



Adult sex ratio influences mate choice in Darwin's finches

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The adult sex ratio (ASR) is an important property of populations. Comparative phylogenetic analyses have shown that unequal sex ratios are associated with the frequency of changing mates, extrapair mating (EPM), mating system and parental care, sex-specific survival, and population dynamics. Comparative demographic analyses are needed to validate the inferences, and to identify the causes and consequences of sex ratio inequalities in changing environments. We tested expected consequences of biased sex ratios in two species of Darwin's finches in the Galápagos, where annual variation in rainfall, food supply, and survival is pronounced. Environmental perturbations cause sex ratios to become strongly male-biased, and when this happens, females have increased opportunities to choose high-quality males. The choice of a mate is influenced by early experience of parental morphology (sexual imprinting), and since morphological traits are highly heritable, mate choice is expressed as a positive correlation between mates. The expected assortative mating was demonstrated when the *Geospiza scandens* population was strongly male-biased, and not present in the contemporary *Geospiza fortis* population with an equal sex ratio. Initial effects of parental imprinting were subsequently overridden by other factors when females changed mates, some repeatedly. Females of both species were more frequently polyandrous in male-biased populations, and fledged more offspring by changing mates. The ASR ratio indirectly affected the frequency of EPM (and hybridization), but this did not lead to social mate choice. The study provides a strong demonstration of how mating patterns change when environmental fluctuations lead to altered sex ratios through differential mortality.

environmental fluctuations | sex bias | mate competition | polyandry | fitness

The adult sex ratio (ASR) is an important property of populations (1, 2). Unlike the primary sex ratio at fertilization and the secondary sex ratio at birth or hatching, the tertiary sex ratio of adults is not under direct parental control. The ASR is therefore subject to social and environmental forces. When those forces result in an unequal sex ratio, the minority sex has greater reproductive opportunities than the majority sex (3, 4). Predictable consequences have been investigated recently by comparative phylogenetic analysis of large numbers of animal species, mainly shorebirds. In agreement with expectations, tests have demonstrated that unequal sex ratios are associated with the frequency of changing mates (divorce) and extrapair mating (EPM; infidelity) (5), sex-specific survival (6, 7), mating system (8, 9), and parental care (7, 10, 11). Species with male-biased populations are more frequently polygamous and have higher indices of EPM than species with female-biased populations, whereas species with female-biased populations exhibit a higher frequency of mate changing than species with male-biased populations (5).

Evolutionary processes that produced differences between species in the past should also be operating within populations at present. Comparative demographic analyses can identify social and environmental factors that currently cause inequalities of ASRs, and quantify mating patterns and fitness consequences (12–15). Such analyses of individuals within populations are

needed to validate inferences of the comparative phylogenetic analyses of populations within species, yet they are rare for two reasons. First, it has been difficult to obtain accurate estimates of male and female numbers, and to pinpoint the time in the life cycle at which sex differential survival originates, even in bird populations, which are the best studied taxonomic group (13, 16–18). Second, research on contemporary populations has been hampered by a relative lack of variation within and between populations of the same species (9). Few populations have been studied long enough to establish whether ASRs are stable through time or whether they change, either gradually and systematically or in a fluctuating manner (7, 13, 17, 19); whether mating patterns also change (20); and what the fitness consequences are for males and for females (12, 14, 15, 21).

Here, we report the results of a 21-y study of Darwin's finches on Daphne Major island in the Galápagos archipelago that largely circumvents these difficulties. Accurate and complete censuses by observation are made possible by marking individuals uniquely, by the tameness and conspicuousness of the birds, and by the small size of the study island [0.34 km² (22)]. Further, the finches are resident, and this minimizes difficulties of estimating numbers of each sex that arise from permanent emigration outside a local study area, and difficulties in distinguishing emigration from mortality (23–27). Finch population sizes and breeding vary as a result of strong annual fluctuations in weather: from dry conditions that prevent or restrict breeding to a single brood to extreme wet conditions in years of El Niño that permit breeding as much as 10 times in 1 y (28, 29). In these features, they differ from well-studied passerine bird populations in temperate

Significance

The adult sex ratio of populations is influenced by various social and environmental forces. When those forces result in an unequal sex ratio, the minority sex has greater reproductive opportunities than the majority sex. Here, we provide evidence of a flexible mating system of Darwin's finches living in a fluctuating environment. Finches form social bonds that are monogamous, polygynous, or polyandrous, and also engage in extrapair mating (EPM). We show that unequal sex ratios are associated with extreme weather conditions, and they influence the frequency of changing mates within a breeding season and EPM. Results largely support the conclusions of comparative phylogenetic analyses, and provide insights into the early stages of evolutionary divergence from a presumed strictly monogamous mating system.

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regions that are often migratory and regularly have a single or, at most, two broods per season (15–17, 30).

Two species are common residents on Daphne Major, *Geospiza fortis*, the medium ground finch (~16 g), and *Geospiza scandens*, the cactus finch (~21 g). *G. fortis* is a generalist granivore, whereas *G. scandens* is a cactus specialist. They live for up to 17 y, nest in cactus bushes (*Opuntia echinos*), and provide biparental care to broods of one to six offspring (SI Appendix, section 1). They differ in territorial system. *G. scandens* males remain associated with the breeding territory throughout the year, whereas *G. fortis* males abandon the territory after breeding and forage elsewhere on the island, as do females and young birds of both species. Thus, the two species experience the same climate but have different ecological niches. Their numbers are limited by different food supplies in the dry season (23), which allows identification of the environmental causes of unequal sex ratios.

We focus on (i) how environmental perturbations cause fluctuations in sex ratio and (ii) how fluctuations in sex ratio affect the mating system. Finches form social bonds that are monogamous, polygynous, or polyandrous. Finches are also promiscuous, engaging in EPM. We show that unequal sex ratios are associated with extreme weather conditions, and these, in turn, alter the frequency of changing mates within a breeding season and EPM. Results largely support the conclusions of phylogenetic analyses, and provide insights into the early stages of evolutionary divergence from a presumed strictly monogamous mating system.

Results

ASRs. We follow Wilson and Hardy (31) and Ancona et al. (18) in expressing ASR as the proportion of adults that are male at the beginning of each year. Both *G. fortis* and *G. scandens* have ratios that are biased toward males (Table 1), as is typical for birds in general (13, 16, 17), but they differ in the degree to which they are biased. The mean ratio departs from 0.5 significantly more strongly in *G. scandens* (0.64 ± 0.016 SE) than in *G. fortis* (0.57 ± 0.016 SE) (paired $t_{20} = 3.14$, $P = 0.0051$). The mean ratio for *G. fortis* is the same as the mean and median ratio (0.57) of 201 pub-

lished estimates for birds compiled by Donald (16). The ratio was not constant in either species, but fluctuated annually in relation to extreme fluctuations in numbers caused by rainfall-induced episodic bursts of reproduction (Fig. 1).

Not all adults breed. The operational sex ratio (OSR) comprises actual breeders together with potential breeders among nonbreeders (13, 32, 33). The potential breeder component is not quantifiable, because we do not know what fraction of the nonbreeders are in a state of readiness to breed, especially in dry years of limited breeding. Therefore, we use instead the breeding sex ratio (BSR), that is, the proportion of breeders that are male, as a proxy for the OSR. ASR and BSR are positively correlated in *G. fortis* ($r = 0.71$, $P = 0.0095$, $n = 12$). They are not correlated in *G. scandens* ($r = 0.15$, $P = 0.2676$, $n = 13$) owing to high annual variation in the nonbreeding component of the adult population.

Environmental Causes of Variation in ASR and BSR. Two conspicuous changes in sex ratios occurred in the 21-y study (Fig. 1 and Tables 1 and 2). Both involved an amplification of the bias toward males, but the environmental causes differed. In the first case, the two species diverged synchronously from a 0.5 sex ratio, followed by a gradual reversal to equal sex ratios. The shifts were associated with a common factor, starvation, and size selective mortality of adults during the severe drought of 1977 (23, 34, 35). Small birds were at a survival disadvantage in both species (23, 36, 37), and females, which are smaller than males by 4–5% on average (34, 38), experienced higher mortality than males (34, 37). In the following two breeding seasons, large males that held large territories had a mating advantage over small males (39).

In the second case, both ASR and BSR diverged from 0.5 in *G. scandens* but not in *G. fortis*. The strong shift was a consequence of an environmental perturbation caused by extreme conditions in the El Niño year of 1983 (SI Appendix, section 1): Prolonged and heavy rain resulted in the destruction of many cactus bushes. Roots rotted in the water-logged soil, bushes became top-heavy with water, and many blew over in strong winds in 1983 (27), and again in the following years. *G. scandens* numbers

Table 1. Annual variation in numbers of adults and sex ratios

Year	Rainfall, mm	<i>G. fortis</i>	Proportion males	<i>G. scandens</i>	Proportion males
1976	135	209	0.56	77	0.62*
1977 [†]	24	119	0.61*	93	0.68***
1978	137	92	0.75****	93	0.73****
1979	69	187	0.63***	64	0.63
1980	53	213	0.62***	128	0.63**
1981	73	199	0.62**	153	0.58
1982	51	212	0.65****	147	0.61*
1983 [‡]	1,359	205	0.65****	180	0.50
1984	53	489	0.45*	110	0.48
1985 [†]	4	350	0.50	285	0.53
1986	49	219	0.48	177	0.70****
1987 [†]	622	192	0.49	81	0.75****
1988 [†]	1	627	0.54*	60	0.71**
1989 [†]	4	547	0.52	117	0.70****
1990	48	424	0.51	108	0.73****
1991 [‡]	195	292	0.52	91	0.71***
1992 [‡]	209	634	0.51	68	0.62
1993 [‡]	234	523	0.52	85	0.64*
1994 [†]	51	424	0.58**	75	0.63*
1995	66	181	0.64***	75	0.66**
1996 [†]	2	103	0.62*	56	0.65*

Mean and SD of frequencies are 0.55 ± 0.07 for *G. fortis* and 0.61 ± 0.10 for *G. scandens*. Significance of departures from a 0.5 ratio (binomial tests) is indicated for 0.05, 0.01, 0.005, and 0.001 by one to four asterisks, respectively.

[†]Breeding was almost absent in drought years.

[‡]Years of El Niño.

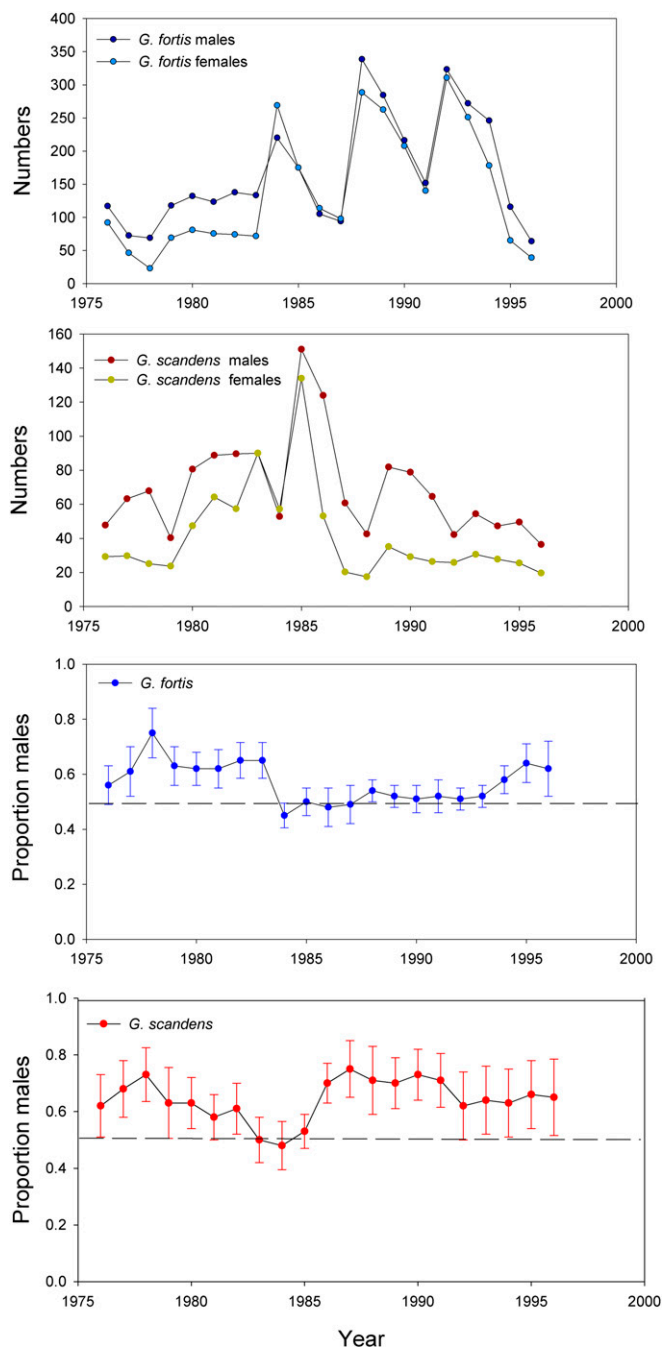


Fig. 1. Annual fluctuations in numbers (*Upper*) and ASRs (*Lower*) with 95% confidence limits.

fell during the drought of 1985, a year without breeding, and females, subordinate to males at cactus food sources, experienced disproportionately strong mortality. Recovery of the population from low numbers was hampered to a small extent by inbreeding depression (40). *G. fortis* was not dependent on this food source and did not increase in ASR (Table 1) or BSR (Table 2).

Mate Choice as a Result of Imprinting. A male-biased sex ratio implies increased opportunity for females to choose high-quality males (39). A previous study of the mating patterns of the finch species on Daphne has provided evidence in support of a hypothesis of mate choice based on parental imprinting (41). According to the hypothesis, the choice of a mate is influenced

by early experience of parental morphology (41–45). Females are expected to choose males with morphological features close to their own parents' morphology under conditions that are favorable for expressing such choice. Since morphological traits are highly heritable in both species (46, 47), offspring are predicted to choose mates that are like themselves, and hence mate assortatively (41) (Fig. 2). With less opportunity to do so, for example, when other factors such as high density, quality of territories, and scarcity of unpaired males affect the mating decision, females are likely to choose males that depart from the imprinted image.

To test the imprinting hypothesis, we contrasted the pairing of *G. scandens* females when choice was restricted in 1984 (mostly single brood only, frequency of males = 0.48; Table 1) with females at the time of the first brood in 1987 when potential choice was much greater (initial frequency of males = 0.75). Contemporary *G. fortis* provides a control for the test because the ASR of this species remained close to 0.5. The prediction is supported by the significant correlation between mates in bill size in *G. scandens* in 1987 ($r = 0.586$, $P < 0.05$, $n = 15$) but not in 1984 ($r = 0.059$, $P = 0.7156$, $n = 40$). The corresponding correlations in *G. fortis* were 0.195 in 1987 ($n = 84$) and 0.161 in 1984 ($n = 73$), and neither was statistically significant ($P > 0.1$). When *G. scandens* females changed mates in 1987 (as discussed in the next section), the effects of imprinting on parental morphology disappeared. At the end of the 1987 breeding season, the correlation in bill size between mates was no longer significant ($r = -0.258$, $P = 0.9335$, $n = 15$).

Sex Ratios and a Change of Mates. Males compete more intensely for mates when females are relatively scarce (6, 25, 26, 33). An unequal sex ratio >0.5 , combined with repeated breeding, provides opportunities for females to change mates within a single breeding season. Some females desert a male after raising a brood to fledging and re-pair with another, while males remain on their breeding territories, singing, defending their territories, and feeding young fledglings (*SI Appendix, sections 1 and 2*). Repeated breeding occurred in 8 y with moderate to extensive rainfall: 1978, 1980, 1981, 1983, 1987, and 1991–1993. Data are available throughout the entire breeding season of the first 6 y. Simple linear regressions of the combined *G. fortis* and *G. scandens* data show that the proportion of females that changed mates is a function of the length of the breeding season ($F_{1,10} = 8.66$, $P = 0.0139$), the mean number of nests per female ($F_{1,10} = 12.43$, $P = 0.0055$), and the BSR ($F_{1,10} = 40.80$, $P < 0.0001$) (Fig. 3), but not the ASR ($F_{1,10} = 0.45$, $P = 0.5179$). Only BSR is a significant predictor of mate change in multiple regression analysis of BSR and the other two significant variables, or BSR and just breeding season length ($F_{2,9} = 18.26$, $P = 0.0007$). The percent variance explained by the BSR variable is 74.91. The simple linear relationship between the proportion of mate changers and BSR is also significant with each species considered separately: *G. fortis* ($F_{1,4} = 15.25$, $P = 0.0175$) and *G. scandens* ($F_{1,4} = 16.10$, $P = 0.0070$).

G. fortis and *G. scandens* differed in sex ratios more strongly in 1987 than in any other year (Table 2): *G. fortis* ratios were equal (ASR = 0.49, BSR = 0.50), whereas *G. scandens* ratios were strongly male-biased (ASR = 0.75, BSR = 0.65). In agreement with expectation, the frequency of mate changes was higher in *G. scandens*, by a factor of 3 throughout the breeding season (Fig. 4). The one-tailed binomial probability associated with the consistent differences is 0.02. In contrast, in 1983, when finches also bred repeatedly (Table 2), BSRs of the two species were similar and so were the proportions of mate changers: 0.13 ± 0.01 for *G. fortis* and 0.16 ± 0.02 for *G. scandens* ($n = 6$ in both cases).

These findings are consistent with phylogenetic evidence of an influence of social environment (sex ratios of adults) on mate

Table 2. ASR and BSR in years of repeated breeding

Year	Species	Breeding season length, in d	Females	Mean no. nests per female	ASR	BSR
1978	<i>G. fortis</i>	95	21	2.9	0.75	0.59
1980	<i>G. fortis</i>	90	29	2.1	0.62	0.52
1981	<i>G. fortis</i>	46	34	2.0	0.62	0.53
1983	<i>G. fortis</i>	249	70	4.8	0.65	0.65
1987	<i>G. fortis</i>	199	126	4.6	0.49	0.50
1991	<i>G. fortis</i>	103	111	2.9	0.52	0.51
1978	<i>G. scandens</i>	118	18	2.8	0.73	0.56
1980	<i>G. scandens</i>	95	47	2.2	0.63	0.50
1981	<i>G. scandens</i>	49	15	2.1	0.58	0.50
1983	<i>G. scandens</i>	260	67	5.2	0.50	0.60
1987	<i>G. scandens</i>	203	22	5.6	0.75	0.65
1991	<i>G. scandens</i>	116	19	3.4	0.71	0.53

changing (5), and contemporary evidence that breeding tactics may respond flexibly to local mating opportunities when BSRs are biased (11, 12, 48–52).

Female Choice of a New Mate. A change of mates might be precipitated by nest failure caused by noncooperative behavior between members of a pair or by frequent aggressive interactions between one of them and an intruder (53), but neither possibility is supported by observations (*SI Appendix, section 2*). Alternatively, a change in mates may be a response to opportunities of pairing with more vigorous males that display readiness to breed, or males with superior territories in terms of defendable nest sites and food resources (14, 15, 53–56). Females are expected to benefit from the change, and to experience higher fledging success and recruitment of their offspring to the breeding population (fitness) than by remaining with the previous mate. Expected benefits have been observed in some studies of passerine birds (12, 14, 21, 57) but not in others (15).

We tested the hypothesis by comparing the reproductive success of females that changed mates with those that did not change with the combined data from 5 y of frequent repeated breeding (Table 3). Females that changed mates gained a clear fitness advantage in terms of numbers of offspring that survived to the following year (fitness 1), and hence potential recruits to the breeding population. However, the potential was not translated into a statistically significant, higher recruitment (fitness 2). The same trend toward higher fitness for mate-changing females is seen in the *G. scandens* data for 1987 alone (*SI Appendix, Table S3*). Full translation of potential to actual recruitment requires favorable conditions for recruitment in the year following repeated

breeding. No breeding took place in the drought years of 1988 and 1989, when many of the potential recruits died. Recruitment of offspring produced before and after a change of mates varied annually and showed no consistent pattern (*SI Appendix, Table S4*).

A possible advantage to females that change mates is they gain a long-term fitness benefit in subsequent years. Females that change mates and survive to the next season may (i) retain the new mate from the previous season, (ii) return to the previous mate, or (iii) pair with a new male. We compared the fitness of females that retained the new mate with those that returned to the previous one when both mates had survived to the season following a change in mates. With data on *G. fortis* and *G. scandens* combined, because the species do not differ and sample sizes are small, more females ($n = 18$) returned to the previous mate than retained the new mate ($n = 17$), which argues against a strong value in retaining a new mate. Further, proportionately fewer retaining females (0.33) than returning females (0.47) produced recruits, and their mean fitness was lower (0.87 ± 0.36 recruits per female) than the mean fitness of those that returned to a previous mate (1.6 ± 0.57 SE).

The default hypothesis is that females gain fitness by a change of mates compared with remaining with the same mate. The hypothesis is not directly testable with field observations, but is plausible because males sometimes show a lack of readiness to breed again when they fail to respond to solicitation of copulations by their social mates (*SI Appendix, section 2*).

Repeated Breeding, BSR, and Mating System. The mating system (58, 59) of Darwin's finches is best described as mixed: Finches display alternative mating tactics (60) of social monogamy, polygyny, or polyandry and nonsocial promiscuity. Females are monogamous, sequentially polyandrous if they change mates after their nestlings fledge (even though they continue to feed them), or simultaneously polyandrous when they lay eggs in the nest of a new male before the nestlings fledge from the nest of a previous male. At the extreme, females have eggs in the nests of two males at the same time (*SI Appendix, section 3*).

Polyandry is expected to occur when adult males outnumber adult females (12, 49, 50). The expected association with BSR is supported by finch data in two ways: by the frequency of occurrence of mate changing by females (Table 4) and by the proportion of females that have more than one social mate (Table 5). The frequency of mate changing by females was highest when BSR was most strongly male-biased, in 1983 for *G. fortis* and in 1987 for *G. scandens* (Table 4).

A male-biased sex ratio facilitates simultaneous polyandry and an increased rate of reproduction. In years of plentiful rain, finches produce several broods in rapid succession and intervals between successive broods vary continuously from positive to negative (Fig. 5). Negative intervals are short: A second clutch of

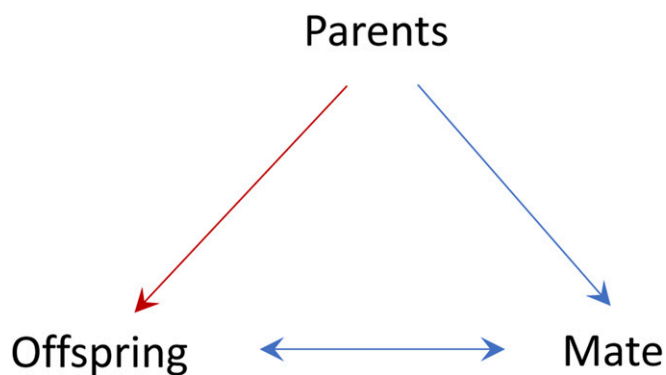


Fig. 2. When offspring imprint on their parents, they are expected to choose mates morphologically like their parents (41). Since offspring resemble their parents (heritability = 0.7–0.8), imprinting should lead to positive assortative mating (41).

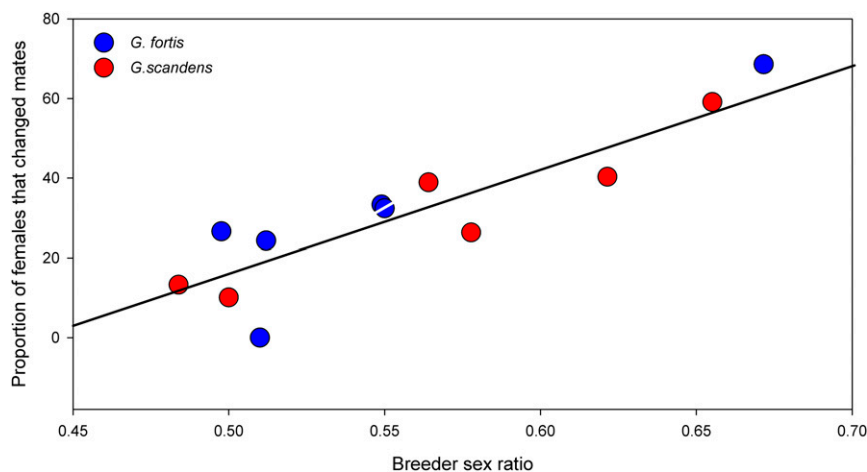


Fig. 3. Proportion of females that changed mates in six productive years: $F_{1,10} = 40.80$, $P < 0.003$, adjusted $R^2 = 0.777$.

eggs is laid in a new nest before offspring have fledged from the first nest (35, 61). Negative intervals are more frequent in *G. fortis* (0.29, $n = 659$) than in *G. scandens* (0.21, $n = 286$) (SI Appendix, section 3 and Table S2). At the three times of BSR $\gg 0.5$ (1983 for *G. fortis* and 1983 and 1987 for *G. scandens*) (Table 2), negative intervals between fledging and egg laying were more frequent among females that changed mates than among those that renested with the same mates (SI Appendix, Table S2). Frequencies are 0.32 versus 0.26 for *G. fortis* and 0.30 versus 0.21 and 0.27 versus 0.21, respectively, for *G. scandens*.

To determine the relative fitness consequences of polyandrous and monogamous breeding, we counted the number of recruits produced over the lifetimes of *G. fortis* and *G. scandens* females from four cohorts: 1978, 1979, 1981, and 1983. Despite the potential reproductive advantage in polyandry, the fitness consequences of the two types of mating were the same in both species (SI Appendix, section 4). Nonetheless some individual polyandrous females were unusually productive (SI Appendix, section 4).

Polygyny, simultaneous pairing of males with two females, is relatively rare, and almost absent in *G. scandens*. Table 5 compares proportions of polygynous males with proportions of simultaneously polyandrous females in years of most repeated breeding. Three conclusions can be drawn from the comparisons.

First, polygyny is more frequent in *G. fortis* than in *G. scandens*. Second, the opposite is true for polyandry. Third, as expected from theory, the most extreme frequencies of polyandry are associated with the highest degree of male bias in the sex ratio (BSR = 0.65): in 1983 for *G. fortis* and in 1987 for *G. scandens*. In contrast, the highest frequency of polygyny in *G. fortis* occurred when the sex ratio was equal in 1987.

EPM and Sex Ratios. Extrapair mating (EPM) is a form of mate choice. It varies in frequency among species in relation to sex ratio (5), and for some species, there is evidence it is adaptive (62–64). A comparative study of 35 species of birds showed that EPM and mate changing were positively correlated (65). The incidence of EPM on Daphne Major island increases with population density and is related to mate changing independent of female age (66). Thus, mate changing, sex ratio, and EPM are all interrelated. One possible consequence is a tendency for a female's extrapair mate to become her social partner later when the sex ratio favors mate changing (SI Appendix, section 5). Some observations are consistent with this possibility. For example, *G. fortis* females that change mates are more likely to have extrapair young than those that do not change mates, and extrapair copulations usually precede the change in mates (66). Further,

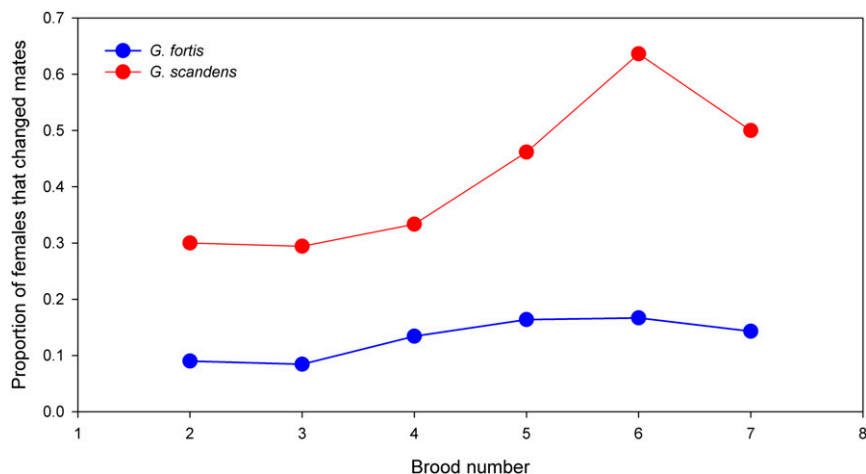


Fig. 4. Proportion of females that changed mates at successive breeding episodes in the 1987 breeding season. The BSR was much higher in *G. scandens* than in *G. fortis* (Table 2). Average proportions of mate-changing females across the second to seventh broods were 0.13 ± 0.01 for *G. fortis* and 0.42 ± 0.06 for *G. scandens*.

Table 3. Breeding success of females that did or did not change mates within a breeding season

Samples	Group	Mates	Nests	Eggs	Fledged	Fit 1	Fit 2
<i>G. fortis</i>							
Mean	Change	2.19	5	17.5	9.4	6.6	1.5
SE			0.3	1.19	0.04	0.06	0.24
<i>n</i> = 36							
Mean	No change	1	3.6	14.1	7.7	4.8	1.31
SE			0.19	0.75	0.53	0.38	0.15
<i>n</i> = 90							
<i>t</i>			3.8	2.44	1.68	2.51	0.75
<i>P</i>			0.0002	0.0162	0.0945	0.0133	0.4531
<i>G. scandens</i>							
Mean	Change	3	6.3	23.4	9.0	5.8	1.4
SE			0.64	2.50	1.61	1.08	0.49
<i>n</i> = 10							
Mean	No change	1	3.4	10.7	5.5	2.3	0.7
SE			0.59	2.28	1.47	0.99	0.44
<i>n</i> = 12							
<i>t</i>			3.31	3.77	1.60	2.37	1.12
<i>P</i>			0.0035	0.0012	0.1242	0.0282	0.2775
Totals							
<i>G. fortis</i>		169	507	1,896	1,035	665	173
<i>G. scandens</i>		44	108	372	163	93	27

Data from 5 y have been combined: 1978, 1981, 1983, 1987, and 1991. Fit 1 refers to survival of offspring to the next year, and Fit 2 refers to recruits to the breeding population. Fit, fitness.

G. fortis females were the initiator in all five extrapair copulations observed in the years 1987–1998, whereas all nine attempts initiated by males failed (66). Females also initiate a change in social mates.

If EPM is a tactic adopted by females in prospecting for future social partners, extrapair males and new social males are expected to be equidistant from the nest of the female's first mate (i.e., they form a common pool of potential mates). However, we found that extrapair males and the new social males were in spatially different domains (Fig. 6 and *SI Appendix, section 6*). Extrapair males often held a neighboring territory (*G. fortis* frequency = 0.47, *n* = 92), and their nests were not far from the extrapair nests in which they had paternity (*SI Appendix, section 6 and Table S6*). New social males of *G. fortis*, on the other hand, were much further away, whether measured as distance in meters (median test: $z = 3.85$, $P < 0.0001$) or number of territories ($z = 4.33$, $P < 0.0001$). The sample of identified EPM *G. scandens* males is too small ($n = 6$) for a meaningful test of their distributions.

A previous comprehensive but not exhaustive analysis of factors affecting EPM patterns (e.g., age, inbreeding, location) failed to identify any benefits (*SI Appendix in ref. 66*). EPM in these and other species of Darwin's finches may be an ancestral trait that occasionally enhances fitness of some individuals in this fluctuating environment but, in the long term, carries no net penalty and confers no net benefit. We conclude that social mating and EPM are not similar manifestations of mate choice, but are alternative reproductive tactics (60).

Hybridization. A further possible consequence of a biased ASR is an increase in hybridization owing to a scarcity of potential conspecific mates (42). Known as the Hubbs principle (comment by E. Mayr in Sibley, ref. 67), it is well supported empirically (42, 68–70). *G. scandens* and *G. fortis* hybridize (22, 71). Hybridization was expected to increase in frequency after 1986, when the *G. scandens* BSR was male-biased. Five interspecific pairs or pairs with a first-generation hybrid were recorded before then ($n = 308$; 0.016), and another five were recorded after ($n = 131$; 0.038). The difference in frequency by a factor of 2 is consistent

with expectation, but is not statistically significant (Fisher's exact $P = 0.1726$). The pairings reflect a taxonomically widespread nonrandom tendency for females to be the smaller sex in hybridizing pairs of species (42, 69–72): Nine of the 10 females were *G. fortis*, the smaller species (two-tailed binomial $P = 0.022$).

Hybridization also occurs through EPM (73). The incidence is expected to be relatively high because courtship, involving species-specific signals and responses, is likely to be minimal or absent in EPM (60, 74). Three of six hybrids (0.5) that could be checked by DNA for paternity were the product of EPM. This is

Table 4. Comparison of male and female polygamy

Year	Males	Proportion	<i>n</i>	Females	Proportion	<i>n</i>
<i>G. fortis</i>						
1978	Polygamous	0.01	1	Polygamous	0.25	8
	Monogamous		68	Monogamous		24
1981	Polygamous	0.00	0	Polygamous	0.29	6
	Monogamous		124	Monogamous		15
1983	Polygamous	0.06	8	Polygamous	0.49	65
	Monogamous		124	Monogamous		68
1987	Polygamous	0.13	12	Polygamous	0.36	35
	Monogamous		82	Monogamous		61
1991	Polygamous	0.05	7	Polygamous	0.20	22
	Monogamous		146	Monogamous		87
<i>G. scandens</i>						
1978	Polygamous	0.00	0	Polygamous	0.14	3
	Monogamous		68	Monogamous		19
1981	Polygamous	0.00	0	Polygamous	0.08	2
	Monogamous		88	Monogamous		22
1983	Polygamous	0.02	2	Polygamous	0.34	29
	Monogamous		90	Monogamous		57
1987	Polygamous	0.00	0	Polygamous	0.68	13
	Monogamous		61	Monogamous		6
1991	Polygamous	0.00	0	Polygamous	0.28	5
	Monogamous		64	Monogamous		13

Frequencies are those of females mating with one (monogamy) or more (polygamy) social mates.

Table 5. Proportions of polygamous males and females

Cohort	Mating type	<i>G. fortis</i>		<i>G. scandens</i>	
		Proportion	<i>n</i>	Proportion	<i>n</i>
1983	Polygyny	0.06	156	0.03	93
	Polyandry	0.13	134	0.13	84
1987	Polygyny	0.10	98	0.00	27
	Polyandry	0.05	122	0.28	18
1991	Polygyny	0.08	110	0.00	17
	Polyandry	0.02	110	0.05	18

Females are counted as polyandrous if mated simultaneously with more than one social partner so that their frequency can be compared with simultaneously polygynous males. The proportion of social partners with one or more mates is shown in Table 4.

significantly higher than the expected fraction of 0.23, based on 93 EPMS of 488 matings with identified paternity (both species combined, one-tailed Fisher's exact $P = 0.045$). The high proportion is further evidence that EPM is an opportunistic, non-adaptive behavior (*SI Appendix, section 7*); a counterexample involving hybridization is provided by Veen et al. (75).

Conclusions

This study addresses the reproductive consequences of variation in ASRs of two populations of Darwin's finches on a small island

in the Galápagos archipelago. It takes advantage of five unusual features of the system: an equatorial location subject to the El Niño phenomenon of strong climatic oscillations, habitat in its natural state, repeated breeding within a single breeding season, a mixed mating system, and precise measurement of sex ratios and fitness. The study is useful in providing insights into patterns derived from phylogenetic comparative analyses of mate changing and EPM. Phylogenetic patterns are the product of evolution over millions of years. Studies of contemporary populations are valuable because they can throw light on the reasons for evolutionary divergence at the earliest stages, just as they are valuable for understanding patterns of morphological and behavioral diversity, speciation, and adaptive radiation (76, 77).

The main findings of the study are as follows: (i) Environmental perturbations cause sex ratios to become male-biased as a result of higher mortality among females than males; (ii) mate choice based on parental imprinting is expressed when $BSR \gg 0.5$; (iii) females change mates more frequently when $BSR > 0.5$; (iv) EPM decreases when $BSR > 0.5$; and (v) females that change mates are polyandrous and produce more offspring surviving to the next year than monogamous females, but this does not necessarily translate into increased recruitment.

Eberhart-Phillips et al. (7) found that offspring in shorebird populations with biased ASRs were predominantly tended by a single parent, suggesting that parental cooperation breaks down with unbalanced sex ratios and gives rise to patterns of mate changing (divorce) and EPM (infidelity) (5, 9). Our study shows

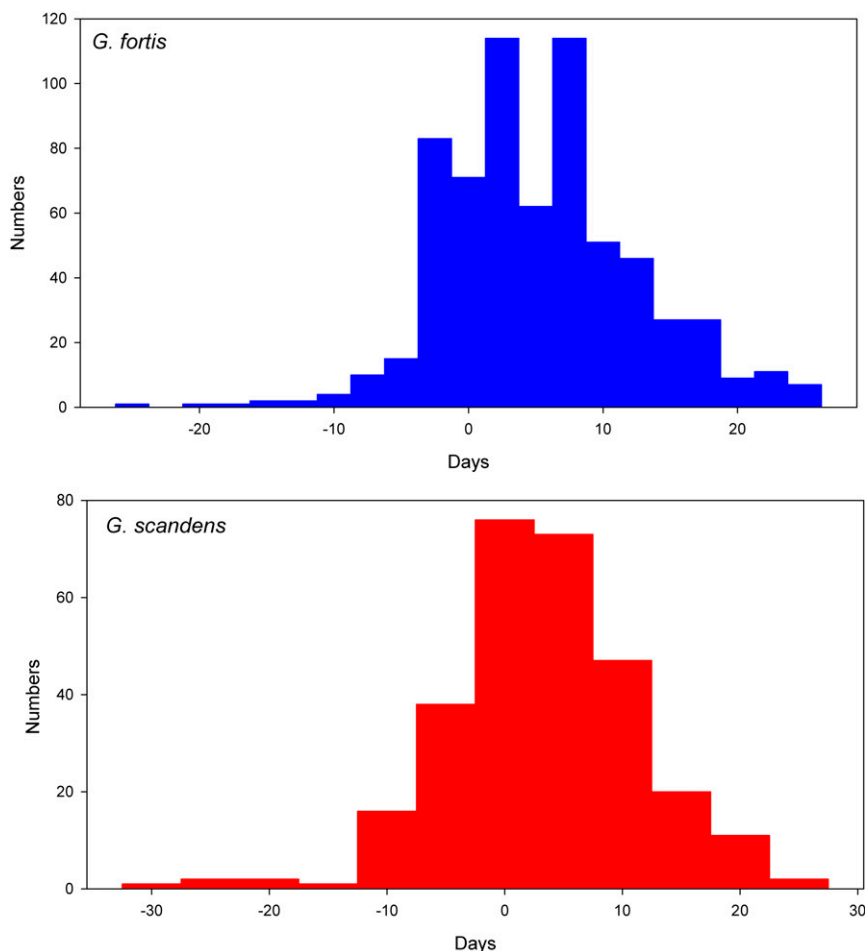


Fig. 5. Frequency distributions of intervals in days between fledging from one nest and egg laying in the next: *G. fortis* (Upper; $n = 657$) and *G. scandens* (Lower; $n = 289$).

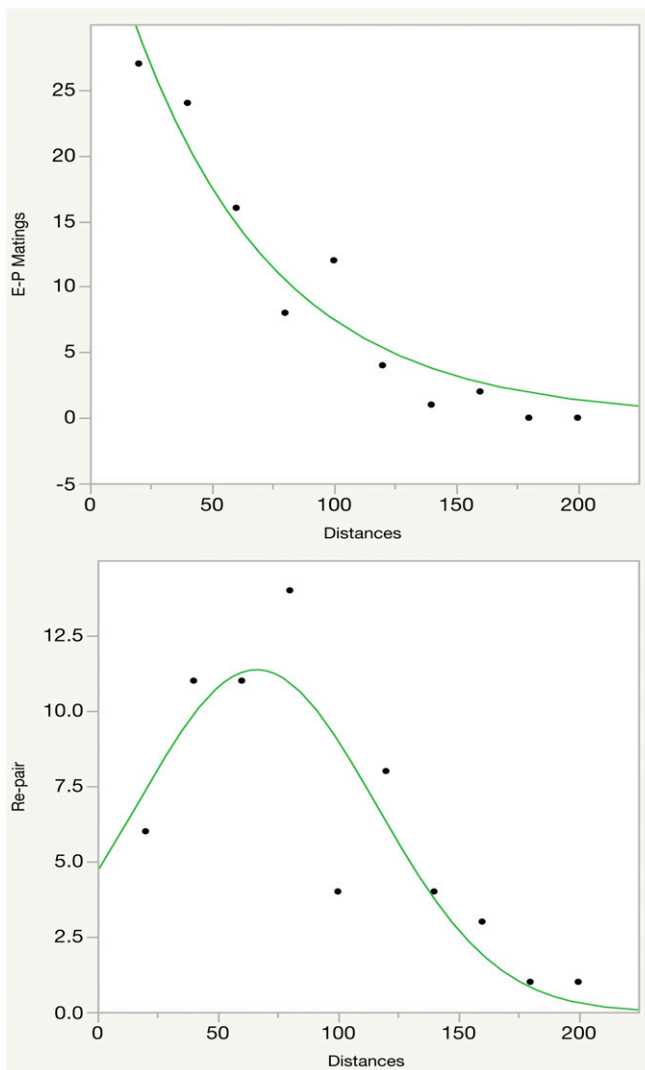


Fig. 6. Distributions of *G. fortis* map distances in meters between current nests and the nests of extrapair males that have fertilized some of the eggs (*Upper*) and between the nests of current and next mates of females that re-pair (*Lower*). R^2 values are 0.93 for the exponential model (*Upper*) and 0.77 for the Gaussian model (*Lower*).

the beginning of the breakdown within a species subject to fluctuating ASRs and BSRs. Results agree with two widely accepted theoretical ideas. The first is that when sex ratios are unequal, the minority sex has greater reproductive opportunities than the majority sex (3, 4) and, consequently, the minority sex is under selection to provide less care (9). The second is that breeding strategies respond flexibly to local mating opportunities when BSRs are biased (11, 12, 48–52).

Our findings differ from two conclusions of phylogenetic analyses. First, Liker et al. (5) found that mate changing (divorce) is twice as frequent in species with female-biased sex ratios than in male-biased ones. This is consistent with the idea that males initiate divorce more often than pair-bonded females when the sex ratio is biased. Mate changing in Darwin's finches, in contrast, increases with male bias in the BSR. This is to be expected with female initiation of a change in mates, and female initiation is supported by observations (*SI Appendix, section 2*), as well as by other studies of passerine birds (12, 49–51, 78). A key factor is movement: Males are tied to territories, and females are free to move. For example, in 1983, 13 of 17 *G. fortis* males

(0.76) that changed mates stayed on territory or acquired a neighbor's territory, whereas only two of 18 females (0.11) stayed locally to that degree.

Second, a phylogenetic comparative study (5) suggested that infidelity (EPM) should increase in male-biased populations when females can pair with preferred males. Our results run counter to this. They indicate that females initially express culturally imprinted mating preferences for social mates under male bias, and then later re-pair opportunistically. Only when the option of re-pairing is much reduced, as when $BSR \sim 0.5$, do females engage in EPM at a high frequency. Variation in mate guarding (74, 79, 80) in relation to BSR may be a contributing causal factor to variation in EPM. A genetic consequence is that diversity of a female's offspring is enhanced by re-pairing with a new social mate and by EPMs (80–82). Genetic diversity may be advantageous under some circumstances in this fluctuating environment.

A previous study of these populations showed that lifetime fitness of finches, as measured by the total number of fledglings produced and the number of those that are recruited to the next generation of breeders, is a function of the total number of eggs produced by a female, which, in turn, is a function of lifespan (66). The present study extends this result by showing the clear fitness benefits of polyandry in the short term. Within a single season of repeated breeding, polyandrous females of both species fledged approximately twice as many offspring as monogamous females. They bred more often, were possibly of higher average quality, and may have received better assistance from their mates. Moreover, more fledglings of polyandrous females than of monogamous females survived to the following year. However, the present study shows that short-term benefits are not always translated into higher recruitment of the offspring. A few females that bred polyandrously experienced fitness benefits as measured by the number of recruits they produced, but, in general, lifetime fitness was not noticeably enhanced by polyandry. Therefore, conditions favoring a strongly male-biased sex ratio would have to persist for longer or occur more often for polyandry to be a regularly advantageous breeding tactic.

We conclude by emphasizing the influence of environmental fluctuations on breeding systems with three diverse examples from Galápagos. Galápagos cormorants, *Nannopterum harrisi*, exhibit serial polyandry with male care of nestlings (83, 84) but not eggs (85). The Galápagos hawk, *Buteo galapagoensis*, has a simultaneously polyandrous, cooperative, breeding system (86–89). Finches are facultatively polyandrous, serially and sequentially. Although their polyandry takes different forms, cormorants, hawks, and finches all experience high prebreeding mortality, occasional shortages of food, and unequal ASRs as well as prolonged breeding seasons and food abundance at other times. This illustrates the theme of the paper. Phylogenetic analysis is needed to reveal the origins of different forms of breeding systems, and analysis of contemporary populations is needed to reveal the conditions to maintain them.

Methods

Sampling Design. Field methods have been extensively described in previous publications (22, 35, 46). The proportion of adults that had been captured in mist nets, measured, and banded uniquely was ~90% in 1979 and ~98% in 1981 (39). By 1992, all breeding adults had been banded. Adults were defined as birds in the year following the hatching year, except in 1983 and 1987, when some birds that hatched that year bred and so are included as adults. ASRs were determined by repeated censusing throughout the island at the beginning of each year. A minor female bias in the estimates is possible because young males are indistinguishable phenotypically from females unless they sing. A large number of nests were followed in the years 1976–1978, but from 1979 onward, all nests on the island were found, their owners (banded + not banded) were identified, and nest locations were recorded on a map every month. Distances between nests were measured on a printed copy of an aerial photograph at a scale of 1 mm = 2 m. Nests were

checked at 2- to 4-d intervals, and nestlings were banded at day 8. Observations of courtship and mating were made opportunistically and during 1-h nest watches conducted in 1987 and 1991 for a total of >200 in each season. Birds were measured as full-grown adults in the year posthatching (71). Microsatellites were used for parentage assignment from blood samples taken from birds captured in mist nets or from nestlings from 1988 onward (71). The Princeton University Animal Care Committee approved the research procedures.

Statistical Analyses. Statistical analyses were performed in JMP (SAS Institute). All tests were two-tailed, unless indicated otherwise.

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