pairs. We defined "bins" corresponding to the normal size range of each allele, and used Genescan and Genotyper software (Applied Biosystems) to assign newly sized alleles to those bins. Automated allele calls were confirmed by visual inspection of electropherograms.

Analysis. We used GENEPOP software (Raymond and Rousset 1995) to check that loci were in Hardy-Weinberg equilibrium, using option 1, suboptions 1 and 2, Hardy-Weinberg exact tests for heterozygote deficiency and heterozygote excess. Genotyping in a project this size is seldom 100% accurate. We estimated genotype error rate by comparing chick genotypes with maternal genotypes. We used the computer program CERVUS (Marshall et al. 1998) to check paternity. CERVUS uses information from co-dominant genetic loci such as micro-

satellites to assign paternity, but unlike a strict exclusion criterion, where only adults that match the offspring at every locus are considered true genetic parents, CERVUS allows for the possibility of incomplete genotypes for some individuals, genotyping errors, mutations and null alleles, and evaluates the relative likelihood of a hypothesized parent being the true genetic parent given the available data. CERVUS calculates an LOD score for each candidate parent. The LOD score is the natural logarithm of the ratio between the likelihood of the candidate male being the true father and the likelihood of a randomly selected male from the population being the true father. Positive values of the LOD score imply that the candidate is more likely to be the father than a randomly picked male, and negative values imply that the candidate is less likely to be the father than a randomly picked male. Given certain characteristics of the studied population (allele frequencies, number of candidate males, thoroughness and accuracy of genotyping), CERVUS uses a simulation procedure that allows the researcher to pick a criterion (an LOD score) such that paternity assignments can be made with a known degree of confidence. We chose a criterion that allowed 95% confidence in paternity assignments (that is, in the simulation, 95% of males who exceeded that LOD score were the true fathers).

RESULTS

Genotyping was 97.8% complete at the six loci. All loci were in Hardy-Weinberg equilibrium except $As\mu 18$, which showed a significant heterozygote deficiency, apparently due to the presence of null alleles at low frequency (estimated by CERVUS at 0.092). Despite the occasional null alleles, this highly polymorphic locus still added to our power to assign paternity using CERVUS, as the information lost to null alleles in a few cases was more than balanced by the exclusion power of the locus in most cases. Two of 280 comparisons (0.71%) between mothers and chicks were mismatches. These were apparent cases of null alleles or preferential amplification of smaller alleles at one locus ($As\mu 18$). Since not every genotyping error will result in a mother-chick mismatch, we estimated an overall genotyping error rate of 2%.

The LOD score that allowed 95% confi-

dence in paternity was 0.82. Forty-two of 47 chick-father comparisons exceeded this criterion, and in fact, all of those tests gave LOD scores in excess of 1.95, corresponding to a confidence level of 97.8% (Fig. 1). Those 42 chicks were considered to have resulted from within-pair copulations. The remaining five chicks could not be assigned to their putative fathers, and in fact, all had negative LOD scores, meaning that their putative father's genotype made him less likely to be the true father than a randomly selected bird from the population. Those five chicks were considered to have resulted from extra-pair fertilizations (EPFs). The EPF rate in our population was thus 10.6% of all chicks, and the 95% confidence interval for the EPF rate ranged from 4–22% of chicks. Three of 18 broods (16.7%) contained at least one extra-pair chick (one chick of four in one brood, two of three in two others). In 2000, two of 13 chicks (15.4%) were due to EPFs; in 2001, it was three of 34 (8.8%).

When all adult males in our sample were tested against the extra-pair chicks, no male emerged as a likely candidate father (none met even an 80% confidence criterion); we could not determine the true father for any of the EPF chicks. Genetic sampling of adult males at the site was not complete in either 2000 or 2001, and we suspect by analogy with other published studies (e.g., Webster et al. 2001) that the genetic fathers of extra-pair chicks were resident, territorial males that we did not sample.

All extra-pair chicks we observed were part of broods with mixed paternity. No nest contained all extra-pair young, as might be encountered if one male took over another male's territory after laying was complete, and fed the young.

DISCUSSION

This population of Seaside Sparrows appears to have a low incidence of extra-pair paternity. Our point estimate of the proportion of EPF chicks is 11%, less than half as high as estimates for Savannah Sparrows (*Passerculus sandwichensis*) of 23% (Freeman-Gallant 1996), White-crowned Sparrows (*Zonotrichia leucophrys*) of 34–38% (Sherman and Morton 1988), Song Sparrows (*Melospiza melodia*) in two large stud-

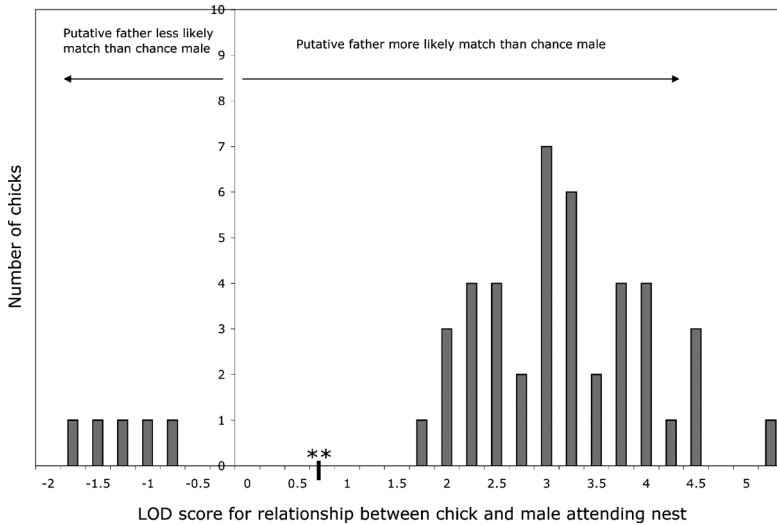


Fig. 1. Frequency histogram showing LOD scores for 47 paternity tests between chicks and putative fathers (the males attending the nests). The bulk of paternity tests resulted in large positive LOD scores, indicating great likelihood that the putative father is the genetic father. LOD scores above 0.82 (marked by “**”) correspond to a >95% confidence that the assigned male is the true father. Negative scores indicate that a randomly chosen male in the population would be a better genetic match than the tested male. The five chicks represented by bars on the left are presumed to be extra-pair young.

ies of about 24% (L. F. Keller, pers. comm.; Hill 1999), and Dark-eyed Juncos (*Junco hyemalis*) of 28% (Ketterson et al. 1998). Another study of Song Sparrows measured an EPF rate of 10.5% (Major and Barber 2004), but the authors used a conservative criterion for excluding social fathers (mismatch at two of three microsatellite loci) and acknowledge that the resulting estimate of EPF may be conservative. Savannah Sparrows are sister taxa to, or possibly should be within, the genus *Ammodramus* (Avisé et al. 1980; Carson and Spicer 2003), and are the closest relatives to Seaside Sparrows for which EPF rates are known. Those are all the New World emberizines for which we have been able to find EPF rates measured by biochemical means. In more distant emberizines such as Old World buntings, rates have been found ranging from 4 to 55% of chicks (Dixon et al. 1994; Hanotte et al. 1994). The 95% confidence interval for our estimate of Seaside Sparrow EPF rate is 4–22%. None of the earlier studies included confidence intervals for their estimates, but it is noteworthy that all but one of the earlier point estimates for New World emberizines fall outside the 95% C.I. for the Seaside Sparrow.

What might keep EPF rates low in Seaside Sparrows? Westneat and Stewart (2003) argue that the most promise for advancing our understanding of the causes of variation in EPP will come not from correlative studies of ecological variables like nesting density, but from close examination of the behavioral interactions between females, paired males, and extra-pair males (Westneat and Stewart 2003). In an intensive study of nesting Seaside Sparrows, female-female aggression was not evident, and males did not appear to guard their mates. Both females and males, however, are aggressive toward conspecific intruders that approach their nest sites, and use specific vocalizations to alert their mates to the presence of intruders of both sexes (Post and Greenlaw 1975). Social monogamy in Seaside Sparrows appears to be maintained by female choice of bachelor males rather than female-female aggression (Greenlaw and Post 1985), and mechanisms of female choice that maintain social monogamy may also encourage females to reject extra-pair advances from neighboring males. In species such as the Seaside Sparrow, where both members of the pair need to cooperate in raising the young, the costs of extra-pair copulations for females may

also outweigh the benefits (Birkhead and Moller 1996). In highly variable habitats such as salt marshes, male aid may be dispensable in some years (Greenlaw and Post 1985), but monogamy may be advantageous for both sexes in the long term.

Mating patterns in Seaside Sparrows are of particular interest because wide variation in nesting density and territorial behavior (Post et al. 1983; Post and Greenlaw 1994) allows for intraspecific tests of the effects of density and territory type on mating patterns. In this study population, males defended small, overlapping nesting territories (\bar{x} 564m²; range, 275–1200m²; $N = 40$). The study population may be classified as occupying grouped territories (Lack 1968) as did another population studied in New York (Post 1974). Both sexes foraged alone, off the nesting territory. Comparison with populations where each resides on a larger, exclusive all-purpose territory (Werner and Woolfenden 1983) might be instructive.

Seaside Sparrows may be ideal subjects for studies of the effects of genetic variation on EPP. Seaside Sparrows, as tidal-marsh nesters, are confined to small, discontinuous patches of habitat across most of their range (Kale 1983; Robbins 1983). Most populations are nonmigratory (Robbins 1983) and in an intensively studied nonmigratory population, extensive banding efforts have documented only limited movement even within an estuary (W. Post, unpubl. data). Although no data on genetic diversity in Seaside Sparrow populations have been published, birds in small, localized populations occupying restricted habitats can show reduced genetic diversity, as has been documented in one population of another marsh-nesting sparrow, *Ammodramus nelsoni* (Seutin and Simon 1988). Future comparisons between populations from different sized habitat islands might allow powerful intraspecific tests of predictions about the effect of genetic variation on EPP rates (Petrie and Kempenaers 1998).

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