

The Relative Size of Darwin's Finch Eggs

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Scott and Ankney (1983) have pointed out I was in error in concluding that Darwin's finches lay unusually small eggs (Grant 1982). I discovered the error independently when trying to reconcile Newton's (1972) statement that European finches lay eggs weighing approximately 10% of adult female body weight with Rahn et al.'s (1975) finding that North American finches lay eggs approximately 20% of adult body weight. As detailed by Scott and Ankney (1983), Rahn et al. (1975) mistakenly equated egg weight with egg value (length \times breadth²) in Amadon's (1943) treatment of North American emberizid data. I repeated the error. In fact, for both groups of finches 10% is the approximately correct figure.

Exactly how do Darwin's finches differ from continental species? To answer this I have followed Amadon's (1943) example and used egg value ($LB^2/1,000$) as an index of volume (cc) rather than manipulate the data to calculate egg weight. Amadon (1943) estimated the intercept and slope of the relationship between egg value and body weight on a double log scale but did not calculate confidence limits on the estimates. Eleven species of continental finches were involved in his analysis, but two were represented twice by two subspecies. To avoid a possible bias that such a repetition might introduce, I repeated the analysis after first eliminating the subspecies with the smallest sample of body weights, namely *Passerculus sandwichensis nevadensis* and *Passerella i. iliaca*. The recalculated values, with 95% confidence limits, are -0.382 ± 0.057 for the intercept and 0.786 ± 0.042 for the slope. I recalculated the relationship with the two subspecies added and, separately, with the inclusion of three more species that Amadon (1943) had excluded because he considered their body-weight data inadequate. The results were almost the same, differing in the intercept by 0.02 and in the slope by 0.01 (maximum).

The relationship between egg value (EV) and adult body weight in grams (W_A) is thus

$$\log_{10}EV = 0.786 \log_{10}W_A - 0.382$$

or

$$EV = 0.415W_A^{0.786}$$

Ten species of Darwin's finches spanning a nearly identical range of adult body weights (Grant 1982) give a very different intercept (-0.055 ± 0.073) and

different slope (0.551 ± 0.058). The relationship can be represented as

$$\log_{10}EV = 0.551 \log_{10}W_A - 0.055$$

or

$$EV = 0.881W_A^{0.551}$$

The two regression lines for Darwin's finches and North American emberizids, respectively, intersect when log body weight is 1.391, or body weight is 24.6 g. This is the approximate weight of *Geospiza conirostris*. The two species of Darwin's finches above this weight, *G. magnirostris* and *Platyspiza crassirostris*, have relatively small eggs compared with the North American birds of similar weight (36 g). All the remaining Darwin's finches have relatively large eggs, not small eggs as concluded earlier (Grant 1982).

Do Darwin's finches have relatively large eggs compared with finches on the nearby South American mainland as well? At the time of my original analysis, I was unable to answer this question, because body-weight data were not available for the species studied by Marchant (1960) in Ecuador. I now have a set of data from Peru, however, kindly supplied by M. D. Williams (pers. comm.; see also Williams 1981a, b). The species, with samples of body weights and egg measurements given in that order in parentheses, are: *Sicalis flaveola* (16, 21), *Piezorhina cinerea* (16, 28), *Volatinia jacarina* (3, 2), *Poospiza hispaniolensis* (6, 2), *Aimophila stolzmanni* (41, 33), and *Sporophila peruviana* (21, 9). The relationship between the means of EV and W_A for these six species is

$$\log_{10}EV = 0.808 \log_{10}W_A - 0.414$$

or

$$EV = 0.385W_A^{0.808}$$

The 95% confidence limits on the coefficients are 0.639 and 0.977 for the slope and -0.196 and -0.632 for the intercept. Strictly, analysis of covariance is required for a comparison of regressions. Nevertheless, it is clear that the relationship for South American species is strikingly similar to the relationship for North American species (above) but is not similar to the one for Darwin's finches. These results strengthen the conclusion that Darwin's finches lay relatively large eggs.

The *high intercept* for the Darwin's finch regression means that the smallest species lay especially large eggs. The point is illustrated by converting egg value to egg weight (W_E) in grams by means of Schoenwetter's equation (in Amadon 1943)

$$W_E = 0.5128EV,$$

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then expressing egg weight as a percentage of adult weight for each species. For the 14 North American emberizids percentage egg weight varies from 9.5 to 12.8, and for the 6 South American species it varies from 9.8 to 13.2, whereas for the 10 species of Darwin's finches it varies from 8.9 to 17.3. The four smallest species of Darwin's finches have higher percentage egg weights than any species in the North American and South American groups: the four species, and their mean weights, are *Certhidea olivacea* (8.8 g), *Camarhynchus parvulus* (13.0 g), *Geospiza difficilis* (11.8 g) and *G. fuliginosa* (13.3 g).

The low slope of the regression means that Darwin's finch eggs increase in size slowly with increasing body size among species. In this respect they differ from most other birds. Martin (1981) deduced that egg weights among birds in general should scale to body size in the manner

$$W_E = k W_A^{0.75},$$

where k is a constant. He performed a test with weights (in milligrams) from 127 species and found good agreement with expectation. The empirical formula was

$$\log_{10} W_E = 0.79 \log_{10} W_A + 2.34,$$

with 95% confidence limits on 0.79 of 0.75 and 0.84. The North American and South American emberizids clearly fit the theoretical expectation, because the slopes (0.786 and 0.808, respectively) of $\log_{10} EV$ regressed on $\log_{10} W_A$ are the same as the slopes of $\log_{10} W_E$ on $\log_{10} W_A$, as EV is multiplied by a constant (0.5128) in each case to give W_E . Darwin's finches do not fit the theoretical expectation, either with calculated egg weights (slope = 0.551) or actual egg weights from a restricted sample of species (slope = 0.48; note the intercept for this equation should be -0.24, not $\log_{10} -0.24$ as reported in Grant 1982).

Why then do Darwin's finches exhibit the unusually low slope and high intercept? I follow the approach adopted earlier toward a similar question (Grant 1982), although not the incorrect details. The surface-area hypothesis of Rahn et al. (1975) and the metabolic hypothesis of Martin (1981) have successfully accounted for variation in relative egg size at higher taxonomic levels, perhaps because of the heterogeneity of the taxa, but neither hypothesis predicts the low slope in Darwin's finches. These two failures suggest that local ecological circumstances need to be considered.

I suggest that the most important ecological factor influencing variation in relative egg size is the resource flush that occurs following the initial heavy rainfall that triggers a breeding response in the finch species (Grant and Boag 1980, Grant and Grant 1980). In general, small-bodied species should be able to take greater and quicker advantage of this than large ones for body-size related energetic reasons (e.g. see

Downhower 1976). They are able to manufacture relatively large eggs quickly. The advantage of relatively large eggs is that the young hatch at a relatively advanced stage of development as a consequence of a relatively long incubation period (Grant 1982), and this gives them a good chance of fledging at a relatively large size (Grant 1981). I suggest further that the risk of nest predation contributes to the selective forces acting on egg size. For example, in mainland environments, where the daily risk of nest predation is higher, the advantage of large egg size is counterbalanced by the attendant disadvantage of a longer (vulnerable) incubation period, and, in fact, both incubation and nestling periods, which generally covary among species for developmental reasons (Lack 1968), are shorter on the Ecuadorian mainland than the Galápagos (Grant and Grant 1980). On the Galápagos, nests of the largest species, *G. magnirostris*, are especially vulnerable to predation by owls (*Asio flammeus*) in a time-dependent manner, the species does not lay relatively large eggs, unlike its smaller congeners, and its incubation and nestling periods are not relatively long (Grant and Grant 1980).

This food-predation hypothesis explains why the small species of Darwin's finches have relatively large eggs and why the slope of the relationship with body size is low, but, as the energetic advantage of small adult female size could be translated alternatively into a large number of eggs, there is a need to consider jointly the factors affecting egg number and egg size (Grant 1982; see also Ricklefs 1968, 1970; Smith and Fretwell 1974).

I thank B. R. Grant, T. D. Price, D. Schluter, R. A. Väisänen, and J. H. Zar for helpful comments on the manuscript, M. D. Williams for allowing me to use unpublished data, and C. D. Ankney and D. M. Scott for showing me an early version of their paper.

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Received 4 June 1982, accepted 26 October 1982.

Further Notes on Variation in Leach's Storm-Petrel¹

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Bourne and Jehl (1982; = B & J) disagree with my taxonomic treatment of *Oceanodroma leucorhoa* (Ainley 1980) at the southern end of the species' range in the eastern North Pacific, particularly my merging of *O. l. chapmani* with *O. l. leucorhoa* and my separation of populations at Guadalupe Island. In regard to *O. l. chapmani*, they attempt to substantiate its validity as a subspecies. They give two reasons for recognizing a sharper distinction between it and more northerly populations than my data indicate. First, they claim their data on ratios of color morphs on Los Coronados and San Benitos (p. 793) are closer to the truth than the patterns in the 103 specimens available in museums (i.e. my Fig. 2, 1980). Their unpublished data cannot be assessed, but, in general, they still help to illustrate the point that I emphasized, namely, that whitest morphs predominate in the north and darkest ones in the south, while those in between are mixed. The situation is thus akin to that of *Fulmarus glacialis* and *Puffinus pacificus* of the Pacific region, where similar color variation has not been given taxonomic significance; B & J should explain why color variation should be treated differently in Leach's Storm-Petrels.

Even if color were a useful character, their second point (p. 796), that 90% of all dark birds in the eastern North Pacific breed on the San Benitos and Coronados, which would therefore validate *O. l. chapmani* as a subspecies, is pertinent only after they first merge *O. l. willetti* (Los Coronados) with *O. l. chapmani*. This is contrary to Austin (1952), to the A.O.U. (1957), and even to Bourne's earlier opinion (*in* Palmer 1962) and thus requires much more support with data than they offered. Furthermore, in their com-

parison of population sizes they do not point out that storm-petrel populations in the Channel Islands have not been well studied and that on islands except San Benitos, and especially on Guadalupe, Los Coronados, and the Channel Islands, populations have been drastically reduced and forced onto adjacent rocks and islets by the introduction of exotic mammals to main islands (e.g. R. L. DeLong and R. S. Crossin, "Status of seabirds on Islas Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados," unpubl. MS, Pacific Ocean Biol. Surv. Progr., Smithsonian Inst.). Thus, most dark-rumped birds do *presently* nest on San Benitos, but, if we applied B & J's 90% rule in regard to color as the only basis for recognizing *O. l. chapmani*, then the subspecies could be invalidated if cats and goats were introduced someday to the San Benitos and the storm-petrel population there was reduced in size as a result!

Finally, they ask that the dark birds found among breeding populations in the Channel Islands and the Farallon Islands be ignored, because these birds were supposedly visiting from the south (p. 795). This is special pleading. Even if these birds were established immigrants from the San Benitos, such an unusually high rate of interchange between islands (6% of the Farallon population would thus have to be derived from San Benitos) would be evidence that we are dealing essentially with only one population. A much higher degree of philopatry, however, is characteristic of storm-petrels and most other species of pelagic seabirds. Many of the dark birds caught on the Farallon Islands have incubation patches during the appropriate season and at least two, which were banded and released, were recaptured there in the same and in subsequent years (PRBO unpubl. data). These facts reduce even more the slim likelihood that these birds were visitors breeding on islands more than 800 km away.

¹ This is Contribution No. 134 of the Point Reyes Bird Observatory.

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