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Low Extrapair Paternity in the Cactus Finch (*Geospiza scandens*)

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Several investigations of Darwin's finches have relied upon observations of adults at the nest for identifying parents. These include estimations of heritable variation and covariation (Grant and Grant 1989, 1994), lifetime reproductive success and genetically effective population sizes (Grant and Grant 1992), and the evolutionary response to selection (Grant and Grant 1995). Studies of other emberizids and cardinalids (related sparrows, finches, and buntings) in the temperate zone have shown that simply observing adults at the nest is not sufficient to be sure of correctly identifying biological parents (Westneat and Webster 1994). Extrapair copulations sometimes result in fertilizations and the rearing of nonpaternal offspring. To determine whether this occurs in Darwin's finches, we undertook a study of microsatellite DNA variation in a socially monogamous, multibrooded species, the Cactus Finch (*Geospiza scandens*), on the Galapagos island of Daphne Major (0°15'S, 90°13'W). The frequency of polygyny has never exceeded 5% in this population (see Boag and Grant 1984, Gibbs and Grant 1987, Grant and Grant 1996 for breeding characteristics and population data).

Methods.—Blood samples were taken from 248 birds in 1988 to 1996. A single drop of blood was taken by brachial vein puncture from nestlings at day 8 and from adults captured in mist nets. Nearly all males on the island throughout the study period were sampled. The largest number of potential breeders was present in 1993 (68 males and 27 females), when 90% of the males and 93% of the females were sampled.

Prior to puncture with a 30.5-gauge hypodermic needle, the area was cleaned with alcohol, and a drop of 0.5M EDTA was placed over the vein. Blood was transferred to EDTA-soaked filter paper, air dried, and stored in drierite at ambient (field) temperatures before being transferred to the laboratory and stored at −80°C.

Eight microsatellite loci developed in the Medium Ground-Finch (*Geospiza fortis*) were used to test parentage in *G. scandens.* Laboratory techniques used for genomic library screening and genetic screening of individual birds generally followed those of Primmer et al. (1995). Detailed methods and primer sequences are available elsewhere (Petren 1998). Measures of variation at these eight loci and exclusion probabilities are given in Table 1. We found no evidence of "null" alleles (Callen et al. 1993) in the pedigree.

Results and discussion.—All 159 offspring had one allele in common with the maternal parent (with the exception of the Z-linked locus). Therefore, mater-

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TABLE 1. The eight microsatellite loci developed in *Geospiza fortis* (Petren 1998) and used to test parentage in *G. scandens*.

Locus	Motif	Alleles (*n*)	H_o[a]	P_I[b]	P_D[c]
Gf1	$(AC)_{23}$	8	0.71	0.08	0.49
Gf2[d]	$(AC)_{11}$	4	0.38	0.11	0.42
Gf3	$(AG)_{17}$	7	0.67	0.09	0.48
Gf5	$(AC)_{14}$	7	0.73	0.10	0.45
Gf7	$(AC)_{22}$	8	0.84	0.06	0.54
Gf8	$(AC)_{21}$	9	0.84	0.04	0.62
Gf11	$(AC)_{28}$	12	0.78	0.03	0.64
Gf16	$(AC)_{15}$	9	0.87	0.02	0.70
Combined				$<2 \times 10^{-10}$	>0.99

[a] Observed heterozygosity.

[b] Probability of identical genotypes for two randomly selected individuals, calculated from observed allele frequencies.

[c] Probability of detection (Westneat 1987).

[d] Z-linked locus. All known females were scored as homozygous and received a single copy inherited paternally.

nity apparently was correctly identified by observation of behavior in all cases, and intraspecific brood parasitism (i.e. egg dumping) was not detected. Twelve of the offspring (8%) in 10 nests had alleles that could not be matched with their assigned (i.e. apparent or social) fathers. Extrapair young occurred in 15% of 66 clutches and 26% of 34 families. None resulted from a change in social breeding partner. Altogether, 7 mothers and 10 apparent fathers were involved, and no obvious pattern existed with regard to the year of breeding. In one case, two nestlings in the same brood had different extrapair fathers. The extrapair fertilization (EPF) frequency (8%) was similar to the observed extrapair copulation frequency (10%; 1 out of a total of 10 recorded).

Some females are more likely to engage in extrapair copulations than others. Two females produced more than half of the extrapair young; one of them produced four while paired successively with two males, and another produced three, also while paired successively with two males. Normal brood sizes are two to four (Boag and Grant 1984, Gibbs and Grant 1987). The age of the female (2 to 10 years) and past breeding experience (0 to 16 broods) were not obvious predisposing factors. Although none of the seven females had previously bred with the true fathers of extrapair young, two subsequently paired and bred with them, but while doing so each engaged in extrapair copulations with other males (see Wetton et al. [1995] for a comparable situation in House Sparrows [*Passer domesticus*]). One female that mated outside the pair bond was the daughter of another female that did so. Female variation in propensity to mate outside the pair bond may be heritable, or may simply reflect opportunistic behavior.

Nine of the 11 extrapair fathers were identified as having a genotype that matched those of the extrapair young. The probability that a random male could provide a match for the two or more "missing" parental alleles (taking into account the mother's genotype) ranged from 7×10^{-5} to 2×10^{-8}. Given the relatively small population size, it is unlikely that true fathers were misidentified.

Extrapair copulations have been interpreted as the result of females seeking males of higher quality than their social mates (see Kempenaers et al. 1997). It might be expected that females are most likely to engage in extrapair copulations: (1) with neighbors; (2) that these neighbors are breeding, if the female's choice of mates is based on an assessment of male quality; and (3) that the females are paired with young and inexperienced males and the neighboring males are older (see Westneat 1987, Westneat and Webster 1994, Kempenaers et al. 1997). Even though we identified most of the true extrapair fathers, the low number of extrapair fertilization events reduces our statistical power to rigorously test these hypotheses; nevertheless, a categorical examination of the data is informative.

The first expectation was realized with regard to *G. scandens*; seven of the nine identified extrapair fathers were neighbors, i.e. holders of contiguously adjacent territories. The other two fathers held territories that were about 200 and 325 m away, corresponding to approximately four and six territory widths, respectively (the maximum possible distance is <700 m). The second expectation was not realized; only one of the true (i.e. extrapair) fathers was breeding (eggs in the nest) at the time the extrapair copulation took place. Two others were paired and bred at the time of the next brood, one paired and bred two broods later, and the other five remained unpaired. The third expectation also was not realized; true fathers were younger than apparent fathers in seven instances, older in two, and the same age in one. The number of previous nests of the apparent father (0 to 21; median 6.5) actually was higher than the number of previous nests of the true father (0 to 12; median 5.5).

Plumage maturation is delayed in this species (Grant 1990), but plumage category was not a factor in extrapair paternity; all apparent and true fathers were in fully mature black plumage. Nor did size appear to be a factor, because the true father was equally likely to be lighter (*n* = 4) or heavier (*n* = 5) in body mass than the apparent father.

Thus, young males are not especially prone to being cuckolded, but the true fathers of extrapair young in the nest are most likely to be neighbors, especially if they are not breeding at the time. The pattern of occurrence of extrapair fertilizations is consistent with the view of Reyer et al. (1997) that a strong stochastic element exists in when and where opportunities for extrapair matings occur.

Depending on its frequency, misidentified parentage could seriously affect the interpretation of sev-

TABLE 2. Estimated frequency of extrapair fertilizations (EPF) in *Geospiza scandens* and related species of emberizids and cardinalids.

Species	English name	% EPF	Reference
Emberiza schoeniclus	Reed Bunting	55	Dixon et al. 1994
Zonotrichia leucophrys	White-crowned Sparrow	38	Sherman and Morton 1988
Emberiza citrinella	Yellowhammer	37	Sundberg and Dixon 1996
Passerina cyanea	Indigo Bunting	35	Westneat 1990
Calcarinus pictus	Smith's Longspur	33	Briskie 1993
Passerculus sandwichensis	Savannah Sparrow	23	Freeman-Gallant 1996
Spizella pusilla	Field Sparrow	19	Petter et al. 1990
Calcarius ornatus	Chestnut-collared Longspur	18	Hill and Gould 1997
Zonotrichia albicollis	White-throated Sparrow	17	Falls and Kopachena 1994
Melospiza melodia	Song Sparrow	15	Keller 1996
Geospiza scandens	Cactus Finch	8	This study
Miliaria calandra	Corn Bunting	5	Hartley et al. 1993

eral behavioral, ecological, and genetical attributes of birds (McDonald and Potts 1997). In the present context, we consider two: (1) calculations of heritable variation (Grant and Grant 1994), and (2) the genetically effective population size (Grant and Grant 1992) of *G. scandens* on Daphne Major. Direct recalculation of previous estimates is not possible because few birds were included in both studies.

Our previously reported heritability estimates are not likely to be seriously affected by an EPF rate of 8%. Inaccuracies due to misidentified mothers should be negligible (assuming low maternal effects; but see Hasselquist et al. 1995), and inaccuracies attributed to misidentified fathers will be diluted because comparisons are made between the father and all young in the nest. Offspring-father regressions were compared with offspring-mother regressions for families of *G. scandens*, excluding known hybrids and backcrosses (Grant and Grant 1994). Heritabilities from offspring-father regressions (0.338 to 0.840 for the six traits, $n = 108$ families) averaged 0.560, which is a few percent lower than the average (0.618) for the offspring-mother heritabilities (0.394 to 0.864; $n = 100$ families). The sympatric congener on Daphne Major, *G. fortis*, also needs to be investigated because differences between offspring-father and offspring-mother heritabilities are larger than in *G. scandens* in some years (Grant and Grant 1999).

The genetically effective population size of *G. scandens* on Daphne Major was estimated by determining lifetime reproductive success of members of the 1978 cohort (Grant and Grant 1992). The estimate is strongly affected by the variance in progeny production (Grant and Grant 1992); however, the lack of a strong trend in extrapair fertilization with male age argues against a serious distortion in our estimate of progeny variance, as does the fact that cuckolds are cuckolded. In two other studies of passerines where extrapair paternity frequencies are comparable to our values, 8 and 11%, respectively, of the estimated effect of misidentifying paternity on calculations of genetically effective sizes was to inflate the sizes by just one individual in each case, or less than 4% (Waite and Parker 1997).

The estimate of 8% extrapair paternity for *G. scandens*, a tropical species, is among the lowest for related emberizids and cardinalids from the temperate zone (Table 2). The only species with a lower frequency, the Corn Bunting (*Miliaria calandra*), is also the only species that frequently is polygynous (Hartley et al. 1993). All tested species show some evidence of extrapair young, and the range of variation in frequency is extremely large, almost as large as the known variation among songbirds in general (see Stutchbury and Morton 1995). Such variation could be useful for identifying the factors that govern extrapair behavior, and for rejecting others (Petrie and Kempenaers 1998). Attempts to do this are presently hindered by a lack of estimates for some species of possibly relevant variables such as breeding habitat structure, sex ratio, age at first reproduction, longevity of breeders, degree of polygyny, male parental investment, and breeding density (e.g. Westneat and Sherman 1997), and by the absence of a reconstructed phylogeny of the group that would enable comparisons to be confined to independent lineages.

Studies of single species have been used to interpret variation among species in two contrasting ways. Stutchbury and Morton (1995) suggested that variation among songbirds in EPF rate can be explained in terms of breeding synchrony, which is under female control. By breeding synchronously, females are best able to compare potential mates and choose among them, and the result is a high frequency of EPF (Stutchbury and Neudorf 1997). This is viewed as being analogous to a lek system in which females can choose among spatially concentrated males. There is statistical evidence for a positive association between degree of synchrony and extent of EPFs across a broad range of passerine taxa (Stutchbury and Morton 1995). Moreover, the relatively less-synchronized tropical species are expected to have lower frequencies of EPFs, but within the tropics, the more synchronized breeders have higher frequencies of EPFs (e.g. Stutchbury et al. 1998). Sample sizes are small, however. Our data from a tropical finch species could be claimed to support this hypothesis in that EPF frequency is low. However, most of the few instances of EPF involved asynchronously breeding or unpaired birds. Moreover, a difficulty with the argument is that females do not have to be breeding synchronously to be able to compare males; rather, males have to be ready to mate.

A contrasting hypothesis emphasizes the inability of a male to simultaneously guard a mate and attract others (Sherman and Morton 1988, Birkhead and Møller 1992) and the inability of a female to simultaneously seek extrapair matings off territory and repel invading females on territory. For either sex, any factor promoting within-pair behavior reduces the opportunity for between-pair behavior, and vice versa. The potential for females to exercise extrapair mate choice is present, but its expression is influenced by the behavior of the breeding partner. It has been suggested that longer prebreeding association of mates and greater synchrony in breeding (Grant and Grant 1989) will lead to males attending to their mates more closely and to females seeking extrapair copulations less frequently. Some observations are consistent with the hypothesis. Migratory species tend to have high frequencies of extrapair young, and the two nonmigratory island species that have been studied (Song Sparrow [*Melospiza melodia*], and Cactus Finch) have the lowest frequencies of extrapair young among the monogamous species (Table 2). An association between extrapair fertilizations and asynchronous breeding has been suspected or observed in other species (Grant and Grant 1989, Petter et al. 1990, Westneat 1990, Reyer et al. 1997, Conrad et al. 1998).

Given the host of ecological and behavioral factors that potentially could influence the frequency of EPFs, as well as the ever-present role of chance, it would be surprising if any single factor could explain a large fraction of the observed variation in EPFs, either within or between species (Birkhead and Møller 1992, Parker and Burley 1997, Petrie and Kempenaers 1998). Explaining the frequency of EPFs, and why only certain individuals are involved, will contribute to our understanding of sexual selection (Petrie and Kempenaers 1998) and the evolution of mating systems.

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