

THE RELATION OF THE FOOD TO THE SIZE AND
SHAPE OF THE BILL IN THE GALAPAGOS
GENUS *GEOSPIZA*.

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THE Fringillid genus *Geospiza*¹ of the Galapagos Archipelago contains about thirty-four species and varieties. Four subgenera may be distinguished on a color basis, but the specific and varietal character are almost entirely in the shape and size of the bill. The bill being the feeding organ, it is most natural to look first for the cause of its variation in a variation of the character of the food.

Geospiza heliobates feeds entirely on insects. But it inhabits exclusively the 'mangrove swamps' where there is nothing but insect food available. The other species are all seed-eaters, although they occasionally pick up a few ants and other small insects. The seeds that they eat are mostly small and they are usually swallowed whole, being found in this condition in the crop. Large seeds when eaten are broken into pieces by the beak before being swallowed, generally only fragments of such are to be found in the stomach. The birds feed a great deal upon the ground, picking up seeds that have fallen from the bushes, and at the same time taking in with the food a considerable amount of gravel.

With a view of determining whether there is any corresponding variation between the bills and the food, Mr. Edmund Heller and the writer, during 1898 and 1899, preserved the stomachs of two hundred and nine specimens of *Geospiza*. These represent *G. pachyrhyncha*, *G. strenua*, *G. conirostris*, *G. fortis fortis*, *G. fortis platyrhyncha*, *G. fuliginosa*, *G. scandens*, *G. scandens fatigata*, *G.*

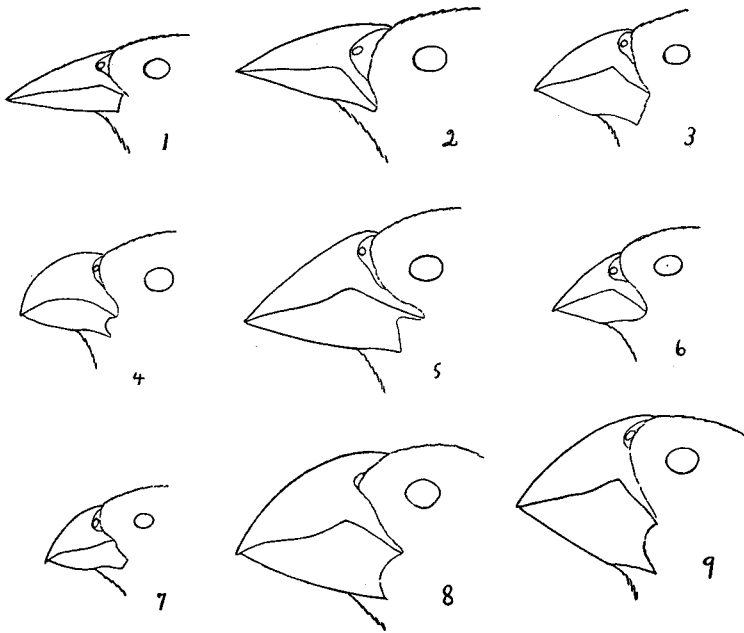
¹ The name *Geospiza* is here used in the same sense as used by Rothschild and Hartert (Novit. Zool., VI, 1899), *i. e.*, to include all of the related Galapagos genera of other authors, such as *Platyspiza*, *Camarhynchus*, *Geospiza* and *Cactornis*. Such a group is certainly a natural one; and in its lines of division are difficult to draw. Ridgway recognizes three genera: *Platyspiza*, *Camarhynchus* and *Geospiza*. The names of species are according to the synonymy in a paper yet to be published by Mr. Edmund Heller and the writer.

scandens rothschildi, *G. affinis*, *G. crassirostris*, *G. prothemelas*, *G. heliobates*. The specimens were collected from the islands of Albemarle, Narborough, James, Seymour, Duncan, Charles, Hood, Barrington, Tower and Bindloe. The dates run from December till June, inclusive.

Comparison has been made of the food of individuals of the same species at different places, and of the food of different species at the same and at different places. The results are somewhat conflicting. In any case one would require a great amount of evidence to come to any definite conclusions. Then, too, there is always a doubt created by the fact that the specimens were not taken on the different islands during the same months, and by the fact that the seasons vary considerably at different localities. What might appear to be evidence of a difference in food habit between a species on one island and a different one on another island, might be nothing more than a seasonal change of diet due to different plants being in seed at the two times. However, a few conclusions may be positively deduced, the results being sufficient to warrant the discussion.

The detailed records of the two hundred and nine stomachs are omitted. The data obtained are given in the following table, and the seeds are illustrated on Plates XII and XIII. The seeds have not been identified, but the names are not necessary. They are drawn to show their relative sizes, and are referred to in the succeeding discussion by their numbers on the plates. Figures 1 to 44, inclusive, except figure 42, are magnified $6\frac{2}{3}$ times. The others are magnified only half as much. The stomachs of Mockingbirds (*Nesomimus*) from eight islands have been examined in the same way. The records of these are given at the end of the table, and the seeds are figured on the plates along with the *Geospiza* seeds. The stomachs of all contained a total of sixty kinds of seeds. Seeds Nos. 59 and 60 are not figured.

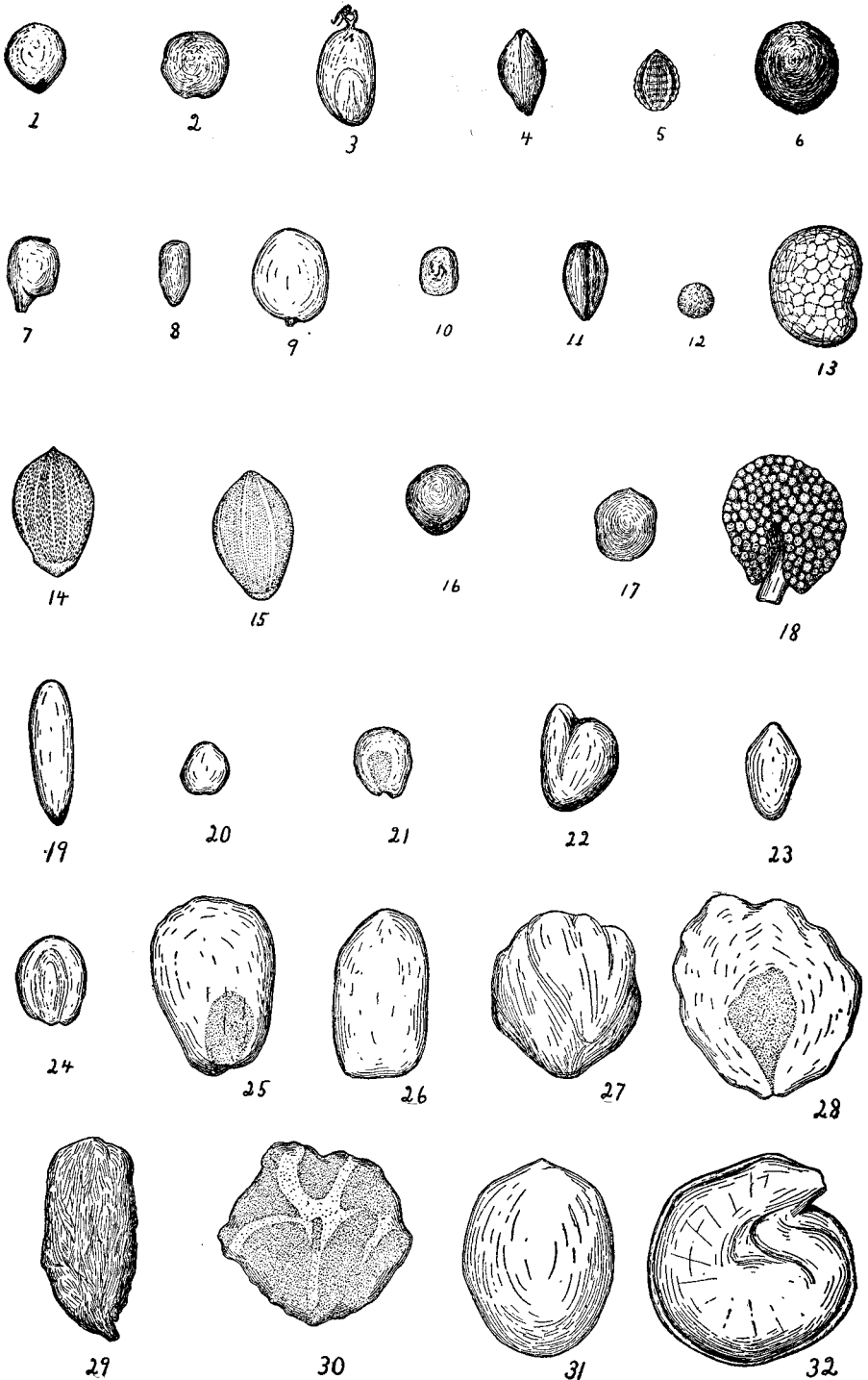
Following is the table (pp. 369-374) containing the records of the examination. It of course does not show the relative numbers of each seed present.



BILLS OF GEOSPIZA.

Natural Size.

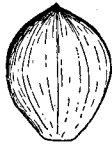
- Fig. 1. *Geospiza scandens scandens*, James Island, from Ridgway.
 Fig. 2. *G. scandens rothschildi*, Bindloe Island.
 Fig. 3. *G. fortis fortis*, Albemarle Island, from Ridgway.
 Fig. 4. *G. crassirostris*, from Ridgway after Gould.
 Fig. 5. *G. conirostris conirostris*, Hood Island, from Ridgway.
 Fig. 6. *G. fuliginosa parvula*, Tagus Cove, Albemarle Island.
 Fig. 7. *G. prothemelas prothemelas*, Albemarle Island.
 Fig. 8. *G. strenua*, Albemarle Island, from Rothschild.
 Fig. 9. *G. pachyrhyncha*, Tower Island, from Ridgway.



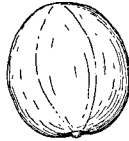
FOOD SEEDS OF GALAPAGOS BIRDS.



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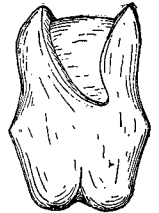
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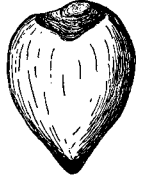
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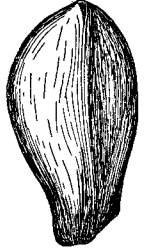
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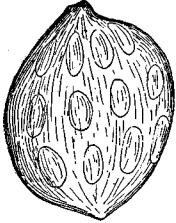
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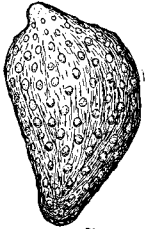
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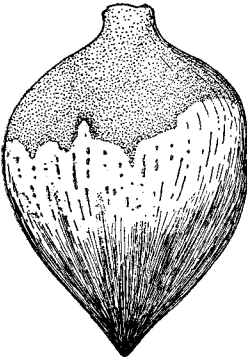
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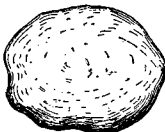
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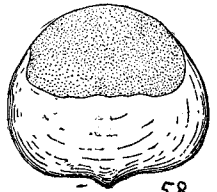
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From the facts given in the table the following propositions may be pretty well established.

I. *The food of GEOSPIZA as a whole differs from that of NESOMIMUS.*

This is evident from the fact that of the twenty-one seeds found in the *Nesomimus* stomachs, only eight were found in *Geospiza* stomachs. Of these seed No. 8, which was the predominant seed in the food of *Geospiza fuliginosa parvula* at Tagus Cove, Albemarle, was found in two specimens of *Nesomimus* from Bindloe Island. Seed No. 18, which occurred in eight *Nesomimus* stomachs, was present in only three *Geospiza* stomachs. The other seeds common to the diets of the two genera were of rare occurrence in each.

Nesomimus eats a great many more insects than does *Geospiza*, being insectivorous and granivorous in about equal proportions. Numerous pieces of large insects were found in nearly all of the *Nesomimus* stomachs, including grasshoppers, flies, beetles, caterpillars, and also spiders and centipedes. The seed part of the diet differs from the food of *Geospiza* in consisting of larger seeds, of seeds that the much smaller-mouthed *Geospiza* could not handle.

II. *The same species at different localities may feed on different seeds.*

The truth of this statement is best shown by a study of the food of *Geospiza fuliginosa parvula* (Pl. XI, Fig. 6) the most widely spread and most abundant form of *Geospiza* on the archipelago. In the stomachs of nineteen specimens of this variety from Tagus Cove, Albemarle Island, collected in January, there was found a total of only eleven species of seeds. Of these, seed No. 1 had been eaten by two birds, No. 2 by one bird, No. 4 by two birds, No. 6 by two birds, No. 8 by nine birds, No. 15 by one bird, No. 22 by five birds, No. 24 by three birds, No. 41 by two birds, No. 58 by one bird, and No. 59 by one bird. This shows that the birds here feed on seed No. 8 more than any other, and that seed No. 22 was second in numbers. Moreover, these two seeds were present in much greater numbers than the others in each stomach in which they occurred.

From Elizabeth Bay, Albemarle, there are only two specimens

and each of these had only seed No. 4 in its stomach. The specimens were collected in February.

Seventeen specimens were examined from Iguana Cove at the southern end of Albemarle, separated from Tagus Cove by a distance of about fifty miles. Here seed No. 1 was eaten by one bird, No. 2 by one bird, No. 4 by one bird, No. 15 by thirteen birds, No. 44 by three birds, and No. 55 by one bird. Thus, the only seed fed on at all constantly by the Iguana Cove birds is seed No. 15 — a seed found in only one stomach at Tagus Cove. The Iguana Cove specimens were collected in December.

Since we do not know what species of plants the different seeds belong to, we cannot say whether the differences in the food of the birds at Tagus Cove and Iguana Cove is due to a difference in the floras of the two localities, to a difference in the time of ripening of the seeds, or to a difference in the preferences of the birds with regard to the seeds at the two places. Since, however, seed No. 15 was found in abundance in the stomachs of birds taken on James, Seymour, Duncan and Barrington Islands in April and May, it would appear that the seeds should be ripe at Tagus Cove in January if they are ripe at Iguana Cove in December. That the plant occurs at Tagus Cove is shown by the fact that the seeds were found here in one stomach. The entire diet of the Tagus Cove birds consisted of seeds Nos. 1, 2, 4, 6, 8, 15, 22, 24, 41, 58 and 59; that of the Iguana Cove birds of seeds Nos. 1, 2, 4, 15, 44 and 55. Of the thirteen kinds of seeds only four are common to both sets. Hence, there is most evidently a difference in the food of the individuals at the two places, at approximately the same time of the year. It is, perhaps, most probable that this difference is due to the same seeds not being available in the same relative numbers at the two places.

Of five specimens from Narborough Island, taken in December, three had in their stomachs only seed No. 8, the other two contained only seed No. 22. These thus fed on the principal part of the diet of the Tagus Cove birds.

On James, Seymour, Duncan and Barrington Islands *Geospiza fuliginosa parvula* feeds almost exclusively on seeds Nos. 14 and 15. Specimens of one or both of these seeds were found in the stomachs of all the thirty-six birds examined, except in one from

James and one from Barrington. Next to these, seeds Nos. 10 and 57 were most abundant, each being represented in ten stomachs. These four seeds were also by far the most abundant wherever they were found. The rest of the diet consisted of seed No. 2, found in two Seymour birds and in one Duncan bird; No. 11, found in one Seymour bird; No. 17, found in one Seymour bird; No. 18, found in one James bird; No. 20 found in one Duncan bird; and Nos. 41 and 59, found in one James bird. These specimens were all collected in April and May.

The facts just detailed certainly show that the individuals of *Geospiza fuliginosa parvula* living on Narborough and at Tagus Cove, Albemarle, during December and January, have a different diet from those individuals living at Iguana Cove, Albemarle, in December, and on James, Seymour, Duncan and Barrington in April and May. The proof, from these facts, of proposition I, however, is somewhat invalidated by the consideration that seeds Nos. 14 and 15 may ripen at Tagus Cove and on Narborough later than January. But seeds Nos. 8 and 22 were not found in any stomachs except in those of birds taken at Tagus Cove. We can see, at least, that the diet of the birds depends on the local prevalence of certain seeds; and that, where the floras differ, the food of a species may differ.

III. *Different species at the same locality may feed on the same kinds of seeds.*

This proposition is much easier to prove than the last. Compare, for example, the food of *Geospiza fuliginosa parvula* (Pl. XI, Fig. 6) and of *G. scandens fatigata* on Seymour and Barrington Islands. As has already been shown, the food of the former species consists almost wholly of seeds Nos. 10, 14, 15 and 57, Nos. 14 and 15 being in the majority. An examination of the table will show that the food of *G. scandens fatigata* on the two islands is practically identical with that of *G. fuliginosa parvula*, consisting mainly of seeds Nos. 14 and 15, with Nos. 10 and 57 second in numbers.

The case of these two species, then, proves that species differing much in the size and shape of the bill (Pl. XI, Figs. 1 and 6) may have absolutely the same food habits. We have not, however, the material at hand to justify the statement of this as a

general truth. We cannot show how far it actually holds true of other species on the archipelago. The similarity in the food of these two common forms on Seymour and Barrington Islands is so striking, however, that one is almost forced to the conclusion that all the species of *Geospiza* eat simply whatever seeds are accessible to them.

IV. *Different species at different localities may feed on the same kinds of seeds.*

The truth of this proposition may be seen by a comparison of the food of *Geospiza conirostris conirostris* (Pl. XI, Fig. 5) on Hood, *G. scandens fatigata* on Seymour and Barrington, and *G. fuliginosa parvula* at Iguana Cove, Albemarle, and on Seymour and Barrington. The largest part of the food of *G. conirostris conirostris* in May consisted of seeds Nos. 14 and 15. Next in numbers were seeds Nos. 10 and 17. All but two of thirteen birds had eaten No. 14, and all but one No. 15, while Nos. 10 and 17 were each represented in six stomachs. Seed No. 5 was found in one bird, No. 23 in one bird, No. 26 in five birds, No. 28 in three birds, No. 29 in one bird, and No. 57 in one bird.

Hence, the food of *G. conirostris* on Hood Island is in the main the same as that of *G. fuliginosa parvula* at Iguana cove, Albemarle, and on Seymour and Barrington Islands, and is also the same as that of *G. scandens fatigata* on Seymour and Barrington. There are thus three species of *Geospiza* with very different bills (Pl. XI, figs. 1, 5 and 6), living at three localities, whose food is almost identical at approximately the same time of the year.

V. *Different species at the same or at different localities may feed on different seeds.*

If the size and shape of the bill is dependent on the character of the food, this proposition should be a general truth. However, the material under consideration affords only a few instances of it.

Geospiza pachyrhyncha (Pl. XI, Fig. 9) is peculiar to Tower Island. The stomachs of seven specimens taken in June contained only seed No. 57. We have no data to show what the food of other species on Tower consists of. Vegetation is extremely scant on the island, and all the birds may be forced to eat the same seed.

A specimen of *Geospiza strenua* (Pl. XI, Fig. 8) taken in January on Narborough had only seed No. 22 in its stomach. Five speci-

mens taken in April on James island had fed as follows; in one stomach were seeds Nos. 11, 26 and 28; in two others seeds Nos. 18 and 26; in another seeds Nos. 57 and 59; in the fifth seeds Nos. 14, 15, 18 and 59. Of two taken in June on Bindloe one had in its stomach only seed No. 46, the other only seed No. 44. These very scant data would seem to indicate that *Geospiza strenua* uses but little selection in the choice of its food. Altogether it has been found to eat seeds Nos. 11, 14, 15, 18, 22, 26, 28, 44, 46, 57 and 59. The James specimens alone had eaten seeds Nos. 11, 14, 15, 18, 26, 28, 57 and 59. This list is somewhat different from the diet of six specimens of *G. scandens fatigata* taken at the same time on James. The stomachs of these birds gave the following: seed No. 2 in one bird, No. 14 in two birds, No. 15 in three birds, No. 18 in one bird, No. 21 in one bird, No. 26 in one bird, No. 41 in four birds, No. 59 in one bird. The species of seeds forming the list in the two cases are almost the same, the main difference is in the proportions of the seeds present. It is a question whether the evidence in this case should not be given to proposition III. It, however, shows the weakness of the proof on which proposition V could be stated as a general fact.

A good example of the proposition under consideration may be derived from a comparison of the food of *Geospiza fortis* (Pl. XI, Fig. 3) at Tagus Cove, Albemarle, with that of *G. fuliginosa parvula* at the same locality. As has already been shown, the food of nineteen Tagus Cove specimens of the latter species was as follows: seed No. 1 had been eaten by two birds, seed No. 2 by one bird, seed No. 4 by two birds, seed No. 6 by two birds, seed No. 8 by nine birds, seed No. 15 by one bird, seed No. 22 by five birds, seed No. 24 by three birds, seed No. 41 by two birds, seed No. 48 by one bird. The table shows the following composition of the food of thirteen Tagus Cove specimens of *Geospiza fortis* taken also during January. Seed No. 2 had been eaten by one bird, seed No. 3 by four birds, seed No. 4 by one bird, seed No. 8 by one bird, seed No. 9 by one bird, seed No. 22 by five birds, seed No. 28 by two birds, seed No. 33 by one bird, seed No. 35 by three birds. The only important difference in these two cases is the predominance of seed No. 8 in the food of *G. fuliginosa* and its scarcity in that of *G. fortis*. These two species have somewhat

similarly shaped bills (Plate XI, Figs. 6 and 3), but that of *G. fortis* is the heavier.

Two specimens of *G. fortis platyrhyncha* from Iguana Cove, Albemarle, taken in December, had eaten only seeds Nos. 38, 40 and 48, seeds not found in the stomachs of any of the Tagus Cove, *G. fortis*, nor in any of the Iguana Cove specimens of *G. fuliginosa*.

Four specimens of the *Geospiza fortis* on James Island, which does not differ from the *G. fortis* of Tagus Cove, had eaten as follows, in April. Seed No. 15 occurred in two stomachs, seed No. 21 in two, seed No. 41 in two, seed No. 57 in one, and seed No. 59 in one. It will be observed that there is no seed common to the three sets, *i. e.*, in the food of the James Island, Iguana Cove, and Tagus Cove specimens of *Geospiza fortis*. The case of the James Island and Tagus Cove specimens belongs to proposition II; the *G. fortis platyrhyncha* differing from *G. fortis fortis* at two other localities belongs to proposition V. It is important to note that the food of all the individuals at any locality does not differ as a whole from that of the others, more than may the food of two individuals at the same locality.

Perhaps the best case under proposition V can be made out from a study of the food of *Geospiza crassirostris* (Pl. XI, Fig. 4) and of *G. fuliginosa parvula* at Iguana Cove, Albemarle. The food of five specimens of the former species, taken the last of December, consisted entirely of seeds Nos. 39 and 40, the former found in only one stomach, the latter in all. As has before been shown, *G. fuliginosa parvula* at Iguana Cove feeds almost entirely on seed No. 15, seeds Nos. 39 and 40 not being found in any of the stomachs.

VI. *Birds with small bills eat only small seeds; birds with large bills eat both small and large seeds.*

Geospiza fuliginosa (Pl. XI, Fig. 6) eats fern seeds larger than Nos. 14 and 15. The only larger one found in their stomachs is No. 57, but this is a thin, flat seed, and is nearly always broken into small pieces before being swallowed. In the stomachs of *G. strenua*, one of the large-billed species (Pl. XI, Fig. 8), there occurred, besides numerous small seeds, such larger ones as Nos. 18, 26, 28, 45 and 58. In the stomachs of *G. conirostris* (Pl. XI, Fig. 5) most of these same larger seeds were found and also No.

29. *G. fortis* (Pl. XI, Fig. 3) eats such moderately large seeds as Nos. 35, 40, and 48 together with larger ones such as Nos. 28 and 57. An examination of the table will show, however, that the larger-billed species by no means confine themselves to large seeds. It appears most probable that they eat the larger seeds simply because their large bills makes it possible for them to eat a greater variety of seeds. There is no evidence that they show a special preference for large seeds.

The foregoing six propositions are about the only conclusions that we can deduce from a study of the material in hand. It is evident that if these propositions were stated severally as general facts they would be mutually conflicting. Each is true only in some cases.

If it be assumed that the various sizes and shapes of bills amongst the *Geospiza* have been developed as adaptations to differences in food habit, then it must be shown that the different species of the genus feed on different species of seeds. This cannot be done. We can prove definitely that some species with very different bills feed on exactly the same kinds of seeds. On the other hand some of the evidence seems to indicate that some of the species and subspecies do have different food habits. We cannot say, however, that these differences of diet are not forced upon different species as a result of their living in different localities. Especially is this probable since, in some cases, we find that individuals of the same species living at different localities feed on different seeds. This is due evidently to flora differences between the two regions.

The evidence, then, seems to be in favor of the general conclusion that *there is no correlation between the food and the size and shape of the bill*. If this is true, then we must look elsewhere for an explanation of the variation of the *Geospiza* bill.