

SEED SELECTION AND HANDLING ABILITY OF FOUR SPECIES OF DARWIN'S FINCHES

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Although Darwin's finches have figured importantly in modern ideas of evolution and ecology, only one detailed study of their feeding behavior has been published (Bowman 1961). In that study stomach contents were analyzed, but the size of seeds and fruits taken was not related in any quantitative way to bill differences among species.

In a 4-month study (by I.A. and L.A.) of the foraging behavior of the *Geospiza* finches at eight sites on seven Galápagos islands, we sought to test the rival hypotheses of Lack (1947) and Bowman (1961) concerning the evolution and ecology of Darwin's finches. During this study, we conducted feeding experiments with four species of *Geospiza* of two islands. The aim of the experiments was to determine feeding rates on rice grains of different hardness and length but of similar depth and width, and to relate these to bill dimensions.

In laboratory studies on feeding using British and American finches, seeds differing in length, width, depth, caloric content, hardness, and sometimes species have been used. Our study differs in that these variables are partially controlled because the "seeds" offered differ essentially in only length and hardness (table 1). The method used by finches to crack seeds and the forces that they exert were explained in detail by Bock (1966) and Newton (1967).

The finches were studied for two weeks at all sites, but on only two islands did the tameness of the finches allow experiments to be run. We spent 1-13 March 1973 on Isla Plaza Sur and 26 May-5 June 1973 on Isla Española at Bahía Gardner. The species involved were *Geospiza fuliginosa*, *G. fortis*, and *G. scandens* on I. Plaza Sur, and *G. conirostris* on I. Española. Despite the large variety of natural seeds and fruits initially made available in the experiments, few finches ate them, even though they were normally eaten. We found by accident that polished rice grains were relished by the finches; these grains are equivalent to hulled seeds.

In our experiments three petri dishes containing water, 20 large rice grains, and 20 small rice grains (large grains broken in half, see table 1), respectively, were placed in line on a platform about 25

cm above the ground. The order of the dishes was changed randomly after each observation, which began when a bird landed on the platform and began feeding. The time spent handling, cracking, and eating grains (with pauses excluded) was measured with a stopwatch. When the bird stopped feeding, the number of grains left in each dish was counted. Some of the birds were color-banded and had been measured, including bill dimensions. Bill length is the length of the culmen from nares to tip, depth is the sum of culmen depth and gonys depth at the nares, and width is the greatest width of the gonys.

Mean feeding rates for each species, and for color-banded individuals in particular, were calculated as harmonic means, i.e., as $N/\Sigma(t/G)$ where N is the number of observations and G is the number of grains cracked and eaten in t seconds during each observation. When rates are averaged, harmonic means are more appropriate than arithmetic means (Steel and Torrie 1960). The dimensions of both kinds of grain were measured with calipers to the nearest 0.1 mm (table 1) and their hardness was determined with a pliers device designed by the McGill University Engineering Department. This registered the force at which a grain was cracked in the range 1.0-40.0 kg force.

In these experiments, satiation level was not controlled. It conceivably could influence feeding rates.

Geospiza fuliginosa, the species with the shortest, shallowest, and narrowest beak, on average cracked and ate both types of rice grain faster than the other species. The species with the largest beak, *G. conirostris*, cracked and ate the grains at the slowest rate (table 2). Although the long grains were about twice as long as the small ones and nearly twice as hard (table 1), in no case did any species take twice the time on average to crack and eat large grains as small ones (table 2); however, a 2:1 ratio of cracking rates (excluding eating) was shown by banded individuals (table 3). These results suggest that large-billed finches have difficulty in getting small seeds into the correct position for cracking.

The feeding rates of the five banded individuals of known bill dimensions (table 3) may be compared with those of the average feeding rate of the respective species (table 2). The Left-Dark Green banded *G. fuliginosa* was close to the average in cracking and eating large grains, but Right-Orange was slower, and Right-White/Dark Green was faster. These results do not bear out the intuitive supposition that, within a species, a deep or wide beak alone confers an advantage in eating hard seeds. In fact, there is an inverse relationship between cracking rate and bill depth and length. Exactly the same order holds with rates of cracking and eating small rice grains. Individuals with long beaks should exert less crushing force at the tip than individuals with short beaks of same depth at the base. Data for *G. fuliginosa* (table 3) tend to support this supposition although

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TABLE 1. Characteristics of rice grains used in experiments. Means and one standard error are shown.

Island		Length (mm)	Width (mm)	Depth (mm)	Hardness (kgf)	Sample size
Plaza Sur	Large grains	5.39 ± 0.13	2.38 ± 0.05	1.55 ± 0.02	4.15 ± 0.23	13
	Small grains	3.24 ± 0.17	2.41 ± 0.09	1.56 ± 0.03	2.83 ± 0.38	11
Española	Large grains	6.03 ± 0.11	2.29 ± 0.06	1.51 ± 0.02	3.93 ± 0.44	10
	Small grains	2.79 ± 0.10	2.26 ± 0.11	1.47 ± 0.04	1.82 ± 0.23	10

TABLE 2. Bill dimensions and feeding rates of four species of finches.

Island	Species	Mean bill dimensions (mm)			Mean feeding rates ^a	
		Length	Depth	Width	Large grains	Small grains
Plaza Sur	<i>G. fuliginosa</i> (52) ^b	8.31 (± 0.05) ^c	6.97 (± 0.05)	6.68 (± 0.05)	23.5 (3-38, 22) ^d	26.5 (4-92, 28)
	<i>G. fortis</i> (10)	10.91 (± 0.22)	10.50 (± 0.21)	9.21 (± 0.15)	12.2 (4-50, 17)	18.6 (5-133, 20)
	<i>G. scandens</i> (18)	14.27 (± 0.21)	8.57 (± 0.11)	7.82 (± 0.11)	18.4 (4-42, 28)	10.1 (1-83, 22)
	<i>G. conirostris</i> (34)	14.60 (± 0.16)	13.14 (± 0.18)	11.24 (± 0.14)	8.8 (3-91, 34)	11.8 (3-81, 35)

^a No. of grains eaten/100 sec.^b Sample size on which bill measurements are based.^c Standard error.^d Range of no. of grains eaten/100 sec, no. of observations.

depth is not constant. All three *G. fuliginosa* were of black plumage, so presumably were adult males.

The single, banded *G. scandens* cracked and ate large grains slightly slower than the fastest *G. fuliginosa*, even though it was larger in all beak dimensions than this *G. fuliginosa*. The banded *G. scandens* was of black plumage, so the comparison is fair in regard to probable age and sex. This *G. scandens* cracked and ate small grains much faster than the fastest *G. fuliginosa*. However, the banded *G. conirostris*, also of black plumage, cracked and ate large and small grains at the same rate as the slowest *G. fuliginosa* (which had the deepest beak of the three *G. fuliginosa*).

The deepest-beaked *G. fuliginosa* showed the greatest range in feeding rates (7-26 grains/100 sec) for large grains, even though its average feeding rate was below that of the population average (table 3).

Three banded *G. fuliginosa* were recorded eating large and small grains 19 and 25 times, respectively, out of 22 and 28 observations with all *G. fuliginosa* (tables 2, 3). One banded *G. scandens* was observed eating large and small grains 18 and 15 times, out of a total of 28 and 22 observations with all *G. scandens*. No banded *G. fortis* were observed often enough. One banded *G. conirostris* was observed 4 and 4 times out of a total of 34 and 35 of all *G. conirostris* eating large and small grains, respectively. Thus these species showed no significant preference

(tested with χ^2) for large grains over small grains or vice-versa. They fed at the petri dish nearest to where they landed on the platform.

Other feeding studies of captive American and British finches have suggested that large-billed species crack and eat seeds faster than small-billed species, and that smaller seeds are preferred. Our results, however, imply that small-billed *Geospiza* finches crack and eat rice grains faster than the large-billed ones, and that no preference exists for size of the rice grain taken. The correlations found for the Palearctic species are, however, most imperfect. Kear (1962:179) found that the Chaffinch (*Fringilla coelebs*), the Greenfinch (*Carduelis chloris*), and the Hawfinch (*Coccothraustes coccothraustes*) husk canary seed at the same rate. Bill length and depth for these species are 12, 8; 14, 10; and 21, 15 mm, respectively. Also, Greenfinches were found to husk hemp seeds faster than Hawfinches.

Working with two White-throated Sparrows (*Zonotrichia albicollis*), Hesperheide (1966) showed that they husked small sunflower seeds more quickly than large sunflower seeds. This agrees with results in tables 2 and 3, with *G. scandens* in table 2 an apparent exception. However, there is high variation in feeding rates, but Hesperheide did not discuss whether this was a result of consistent differences between individuals, along the lines of our table 3. Cardinals (*Cardinalis cardinalis*) too have been shown

TABLE 3. Bill dimensions and feeding rates of color-banded birds.

Island	Species and band	Bill dimensions (mm)			Mean feeding rates ^a	
		Length	Depth	Width	Large grains	Small grains
Plaza Sur	<i>G. fuliginosa</i> Left-Dark Green	8.2	6.7	6.5	23.3 (17-33, 10) ^b	41.3 (20-92, 14)
	<i>G. fuliginosa</i> Right-Orange	8.8	7.1	6.6	15.7 (7-26, 5)	36.0 (21-78, 6)
	<i>G. fuliginosa</i> Right-White/Dark Green	7.9	6.5	7.0	31.4 (26-36, 4)	58.2 (48-67, 5)
	<i>G. scandens</i> Left-Dark Blue	15.0	9.2	8.4	30.1 (21-42, 18)	78.0 (41-83, 15)
Española	<i>G. conirostris</i> Left-Light Blue	16.6	14.7	12.5	15.4 (13-17, 4)	30.2 (20-42, 4)

^a No. of grains eaten/100 sec.^b Range of no. of grains eaten/100 sec, no. of observations.

TABLE 4. Characteristics of canary, millet, rape, oat, and sunflower seeds. Means and one standard error are shown.

Seed	Length (mm)	Width (mm)	Depth (mm)	Hardness (kgf)	Sample size
Canary	5.17 ± 0.09	1.89 ± 0.02	1.43 ± 0.03	2.34 ± 0.09	20
Millet	2.82 ± 0.03	2.10 ± 0.05	1.60 ± 0.03	1.96 ± 0.08	20
Rape	1.48 ± 0.03	1.21 ± 0.03 ^a		≤ 1.00 ± 0.00	20
Oats	9.11 ± 0.14	2.65 ± 0.06	2.17 ± 0.06	2.35 ± 0.17	20
Sunflower	11.93 ± 0.24	6.56 ± 0.13	3.90 ± 0.12	≤ 1.37 ± 0.12 ^b ≤ 2.24 ± 0.21 ^c	20-28

^a It is not possible to distinguish depth and width as the seeds are subspherical.

^b Hardness of testa.

^c Hardness of kernel.

to husk small sunflower seeds more quickly than large ones (Willson 1971).

Seven species of North American sparrows took on average 1.6, 2.8, 2.9, 3.2, 3.9, 4.0 and 4.9 sec to crack and eat one millet seed whereas Cardinals (beak depth 12 mm) took 5.4 sec (Willson 1971). Millet (*Panicum*) seeds are about 1.6 mm deep and nearly 2 kgf in hardness (table 4), which is probably similar to Willson's millet samples. Willson's conclusion that large-billed species do not necessarily crack large seeds more rapidly than small-billed ones may have resulted from her choice of seeds, most being thin (< 2 mm deep) and not very hard (< 3 kgf) (table 4). A greater range of seed or fruit depth and hardness, such as was found in the Galápagos where depths range from 0.1 mm to about 10 mm and hardnesses from about 1 kgf to over 40 kgf, is necessary to test such an hypothesis. Willson (1972) has suggested that not all types of seeds push the limits of the abilities of the finches she studied.

Although the *Geospiza* finches showed no preferences for small grains over large grains, Hespeneheide (1966) found that White-throated Sparrows and Dark-eyed Juncos (*Junco hyemalis*) most often chose the smallest sunflower seeds. Willson (1972) confirmed this with other small-billed finch species. Cardinals showed hardly any preference.

Small-billed finches, presumably because of their small gape and relatively less powerful jaw musculature, must be unable to handle and crack very large fruits and seeds. This has been confirmed for the *Geospiza* finches on seven islands (Abbott, Abbott, and Grant, unpubl. data.). No one appears to have determined the maximum size seed that a small-billed species can crack. Probably the critical factors are seed depth (the smallest dimension of the seed), because the seed must be small enough to fit into the gape, and seed hardness, because the seed must be soft enough to be cracked by the jaw musculature. In the Galápagos, the largest-billed finch, *G. magnirostris* (bill depth 14-17 mm), was not recorded eating grass seeds (virtually the smallest type of seed most widely distributed) by either Lack (1945), Bowman (1961), or us. Also, the tree *Bursera graveolens*, which is widely distributed throughout the archipelago, produces a subglobular drupe fruit of approximately 10 × 9 × 8 mm and hardness of 4-6 kgf, varying from island to island. The fruit contains a seed, approximately 5 × 5 × 4 mm and hardness of 5 kgf, surrounded by a red aril. *G. fuliginosa* (bill

depth of 6-8 mm) was never recorded cracking a *Bursera* fruit or seed, but it does eat the aril. *G. fortis* on I. Daphne (bill depth of 8-11 mm) commonly cracks *Bursera* seeds, which it finds on the ground or from a dehiscing fruit, but was occasionally seen cracking unripe *Bursera* fruits (see also Beebe 1924). On I. Gardner adjacent to I. Española, *G. conirostris* (bill depth 12-14 mm) was often recorded cracking open unripe fruits to get the seeds as was *G. magnirostris* (bill depth 14-18 mm) on I. Daphne, I. Genovesa, and I. Rábida. These observations suggest that: (1) *G. magnirostris* is unable to manipulate very small seeds into position to crack quickly and so for energetic reasons avoids such seeds; (2) that gape size determines whether *Bursera* fruits or seeds or neither are able to be held in position for cracking; and (3) although small-billed finches can crack and eat rice grains of about 1.5 mm depth and hardness of 2-4 kgf faster than larger-billed species, these latter are able to handle larger and harder seeds which *G. fuliginosa* would find impossible to handle.

From these considerations, if depth of the rice grains used in the experiments had been increased from 1.5 to 3.0 mm, we would expect the feeding rate of *G. fuliginosa* to decrease, but that of the larger-billed species to increase. If grain of 4 mm depth had been offered, we would expect that *G. fuliginosa* would be unable to fit them into the gape. Similarly, if depth remained at 1.5 mm but hardness were doubled from 3 to 6 kgf, the larger-billed species should be able to crack and eat seeds of greater depth and hardness faster than small-billed species (if these can), but small-billed species should continue to crack and eat thin and soft/moderately hard seeds faster than the large-billed species. These hypotheses deserve testing in the laboratory, though not necessarily with Darwin's finches.

SUMMARY

The time taken by four species of wild *Geospiza* finches on two Galápagos islands to crack and eat long-hard and short-soft rice grains was measured. *G. fuliginosa*, the species with the smallest beak, on average cracked and ate both types of grain faster than the other species. All species (except *G. scandens*) cracked and ate the short-soft grains faster than the long-hard ones.

The feeding rates of three banded *G. fuliginosa* (of known bill dimensions) were such that the smallest-billed individual cracked and ate both types of

grain faster than the others. A banded *G. conirostris* (largest bill of all species studied) was slowest. We suggest that the very large-billed finches may have difficulty in quickly positioning small seeds for cracking.

In the experiments conducted, the large-billed *G. conirostris*, *G. fortis*, and *G. scandens* showed no significant preference for large grains, nor did *G. fuliginosa* prefer small grains.

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ORIENTATION OF ADÉLIE PENGUINS ON THEIR TERRITORIES

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Adélie Penguins (*Pygoscelis adeliae*) nest in dense colonies on the shores of the Antarctic continent and off-lying islands. Nests are situated in small nesting territories within the colonies. The position of established territories often influences the positioning of new territories, especially on uniform flat terrain (Spurr 1972). That is, behavioral interactions between penguins influence the arrangement of territories in a colony. This paper shows that behavioral interactions between penguins also affect the orientation of penguins on their territories.

Observations were made during the summer of 1968-69 at the University of Canterbury field station, Cape Bird, Ross Island, Antarctica (77° 13' 10" S, 166° 28' 30" E). I made two sets of observations to determine the effect of wind speed on orientation of penguins lying down and incubating eggs—one set on a calm day (wind speed 1.6 m/sec) and the other when a strong southerly wind was blowing (8.5 m/sec). Counts were made of the number of penguins facing into the wind or in other directions away from the wind. I read wind speeds from a small hand anemometer held 20 cm above the ground on the windward side of the colony.

Other observations were made at wind speeds less than 3 m/sec. The positions of 893 penguins, lying undisturbed on their territories during the incubation period, were plotted on colony maps. These were then analyzed with respect to geographical position and orientation of neighbors. Analyses were made with reference to eight compass directions (0, 45, 90, 135, 180, 225, 270, and 315 degrees).

The term, "central penguin," refers to a penguin that is surrounded by others. In Figures 1A and 1B, the central penguin is surrounded by eight others,

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corresponding to the eight compass directions. In the field, central penguins had no more than six neighbors; for analysis each was allocated to one of the eight compass directions.

The direction in which incubating penguins face is strongly influenced by wind speed (table 1). In strong winds, penguins incubating eggs tend to face into the wind. Thus, most penguins face in the same direction, usually either north or south (the predominant wind directions at Cape Bird). In calm conditions, or with light winds, orientation became random with respect to geographical position, but was strongly influenced by neighboring penguins. Fewer nests were located directly in front of a penguin (0° in table 2) compared to other locations (e.g. 45° from the front of a penguin). This means that penguins tend to face into inter-nest spaces, rather than directly towards another nest.

When penguins did face toward a neighboring nest, the orientation of the neighbor on that nest was significantly different from that of other neighbors (table 2). The neighbor directly in front never rested facing directly towards the central penguin, though penguins on other surrounding nests sometimes faced toward the central nest (fig. 1A), or in the opposite direction (180°) to the central penguin (fig. 1B). When penguins are undisturbed they show a significant tendency to avoid facing another penguin's head.

Penguins did not directly face one another when resting, but when a neighbor started rearranging nest stones near its boundary, a penguin would turn to face (and maybe threaten) that neighbor. When the neighbor stopped rearranging stones, the other pen-

TABLE 1. Orientation of penguins in relation to wind speed (χ^2 probability < 0.01).

Wind speed (m/sec)	No. of penguins facing		
	into wind	with wind	other
8.5	48	8	5
1.6	2	2	56

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