Supporting Information

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SI Methods

Sampling. When fully grown at age 60 d or older, finches were captured in mist nets placed in all habitats and measured (1). From 1988 onward, a small drop of blood was obtained from the brachial vein of 8-d-old chicks in the nest and adults captured in mist nets. Microsatellite data were used to identify the paternity of offspring in the nests of members of the 1987 cohort. Here we report analyses of paternity of all offspring of known parents (regardless of cohort membership) hatched in 1987, 1991, and 1998 and offspring from the first two broods in only 1992, 1993, and 1995. There was little or no breeding in the remaining dry years between the first and last of these. The percentages of extrapair fathers of *G. fortis* that could be identified unambiguously by microsatellite matching are 56.5 in 1987 ($n = 46$), 73.1 in 1991 ($n = 108$), 67.7 in 1992 ($n = 15$), 74.2 in 1993 and 1995 ($n = 31$), and 34.8 in 1998 ($n = 23$). Others could not be identified because not all males were genotyped.

We compared the ages of extrapair mates and social mates, and assessed spatial variation in the incidence of EPY in nests and fitness consequences of EPM. Individual females were entered into each analysis only once.

We estimated the random expectation in a given year of a female mating outside the pair bond with a male older, younger, or the same age as the social mate from the frequencies of nesting males of each age (1–12 y) in the population at that time. There are no floating males without territories in the study species. We combined and averaged the age-specific probabilities in the 6 years. For each age of the social mate, and for both *G. fortis* ($n = 97$) and *G. scandens* ($n = 15$), we compared the median expected age of extrapair males with the median observed age of the extrapair males. Where *G. fortis* females mated with two extrapair males ($n = 9$), both males were entered into the analysis. The extrapair males differed in age in four cases. There are gaps in the *G. scandens* data; for example, there are no data for ages 2, 3, 6–9, and 11 y, owing to small sample sizes and drought years of no breeding.

To examine spatial patterns of variation in the incidence of EPY in nests, we entered nest locations on a scaled map of the island, divided into 20 sectors for convenience (2). Observations of courtship, copulations, and nesting behavior were made at all locations on the island on an opportunistic basis in all years and during systematic monitoring of nests in 1987 and 1991. There were 161 nest watches of 45- to 65-min duration involving 51 pairs of *G. fortis* in 1987 and a comparable number of nest watches of both species, but of variable duration, in 1991.

We assessed fitness consequences of EPM in males by comparing gains from EPM with losses from cuckoldry at each age. Data for all years were combined. At the population level, gains equaled losses, subject to sampling variation. Losses were known precisely from focal nests, but gains were estimated from incomplete nest data (except in 1991). The discrepancies were approximately one-third of *G. fortis* gains and approximately one-half of *G. scandens* gains. Therefore, assuming that the distribution of unknown gains across male age groups was exactly the same as the distribution of known gains, we made an adjustment to the gain column by adding ≈50% to each entry in the gain column of *G. fortis* and doubling the *G. scandens* values so as to equalize the totals of gains and losses for each species.

It is possible that our samples of genotyped individuals were biased in ways that have affected the results. For example, young (or old) birds might have been missed to a disproportionate extent, thereby biasing the comparison of age in social and extrapair males.

The sampling program was comprehensive, and we have been unable to detect any bias. Several factors account for this. First, mist nets were placed widely in locations around the island and operated before and shortly after dawn to capture large numbers of finches. Individuals are capable of traversing the island in a few minutes, and sometimes fly long distances out of their territories. Second, nets capture both young and old birds without any bias known to us. Birds that have been captured before are less likely to be caught than inexperienced birds, but this is not a factor in our sampling. Third, there was no bias in sampling offspring in nests. Blood samples were obtained from all chicks in a nest. Apart from one or two nests that were missed, all nests on the island were found in each year through daily searches, social parents were identified, and blood samples were obtained when chicks were banded.

Most analyses are restricted to *G. fortis*, the most common species, for reasons of sample size. The number of breeding females varied between years (1987–1998) from >45 to 267 for *G. fortis* and from 19 to 38 for *G. scandens* (Table S1). A third species, *G. magnirostris*, also breeds on the island but in low numbers, only 4–28 females in the study period.

Morphology. Adults were weighed and wing, tarsus, and beak length and beak depth and width were measured (2). Principal components derived from six morphological measurements per bird were used to test for nonrandom EPM based on body size, beak size, and beak shape.

Two principal components analyses were performed on the combined sample ($n = 126$) of *G. fortis* breeding females and their social and extrapair mates. Weight (g), tarsus length (mm), and wing length (mm) were entered in the first analysis. The first principal component is interpreted as a measure of body size because the three variables have uniformly high and positive loadings (0.72–0.88). The percent variance explained by the first component is 71.6. Beak length, depth, and width (mm) were entered in the second analysis. The first principal component is interpreted as a measure of beak size (loadings, 0.72–0.88; percent variance explained, 87.8), and the second component (percent variance explained, 8.6) is interpreted as a measure of beak shape, because length has a positive loading (0.48) and depth and width have similar and positive loadings (−0.21 and −0.20, respectively).

SI Results

Morphological Analyses. Social and extrapair mates of *G. fortis* females are compared in Table S2. Component scores were used to test the hypothesis that social and extrapair mates differ in mean morphology. None of the differences in mean scores are significant by paired *t* tests (all $P > 0.1$).

A similar principal components analysis was performed with *G. fortis* females with and without extrapair mates. The mean values are compared in Table S3. The hypothesis that females with extrapair mates differ morphologically from those without extrapair mates was not supported by any of the *t* tests on the three sets of principal components means. Furthermore, measurements of social and extrapair mates were not correlated, nor were there any associations between the female's parents and her mates in those measures, as revealed by multiple regression analyses with mate measurement (within-pair or extrapair) regressed on each of the two parental measurements (all $P > 0.1$). Inspection of the data shows no indication of complementarity in the pattern of measurements, such as females paired with small males having large extrapair mates. With regard to the females,

those with extrapair mates did not differ from those without extrapair mates in any morphological feature (Table S3; all $P > 0.1$, paired t test).

Song Analyses. Experiments on Daphne Major and other islands have demonstrated that ground finches are able to discriminate between their own and a closely related congener on the basis of song in the absence of visual cues (3). We tested the hypothesis of intraspecific mate choice based on song using the four song types recognized in previous studies of *G. fortis* on Daphne Major (4, 5). Males sing a single, structurally simple song type, which they retain for life. Females do not sing. The song types of fathers, social mates, and extrapair mates are known for 50 *G. fortis* females from tape recordings (5). Some 30% of social mates sang the same song type as the father of their female. The null expectation is 26%, which is the sum of the squared frequencies of the different types, scarcely different from the observed 30%. Some 38% of extrapair mates sang the same song type as the father of the female. Although this value deviates more from the null expectation, the deviation is not significant ($P = 0.284$, Fisher's exact probability). There is no evidence that extrapair males are chosen on the basis of the songs that they sing.

Environmental factors: Location, neighbors, and density. Production of extrapair *G. fortis* young is spatially heterogeneous. Most *G. fortis* (73.3%; $n = 75$) nest on the outer slope of the cone-shaped island. Proportionally more of them (63.4%) had at least one EPY in the nest compared with those (33.9%) nesting on the inner slope and plateau ($\chi^2_1 = 5.43$; $P = 0.02$). The analysis is restricted to the 72 females that produced at least six young when paired with the same social mate because the overall frequency of EPY (0.171) is one in six, but an unrestricted analysis gave the same result. Approximately half of the extrapair mates were nearest neighbors, as classified by the lack of intervening territories regardless of distance: 40% for *G. fortis* ($n = 63$) and 57% for *G. scandens* ($n = 14$). For both species, the maximum distance from the focal nest to the territory of the extrapair male exceeded 400 m.

The number of *G. fortis* females with EPY ($n = 30$) increased with local nest density across 16 sectors of the island ($R^2 = 0.623$; $F_{1,14} = 25.75$; $P = 0.001$), whereas the number without EPY ($n = 42$) did not ($R^2 = 0.163$; $F_{1,14} = 3.92$; $P = 0.068$). The slopes of the two simple regressions $b = 0.459 \pm 0.090$ and $b = 0.107 \pm 0.054$ differed significantly ($F_{1,36} = 7.25$; $P = 0.017$, ANCOVA), indicating that the proportion of nests with EPY increased with increasing density. For *G. scandens,* no relationship with local nest density was detected in *G. fortis* females with extrapair mates ($n = 5$; $R^2 = 0.210$; $F_{1,8} = 3.40$; $P = 0.103$).

Gains and losses of male paternity. Social males of both species may lose fitness from cuckoldry throughout life (Fig. S1). To test whether frequencies of gains and losses vary with age, we compared the numbers of females and their social mates that had EPY in the nests with the numbers in their respective categories without EPY at each age. We also compared the number of males that sired EPY and did not sire EPY at each age. We tested the null hypothesis of equal proportions of extrapair parents and social mates across all age groups with data grouped in 2-y categories (1–2, 3–4...11–12 y), with samples of >10 individuals per category. The hypothesis was rejected in all *G. fortis* tests: females, $\chi^2_4 = 20.438$, $P = 0.0004$; social mates, $\chi^2_5 = 12.256$, $P = 0.0314$; extrapair males, $\chi^2_5 = 83.276$, $P < 0.0001$. The null hypothesis was not rejected by any of the *G. scandens* tests: females, $\chi^2_3 = 1.738$, $P = 0.6286$; social mates, $\chi^2_5 = 5.122$, $P = 0.4012$; extrapair males, $\chi^2_4 = 7.779$, $P = 0.1000$.

G. fortis males are most vulnerable to losing paternity through EPM when young (Fig. S1). The gain to a male from EPM might be offset by loss of paternity from EPM of his social mate. Net benefits (gains > losses) are age-related. The probability of a *G. fortis* male gaining paternity from EPM is close to 0 until age 5–

6 y, and gains exceed losses on average only when males reach age 7 or 8 y (Fig. S2). *G. scandens* are different. The probability of gaining paternity is 0 only for the youngest age group of 1- to 2-y-olds, and males obtain a net benefit on average at the next youngest age (3–6 y). Females of both species are least likely to gain EPY at the youngest age (1–2 y) and most likely to gain EPY at 3–4 y.

In contrast to *G. fortis*, a high incidence of EPM of young females with old males was not found in *G. scandens*. Young *G. scandens* males also demonstrated greater success from EPM than old males (Fig. S2). The difference between species is associated with differences in territoriality, feeding ecology, and sex ratio (6). As a result of strong defense of cactus bushes, male *G. scandens* survive better and outnumber females. Most extrapair *G. scandens* males (8 of 10) were unpaired, and half (5) were young (< 6 y), whereas only 7 of 62 extrapair *G. fortis* males lacked social mates, and of these, only 3 were young. The species differ in the proportion of extrapair males that were unpaired ($P = 0.007$, Fisher's exact probability).

Change of social mates within a breeding season. Some females change mates within long breeding seasons and reproduce rapidly by starting a clutch of eggs with a new social male just before or immediately after the fledging of nestlings (2, 7). The previous social male feeds the fledglings. Females that changed social mates within a breeding season were more likely to have EPY than those that did not. In 1987, an El Niño year of extensive rains when as many as five broods were produced by some females, proportionally more *G. fortis* females that changed mates ($n = 11$) had EPY (0.818) than those that did not (0.286; $n = 35$; $P = 0.004$, Fisher's exact test). This difference was repeated in 1991, another El Niño year, when again more *G. fortis* females that changed mates had EPY than those that did not (0.750, $n = 12$ vs. 0.394, $n = 66$; $P = 0.029$, Fisher's exact test). More of the females that changed mates had EPY before the change than afterward, although the difference was not significant ($n = 21$; binomial $P = 0.384$). Female age is not a factor in these analyses; the median age of all groups is 4 y. Moreover, the two groups of females did not differ in terms of any of our morphological or genetic measures. The data for *G. scandens*, three in 1987 and nine in 1991, are too scant to allow meaningful analysis but nonetheless show no indication of a difference comparable to that for *G. fortis*.

Possible benefits of EPM. Davies (8) has suggested that male passerine birds generally compete with each other for mating after securing a territory to breed, and that females compete with each other not for males, but for food resources and nest sites. EPM is a plausible outcome that brings the two competitive functions together. By engaging in EPM, males increase their offspring and females increase their reproductive opportunities.

Male courtship and mate-guarding behavior of socially monogamous Darwin's finches are consistent with the proposed division of competitive functions, as are female–female interactions and occasional visits by females to the nests of others. However, the keys to male reproductive success are obtaining a good territory and living long (9), because most of their young are raised in their territories; EPY are in the minority (Fig. S1). Females compete for social mates at successive breeding attempts as a means of obtaining good nest sites and food resources. In the extended breeding seasons sometimes experienced by Darwin's finches, females gain rewards by reproducing rapidly. A female may start another clutch with a new partner if the social male is feeding fledglings and not ready to breed again (2, 7). If the attempt to repair fails after a few days, she may return to the first partner and breed again with him. In either case, the ensuing clutch of eggs may have mixed paternity. Attempts at repairing are likely to be underestimated, because the failures are rarely observed and recorded. EPY in the nest may be the signature of

those attempts. In this respect, EPM is a reflection of a female keeping her reproductive options open.

This interpretation is supported by our finding that females that changed social mates within a breeding season were more likely to have EPY compared with those that did not do so. Observations of copulations provide additional support. In the years 1987–1998, we recorded five extrapair copulations (*G. fortis* and *G. scandens* combined), compared with 103 within-pair copulations. Females initiated all of these copulations; an additional nine attempts initiated by males all failed. These might have been attempts to form a new pair bond, as they all occurred within 3 m of a new nest. Most (91.7%) within-pair copulations of the two species occurred conspicuously on the bush containing a pair's nest or within 5 m of it ($n = 48$).

A possible reward of EPM for females is the gain of a better social mate, territory, and nest sites. By mating outside the pair bond when the first clutch is initiated, a female might gain the male as a social mate later in the breeding season. However, there was only a single example of this (in *G. fortis*), and only one example of EPM in one year followed by social pairing with the same male in the next year.

Untested Bases of Extrapair Mate Choice. Our original conclusion from a study restricted to social mates (10) that mating is essentially random with respect to morphology and song still stands and is now extended to heterozygosity at microsatellite loci. It is possible that the loci are the wrong ones to use for such investigations, because they are selectively neutral and not linked to salient loci. Alternatively, there really is no choice based on genetic characteristics that females are able to detect.

Extrapair mates could have been unusual in features that we did not measure. For example, some investigators have found that extrapair males are more diverse at MHC loci than the social males (11), implying selective EPM. Others have found that EPY have higher cell-mediated immunity than within-pair sibs (12), also implying selective EPM. Darwin's finches are periodically affected by avipox, and the degree to which they display symptoms might be a factor in females' choice of an extrapair mate. Nevertheless, the incidence of pox on Daphne Major was at or close to 0 in the years of study reported here except in 1983 (13), and no other disease was observed.

EPM may be sought by females as a means of alleviating the deleterious effects of close inbreeding, especially in cooperatively breeding species (14) and very small populations (15). Although close inbreeding does occur in all three species on Daphne Major and carries a fitness cost (16), it is rare, and there is no evidence of an avoidance of breeding with close relatives (17). Given the lack of evidence of deleterious genetic effects when *G. fortis* and *G. scandens* hybridize (18), it is unlikely that conspecific EPM permits females to choose genetically compatible fathers through sperm competition (e.g., ref. 19).

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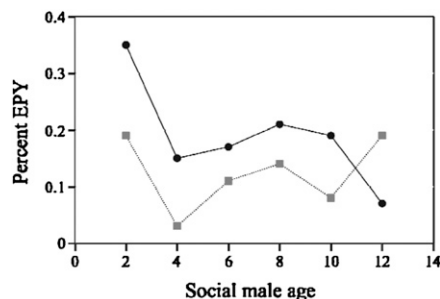
Fig. S1. Proportion of EPY in nests in relation to the age of the social male. Proportions vary similarly with female age. Sample sizes of offspring with respect to increasing age are 46, 576, 238, 215, 93, and 74 for *G. fortis* (black circles) and 16, 71, 97, 64, 73, and 37 for *G. scandens* (gray squares).

Fig. S2. Net benefit of EPM. Gains of fitness to males from EPM as a proportion of total gains plus losses from being cuckolded. Sample sizes with respect to increasing age are 15, 134, 68, 96, 45, and 12 for *G. fortis* (black circles) and 3, 14, 26, 17, 17, and 3 for *G. scandens* (gray squares). Proportions for the youngest and oldest age groups of *G. scandens* are omitted from the figure due to small sample sizes.

Table S1. Numbers of breeding females

Year	*G. fortis*	*G. scandens*	*G. magnirostris*
1987	127 (0.93)	23 (0.96)	4 (0.50)
1991	122 (0.98)	19 (1.00)	5 (0.75)
1992	156 (0.90)	19 (1.00)	10 (0.90)
1993	267 (0.65)	22 (0.86)	9 (0.67)
1995	88 (0.45)	38 (0.66)	13 (0.69)
1998	45+ (<0.29)	38 (0.42)	28 (0.25)

Proportions banded are in parentheses. *G. magnirostris* is included for completeness.

Table S2. Morphological characteristics of social and extrapair mates of *G. fortis* females (*n* = 66)

	Social mates	Extrapair mates
Body size, mean ± SD	−0.096 ± 1.036	−0.263 ± 0.998
Beak size, mean ± SD	0.028 ± 1.125	0.178 ± 1.158
Beak shape, mean ± SD	0.285 ± 0.896	0.401 ± 1.107

Body size is the first component from a principal components analysis of weight and wing and tarsus length. Beak size and shape are the first two components from a principal components analysis of beak length, depth, and width. Beak shape is a measure of pointedness. There are no differences between the groups by paired *t* test (all *P* > 0.1).

Table S3. Morphological characteristics of breeding *G. fortis* females with (*n* = 65) and without (*n* = 82) extrapair mates

	With extrapair mates	Without extrapair mates
Body size, mean ± SD	0.618 ± 0.897	0.703 ± 0.876
Beak size, mean ± SD	0.330 ± 1.024	0.305 ± 1.013
Beak shape, mean ± SD	0.287 ± 0.956	0.171 ± 0.956

Body size is the first component from a principal components analysis of weight and wing and tarsus length. Beak size and shape are the first two components from a principal components analysis of beak length, depth, and width. Beak shape is a measure of pointedness.