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ON PLUMAGE VARIATION IN MALE
DARWIN'S FINCHES¹

RESULTS OF THE GERMAN GALAPAGOS-EXPEDITION 1962/63. V.

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A. PLUMAGE VARIATION AND ITS INTERPRETATION

As has been well known for a long time, the males of Darwin's finches (Geospizidae) exhibit a high degree of plumage variation (cf. Rothschild and Hartert 1899, Snodgrass and Heller 1904, Swarth 1931, Lack 1945, 1947, Bowman 1961). In the six species of *Geospiza*, the plumage occurs in an intergrading series from the streaked female-like condition to an almost entirely black plumage; in this black plumage, only the undertail coverts are more or less broadly margined with whitish or pale buff. This continuous series of plumages was divided by Bowman (1961, p. 180) into seven approximately equal classes, in which class "1a" denotes black, with the exception of the undertail coverts; "1b" black, except for faint white margins to feathers of lower belly and undertail coverts; "2"- "4" increasing reduction of black from the belly up to the head; "5" a faint suggestion of black at the base of the bill; and finally, "6" denotes the grey plumage devoid of any black patch.

On this scale the males of *Camarhynchus* and *Platyspiza* fall only within the classes 3-6; i.e., they never attain the full black plumage. In the two species of *Cactospiza* there is no suggestion of black in the male. However, Lack (1947: 47) mentions one male specimen each of *Platyspiza crassirostris* and of *Camarhynchus psittacula* of almost entire black appearance; moreover, among hundreds of woodpecker finches (*Cactospiza pallida*) seen by him in the field, one male had a black head. The warbler finch (*Certhidea olivacea*), which shows variation of an orange patch at the male's throat, and the Cocos finch (*Pinaroloxias inornata*) are omitted from the following consideration.

Two general views as to the nature of this variable coloration have been proposed. Swarth (*l.c.*) calls the black males "perfect plumaged", "high plumaged", "adult" or "perfect adult" (see also Rothschild and Hartert 1899); the partly black and streaked males he considers as "variants" (p. 144). One can only guess that by these "variants" he thought of young males in contrast to "adult" males. However, Swarth (*op. cit.*, p. 24) admits the possibility that the plumages represent "color phases" independent of age. Lack (1945: 58 ff.) favored the view that the plumages represent age-dependent stages in the development of the individual. However, quoting from Orr's observations on captive *Geospiza* individuals in California, Lack states that "there is much individual variation, so that these stages overlap" (Lack 1947: 46). Beyond this he presents evidence that there is a good positive correlation between wing length and the amount of black in the plumage. Moreover, his field observations indicated that the black males breed earlier than the others. From these facts he concludes in analogy with other songbirds that the black males are *older* than the streaked males.

On the other hand, Huxley (1955) thinks of the geospizine plumages in terms of "continuous morphism" (i.e. a genetic polymorphism). Further, as the grey males tend to breed later than the black ones, they are supposed to be forced into the suboptimal arid lowland zones. This, in turn, is interpreted as "a secondary differ-

ential ecogeographical distribution of the two morphic types, so that here again the morphism spreads the species over a wider range of habitats" (p. 316). We want to comment on the concept of "continuous morphism" below. Here it will suffice only to stress, first, that there are typically no "two morphic types"; instead there is a complete intergradation of plumages in the male. Second, polymorphism is defined as having a genetic basis. However, not even offspring of single geospizine broods have been analysed with regard to plumage (cf. for example Hrubant 1955). This is one of the reasons why we think it premature to label the variation in the finches as polymorphic in the accepted genetic sense. Finally, Bowman (*l. c.*, p. 202) adopted Huxley's view that "the male plumages in *Geospiza*, *Camarhynchus*, and *Platyspiza* are examples of 'continuous morphism'".

B. METHODS AND ACKNOWLEDGMENTS

With these conflicting views in mind we began studying Darwin's finches. Since we stayed for an entire year (Sept. 1962 to Sept. 1963) on the islands—i.e. longer than any previous expedition studying the finches—we are able to present new data concerning the plumage variation. Our method was capture-recapture of color-banded finches on four islands, assessing their age by examining the cranial vault in the living bird (cf. Miller 1946), and their sex by laparotomy. The detailed data on plumages, molt, and breeding season will be set forth later (Curio and Kramer in prep.); here we report only on the plumage variation.

The birds were caught with mist nets and ground traps on Indefatigable Island; beyond this, we employed a hand-net on Tower and on Wenman Island as *G. difficilis* was very tame there. On Wenman Island, we were also successful in lowering a horizontally manipulated mist net swiftly on birds feeding at a bait station.

In order to assess the age of individual birds, various criteria were used. These consist of (a) the pneumatization of the skull, (b) the color of the bill, (c) the size of the testes, and (d) the stage of molt of the flight feathers. We consider none of the listed characters to be reliable when applied singly, yet meaningful when applied concurrently.

a) Generally, it may be presumed, that age in a songbird is reflected by the degree of its *cranial pneumatization* (for a review see Bowman 1961). There are however exceptions to this rule. According to Bowman's thorough study of skull pneumatization in the Geospizines it was evident that the correlation between the degree of ossification (i.e. the formation of a double-layered cranial vault), and plumage color in male *Geospiza* individuals is only suggestive. There are males in *G. magnirostris* and *fortis* possessing a fully pneumatized skull but grey plumage. Moreover, there are male *G. magnirostris*, *conirostris*, *fortis*, and *fuliginosa* which are black (1a) but have only a poorly pneumatized cranium (*l. c.*, table 40). Unfortunately, the data for *G. difficilis* are too meager to allow a similar comparison: among 9 skulls examined none was pneuma-

tized (table 38; the percentage of fully pneumatized skulls reads as 100% instead of 0%; this should be corrected in *Pinaroloxias inornata* too). Further, only two of the nine skulls were from males. Similarly, there is but a poor correlation between the two characters in question in *Camarhynchus* and *Platypsiza*, *Certhidea* possibly forming an exception (*l. c.*, table 41). Thus, it is only reasonable that Bowman concludes "that the rate of cranial pneumatization in the Geospizinae is subject to a lesser degree of individual variation than the timing of the molt or the amount of black plumage that is eventually acquired in males of certain genera" (p. 183). The minimal age at which the skull no longer possesses "windows" of single-layered bony tissue is not known. It could only be ascertained that a *G. scandens* male of at least 1.6 years of age from Indefatigable Island, which died in captivity (cf. Orr *l. c.*), showed considerable posterior "windows". Also, there are indications that complete ossification may be delayed up to six years of age (Bowman *l. c.*, table 39).

However, in living Tower *G. difficilis* individuals we found only pneumatized or fully opaque and single-layered conditions in an area of the cranial roof which could be exposed by a short slit of 6-8 mm in length. It was thus possible to view the whole area between the orbitals, the base of the zygomatic processes, the posterior border area of the parietals, and the parietals up to a line which connected more or less the anterior border of the orbita. In only one male with an otherwise pneumatized cranial roof we discovered tiny "windows" at the posterior border of the parietals (corresponding to Bowman's fig. 46-VI, p. 172, in *G. fuliginosa*). The important fact to be stressed here is that there was a clear-cut difference between skulls with large symmetrical "windows" and skulls with no detectable "windows".

After cutting a few feathers from the crown, a short slit was made with a scalpel in the sagittal plane; then the skin was gently lifted with pointed forceps, so that the whole accessible area of the cranial vault could be scrutinized. There was practically no bleeding. In *G. magnirostris* and *conirostris* the slits were correspondingly longer, in *G. fuliginosa* equally long as was found to be useful in *difficilis*. After examining the bone, the skin was immediately closed with a tiny patch of sticky tape. After \pm 10 days this had fallen off and the wound could be located only by the shortened crown feathers. The operation did not seem to disturb the birds seriously; at least those recaptured had not lost weight.

b) The color of the bill is highly indicative of reproductive conditions in the Geospizine finches (Swarth 1931, Lack 1945, 1947). Shortly before and during the breeding season the bill color changes from a pale yellowish (often mixed with pinkish), through a partially dark colored stage, or an intermediate one between black and yellow, to full black. In the intermediate condition the base of the mandibles or of only the lower mandible is yellowish whereas the rest of the bill stays dark brown or black. And in full breeding condition all adult birds possess black beaks, the females' sometimes being more brownish.

c) According to Bowman's (*l. c.*) analysis there is no convincing correlation between *plumage class* and the size of the *gonads* on Indefatigable Island; this conclusion applies to *Geospiza magnirostris*, *fortis*, *fuliginosa*, *Camarhynchus parvulus*, *C. psittacula*, and *Platyspiza crassirostris*. We shall not discuss his data in detail; instead we merely want to point to an opposite condition in our Tower finches, (p. 37.). Since, in general, we examined the gonads by laparotomy, the size of only the left testis or ovary could be assessed. The wound caused by the operation healed extremely well in all birds which we later caught repeatedly; after 8-10 days the scar could be hardly located.

d) Furthermore the stage of *molt* of the wing feathers offers excellent means for distinguishing both age groups. The reader is referred to section C 2 d.

Moreover, one supposedly old *G. difficilis* male on Tower refused to feed upon our Canary seed otherwise readily accepted by all birds that were certainly young (see later). We encountered this difficulty only in several other grey birds which turned out to be *old* females.

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C. NEW EVIDENCE ON PLUMAGE VARIATION

1. *Seasonal changes in the plumages of populations.*

Since our main purpose was an investigation of enemy recognition in the finches, our data on side-lines of research remained necessarily fragmentary. Yet, for some island populations we collected more extensive data on finches than had previously been collected in a single period of time (table 1 a). It is surprising to find that *Geospiza difficilis acutirostris* (Swarth's *G. acutirostris*) on Tower Island exhibits no continuous range of variation; instead, merely the extremes of the continuum of plumages, namely black and grey males, occur. The same applies to birds only seen but not caught, although the possibility that a class 2 bird or class 5 bird might have been overlooked cannot altogether be ruled out. However, males collected in other months, probably including December, belong to intermediate plumage types (table 1a).

The breeding season of *G. difficilis* on Tower Island had just finished when we began work. The young birds were not older than 3-4 months, for in the beginning of Jan. 1963 there had been no breeding activity on Tower Island. The difference of class-distribution between Lack's and our samples may be ascribed to the fact that our birds of the year were only several weeks old while those

TABLE 1. SEASONAL VARIATION

Island	Species	Time of year	Relation to Breeding Season
- a -			
Tower	<i>G. difficilis</i>	May 28-July 30	after
		June ¹⁾ Sept. ¹⁾	" /before
		June, Sept.; probably Dec. ²⁾	" / "
Tower	<i>G. conirostris</i>	May 28-July 30	"
Tower	<i>G. magnirostris</i>	"	"
Wenman ⁴	<i>G. difficilis</i>	Jan. 8-Feb. 14	before
- b -			
Indefatigable	<i>G. fuliginosa</i>	Aug. 8-25; Sept. 13-16; Sept. 9- Oct. 5; Nov. 15- Dec. 2	before
		Apr. 30-May 9	end + after

¹⁾From Swarth (1931, p. 184, 186).²⁾From Lack (1945, p. 56) and Swarth (*op. cit.*, p. 184); females omitted.³⁾Intermediate plumage classes were distributed between adjacent classes.⁴⁾See also table 2.

reported by Lack must have been several months older. The preponderance of black birds in Lack's sample might mean (a) that grey males had died in larger numbers than black males after the first half of the calendar year; or, (b) that grey males had largely molted into a black plumage. This point will be discussed below. The idea that the collectors might have biased the sample by favoring black birds is unlikely since one and the same man shot samples of quite different proportions of black to grey males on different islands and at different times of the year (Swarth 1931, Lack 1945, see later).

The data for *G. conirostris* and *magnirostris* reveal similarly that the intermediate males are scarcer than the extreme plumage classes. This holds for Lack's samples too, at least with regard to *G. magnirostris*.

It is possible to arrive at a more accurate estimate of the proportion of the two classes in *G. difficilis* than we have done so far. Assuming (a) that males and females are approximately equal in number, (b) that all black males are older than one year, and (c) that the grey males are young, we can assess the proportion of young birds among the unsexed grey individuals as follows. By subtracting 22 old females from the 180 unsexed *difficilis* (table 1 a) we obtain 158 young birds of both sexes. To these we have to add the 7 grey males. Taking for granted a balanced sex ratio among these young birds means that there are roughly *four times* as many young than old males in June and July (82: 22). This estimate rests entirely on the assumption that there are no old grey males

IN FOUR SPECIES OF *Geospiza*.

Plumage class (Bowman 1961)								Total Birds
1a + 1b	2 ♂ ♂	3	4	5	6	6 ♀ ♀ + sex ?		
- a -								
22	—	—	—	—	7	180		209
7	—	—	—	—	1	2	♀ ♀	9
10	—	—	—	—	—	4	♀ ♀	14
44	— 6 —			—	3	—		53
3	1	3	—	—	1	96		104
4	2, 5 ³	0, 5 ³	—	—	1	87		95
6	2	—	2	9	3	29		51
- b -								
26	14	4	0, 5 ³	2, 5 ³	4	104		155
1	1, 5 ³	1, 5 ³	—	—	1	14		19

(see below). This proportion of black versus grey males is drastically reversed later on in the year (cf. Lack's sample).

By assuming that all males of class 1-3 are older than one year, we arrive at similar ratios in *G. conirostris* and *magnirostris* respectively (table 1 a); for *conirostris* it amounts to 7:1 (grey : black) and for *magnirostris* to 6:1. The magnitude of this ratio might theoretically be biased by the fact that the black individuals tended to avoid traps. However, observations at our automatic ground traps and mist nets demonstrated no detectable difference in behavior between the two groups.

On the other hand just before the breeding season black and partly black males definitely outweigh the light-colored ones on Wenman Island (table 1 a), the computed ratio being 3:1 (black : grey). This would be a corroboration of Lack's sample of *G. difficilis* on Tower Island.

It would be highly desirable to examine the plumages on one and the same island in different seasons. We were able to catch finches repeatedly on Indefatigable Island; we can thus compare the proportions of dark and grey birds at different times of the year (table 1 b). The data (on both sexes) in *G. fuliginosa* reveal strikingly different proportions with regard to the end of the breeding season. Preceding the end we obtained a ratio of approximately 1:2 (47 dark: 108 grey), and just at the termination of the reproductive season a ratio of 1:4 (4:15). Thus we see that data collected by the same observer under identical circumstances confirm the relative increase of grey males as the breeding season

draws to an end. Hence, we are left with the question whether or not our assumption is correct that all black or partly black males are older than one year, and whether all grey males are younger than this.

From the material published by Swarth (1931), one can obtain the time of year that certain island samples had been collected. We divided the available data on male plumage distribution in the *Geospiza* and *Camarhynchus* species with regard to the breeding season. Although we accumulated field evidence that the breeding season, especially on islands with a humid zone, is longer than is generally assumed, we consider the breeding season to last only from December up to May. This is done because Swarth's material includes males from many islands with only a dry zone (for example: Wenman, Tower, Bindloe, Duncan, Jervis, Barrington, Hood, and Gardner near Hood Islands). The result of the comparison is set out in table 2. The meager data for the Wenman Island *difficilis* have been included for the purpose of a comparison with our data for the Tower Island *difficilis* (table 1 a).

As can be readily seen, black males predominate just before and in the beginning of the reproductive season, while grey males predominate after breeding. This is revealed by the overall ratio comprising all species listed, as well as the ratios of specific populations; there is no exception to the rule. By lumping all months of the year excepting those in the first two columns (table 2) a ratio of black versus streaked males is obtained which is more balanced; it lies in the approximate middle of the former ratios. In nearly every single island sample the black males tend to outweigh the streaked males (we comment on this imbalance below).

There are, however, two noteworthy exceptions. First, in *Camarhynchus parvulus* from Chatham Island black-headed males are only poorly represented—a fact which has already been noted by previous authors (Swarth 1931, Lack 1945: 47). On Charles, on the other hand, *C. parvulus* is predominantly black-headed (70 % out of 87 males Lack 1947: 48; this figure is obtained when the data set forth in table 2 are enlarged by other expeditions' material). However, two other related finch species on Charles exhibit a low proportion of black males (*C. pauper*; *Platyspiza crassirostris*, not contained in table 2 as there are no collecting dates in the reports). These differences between the *parvulus* populations were interpreted as genuine inter-island variation and not as sampling error (Lack *l. c.*, Huxley *l. c.*).

Second, *G. difficilis* collected in September on Wenman Island, were comprised of mainly grey birds, some of which had just fledged thus indicating that some breeding had taken place at that time. Whether breeding had not yet reached its climax remains an open question. Only three months later this ratio was reversed, although the number may be too small to allow generalization. However, the ratio obtained during our field work on Wenman Island had already shifted in favor of black males; the proportion of 6:16 (black : grey) lies between the two samples of museum specimens (cf. table 1 a). With regard to our sample of Wenman male records

TABLE 2. SEASON AND PLUMAGE RATIOS OF MALE *Geospiza*
AND *Camarhynchus*

In general only samples of more than 15 males included; data from Swarth (1931) representing specimens from Academy and Stanford collections.

Species	Island	collected in months	Relation to breeding season (Dec.-May) black : grey		
			before + begin	end + after	between seasons + whole year
<i>G. magnirostris</i>	Abingdon	6, 9		5 : 16	
	James	1, 4, 8, 12			23 : 14
	Jervis	12	20 : 1		
<i>G. fortis</i>	Abingdon	6, 9		3 : 19	
	Indefatig.	1, 7, 10, 11			19 : 19
	Seymour	4, 7, 11			15 : 3
	Daphne	7, 11			15 : 1
	Duncan	8, 12	17 : 4		
	Albemarle	1, 2, 3, 4, 5, 6, 8, 11, 12			52 : 25
<i>G. fuliginosa</i>	Charles	2, 3, 5, 6, 10			92 : 55
	Chatham	1, 2, 5, 6, 7, 9, 10			39 : 19
	Indefatig.	1, 4, 7, 10, 11			25 : 12
	Seymour	4, 5, 7, 11			26 : 7
	Duncan	5, 8, 12			34 : 22
	Albemarle	1, 2, 3, 4, 5, 8, 9, 10, 11, 12			33 : 17
	Barrington	5, 7, 10			28 : 2
	Hood	1, 2, 5, 6, 7, 9, 10			20 : 3
<i>G. difficilis</i>	Chatham	1, 2, 5, 7, 9, 10			44 : 29
	Wenman	9		3 : 29 ¹⁾	
	"	12	(5 : 1)		
	James	1 ²⁾ , 8 ³⁾ , 12 ³⁾	29 : 0		
	Indefatig.	1 ²⁾ , 7 ⁴⁾ , 11 ⁴⁾	19 : 4		
<i>G. scandens</i>	"	1, 7, 10, 11			25 : 9
	Seymour	7, 11			12 : 16
	Albemarle	3, 4, 8, 11			8 : 9
	Barrington	7, 10			45 : 0
	Charles	2, 3, 5, 6, 10			46 : 29
<i>G. conirostris</i>	Hood	1, 2, 5, 6, 7, 9, 10			41 : 18
	Gardner				
	near Hood	2, 5, 6, 9			34 : 34
<i>C. psittacula</i>	James	1 (5), 8 (2), 12 (6) ⁵⁾	12 : 0		34 : 34
	Bindloe	9			8 : 9
<i>C. pauper</i>	Charles	2, 3, 5, 6, 10			16 : 58
<i>C. parvulus</i>	James	1, 8	9 : 6		
	Albemarle	3, 4, 8, 11			19 : 17
	Charles	2, 3, 5, 6, 10			38 : 42
	Chatham				6 : 67
Total ratio			111 : 16	11 : 64	763 : 519

¹⁾Classified here because Gifford (1919, p. 242) had taken 4 young "which had been out of the nest but a few days" (Sept. 24th).

²⁾Two days collected.

³⁾Altogether four days.

⁴⁾Altogether seven days.

⁵⁾() = individuals; not all males.

Note: "Grey" includes grey and partly grey birds, i.e. classes 1b or 2 to 6.

we may be completely confident that it was obtained *before* egg-laying started, though vigorous courting and territorial fighting were well underway. This took place after the heavy rains in the end of January. Thus we may conclude that male *G. difficilis* on Wenman Island change from a predominantly streaked condition (including partly black males, after Swarth (*l. c.*)), right after breeding to a more black plumage, possibly within a few months. If one ascribes this shift to a differential mortality of the male groups involved one has to postulate that the majority of the grey males dies during this period but not in the much longer spell of time between the termination of the breeding season and September. In the face of modern work on population ecology this seems to be an unreasonable assumption.

In conclusion we may state that there is a striking change in the male plumage which occurs around the breeding season. How this is brought about will be explained now.

2. Plumage color and age

After having ascertained that *Geospiza difficilis* males on Tower Island comprised only fully black and fully grey, i.e. female colored, individuals (table 1 a) we must test our hypothesis that the black males are older than the rest. In fact, 19 of 22 black males of type 1a (11) and 1b (11) proved to be old as judged from various criteria. The remaining three males were regrettably not aged, when we were still unaware of the unique situation in the Tower *difficilis* (table 3).

TABLE 3. PLUMAGE CLASS, AGE, AND SEX IN INDIVIDUALS OF THE THREE *Geospiza* SPECIES ON TOWER ISLAND. MAY 28-JULY 30, 1963 (TYPES 4 AND 5 DID NOT OCCUR).

Species	Plumage	♂ ♂			♀ ♀			Sex ?		Total
		ad.	juv.	age?	ad.	juv.	age?	ad.	juv.	
<i>G. difficilis</i>	1a + 1b	19	—	3	—	—	—	—	—	—
	6	—	5	2	12	1	2	2	123	40
<i>G. conirostris</i>	1-3	7	—	—	—	—	—	—	—	—
	6	—	—	1	1	1	—	2	21	71
<i>G. magnirostris</i>	1-3	7	—	—	—	—	—	—	—	—
	6	—	—	1	1	1	—	—	10	75

a) *Skull*.—We examined the skull of 5 of our 22 black males (cf. table 3) and judged them to be fully pneumatized whereas the majority of the grey birds, i.e. 91.4% of 139, had a juvenile skull (see page 29).

b) *Bill color*.—A dark beak indicates old age (page 30). In our sample of *difficilis* from Tower Island no grey bird excepting a few adult females (see below) had a black beak, the bill being intermediately colored, but mostly yellowish. The distinction between old females and young birds from a distance was very insecure, however. On the other hand five of our 22 black males had a black

bill; four of them were caught before June 16th, and only one on July 11th. All others, before and after, had a dark brown bill, the base of which was sometimes light brown in the lower mandible; only once were the distal two thirds lighter brown in an 1b male. Twelve old females possessed a brown bill becoming lighter toward the tip, which itself was generally blackish; in only one the bill was nearly black with a lighter patch at the base of the lower mandible. Thus, *no grey bird*, judged to be juvenile, from the condition of its skull, possessed a *black bill*. The same holds true of the two other *Geospiza* forms on Tower Island; here the presumably young birds had a yellowish or even pinkish first half of the lower mandible, the rest of the bill being brownish. This condition of a clearly double-colored lower mandible was found in no bird with a fully pneumatized skull.

c) *Gonad size*.—From table 4 two facts become evident: (1) the grey males tend to have smaller testes than the black males, and (2) black males exhibit a clear decrease in testes size as the non-reproductive season advances, so that in the end of July the males

TABLE 4. PLUMAGE, TESTIS SIZE, AND SEASON IN MALE *Geospiza* ON TOWER ISLAND IN 1963.

Species	black			grey			
	class	date	left testis ¹⁾ mm.	class	date	left testis ²⁾ mm.	skull
<i>G. difficilis</i>	1a	May 28	3 x 2.5	6	June 16	1.5 x 1	juv.
	1b	June 19	3.5 x 2	6	" 19	1.5 x 1	"
	1a	" 22	3 x 2	6	July 10	2 x 1.5	"
	1b	" 23	3 x 2.5				
	1b	" 23	2 x 2.5				
	1b	" 27	3 x 2				
	1b	" 27	2.5 x 2				
	1b	" 28	2.5 x 2				
	1a	" 28	2.5 x 2				
	1b	July 4	2 x 1.5				
	1b	" 5	2 x 1.5				
	1a	" 10	1.5 x 1				
	1a	" 14	1.8 x 1.2				
	<i>G. difficilis</i> x <i>conirostris</i>				6	July 26	1.0 x 0.8

¹⁾Because of laparotomy other testis not examined.

could no longer be distinguished by this means. Such a state of affairs permits only two assumptions: (1) either some of the grey males are as old as the black males, but because of some reason their testes have not become mature; or, (2) the grey males are birds of the last breeding season and therefore still have immature gonads. Contrary to the first assumption all of the grey males in table 4 do

have juvenile cranial vaults. As there was no grey male with a pneumatized skull (see above), the second assumption seems more reasonable to us.

d) There was no clear-cut difference with regard to the *molt* of the contour feathers between the grey and black birds; few birds in either group renewed them during our stay. Some black birds had just finished the molt. But there was a plain difference in the molt of the flight feathers. Up to June 28th nearly all (i.e. 10 out of 12 old males and females) molted primaries *and* secondaries. In five of these birds whose age was judged mostly from the skull (including one of the two that did not renew their wing feathers), we observed shedding of the tail feathers as well. The mode of replacement of the old feathers need not concern us here; it will suffice to say that *all* secondaries were eventually involved. After that date molt occurred in only the secondaries in 10 out of 23 birds; the others had obviously fresh feathers and had thus previously finished the renewal of their wing feathers.

On the other hand the grey birds tended to replace only the three innermost secondaries ("Schirmfedern" in the terminology of V. Stresemann (1963, p. 104), i.e. "shelter feathers"). Among 127 young (as judged from the skull) birds only seven molted primaries. However, in each case it was only one primary (numbers 2, 3, 3, 5, 8, 8, 9)¹; in these individuals the renewal of the primaries was asymmetrical and thus probably abnormal.

Hence, we may conclude that the molt of the primaries, as well as the molt of the secondaries other than the three innermost ones, was clearly diagnostic of older birds. The replacement of only secondary feathers never occurred in an old bird, and is thus indicative of young age. In general, the same was true of *G. magirostris* and *conirostris* as well, yet strictly speaking of only the old birds. The young *conirostris* were liable to molt some or all the secondaries and the young *magirostris* some of the six innermost secondaries.

In summarizing the evidence for a distinction of old and young males in *G. difficilis* we conclude: there is a close correlation between (a) the type of plumage, (b) cranial condition, (c) bill color, (d) testis size, and (e) molt. There were no exceptions. Two of the characters examined were more indicative of age than the rest: the bill color and the testis size revealed that the bird in question had been reproductively mature or not and was thus over a year old or not. This leads us again to the assumption that the grey males are young birds.

Of this we became entirely convinced when checking the sex of the grey *G. difficilis* which were old according to their skull condition. When we performed laparotomies 12 grey birds with a windowless skull all turned out to be *females* (table 3); the young grey birds consisted of females *and* males, as some cases proved which we were able to check. Likewise a grey *and* old bird of each *G. magirostris*

¹Primaries were numbered from innermost to outermost.

and *conirostris* turned out to be a female. There are two old, grey *G. difficilis* which were not sexed.

Thus we conclude that, at least in *Geospiza difficilis* on Tower Island, all black birds are males and are older than one year of age, and that grey males are younger; the latter can be told apart from females only by examining the bird in the hand.

3. Seasonal plumage changes in individual birds.

The most direct evidence of our theory that male coloration is age-dependent—which one is tempted to generalize for all Darwin's finches—could be obtained by following individual males through the seasons. As the recovery rate of banded finches was small because of their long range movements the data are meager but a welcome corroboration.

For four species we are able to show that a male may molt from plumage class 6 into 2 or 5 (*Camarhynchus parvulus*, table 5). The shortest spell of time after which we noted a color change of the body was three weeks in *G. difficilis* on Wenman Island (No. 331). There are three *G. difficilis*, five *fuliginosa*, four *fortis*, and one *Camarhynchus parvulus* male which molted from a light plumage to a darker one. The reverse was never observed. In seven of those cases the bird was re-captured after having acquired an intermediate type plumage. Yet, it cannot be concluded that this meant a final stage for the particular molt, as five of these birds had not yet finished molting at the time of re-capture. The *G. fuliginosa* Nos. 287, 302, and 1155 as well as the *fortis* Nos. 303, 306, and 1079 would suggest several stages in the development of the final plumage, as the birds had a freshly molted, intermediate plumage when they were captured for the next-to-last time. There are only two birds with faint white margins in their black plumage who had, after more than 10 months, *not* acquired the fully black feathers (Nos. 1, 306). The change from the next-to-last plumage to the final one may be very slight (No. 287), or may be a veritable jump (Nos. 302, 1079). Therefore, an intermediate plumage cannot be a highly reliable indicator of age. This is well in accord with the words of Orr (1945, p. 102) having studied captive finches (*G. magnirostris*, *fortis*, *fuliginosa*, and *scandens*): "In captivity the males, at the completion of the postjuvinal molt, possessed a female-like plumage which normally was retained for one year. Second year plumage showed black on the head and throat of the male. In the third year plumage this black coloration extended down to the breast and the anterior part of the back. Full black plumage was usually attained the fourth year. A great deal of individual variation in the amount of black present in the various male plumages after the first year resulted in some overlapping. That this occurs in the native state is born out by museum specimens."

From this it appears that several years may elapse until the fully black plumage is attained; However, we think that many males attain a black plumage right before the first breeding season (see also Snodgrass and Heller 1904, p. 303). This is deduced from (1) a comparison of proportions of grey versus black males at different

TABLE 5. CHANGES IN PLUMAGE CLASS IN INDIVIDUAL FINCHES. SIX *difficilis*, WITHIN 3/4 TO 1 1/4 MONTHS ARE OMITTED. THE SAME APPLIES TO 1 FEMALE 1 TO 11 MONTHS.

Island	species	field No.	date		1st capture	
					plumage	molt
Wenman	<i>G. difficilis</i>	316	Jan.	8, 62	6	—
		327	Jan.	13, 62	6	centr. tail
		331	Jan.	17, 62	6	—
		326	Jan.	13, 62	6	—
Indefatigable	<i>G. fuliginosa</i>	1	Sept.	13, 62	1b-2	—
		287	Nov.	23, 62	2(-3)	head
	302	Nov.	27, 62	6	—	
	1150	Aug.	23, 63	1b-2	belly	
	1155	Aug.	24, 63	1b	— (fresh)	
	<i>G. fortis</i>	288	Nov.	23, 62	3	body
		303	Nov.	27, 62	2	— (fresh)
		306	Nov.	29, 62	3-4	"
	<i>Camarhynchus parvulus</i>	1079	Aug.	8, 63	4	"
24		Sept.	23, 62	6	—	

¹)As females only exceptionally attain black at the head, the fact that the unequivocally to sex.

²)Re-captures by Dr. David Snow, who kindly supplied his data, of finches

times of the year (p. 33 ff.), (2) that obviously all males in *G. difficilis acutirostris* attain the black plumage (1a, 1b) before they are a year old (an assumption made already by Swarth (*l. c.*, p. 24) but refuted by Orr (*l. c.*) along the lines of alleged sampling errors), and thus pass through the intermediate stages *within one molt only*. (3) One *G. fuliginosa* passed from class 6 plumage to a black plumage within nine months, i.e. within one molt cycle.

The relative rapidity which is taken by the prenuptial molt appears to be in good accordance with what we found: lumping the birds of all months of the year yields a ratio of black to grey males which is definitely not intermediate to the ratios obtained by combining both the pre-breeding-season and post-breeding-season records from museum specimens; instead it shows a striking preponderance of black males. This might be ascribed to the fact that the molt is passed through within a few months only.

There is one female *G. difficilis* which changed its color from typical female plumage to class 5 and perhaps further. However, this is not altogether unexpected as one female on Tower Island too (of the smaller *acutirostris*) had been found with "the head and upper breast almost solidly black" (Swarth 1931, p. 178). We are inclined to believe that such are exceptions to the rule that the female stays in its streaked grey plumage throughout its life.

There are a number of Wenman *difficilis* that had not changed

2 MALES AND 4 BIRDS OF UNKNOWN SEX, WHOSE PLUMAGE DID NOT CHANGE AND 10 UNSEXED *fuliginosa* INDIVIDUALS WHO WERE RE-CAPTURED AFTER

date	2nd capture plumage	molt	months apart	Sex
Feb. 7, 62	5	in process primar., tail	1	0 ¹⁾
Feb. 13, 62	4	in proc., se- condar., tail	1	♂
Feb. 10, 62	5	<i>idem</i>	3/4	♂, testes: left : 7 x 5 mm. right : 5 x 5 "
Feb. 11, 62	5	head black	1	♀, ovary: 3 x 4 "
June 3, 63	1a-1b	? ²⁾	10	♂
Apr. 4, 63	1b	? ²⁾	4	♂
Feb. 4, 64	1a	? ²⁾	9	(3rd capture)
Aug. 21, 63	2	head	9	♂
Nov. 25, 63	1a	? ²⁾	3	♂
June 9, 64	1a	? ²⁾	9 1/2	♂
April 10, 63	2	? ²⁾	4 1/2	♂
Feb. 6, 64	1a	? ²⁾	14	♂
Nov. 8, 63	1b-2	? ²⁾	11 1/2	♂
Dec. 12, 63	"	? ²⁾	12 1/2	(3rd capture)
Oct. 24, 63	1a	? ²⁾	2 1/2	♂
Feb. 29, 63	5	throat	5	♂ (song)

individual in question molted into type 5 alone is not considered here to point banded by the authors.

body color within a time during which others had. This might mean that they were females, or, that they acquired a darker plumage after we had caught them for the last time (although then the breeding season was drawing quite close), or, that they stayed grey for at least one breeding season. A similar state of affairs holds true for a number of Indefatigable *fuliginosa* (see table 5).

The sequence of molts in the male *Geospiza* we visualize is then as follows. After the nestling plumage a postjuvenile plumage is attained which is basically colored the same. The latter is then replaced during a prenuptial molt by the black plumage (or an intermediate one). In part of young *Geospiza* males on Indefatigable Island, however, there is obviously no prenuptial molt as some of them breed when still grey. From then on there may be one complete molt per year, in *G. difficilis* following the breeding season, or two as indicated by *G. fuliginosa* (table 5) and by Orr's observations in captivity.

D. DISCUSSION AND CONCLUSIONS

After having ascertained for at least some *Geospiza* species and *Camarhynchus parvulus* that acquiring the black plumage does depend on age, one may ask whether this is so exclusively.

Obviously Huxley (1955), when classifying the plumage variation in the Geospizines, held the view that this is an expression of only

genic variation in males; this view was subsequently adopted by Bowman (1961). However, on one hand Bowman (*l. c.*, p. 180) quoted verbatim a passage from Orr (here on p. 39) interpreting the different plumages in terms of age; on the other hand he holds the view that "the male plumages in *Geospiza*, *Camarhynchus*, and *Platyspiza* are examples of continuous morphism" (*l. c.*, p. 202). He believes that "there is reason to think that certain morphs (in the Geospizinae) are genetically fixed" (p. 197). Now, morphism (Huxley *l. c.*) is defined as genetic variation within a population. Apart from stating a tautology Bowman does not give the reasons for assuming genic variation of plumage, thereby leaving the conclusion open to question.

We here briefly comment on the concept of "continuous morphism" (Huxley *l. c.*). First of all, one of the essentials of morphism (polymorphism of Ford (1945) and others) is the existence of *discontinuously* distributed variants or morphs within one and the same population. This definition has now become so generally accepted that it needs no further elaboration. However, by calling intraspecific variation "continuous morphism" one deprives the concept of morphism of its meaning; logically then each character of an organism which does not vary discontinuously (i.e., the huge majority) would fall within a "continuous morphism". Restriction of the term to rather spectacular cases, such as the plumage variation in Darwin's finches, allows only for an arbitrary judgment which cannot satisfy the need for a clear distinction between discontinuous and continuous variation. Therefore, we are inclined to discard the concept of a "continuous morphism".

Discarding "continuous morphism" does not exclude the possibility that the genetic material underlying continuous variation may be discontinuous; this is even probable (cf. Huxley's concept of rate genes). But accepting this does not affect our argument, which is based on typological reasoning.

A minor qualification applies to the term "morphism" (Huxley). As Mayr (1963, p. 151) points out, in our view correctly, "morphism fails to bring out what the poly-component indicates, namely the occurrence of several variants". However, it is suitable to call the single variants "morphs" as was done by Huxley. Therefore, following Ford (1945), Mayr (*l. c.*), and others we would prefer "polymorphism" denoting a genetic and discontinuous variation, (as opposed to "polyphenism" denoting a discontinuous, non-genetic variation; Mayr *op. cit.*, p. 150).

Our data do *not* disprove the possibility that the age in which the fully black plumage is acquired varies genetically, or the mode of attaining the plumage, e.g. whether by a single molt or after only several molts. Finally, both the age and the mode of acquisition of the black plumage might vary. Even if this be so one is still not justified in labelling this "polymorphism", unless it is shown that at least one of these components varies discontinuously (see above).

The males of some Geospizines may have to pass through intermediate plumages before becoming black. However, this is definitely not so in *G. difficilis* on Tower Island consisting of only black and

grey males although the fullest perfection of black, i.e. class 1a, may only be acquired after the second molt. And no proof for this could be adduced by following individual males through their life, although on this point our data are too meager.

The inter-island variation of plumage types in *Platypiza* and *Camarhynchus parvulus* which we mentioned earlier (p. 34) would also not constitute a case of polymorphism but rather a geographic variation in the proportion of males attaining the final plumage. It is almost certain that such situations do not reflect varying age class composition on different islands, because this would mean that the *parvulus* population with predominantly black-headed males, in this case on Charles, would be composed of much more old than of young males. This would not be in accord with recent findings in population ecology of songbirds demonstrating that the older age classes form only a minor fraction of the population (see review of Lack 1954).

SUMMARY

Views as to how individual variation in the male plumage of Darwin's finches is brought about are briefly represented. Then new evidence is put forward that acquisition of the fully black plumage is dependent on age. At least in *Geospiza difficilis* on Tower Island the male does not pass through intermediate stages during successive molts; instead it attains the black plumage during the first molt following the post-juvenile replacement of feathers. This is deduced from (1) that after the breeding season there is no black male with juvenile characters, i.e. a non-pneumatized skull, molt of only the three innermost secondaries, a juvenile bill coloration, and testes of less than 2 mm length. (2) All grey birds had a non-pneumatized cranial vault, had never a black beak, molted in general only the three innermost secondaries, and three of the grey males examined had testes of less or up to 2 mm length. (3) Those few grey birds which were old according to all or some of these criteria proved to be females.

During the time preceding the breeding season black males outnumber grey males; this ratio is reversed after the breeding season in *Geospiza* and *Camarhynchus* species. This is regarded as a corroboration of the theory that age determines the final plumage coloration. Accordingly, individual males of *Geospiza difficilis*, *fuliginosa*, and *Camarhynchus parvulus* changed from a grey to a black plumage. This may be acquired in only one or several molts.

There is no support for the idea that plumage variation in Darwin's finches constitutes a case of polymorphism.

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