SHORT COMMUNICATIONS

Breeding of Darwin's Finches at an Unusually Early Age in an El Niño Year

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The age at which an organism first breeds has an important effect on its relative fitness. Passerine birds usually breed for the first time at an age of 1 yr or more. In arid regions of the world they may breed in the year of their birth. This is suggested by laboratory studies of reproductive maturation (Marshall and Disney 1957; Sossinka 1980a, b) and by occasional observations of birds in the wild (Immelmann 1963, Davies 1977, Kikkawa 1980). Here, we report the breeding of two species of Darwin's finches on the Galápagos Islands at an age of 3–6 months. This is the first demonstration of unusually early breeding and its short-term consequences in wild birds whose ages are precisely known. The results have important implications for the evolution of maturation rates in birds.

Populations of the Medium Ground Finch (*Geospiza fortis*) and Cactus Ground Finch (*G. scandens*) on Isla Daphne Major have been studied every year since 1975, and almost all individuals have been uniquely color banded. Breeding of the finches is governed by rainfall and the ensuing production of plants and arthropods (Grant and Boag 1980). From 1976 to 1982, the maximum annual total of rain was 137 mm, which fell over a 4-month period in 1978 (Boag and Grant in press). In late November 1982, rain began falling heavily, associated with an El Niño event that has been described as the most severe of the century (Cane 1983, Kerr 1983). Rain continued until mid-July 1983. The rainfall total on I. Daphne for the 8-month period was 1,359 mm, i.e. 10 times the previous annual maximum.

Finches started laying eggs in late November and early December 1982. The last nestling fledged in early September 1983. During this 9-month period, individual pairs bred as many as seven times; the previous maximum had been five clutches produced by a single pair of *G. scandens* in 1978. We found all the nests, uniquely banded the chicks at 8 days of age with one metal and three color bands, identified the parents by their bands, and monitored the success of each breeding attempt.

From April 1983 onwards the breeding populations of both species were augmented by birds born a few months earlier. Ages at first reproduction (clutch initiation) are displayed in Fig. 1. The youngest *G. fortis* attempting to breed was 81 days old, and it fledged two young. The youngest *G. scandens* was 89 days old, and it fledged none. The youngest *G. scandens* to breed successfully laid her first egg when she was 97 days old. These values confirm the supposition, based on estimates of age from plumage and skull characters, that passerine birds can breed in the wild when about 3 months old (see also Orr 1945). Early breeding may be common in regions where suitable conditions for breeding persist for more than 3 or 4 months, but the only record we have been able to find of a banded bird in the wild breeding at a comparably early age is of a female Zebra Finch (*Poephila guttata*) in Australia, which laid her first egg when she was 86 days old (Immelmann 1963).

Geospiza fortis individuals breeding in their year of birth were younger, on average, than their *G. scandens* counterparts, as is revealed by Mann-Whitney *U*- and *t*-tests (data ln-transformed to correct for skewness, $t_{188} = 2.11$, $P < 0.05$; see also Table 1). This may be related to their different growth rates; asymptotic size is reached in less than 60 days in *G. fortis*, but some dimensions in *G. scandens* increase for 80 days (Boag 1983).

The parents of these birds bred for the first time when they were 22–24 months old on average (i.e. nearly 2 yr old); the two species did not differ in this respect ($t_{80} = 0.90$, $P > 0.1$; Table 1). Despite the great difference between the 1982–1983 cohort and their parents, there is a significant correlation between them in age at first reproduction. We show this for *G. fortis* by using mid-parent values (i.e. the average of the ages of mother and father when they first bred) and family mean values for the offspring born in 1982–1983 who subsequently bred. The parametric correlation coefficient for 15 families is 0.534 ($P < 0.05$). Correlations based on father alone (0.464) or mother alone (0.496) are not quite significant. The significant correlation is consistent with the possibility that the relative age at first reproduction is partly under genetic control.

More female (106) than male (39) *G. fortis* bred in their first year, but the majority of both sexes did not breed. In the absence of external distinguishing features of the sexes of these young birds, we assume a 1:1 sex ratio of young available to breed. Proportionally more females bred than would be expected by chance ($\chi^2_1 = 27.7$, $P < 0.001$). Six male and 39 female *G. scandens* bred in their first year, the proportions again differing from an expected 1:1 ratio ($\chi^2_1 = 24.2$, $P < 0.001$). In addition, *G. fortis* females, with an average age at first reproduction of 109.2 ± 21.0 (SD) days, bred earlier than males (131.9 ± 24.3 days; $t_{143} = 5.50$, $P < 0.001$). *Geospiza scandens* females and males, however, did not differ in age at first reproduction ($t_{43} = 0.13$, $P > 0.1$).

These differences between sexes are not likely to be caused by intrinsic differences in maturation rates,

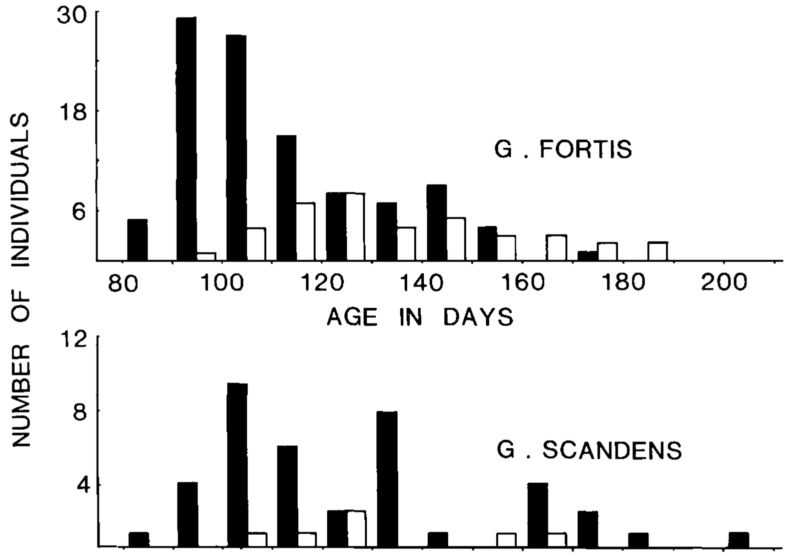

Fig. 1. Ages at first reproduction of female (solid bars) and male (open bars) finches born in the 1982–1983 breeding season. Ages are from birth (hatching) to the day the first egg was laid.

because other studies have shown that male birds generally produce gametes at an earlier age than do females (Immelmann 1963, Serventy 1971, Sossinka 1980b). Rather, they probably reflect greater opportunities for the breeding of females than of males, resulting from a male-biased sex ratio in the adults of both species. The bias arose through differential mortality during the drought of 1977 and has persisted ever since (Boag and Grant 1981, Price 1984). There were more mates available for females than for males, and males had the additional task of establishing territories.

TABLE 1. Mean ages at first reproduction in days (±1 SD) for birds breeding in their year of birth and for their parents. Ages were determined from the date on which the first egg was laid by the birds or by their mates. Only data from parents (~90%) of exactly known ages are included. Males and females have been combined. The range of ages are shown in parentheses; n is sample size.

Species	The 1982–1983 cohort	Their parents
G. fortis	115.3 ± 24.12 (81–183) $n = 145$	745.4 ± 247.7 (365–1,154) $n = 68$
G. scandens	125.8 ± 27.7 (89–203) $n = 45$	680.6 ± 231.8 (415–1,157) $n = 14$

Both *G. fortis* and *G. scandens* bred successfully in their first year when paired with older birds (Table 2). To compare their performance with the performance at the same time of older birds of the same species that had bred previously, we first combined clutches into three groups of comparable sample sizes: 1–2 eggs, 3 eggs, and 4–6 eggs. For *G. fortis*, old females paired with old males laid proportionally more large clutches than did young females paired with either old males ($\chi^2_2 = 7.78$, $P < 0.02$) or young males ($\chi^2_2 = 13.22$, $P < 0.001$). We then compared pairs that hatched at least one egg (Table 2) but fledged no offspring with those that fledged one or more offspring. Again, the old pairs of *G. fortis* did proportionally better than either the mixed pairs (Fisher's Exact Probability = 0.0004) or young pairs ($P = 0.029$). In contrast to *G. fortis*, there were no detectable differences in breeding success between young and old *G. scandens* (see also Table 2).

The relatively low reproductive success of young *G. fortis* appears to be due to their youth rather than to their inexperience at breeding. We reach this conclusion from the absence of any detectable difference in reproductive success between *G. fortis* females ($n = 18$) born in 1981 and breeding for the first time in December 1982 or January 1983 and older (experienced) females ($n = 41$) breeding in the same months ($P > 0.1$ in each case). This does not preclude the possibility that the low reproductive success of young *G. fortis* in 1983 was attributable, in part, to a controlled, sub-maximal, reproductive effort (cf. Curio 1983).

TABLE 2. Breeding success of pairs containing 0, 1, or 2 birds born in 1982–1983 (Young) or in 1981 and earlier (Old) and that hatched at least one egg. No pairs comprised young males and old females, and none contained birds born in the normal breeding season of 1982 (they had all died). Data for old pairs were restricted to the period when young birds were breeding (n is sample size).

	Pair type		
	Young ♂ × Young ♀	Old ♂ × Young ♀	Old ♂ × Old ♀
G. fortis			
n	10	32	123
Mean clutch size ± SD	3.40 ± 0.5	3.70 ± 1.7	4.0 ± 1.2
Mean number of fledglings ± SD	0	0.75 ± 1.2	0.94 ± 1.3
G. scandens			
n	—	33	102
Mean clutch size ± SD	—	3.76 ± 1.6	3.81 ± 1.0
Mean number of fledglings ± SD	—	0.93 ± 2.1	0.99 ± 1.3

In only 1 yr out of 8 was the wet season long enough to permit finches to breed in the season of their birth. This frequency may be misleadingly high. Since 1950 (excluding 1983), the wet season has lasted for more than 4 months only three times in the coastal areas of Islas San Cristóbal and Santa Cruz, in other words about once a decade. Individual finches of both species can live for more than 10 yr in the wild (unpubl. obs.) The chief implication of these results is that rare events are important selective determinants of maturation. The breeding of young birds paired with old birds was remarkably successful, but whether or not it extracted a cost in terms of lowered probability of survival during the nonbreeding dry season or subsequently remains to be seen.

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