

ORNITHOLOGICAL LITERATURE

EVOLUTION OF THE RAILS OF THE SOUTH ATLANTIC ISLANDS (AVES: RALLIDAE). By STORRS L. OLSON. Smithsonian Contributions to Zoology, No. 152, Smithsonian Institution Press, 1973:iv + 53 pp., 11 pl., 8 text figs. Paper cover. \$0.95. (Obtainable from Superintendent of Documents, U. S. Govt. Printing Office, Washington, D.C.).—Storrs Olson has spent a number of years studying rails, and this paper presents the results of his Ph.D. thesis. He summarizes and extends our knowledge about the rails of Ascension, St. Helena, Tristan da Cunha, and Gough Islands. People interested in the distribution of rails and in the evolution of flightlessness on islands will find this paper informative and necessary reading.

A new species of flightless extinct rail is described from Ascension and placed in the genus *Atlantisia*, previously containing only a rail from Inaccessible Island. Olson also adds another species to *Atlantisia*, as he synonymizes *Aphanocrex*, a monotypic genus from St. Helena. Thus, the expanded *Atlantisia* is now considered to be composed of three species of flightless rails on as many separated South Atlantic Islands. Olson believes *Atlantisia* is related to the "*Rallus* assemblage," although other than saying that there are skeletal similarities among these birds, he presents no strong evidence for this conclusion. He envisions *Atlantisia* having been derived from a single species that was given to wandering or from two closely related species. It would appear that the only recourse to these speculations is to determine the phylogenetic relationships of the recent species of rails and then fit *Atlantisia* into this scheme.

Olson also describes as new an extinct species of *Porzana*, *P. astrictocarpus*, from St. Helena. This rail was also flightless, having a greatly reduced coracoid and scapula but with a normally developed wing skeleton.

Olson takes up the problem of why some species appear to be good colonizers whereas others do not. *Porphyryula*, for example, has reached various South Atlantic islands, but it has neither colonized nor differentiated. *Gallinula*, on the other hand, has colonized and evolved flightless forms. Skeletal measurements suggest greater variability in *Gallinula*, and Olson postulates that a greater genetic plasticity has enabled *Gallinula* to adapt itself to variable environments more easily than *Porphyryula*. Olson extends this same type of argument to the Rallidae as a whole, claiming their "generalized nature" has permitted this family to successfully colonize islands. Perhaps this is so. The variability-colonizing hypothesis is an old one, and now that we are beginning to study genetic variability in natural populations through electrophoretic techniques, supportive evidence may be forthcoming.

Olson closes his paper with a discussion on the evolution of flightlessness in rails. He argues that flightlessness is an adaptation, in that a reduction of the pectoral musculature would permit a saving in energy that could be redirected to reproduction. Again, this is an old argument, perhaps reasonable—although probably not the whole story. This hypothesis is amenable to some testing, and it would be most instructive to compare the physiology and energy budgets of flightless *Gallinula* with their flying counterparts.

Perhaps the most interesting part of this paper is the discussion of how, morphogenetically, flightlessness develop. Young individuals, presumably of most species of rails, exhibit the same skeletal proportions as do the adults of flightless species. Thus, it is easy to see that if proportions of young birds were maintained through the growth process, the adults would be flightless. Various factors of the growth process might

also explain why rails more than other groups of birds frequently become flightless. In most birds that have been studied, the sternum is partially ossified at hatching or relatively soon thereafter, but in rails it apparently does not ossify until well after hatching. Much more comparative developmental data are needed, but as Olson notes, these differences in rates of ossification very possibly "preadapt" groups such as rails to flightlessness. Olson suggests that these ontogenetic changes would require little genetic modification. This may be true, but so might be the opposite speculation; I doubt whether there is evidence for either viewpoint. In any case, the degree of genetic modification does not bear on the phylogenetic usefulness of flightlessness, as he supposes. All features are of potential value in discerning monophyletic groups and cannot be rejected prior to a comparative analysis. Only after study of one or more other features that suggest alternative relationships can we say that any particular feature does or does not appear to be phylogenetically useful.

In summary, Olson has written a stimulating paper on some interesting birds and problems, and ornithologists of varying persuasions will find it worthwhile reading.—
JOEL CRACRAFT.

INTRA-ISLAND VARIATION IN THE MASCARENE WHITE-EYE *ZOSTEROPS BORBONICA*. By Frank B. Gill. Ornithological Monographs No. 12, American Ornithologists' Union, 1973:66 pp., maps, charts, drawings, photographs, color plate by W. A. Lunk. Paper cover. \$2.00 (\$1.60 to A.O.U. members). (Obtainable from Burt L. Monroe, Jr., Treasurer, A.O.U., Box 23447, Anchorage, Ky. 40223).—In 1964, Robert Storer and Frank Gill visited Reunion Island (500 miles east of Madagascar) and discovered that the endemic *Zosterops borbonica* was remarkably variable in certain plumage characteristics. They decided to recognize a record-breaking four races of the species on this single island (Storer, R. W. and F. B. Gill, Occ. Pap. Mus. Zool. Univ. Michigan No. 648, 1966), a bold decision in this age of lumpers. Gill returned to the island in 1967 for nine months, in order to gather detailed information on geographical distribution of the phenotypes and to answer the question—why, on an island so small (about 1000 square miles in area) is variation so great?

His conclusion contained in this monograph, was arrived at from an analysis of the plumage and size variation in relation to altitude and rainfall of 759 specimens collected at 76 localities; this is supplemented by information on courtship, feeding, movements, activity, etc. of banded birds. Gill recognized three categories of plumage variation. First were birds with gray, brown, or intermediately colored backs. As only 42 adult specimens fell into the intermediate class, and as brown and gray birds are extensively sympatric, interbreed, and produce viable offspring, this he considered an example of genetic polymorphism. Second were brown birds only, varying in head color from fully brown to fully gray, through several intermediates. Although fully brown and fully gray heads predominate, intermediates are more frequent than in the case with back color, hence this is not treated as a genetic polymorphism. Third were birds whose underpart coloration varies from nearly pure white to lead gray, with various amounts of brown in some specimens (confined to the breast and flanks). The predominance of browns and grays in the plumage, by the way, is highly usual in the white-eye family.

What does this plumage variation mean? It turns out that there are clear and interesting geographical patterns of distribution of the phenotypes. Lowland populations are 100

percent of the brown back color morph. The proportion of brown morphs decreases gradually with altitude, and gray morphs predominate at the highest altitude. Within the brown morph, gray-headed birds are found in the wet northern and eastern lowlands (below 1380 m), while brown-headed birds are found on the dry western slopes (above 1400 m). The transition between these two types on the eastern slopes is continuous and steeply clinal, but it is abrupt in the lowlands on each side of rivers and recent lava flows. Variation of underpart color is related to altitude, as shown by regression analysis, and rainfall is additionally correlated in each of the three brown morphs but not the gray morph. In other words, some of the geographical patterns are continuous, others are discontinuous. Gill considers these patterns to indicate adaptation, possibly in relation to thermoregulation but not to predation.

The analysis of variation in wing, tarsus, and bill lengths yields a couple of surprises. Wing and tarsus lengths increase with altitude in the brown morphs but not in the gray morphs. Bill length, in contrast, bears a non-significant positive relationship to altitude in the brown-headed (brown) form, yet a significantly negative relationship to altitude exists in the gray morphs. Thus there is the interesting possibility that the two morphs respond differently to the same set of environmental factors, possibly food supply. The gray-headed brown birds show a hint of a positive relationship at low altitudes, as in the brown-headed brown birds, and a negative relationship exists at higher altitudes, as in the gray morphs. Part of these findings may be a correlated effect of body size variation, but whether we should be looking at body size, bill size, or both, the situation has greater fascination and bearing on the evolutionary history of the species than is indicated by Gill's discussion.

These are the skeletal facts of the variation, and in amassing and presenting them, Gill has done a thorough job. One may quibble with small points: coefficients of determination are woefully small; Fisher's exact test would have been more appropriate than χ^2 for the analysis of data given in Table 6; plumage might have been studied colorimetrically; multivariate statistics might have been used for unravelling the complicated co-variation of plumage and dimensions, and so on. Regardless, I doubt that the results of the descriptive study would be altered much.

In the final section, Gill attempts to reconstruct a probable evolutionary history of the species and discusses its variation, adaptation, and taxonomy. He postulates that limited primeval forest-edge habitat suitable for the species originally existed, this dissected into partially isolated patches. After the ancestral species arrived on Reunion, it lost its plumage carotenoids and the eye-ring, changes which facilitated coexistence with the aggressive and already established *Z. olivacea*. Gill supposes that *Z. borbonica* would, at that time, have resembled the present, gray *Z. b. mauritiana* on Mauritius Island (rather than being of the brown morph), because extensive phaeomelanin (brown) pigments are rare in the Zosteropidae. Next, a phaeomelanic morph may have arisen by mutation in the Reunion lowlands, where it enjoyed some unspecified selective advantage over the gray morph. There the mutant quickly spread. In response, the gray morph became better adapted to the cold temperatures and scrub vegetation of high altitudes, to which it was increasingly restricted, while the brown morph differentiated in the semi-isolated pockets of lowland habitat into the several head-color forms. The advent of man in 1663, with his subsequent habitat destruction and creation of edges, broke down the isolation. This enabled the lowland birds to increase in numbers and expand upwards and outwards, making more contacts with the gray morph. All this resulted in the pattern of distribution which is found today.

Plausible as this outline is, Gill presents it as an opinion without discussing alterna-