

# SONG INHERITANCE AND MATING PATTERNS IN DARWIN'S FINCHES

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**ABSTRACT.**—The song types of two populations of Darwin's finches, the Medium Ground-Finch (*Geospiza fortis*) and the Cactus Finch (*G. scandens*) on I. Daphne Major, Galápagos, were studied from 1979 to 1981. Four discrete song types, easily distinguished by ear, are present in the *G. fortis* population, and two are present in the *G. scandens* population. A male generally sings his father's song type. Females mate randomly with respect to their fathers' song types. There is no evidence that song is used as a cue to avoid either extreme inbreeding or outbreeding. Received 10 April 1984, accepted 18 October 1984.

DARWIN'S finches have simple repeated songs (Bowman 1983, Ratcliffe and Grant 1985). Within each population individuals generally sing one of a number of discrete song types. The possible adaptive significance of the simplicity of the song and of song differences among individuals can be investigated using information on the way in which song is acquired in males and on mating patterns with respect to song type (Grant 1984). Grant (1984) has supplied the relevant information for a population of the Large Cactus Finch (*Geospiza conirostris*) on I. Genovesa, Galápagos. We present here the results from a study on two other species of Darwin's finches, the Medium Ground-Finch (*G. fortis*) and the Cactus Finch (*G. scandens*), on I. Daphne Major.

We show that sons generally sing the same song types as their fathers and that females appear to mate randomly with respect to their fathers' song types. We discuss the adaptive significance of songs and song variation in the light of these results and consider the possibility that songs are used to avoid either extreme inbreeding or extreme outbreeding.

## METHODS

We studied populations of *G. fortis* and *G. scandens* on the 40-ha I. Daphne between 1979 and 1981. We mapped territories of individual males, located many nests, and color-banded adults and nestlings (see Boag and Grant 1984a). During our study population sizes varied between 100 and 400 individuals (Price et al.

1983, Price 1984). All males more than 1 yr old had territories and sang fully developed songs. The song types of all singing males were noted.

The songs of 40 male *G. fortis* and 10 male *G. scandens* were recorded with a Panasonic cassette tape recorder. Birds were recorded between 1 and 6 times from a distance of 2–4 m. Spectrograms were made on a Kay spectrograph using a wide-band setting.

## RESULTS

**Song types.**—Four song types, sounding very different to the ear, are present in the *G. fortis* population (Fig. 1). The spectrograms were prepared by TDP and classified "blind" by SJM. Both of us were able to categorize each of the 40 prepared spectrograms to one of these song types, and in each case our categorization conformed to the categorization made by ear in the field. Song subtypes (Grant 1984) are recognizable both on spectrograms and in the field, but because only a sample of all the males were tape-recorded, and there are possible ambiguities in aural classification of subtypes, song subtypes are not considered further in this paper. Each male sang one song type, and no birds have ever been known to change their song either within or between years. Each of the *G. fortis* song types differs clearly in the number of elements per song and in temporal patterning (Fig. 1). Song-type 2 is a faster, 3-element version of the 2-element song-type 1. Song-type 3 is a more condensed version of song-type 1, with certain features missing. Song-type 4 is more dissimilar, being longer with repeated single elements of lower pitch (Fig. 1). Ratcliffe (1981) found similar variation and presented additional spectrograms of song-types 1 and 2.

In *G. scandens*, two principal song types are

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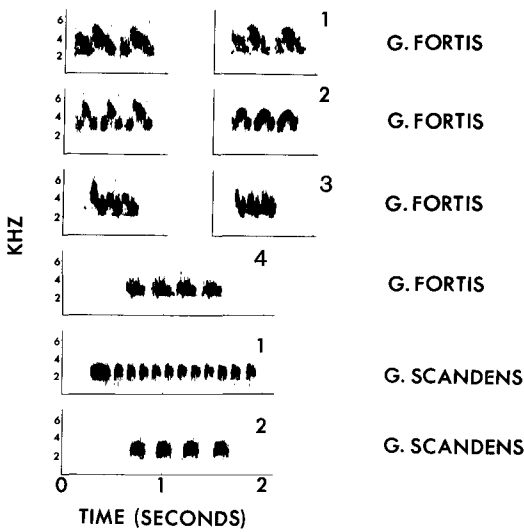


Fig. 1. Spectrograms of the major song types on Daphne Major. For *G. fortis* song-types 1, 2, and 3, songs of a father (left) and a son (right) are shown.

present in the population: a fast "churr" (song-type 1) and a rarer, slower version of this (song-type 2, Fig. 1). On the spectrograms *G. fortis* song-type 4 ("clang clang clang . . .") and *G. scandens* song-type 2 ("che che che . . .") appear very similar, but they are easily distinguishable by ear.

The number of males singing each song type among the 182 territorial *G. fortis* and 120 *G. scandens* on the island in March 1981 is given in Table 1. Two *G. fortis* males sang a mixture of *G. fortis* song-types 1 and 2 in irregular sequences, and one male sang a *G. scandens* song-type 1. Two *G. scandens* males sang a mixture of *G. scandens* song-types 1 and 2, another sang a typical *G. fortis* type 1, and a fourth a typical *G. fortis* type 2.

*Song transmission.*—In both species males have usually sung their father's song type and brothers have always sung the same song type as each other. Among the two species combined, males from only 3 of 63 nests (4.8%) had a song type different from that of their father (Table 2). In *G. scandens* the father had a mixed song and the son sang the commoner type-1 song. In *G. fortis* 3 brothers from the same nest sang type-2 songs whereas their father sang type 1, and in the other instance a singleton sang type 1 whereas its father sang type 2. In these cases it is possible that the parent was

TABLE 1. Numbers of males singing different song types in 1981.

Song type <sup>a</sup>	<i>G. fortis</i>	<i>G. scandens</i>
1	115	107
2	41	9
3	16	—
4	7	—
Mixed 1 and 2	2	2
Heterospecific <sup>b</sup>	1	2

<sup>a</sup> Note that the labeling of song-types 1 and 2 within each species is simply for convenience and does not indicate any homology across the two species (see Fig. 1).

<sup>b</sup> Individuals singing the other species' song.

misidentified or that the young became imprinted on another male.

We found no evidence that young birds learned their neighbor's song type, either at the time of fledging or when setting up their own territory (cf. Kroodsma 1974, Jenkins 1978, Payne et al. 1981, McGregor and Krebs 1982a). Four *G. scandens* males were raised in territories in which the nearest neighbor sang a song type different from that of their father: none sang their neighbor's song type. Three individuals singing song-type 2 settled in territories surrounded by males singing song-type 1 but never sang that song.

The corresponding data for *G. fortis* are presented in Table 3. When these data are viewed in the light of the proportion of males singing each song type on the island (Table 1), it is clear that there is no influence of nearest neighbor at the time of fledging or at the time of setting up a territory.

*Mating patterns.*—During the study there were between 2 and 3 times as many males as females on the island (Millington and Grant 1984, Price 1984), giving plenty of opportunity for females to exercise choice of mates based on song type. The mating patterns of females for which the song type of both the first mate and the father are known are shown in Tables 4 and 5.

Female *G. fortis* appear to mate at random from among the available males with respect to song type (Table 4). For each paternal song type of the females, we calculated the distribution of song types of unmated males in the population and compared this to the distribution of song types of the first mate (Table 4). The pattern is very similar to that expected on

TABLE 2. The relationship between the songs of fathers and sons. Only one male from each nest is counted because all siblings sang the same songs. Except where otherwise noted, each nest had a single male offspring surviving to sing.

Offspring song type	Father song type						
	<i>G. fortis</i>				<i>G. scandens</i>		
	1	2	3	4	1	2	Mixed
Same as father	25 <sup>a</sup>	10	1	1 <sup>c</sup>	23 <sup>d</sup>	1 <sup>c</sup>	0
Different from father	1	1 <sup>b</sup>	0	0	0	0	1

<sup>a</sup> Includes 4 sets of twins, 2 sets of triplets, and 1 quadruplet.

<sup>b</sup> A triplet.

<sup>c</sup> A set of twins.

<sup>d</sup> Includes 7 sets of twins.

the basis of random mating. To test the result statistically, it is necessary to compare mating patterns of females with respect to paternal song-type 1 and the other song types combined, giving, in a goodness of fit test,  $\chi^2_1 = 0.025$ ,  $P > 0.95$ . A pattern of random mating is also observed among females that have had more than one mate during the study. Forty-five percent ( $n = 48$ ) of the females that mated with more than one male had two mates differing in song type. Applying a similar goodness of fit test, we found no association (either positive or negative) between first and second mates' song types ( $\chi^2_1 = 0.4$ ,  $P > 0.9$ ). Ratcliffe and Grant (1985) reported a similar result for *G. fortis* mate switches on Daphne in 1978.

In *G. scandens*, the results do suggest a deviation in the direction of assortative mating (Table 5), but this is not significant, given the small numbers of song-type 2 (binomial test, excluding mixed-song birds,  $P > 0.25$ ).

#### DISCUSSION

Laboratory studies have shown that young birds of several species will learn their fathers' songs (Nicolai 1959, Immelmann 1969, Böhner 1983). However, field studies, albeit in quite different species from those observed in the laboratory, have not demonstrated paternal copying, but rather copying from neighbors at the time of settling (Kroodsma 1974, Jenkins 1978, Payne et al. 1981, McGregor and Krebs 1982a). In only one other species of Darwin's finch, *G. conirostris*, has it been shown that males consistently sing their father's song type (Grant 1984). Our results, together with those of Grant (1984), suggest that paternal transmission of song is likely to be general in the *Geospiza*.

The sensitive period in several other species comprises both a predispersal and postdispersal phase (Kroodsma 1978, Slater and Ince 1982) and is subject to environmentally dependent modification (Kroodsma and Pickert 1980). In Darwin's finches the sensitive period is estimated by Bowman (1983) to be very short, between 10 and 40 days after hatching. Grant (1984) links the short sensitive period in *G. conirostris* to the need for a simple, precisely copied song for species recognition. The importance of song for species recognition on Daphne is suggested by playback experiments (Ratcliffe and Grant 1985) and the observation that in 1980 a *G. scandens* female paired with the *G. fortis* male that sang the *G. scandens* song.

Because sons usually sing their fathers' songs, song could be used as a cue to avoid inbreeding. We find no evidence for this: females appear to mate randomly with respect to song type. Grant (1984) found a similar result for *G. conirostris*. However, she found a tendency for females not to mate with males that sang the same song subtype as their father (given sample sizes, this result was not significant). Although it is possible that females are using fine structure elements in songs to avoid inbreeding on Daphne, it does not appear that inbreeding is in fact being avoided. Two sib-sib matings have been observed during the study, one each in *G. fortis* and *G. scandens*. Given the small proportion of known relatives on the island it is not possible to ascertain if this represents any deviation from random mating. The *G. scandens* case was the only mating in which the female's mate and her father both sang the rare song-type 2 (Table 5).

It has been suggested that song types also could be used to avoid extreme outbreeding

TABLE 3. The association of a male's song type with its nearest neighbor's song type at the time of fledging and at the time of settling in *G. fortis*. Only males for which both the father's and neighbor's songs were known are included in each analysis.

	Nearest neighbor's song type	Father's song type	
		Same	Different
Fledging males	Same	26	0
	Different	18	1
Settling males <sup>a</sup>	Same	16	1
	Different	22	3 <sup>b</sup>

<sup>a</sup> Does not include 1 male that sang part of its nearest neighbor's and part of its father's song.

<sup>b</sup> The three brothers in Table 2.

(McGregor and Krebs 1982b). Although we have not attempted to use a test that ranks song types on the basis of similarity, there is no evidence to support this on Daphne. Indeed, extreme outbreeding is not avoided: immigrant female *G. fuliginosa* on the island regularly hybridize at low frequency with resident male *G. fortis* (Boag and Grant 1984a, b). This is despite the presence of unmated immigrant male *G. fuliginosa* holding territories on the island. These immigrants do have songs similar to those of *G. fortis* song-type 1 (Ratcliffe 1981), but they are recognizable as distinct to the human ear.

TABLE 4. Comparison of observed mating patterns in *G. fortis* with those predicted under the hypothesis of no assortment by song type. The proportions of the song groups (1, 2, and 3 and 4 combined) did not differ between 1979 and 1981 ( $\chi^2_2 = 0.33, n = 117, P > 0.9$ ). The average proportions for these two years (0.64 for song-type 1, 0.23 for type 2, and 0.14 for types 3 and 4 combined) were multiplied by the number of females of each paternal song type to give expected values.<sup>a</sup>

Mate's song		Father's song <sup>b</sup>		
		1	2	4
1	Observed	13	7	2
	Expected	11.5	6.4	2.6
2	Observed	3	2	2
	Expected	4.2	2.3	0.9
3 and 4	Observed	2	1	0
	Expected	2.4	1.4	0.5

<sup>a</sup> One female of paternal song-type 1 mated to a male of mixed song and is not included in this table.

<sup>b</sup> There were no known fathers singing song-type 3.

TABLE 5. Mating patterns in *G. scandens*.

Mate's song	Father's song		
	1	2	Mixed
1	20	0	1
2	0	1	0
Mixed	0	0	1

Given the data presently available we suggest that there may be little adaptive significance to song-type variation (see also Wiens 1982). However, we cannot assess the significance of variation in song subtypes, nor do we have large numbers of birds on the island that are known to be related. There may also be selection pressures on the song types at other times that were absent during our study. First, strong sexual selection for other male characteristics (Price 1984) may have obscured any potential preferences based on song. Second, because song is a species recognition cue, Grant (1984) suggests that the presence of just a few discrete types within each population is a result of selection against rare variants, which fail to be recognized by females.

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