VARIATION IN THE SIZE AND SHAPE OF DARWIN'S FINCH EGGS

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ABSTRACT.—Egg size and shape variation was analyzed in 10 species of Darwin's finches. Egg shape varies among species: eggs of the tree finches are relatively long, those of the warbler finch are relatively short, and eggs of the ground finches are intermediate. *Geospiza conirostris* is unusual among the ground finches in laying eggs of similar shape to those of tree finches. These variations parallel to some degree the variation in egg shape among ecologically similar groups of species in continental regions. Egg size and adult body size are positively correlated, both intraspecifically and interspecifically. Darwin's finches, especially the larger species, lay relatively small clutches of small eggs in terms of egg or clutch weight in proportion to adult weight. They also have short incubation periods. These are considered to be adaptations that enhance repeated and rapid breeding at irregular intervals. *Received 24 September 1980, accepted 27 August 1981.*

AT the familial and ordinal level, egg size is a positive function of body size in a large variety of birds (Lack 1968, Rahn et al. 1975). A similar relationship between egg size (and shape) and body size has been demonstrated at the intraspecific level with a few species (e.g. Svensson 1978, Ojanen et al. 1979, Otto 1979). This paper deals with variation at an intermediate taxonomic level, the level of species within a subfamily. I report the results of an analysis of egg size and shape variation within and among species of Darwin's finches (subfamily Geospizinae) from the Galápagos Islands, and then compare size and shape relationship with other species of passerines, particularly finches, in continental regions.

METHODS

During a field study of Darwin's finches on Isla Genovesa in 1978 (Grant and Grant 1980a), I measured complete clutches of eggs of four species and, for comparison, two non-finch species: *Geospiza magnirostris, G. conirostris, G. difficilis, Certhidea olivacea, Nesomimus parvulus* (mockingbird), and *Zenaida galapagoensis* (dove). Maximum breadth and length were measured to the nearest 0.1 mm with callipers and weight was measured to the nearest 0.1 g with a Pesola® spring balance. Some of the parents were captured in mist nets and weighed to the nearest 0.1 g. A few eggs of *G. difficilis* were also measured on Isla Wolf in April 1978, and a few eggs of *G. fortis* and *G. scandens* were measured on Isla Daphne Major in March 1976.

I also measured the length and breadth of finch eggs in the California Academy of Sciences collec-

tion. This amounts to 69 partial or complete clutches of eight species. They were collected mainly on Islas San Cristóbal and Santa María in 1906, with a few from Islas Isabela (8), Española (3), and Fernandina (1). I disregarded the measurements of only one clutch of one egg. This was labelled as *G. crassirostris* (=*Platyspiza crassirostris*) from a nest at 1.5 m in cactus on Isla Isabela, but the egg dimensions and the nest placement strongly suggest that the identification was wrong.

To calculate egg volume, I used the formula from Tatum (1975):

$$V = \frac{\pi L B^2}{6}$$

where L is length and B is maximum breadth. Shape coefficients that characterize departures from a perfect ellipse make the estimate of volume more precise (Tatum 1975), but their elimination here for reasons of simplicity does not seriously bias the estimates with the present material. I have analyzed size and shape by subjecting clutch means to analyses of variance and covariance, t tests, parametric correlation, and regression (Steel and Torrie 1960, Rahn et al. 1975). I excluded repeat clutches.

Consistency of measurements was determined by measuring small samples of eggs of each species twice on different days about a week apart, pooling the data from different clutches, and then expressing the between-egg variance as a percentage of the total between- and within-egg variance. Consistency of length and breadth measurements expressed in this way exceeded 97% in all instances. Consistency of weights was lower because of the systematic decline in weight with age as a result of diffusive loss of water. The effect of daily weight loss upon sample parameters was minimized by restricting most

Table 1. Mean, standard error of the mean, and variance of egg dimensions (mm) and weights (g). n = sample size. Clutch numbers were assigned by time of breeding, and therefore correspond to early, middle, late, and very late times in the breeding season, January to May 1978 (Grant and Grant 1980a).

	Clutch 1			Clutch 2			Clutch 3			Clutch 4		
	$\bar{x}$	SE	s^2	$\bar{x}$	SE	s^2	$\bar{x}$	SE	s^2	$\bar{x}$	SE	s^2
Geospiza magnirostris												
Weight	3.16	0.04	0.0764	3.14	0.03	0.0575	3.19	0.05	0.1166			
Length	22.47	0.10	0.5211	22.01	0.15	1.2190	22.19	0.12	0.6413			
Breadth	16.55	0.05	0.1463	16.68	0.07	0.2662	16.74	0.07	0.2306			
n	54			58			43					
Geospiza conirostris												
Weight	2.63	0.04	0.0249	2.72	0.04	0.0624	2.74	0.04	0.0495	2.64	0.05	0.0379
Length	21.28	0.26	1.1707	21.41	0.12	0.7914	21.31	0.13	0.7720	20.72	0.13	0.3054
Breadth	15.53	0.06	0.0674	15.83	0.07	0.2777	15.86	0.07	0.2096	15.47	0.10	0.1915
n	17			61			43			18		
Geospiza difficilis												
Weight	1.77	0.02	0.0328	1.63	0.03	0.0554	1.73	0.02	0.0234	1.68	0.03	0.0306
Length	18.08	0.12	0.7017	17.93	0.09	0.6086	17.56	0.12	0.8497	18.08	0.18	0.7925
Breadth	13.66	0.06	0.1635	13.57	0.06	0.2498	13.70	0.06	0.1791	13.55	0.09	0.1884
n	52			69			55			25		
Certhidea olicacea												
Weight	1.55	0.03	0.0206	1.52	0.04	0.0186						
Length	16.80	0.12	0.2815	16.66	0.15	0.2942						
Breadth	13.31	0.07	0.0959	13.37	0.08	0.0740						
n	21			13								
Nesomimus parvulus												
Weight	4.88	0.06	0.1786	4.91	0.08	0.1420						
Length	26.45	0.14	1.0277	26.33	0.17	0.6962						
Breadth	19.10	0.07	0.2764	19.09	0.11	0.3077						
n	51			24								
Zenaida galapagoensis												
Weight	6.35	0.08	0.2984	6.74	0.11	0.3074						
Length	27.66	0.13	0.8079	28.06	0.21	1.1041						
Breadth	21.05	0.09	0.4004	21.53	0.12	0.3488						
n	49			25								

(>90%) measurements to the first 3 days after the clutches were completed.

Results

Sources of variation within populations.— Weights and dimensions of eggs measured on I. Genovesa are summarized in Table 1. There is a small amount of variation in egg size among clutches in early, middle, and late season. For example, egg length is significantly more variable in mid-season clutches of *magnirostris* than in early-season clutches laid by the same seven females ($F_{6,6} = 8.54$, $P < 0.05$). Some of the differences in means between clutches produced at different times by different groups of females (see Table 1) are also significant. The regression relationship between egg length and breadth is almost significantly different in *magnirostris* clutches laid in early and middle season (ANCOVA, $0.1 > P > 0.05$);

eggs were longer relative to their breadth in early clutches than in later clutches (see also Table 2). But most tests for seasonal differences were not significant, and significant ones showed no systematic trends. Therefore, except where specified I have ignored seasonal variation, and in subsequent analyses I have used only the first clutch I measured for each pair of birds.

Variation in egg weight, volume, length, and breadth of each species was partitioned, in separate one-way ANOVAs, into between-bird and within-bird components for each of the six species. In all cases there was significant ($P \ll 0.05$) between-bird variation, and its contribution to total variation fell between 60 and 98% (mode $\simeq$ 90%). This is in agreement with reports in the literature of other species (Ricklefs 1977, Ricklefs et al. 1978, Ojanen et al. 1979). It suggests that much of the variation is

TABLE 2. Repeatabilities (r) of egg dimensions, using means of successive clutches laid by the same female for n females. Clutch sizes did not differ between successive clutches (Grant and Grant 1980a). Egg weights have not been included because consistency of measurements is low. * = $P < 0.05$; ** = $P < 0.01$.

	n	Length	Breadth	Length/breadth	Volume
Geospiza magnirostris					
1st–2nd clutch	7	−0.544	0.908**	−0.436	0.624
2nd–3rd clutch	6	0.908*	0.962**	0.954**	0.717
Geospiza conirostris					
2nd–3rd clutch	9	0.810**	0.715*	0.799**	0.723*

heritable, as has been shown for both egg size and shape with a few species (Väisänen et al. 1972; Jones 1973; Kendeigh 1975; Ojanen et al. 1979; van Noordwijk et al. 1980, 1981). Also in agreement with these reports, the repeatabilities (correlations) of egg characteristics in successive clutches laid by the same female were generally high (Table 2). The maintenance of differences between females in successive clutches could reflect the consistent expression of different genetic factors among females, or it could reflect the consistent differences in environmental factors affecting females that laid successive clutches in the same territories. But repeatability values in these other studies were approximately the same as heritabilities estimated by standard parent-offspring regressions. This and other evidence (see van Noordwijk et al. 1981, for more extensive discussion) suggest that high repeatabilities reflect genetic differences in egg characteristics among females. This is important for arguments about the adaptive significance of egg dimensions.

Egg size in relation to adult size.—Mean egg size is positively correlated with mean adult size among species. This was established with 10 species of finches, using volume as a measure of egg size and adult weights taken from I. Genovesa, I. Santa Cruz (unpubl.), and I. Daphne (Grant et al. 1975). The product-moment correlation is large ($r = 0.99$) and highly significant ($P < 0.01$).

It is more customary to use egg weight as a measure of egg size (Heinroth 1922, Huxley 1927, Rahn et al. 1975) and to transform to logarithms in making interspecific comparisons. Estimates of mean egg weights are available for the four finch species on I. Genovesa (Table 1) and for the two finch species on I. Daphne. There is a strong positive correlation ($r = 0.96$, $P < 0.01$) between mean egg weight and mean adult size for this small sample. The sample size can be increased by first establishing by regression analysis a relationship between log egg weight and log egg volume for these six species, and then using the regression equation to predict log egg weight in the remaining four species for which only mean egg volume is known. Using these predicted values, I obtain an almost identical correlation coefficient ($r = 0.97$, $P < 0.005$). A further noteworthy feature is that the slopes of the regressions of log egg weight on log body weight are identical for the restricted sample ($b = 0.48 \pm 0.07$) and for the extended sample ($b = 0.48 \pm 0.04$; Fig. 1). Both are significantly lower than the common slope of 0.675 ± 0.015 (95% confidence limits) for 17 orders of birds (Rahn et al. 1975).

Mean egg size is positively related to mean adult size among populations of the same species. I do not have enough data to test this by correlation analysis. However, all dimensions of *difficilis* eggs from I. Wolf are significantly larger ($P < 0.001$) than those of *difficilis* eggs from I. Genovesa, and the mean adult weight on I. Wolf (20.2 g, $n = 20$) is significantly greater ($P < 0.001$) than the mean weight on I. Genovesa (11.6 g, $n = 105$). The differences in egg dimensions and body weights are approximately similar. The egg volume on I. Wolf can be predicted from the interspecific regression equation describing volume (Y) as a function of adult weight (X) (see Rahn et al. 1975 for a justification of this type of regression). The predicted volume is calculated to be 2,470 mm³. The volume estimated from the mean length and breadth of 23 eggs is 2,386 mm³. Thus, the predicted volume is within 4% of the estimated volume and well within the range of sampling error. The association between egg size and adult size is also shown by a comparison of dimensions of *fortis* eggs from I. Daphne and the combined sample of *fortis* eggs from Islas Santa María, San Cris-
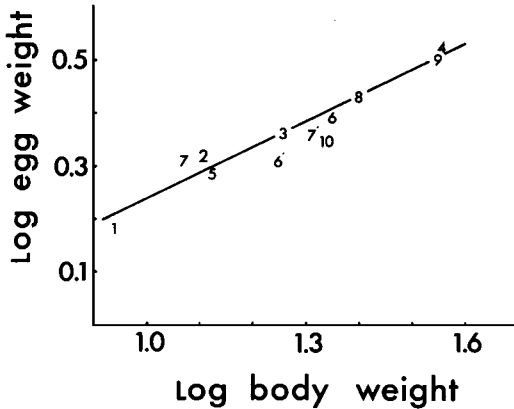
Fig. 1. The relationship between average egg weight and average adult body weight for 10 species of Darwin's finches; see text for sources of data. Symbols: 1 = *Certhidea olivacea*, 2 = *Camarhynchus parvulus*, 3 = *Cactospiza pallida*, 4 = *Platyspiza crassirostris*, 5 = *Geospiza fuliginosa*, 6 = *Geospiza fortis* (Islas San Cristóbal, Santa María, and Isabela), 6' = *Geospiza fortis* (Isla Daphne Major), 7 = *Geospiza difficilis* (Isla Genovesa), 7' = *Geospiza difficilis* (Isla Wolf), 8 = *Geospiza conirostris*, 9 = *Geospiza magnirostris*, 10 = *Geospiza scandens*. The regression equation for the 10 species (omitting 6' and 7' populations) is log Y = 0.48 log X − log 0.24; r = 0.97, P < 0.005.
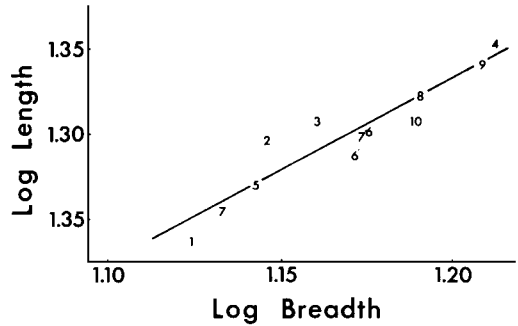

Fig. 2. The relationship between average egg length and average egg breadth for 10 species of Darwin's finches. Symbols as in Fig. 1. The regression equation is log Y = 1.10 log X + log 0.01; r = 0.96, P < 0.005.

tóbal, and Isabela. Egg dimensions are significantly smaller in the Daphne sample, and adult *fortis* are smaller on I. Daphne than anywhere else in the archipelago (Lack 1947).

Mean egg size is also probably related to mean adult size among individuals of the same population, but my samples (n = 16) of measured adults are too small to demonstrate it. In several tests with Genovesa data, mean egg dimensions were positively correlated with parental size (weight or tarsus) at P < 0.1, but only one correlation was significant at P < 0.05.

Egg shape.—The relationship between mean egg length and mean egg breadth among species (Fig. 2) is highly significant (r = 0.96, P < 0.005). It is even higher if just the six *Geospiza* species are considered (r = 0.99, P < 0.001). The slopes of the two regressions do not depart significantly from 1.0; they are 1.10 ± 0.12 (SE) for all 10 species and 1.08 ± 0.04 for the six *Geospiza* species. Both lines pass through the origin. In these respects, variation

in egg proportions among Darwin's finches does not differ from variation among a group of six species of unrelated finches on the Ecuadorian mainland. Using Marchant's (1960) data, I calculate the slope of the regression to be 0.98 ± 0.13, and this slope also passes through the origin.

The relationship in Fig. 2 obscures small but significant differences between species. Following Preston (1969), I have calculated indices of elongation by dividing length by breadth. The values in Table 3 show, as does Fig. 2, that the tree finches have relatively long eggs and the warbler finch has relatively short eggs; only 1 of 11 clutches of *Certhidea* (warbler finch) has an elongation index in the range of the 9 clutches of the tree finches. A difference between the groups as large as this is not expected by chance (Mann-Whitney U = 1, P < 0.001).

Ground finches are intermediate. To test for heterogeneity among them I have performed a one-way ANOVA on the decimal values given in Table 3, converted to percentages. I did not use the customary angular or inverse sine transformation because all but two of the percentages are outside the range of 0 to 20 (see Steel and Torrie 1960: 158). Significant heterogeneity was demonstrated ($F_{5,120}$ = 3.10, P < 0.025). By the Duncan's new multiple range test, *conirostris* values lie significantly (P < 0.05) outside the range of all of the other five species, whereas these five species are statistically homogeneous. Therefore, *conirostris* eggs are relatively long, like tree finch eggs.

Certhidea eggs were not included in this analysis, even though the sample of clutches is sufficient. They differ significantly from *G. difficilis* eggs, which are the least pointed among ground finch eggs (percentages log-transformed to correct for unequal variances, $t_{44} = 2.54$, $P < 0.02$).

Within species there is a positive relationship between length and breadth for only *difficilis* clutches ($r = 0.361$, $P < 0.05$) and *Zenaida* clutches ($r = 0.373$, $P < 0.05$). As these two species are represented by the largest samples (Table 3), there may be similar but weak positive relationships in the other species that only much larger samples would reveal.

As judged by eye, other shape parameters, such as asymmetry and bicone (Preston 1969, Paganelli et al. 1974), did not vary much among the eggs of Darwin's finches, although the shape of some late-season *magnirostris* eggs approached an ellipse without asymmetry. These parameters were not the same for Darwin's finch and dove eggs. A basic ellipse without asymmetry is the standard shape of dove eggs, whereas asymmetry is characteristic of the finch eggs. The difference between taxa is not reflected in the elongation indices (Table 3).

COMPARISONS WITH OTHER SPECIES AND DISCUSSION

Egg size.—It has been known since Huxley's (1927) analysis of Heinroth's (1922) data that egg weight increases among species as a power function of adult body size. Rahn et al. (1975) have shown that the slope of log egg weight regressed on log body weight, which is the same as the exponent of a power function equation, is remarkably constant for a variety of bird families and orders. The common slope is 0.675 ± 0.015 (95% confidence limits) for 17 orders of birds. The slope for Darwin's finches is 0.48 ± 0.04, and hence clearly significantly lower.

The slope of the relationship among Darwin's finches is low when compared with other subfamilies of the Fringillidae and related passerines. Amadon (1943) calculated a power function exponent of 0.786 for 10 temperate zone species of Emberizinae. Payne (1977) gave regression slope values of 0.54 for 8 species of Viduinae, 0.80 for 28 species of Estrildidae, 0.68 for 24 species of Ploceinae, and 0.61 for 6

TABLE 3. Elongation indices of eggs. An index was calculated for each clutch by dividing the clutch mean egg length by the clutch mean egg breadth, then the mean index for each species ($\bar{x}$) was obtained by dividing the sum of the clutch indices by the number of clutches (n). Samples are the same as in Fig. 1, except that 6 and 7[7] are not included.

	n	$\bar{x}$	Range
Ground Finches			
Geospiza magnirostris	22	1.339	1.16–1.40
Geospiza conirostris	16	1.374	1.28–1.45
Geospiza scandens	6	1.333	1.24–1.40
Geospiza fortis	20	1.325	1.22–1.44
Geospiza fuliginosa	27	1.324	1.22–1.44
Geospiza difficilis	35	1.310	1.18–1.42
Tree Finches			
Platyspiza crassirostris	3	1.380	1.35–1.41
Cactospiza pallida	3	1.383	1.30–1.47
Camarhynchus parvulus	3	1.430	1.38–1.47
Warbler Finch			
Certhidea olivacea	11	1.264	1.23–1.32
Mockingbird			
Nesomimus parvulus	16	1.385	1.32–1.47
Dove			
Zenaida galapagoensis	35	1.314	1.23–1.40

species of Passerinae. Tropical and temperate zone species were combined in the analyses. An unweighted mean of these slopes is 0.657, close to the common slope of 0.675 estimated by Rahn et al. (1975). Thus, Darwin's finches exhibit an unusually low slope. The intercept of the line (-0.25 ± 0.23) is also significantly lower than the 0.413 given by Amadon (1943); hence, the two groups of finches exhibit different proportionalities.

Rahn et al. (1975) used the same data assembled by Amadon (1943) to determine that egg weights of Fringillidae are about 20% of adult body weight when scaled to a 30-g bird. By the relationship in Fig. 1, a 30-g Darwin's finch lays a 3.0-g egg, which is only 10% of adult body weight. In fact, all Darwin's finches studied lay proportionally smaller eggs than Amadon's finches. On I. Genovesa the two small species, *Certhidea* ($\sim$7 g) and *difficilis* ($\sim$12 g), lay eggs of similar proportional weight, 17.4 and 17.1%, respectively, which compares with 25% for a 10-g finch in Amadon's group. The two larger species, *magnirostris* ($\sim$35 g) and *conirostris* ($\sim$25 g), lay proportionally much smaller eggs, 8.9% and 10.7%, respectively. The values for *scandens* and *fortis* on I. Daphne are 10.3 and 11.6%, respectively. One expects

egg weight as a proportion of body weight to decrease as body size increases (Lack 1968, Rahn et al. 1975), but not to the degree exhibited by Darwin's finches. Thus, it is the larger species of Darwin's finches that are particularly unusual. A consequence of laying relatively small eggs is that their nestlings hatch relatively underdeveloped (Grant 1981).

The relatively small eggs of Darwin's finches can be explained in two ways. The first is that they are determined by a set of maternal anatomical and physiological constraints peculiar to the Geospizinae that evolved before or soon after the colonization of the Galápagos. The adaptive reasons, if any, for these constraints and for the resulting egg sizes must be sought in the environmental conditions that the ancestors experienced. The second explanation is that relative egg size is determined by current environmental conditions through natural selection. The first is a phylogenetic hypothesis that cannot be tested directly, so it has an appeal in proportion to the failure of the second. I shall therefore develop the second and outline some tests.

I suggest that the relatively small eggs of Darwin's finches are a consequence of selection for high reproductive rates in all species under the peculiar conditions prevailing on the Galápagos. The amount, duration, and pattern of rainfall, which is highly variable and unpredictable (Grant and Boag 1980), determines the length of the breeding season. There are years of virtually no rain when some species do not breed at all (Boag 1981, Grant and Grant 1980b) and years of rains sufficiently prolonged that finches rear as many as five broods (Grant and Grant 1980a) and possibly more. There is considerable unpredictability regarding the duration of conditions suitable for breeding in any one year. Thus, the finches have to cope with a variety of conditions with very contrasting extremes; long periods without rain when survival is at a premium and occasional highly suitable conditions when rapid breeding is at a premium (Grant and Grant 1980a, b). Therefore, they are not solely r-selected or K-selected. I suggest that the relatively small eggs represent a compromise between conflicting selection pressures affecting reproduction and survival. Reproduction is maximized by the production of large clutches of small eggs, while post-breeding chances of survival to the next breeding episode are maximized by the production of small clutches of larger eggs. The compromise in Darwin's finches is a relatively low reproductive effort (egg or clutch weight) without a correspondingly low clutch size. The important point is that physiological capabilities of repeat breeding are enhanced, without a marked reduction in the chances of long-term survival, by the production of smaller than maximum eggs (cf. Williams 1966). This enhancement is greatest for the largest species because they experience energetic difficulties to a disproportionate extent in attempting to breed rapidly and repeatedly. The evidence for this is that in general the larger species of ground finches start breeding later and cease earlier than the smaller species (Downhower 1976, Grant and Grant 1980a).

The repeat-breeding hypothesis would be falsified if clutch size compensated for egg size (cf. Smith and Fretwell 1974), such that total clutch weight was the same or a higher proportion of adult body weight than in other groups of fringillids. Values of clutch weight for 10 other species of fringillids fall in the range of 95 to 110% of adult body weight (Rahn et al. 1975). Modal clutch sizes on I. Genovesa were three eggs for *Certhidea* and four eggs for the three *Geospiza* species in a year of extensive rains (Grant and Grant 1980a). From these figures I calculate total clutch weights to be 52% of body weight for *Certhidea*, 68% for *difficilis*, 43% for *conirostris*, and 36% for *magnirostris*. Maximum clutch sizes were 4 eggs for *Certhidea*, 5 eggs for *conirostris*, and 6 eggs for *magnirostris* and *difficilis*. These convert to proportional egg weights of 103% for *difficilis*, 70% for *Certhidea*, 54% for *magnirostris*, and 53% for *conirostris*. Modal and maximal values for *fortis* and *scandens* also lie in the range of 50 to 75%. Thus, only *difficilis*, when producing its largest clutches, reaches the range of values for other fringillids. Therefore, egg number does not compensate for egg size, and the hypothesis has withstood the test.

A consequence of low egg and clutch weights should be a short incubation period (Lack 1968). This appears to be correct. Incubation period (I) is given by the formula $I = 9.105\ B^{0.167}$, where B is body weight (Rahn et al. 1975). This permits the estimation of an incubation period of 13.09 days for *Certhidea* and 13.75 days for *difficilis*. These values fall just

outside the observed range of 10–13 days for both species (Grant and Grant 1980a). The differences are greater, however, for the larger two species. Estimations of 15.60 days for *conirostris* and 16.51 days for *magnirostris* fall well above the observed ranges of 11–13 and 10–14 days, respectively. These differences are difficult to evaluate because the confidence limits on the estimates given by Rahn et al. (1975) are broad. Nevertheless, the differences are in the predicted direction.

Other tests for the repeat-breeding hypothesis can be devised by comparing relative egg weights in different environments. Grant and Boag (1980) presented an argument for supposing that populations of finches living at high altitudes on the Galápagos experience more stable conditions than do those at low altitudes, and in consequence they are selected more toward the K end of the r–K spectrum. From this I predict that egg weights should be proportionally higher, and incubation periods longer, in high altitude populations than in low altitude ones. I also predict the traits of high altitude populations to be exhibited by *Pinaroloxias inornata*, the geospizine finch that occurs in humid forest on Cocos Island.

In a climatically similar region of the Ecuadorian mainland, proportional egg weights in unrelated finch species should be the same as in Darwin's finches. Marchant's (1960) study of several finch species in an arid coastal region of the Ecuadorian mainland yielded measurements of eggs and estimates of clutch sizes. Unfortunately, no adult weights were given, and I can only make a single crude comparison. Assuming that the adult weights of *Volatinia jacarina* are the same in Ecuador (unknown) and Central America ($\bar{x} = 9.6$ g, D. Steadman pers. comm.), and that egg weight can be predicted from egg volume by the same equation that describes the relationship for Darwin's finch eggs, I calculate mean egg weight to be 1.5 g, which is 16% of adult weight. This is similar to the proportional weight of Darwin's finch eggs. *Volatinia jacarina*, with a clutch size of three eggs (Marchant 1960), also produces a proportional clutch weight (48%) similar to Darwin's finches.

The most comparable set of data from a tropical region elsewhere are from Payne's (1977) study of nine species of nesting and repeat-breeding finches in south-central Africa. These species laid eggs in the range of 10 to 15% of adult body weight (i.e. similar to Darwin's finches). A separate group of brood-parasitic finches, which are opportunistic repeat-breeders with high seasonal egg production, generally laid smaller eggs relative to body size than did the most closely related nesting finches living in the same area (Payne 1977). Clutch weights were also unusually low in the parasitic finches (20–35% of adult body weight).

These facts are consistent with the hypothesis. This discussion, however, has ignored clutch size as an alternative or additional parameter to egg size that can be modified by natural selection to maximize repeated breeding. There is a need in future studies to consider these two parameters jointly, and to integrate them with other components of reproductive potential such as the duration of incubation and nestling periods and the interval between successive clutches (see Burley 1980, Grant and Grant 1980a).

Egg shape.—Shape differs between families of birds (Lack 1968, Preston 1969), but the significance of this variation is not understood. Lack (1968) argued that, whatever the biological meaning of the variation, egg shape is adaptive. This assumes that the variation is at least partly determined genetically. It is a reasonable assumption, because variation within a population of Great Tits (*Parus major*) is highly heritable (van Noordwijk et al. 1980, 1981).

Variation in egg shape among Darwin's finch species may also be adaptive. If variation among families in continental regions is adaptive, I would expect parallel variation among Darwin's finches, because adult finches have converged in body form and beak proportions on members of different continental families (Lack 1947). Bowman (1963) has identified some of these convergences, and Preston (1969) has provided egg shape (elongation) indices (E) for many families of birds. Using this information and the data in Table 3, I find there are some correspondences in egg shape between finches and their systematically unrelated ecological homologues elsewhere.

Thus, the warbler finch ($E = 1.26$) is similar to the Sylviidae (mean 1.28; range 1.26–1.30) and Parulidae (1.30; 1.25–1.37). Almost all other passerines have relatively longer eggs. Bowman (1963) identifies tangers (Thraupidae) as

the ecological equivalent of the tree finch *Cactospiza pallidus*, and in both cases the elongation index is 1.38. Finches (Fringillidae) have a mean value of 1.32, almost identical to most *Geospiza* species. *G. conirostris* on I. Genovesa shows resemblances to orioles (Icteridae), and its index of 1.37 is almost the same as the icterid index of 1.38.

Against these correspondences are two exceptions. *G. scandens* also resembles icterids, but its elongation index is typical of the finches at 1.33. The tree finch *Camarhynchus parvulus* resembles tits (Paridae) (Bowman 1963), but the parid index (1.32; 1.26–1.39) is much lower than the *C. parvulus* index of 1.43. It is difficult to evaluate these exceptions as they both involve small samples of measurements. It should also be mentioned that, whereas *Nesomimus parvulus* (1.38) is typical of the Mimidae (1.36; 1.33–1.43), *Zenaida galapagoensis* has an unusually small index (1.31) for its family (1.33–1.36). This suggests that some departures from expectation might occur among Darwin's finches for reasons (unidentified) other than incorrect assessment of ecological homology.

If egg shape variation is adaptive, its significance lies in incubation; different egg shapes are optimal for incubation by birds of different bodily proportions in nests of similar shape (Orr 1945, Lack 1947). This could be tested by experimentally varying the shape of artificial eggs and measuring their temperatures beneath incubating birds.

The nonadaptive alternative hypothesis is that egg shape variation is a consequence of variation in the body proportions of adult females for anatomical and physiological reasons governing egg formation in the oviduct. In this case, body size and egg size may be adaptive, but egg shape is a byproduct of those adaptations. The influence of body size is mediated by the oviduct, whose maximum extensibility sets an upper limit to egg breadth among eggs of various sizes; egg length is not so constrained. Beyond a certain egg breadth, therefore, increases in egg volume should lead to disproportionately long eggs as breadth remains constant or even declines (van Noordwijk et al. 1981). Thus, over the full range of intraspecific variation in egg size there may be no correlation between egg length and breadth, and breadth should vary less than length. Both

of these characteristics were observed in the present study. Moreover, mean egg width was also more strongly correlated with mean adult female weight in the 10 finch species ($r = 0.991$, $P < 0.001$) than was mean egg length ($r = 0.943$, $P < 0.001$), which is in agreement with the above reasoning. A further indication that egg shape variation is a consequence of egg size variation is to be seen in the similarity of Fig. 1 and Fig. 2. There is an approximate correspondence between orthogonal deviations from the egg size–body size regression in Fig. 1 and deviations of the same species from the length-breadth regression line in Fig. 2. The two sets of deviations are significantly correlated when ranked ($r_s = 0.594$, $P < 0.05$, one-tailed).

The nonadaptive hypothesis outlined here can explain why tree finches have relatively long eggs. They are selected to lay relatively few large eggs because, living generally at higher altitudes than ground finches (Lack 1947), they are less subject to annual variations in climate and food supply, and so have more stable populations. The hypothesis, however, does not explain why continental fringillids lay much heavier eggs relative to body weight than do Darwin's finches but produce eggs of similar shape. This would have to be explained by a relatively wider oviduct in the mainland finches. In conclusion, although there is much support for the hypothesis that egg shape is to some extent a consequence of egg size and oviduct constraints and selection acts on heritable variation in egg size, there is enough uncertainty to justify a repeat of Lack's (1968) call for more research into the significance of egg shape variation.

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NOTE ADDED IN PROOF

After this paper was written, I measured the eggs (in the British Museum) of one of the species missing from the original analysis, *Camarhynchus psittacula*. The mean elongation of the single clutch of three eggs from Isla Pinta was 1.45 (cf. Table 3). The mean dimensions lie above the regression line in Fig. 2, and, making the appropriate calculations using unpublished body-weight data, I find a similar placement above the regression line in Fig. 1. In these respects, *C. psittacula* closely resembles *C. parvulus*.