VARIATION IN RELATIVE HEART SIZE OF CERTAIN PASSERINES WITH INCREASE IN ALTITUDE

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RENSCH (1931) has attempted to show that in certain passerines (*Dicaeum igniferum, Acmonorhynchus annae,* and *Cinnyris jugularis ornata*) from tropical regions the ratio of heart weight to body weight, or "heart ratio," increases markedly with increase in altitude. Although Rensch's data and conclusions were accepted by Stresemann (1927–1934), Moreau (1944) maintained that whereas such a trend might be expected on physiological grounds, the evidence presented by Rensch was unsatisfactory. Because Rensch had only small series of specimens and had not fully explained the method by which his data were obtained, Moreau expressed the need of standardized procedure by listing and briefly discussing possible sources of error. These sources included differences in age, sex, or physiological condition of specimens; in time of day of collection (birds weighing more in the afternoon than in the early morning); in lapse of time between collecting and weighing (the longer the time, the greater the weight loss through desiccation); in method of collecting (if shot, loss in body weight possibly resulting from loss of blood); and in preparation of hearts for weighing. Moreau also pointed out the need of larger series, statistical treatment of data, and investigation of intrapopulation variation as a necessary preliminary to comparison of populations at different altitudes. While Moreau's critique in general seems valid, we believe nevertheless that Rensch's data, albeit scanty, do provide a rough reflection of an actual pattern of increasing heart ratio in birds with increasing altitude.

Even before the appearance of Rensch's paper, Clark (1927:79,80) made the generalization that "animals living in cold climates appear to have higher heart ratios than similar animals living in warmer climates." Clark's evidence was based on reports by Strohl and by Hesse who dealt with ptarmigan (two species of *Lagopus*), House Sparrows (*Passer domesticus*), and squirrels (*Sciurus vulgaris*), comparing high-latitude or high-altitude forms with their counterparts from warmer regions. As these findings suggest and as Moreau (*op. cit.*) readily granted, an increase in heart size relative to body size at high altitude might be expected not only because of cooler temperatures but also because of the more rarified air. The following data on twelve species of passerine birds from a Temperate Zone region provide further evidence for the relationship between heart ratio and altitude (Fig. 1).

METHODS

Most of the specimens furnishing ratio values used in Figure 1 were taken with shotguns, placed in paper cones, and weighed within a few hours. The

birds were weighed to the nearest 0.1 grams on a double-beam balance; the hearts, to the nearest 0.01 grams on a triple-beam balance. It was found through testing that weights of hearts freshly excised and prepared (which included cutting off stumps of blood vessels and removal of blood or clots from the auricles) were not significantly different from weights of the *same* hearts preserved in 10 per cent formalin and later re-weighed. Specifically, among 84 hearts of Scrub Jays (*Aphelocoma coerulescens*) and Steller Jays (*Cyanocitta stelleri*) so treated, there was a mean weight loss of 1.56 per cent in the preserved hearts. Hearts in formalin were therefore considered comparable to ones freshly weighed. All the high-altitude data included in the present report pertain to weights of formalin-fixed hearts (all removed from solution, carefully trimmed, washed out, gently blotted, and weighed by the senior author). No attempt was made to correct for possible weight loss of the order of 1 or 2 per cent. All the lower-altitude data pertain to fresh-heart weights (again prepared and weighed by the same person in a standard way). The high-altitude specimens were obtained in the White Mountains of extreme east-central California and adjacent Nevada by the junior author, who accompanied a collecting expedition led by W. C. Russell and sponsored by the Museum of Vertebrate Zoology. The hearts of passerines taken at elevations from 6750 to 10,500 feet were excised and labeled individually (being pierced with insect pins bearing heavy-paper tabs for field catalog numbers). Thus, hearts could later be associated with individual specimens and their corresponding body weights.

Most of the specimens of lower-altitude populations represented in Figure 1 were obtained at elevations between 100 and 800 feet, usually in Alameda, Contra Costa, or Marin counties in central-coastal California. Exceptions are (1) the "lower-altitude" specimens of *Cyanocitta stelleri,* which were shot in Tuolumne County, California, at approximately 2000 feet, and (2) the Yellow throats (*Geothlypis trichas*) and Chipping Sparrows (*Spizella passerina*), of which the lowland samples came from southern Georgia. It should be added that the lowland Fox Sparrows (*Passerella iliaca*) were wintering birds from near Berkeley, California. While it is possible that these Fox Sparrows represent breeding stock from high altitudes, it is not likely that they do. With these exceptions, the highland and lowland samples were both taken shortly before or during the breeding season and are both essentially Californian, coming from high Sierran and low coastal hill regions, respectively.

Extremely fat specimens were not used in this study. In specimens with limited deposition of subcutaneous and intraperitoneal fat, there is also some deposition on the heart, this tending to minimize variability in the ratios. For the present we are assuming that the myocardium does not undergo seasonal

variation in size. Because this report is of preliminary nature, the assigning of geographic race names to populations is deemed unnecessary.

Acknowledgments

Most of the jays (*Cyanocitta* and *Aphelocoma*) were salvaged from a jay shoot in Tuolumne County, California, by Dr. Frank A. Pitelka. Robert S. Hoffman, Victor Lewin, Jr., and Ralph J. Raitt were helpful in providing a number of the fringillids. Determination of ratios was facilitated by use of a calculator in the Museum of Vertebrate Zoology.

Results and Discussion

The graphs shown in Figure 1 are rather striking in that heart ratios of high-montane samples or individuals are higher in all species than are ratios from lower altitudes. The trend lines for *Cyanocitta stelleri* approach the vertical more closely than those of other species; this might be due not only

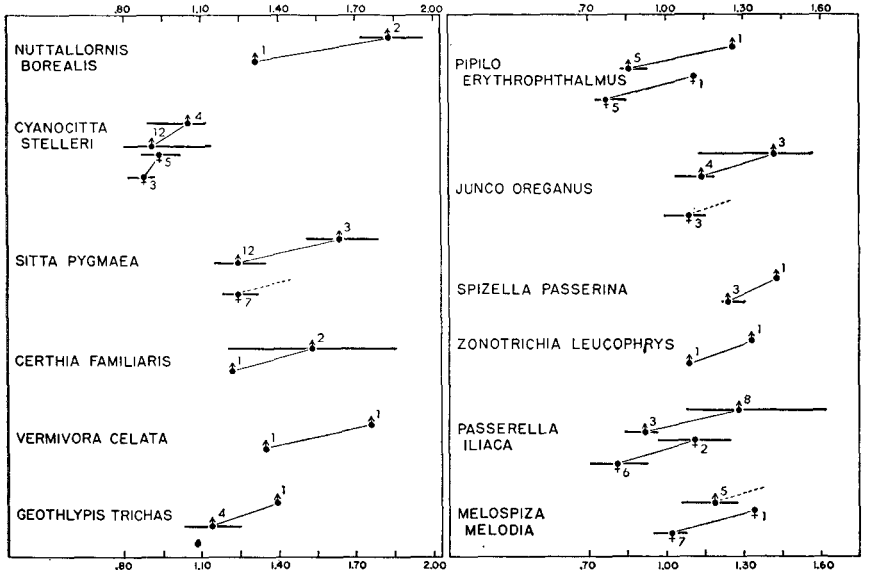

Fig. 1. Variation in heart ratio (heart weight divided by total body weight) of twelve passerine species in relation to altitudinal increase. Sex symbols designate both the sex and mean (or sole, individual) ratio; for each species, symbols to the right refer to the higher altitudes; small numbers near symbols show the number in the sample; heavy horizontal lines indicate the range of ratio values for a given sample; diagonal lines connecting like symbols serve to accentuate the regular trend toward higher heart ratio with increasing altitude.

to the fact that the "lowland" population itself came from 2000 feet, but also because of the large size of jays in comparison with the other passerines. Whatever the altitude, both *Cyanocitta stelleri* and certain fringillid species show higher heart ratios in males than in females. (This is likewise true of *Aphelocoma coerulescens* and other passerines not included in Figure 1.) In the lowland population of Pigmy Nuthatch (*Sitta pygmaea*) the sexes average the same. The two montane specimens of Brown Creeper (*Certhia familiaris*) show marked and probably aberrant difference in heart ratio, due possibly to desiccation or to technical error; both this sample and those of other species, notably the Orange-crowned Warbler (*Vermivora celata*), *Geothlypis trichas*, *Spizella passerina*, and the White-crowned Sparrow (*Zonotrichia leucophrys*) are admittedly poor and unsatisfactory, but since trends suggested by them agree with those shown by other species, they are included in Figure 1.

TABLE 1

PRECISE VALUES FOR THE DATA PLOTTED IN FIGURE 1

Samples are represented by extreme ratios and means (in parentheses)

Species	Lowland Males	Highland Males	Lowland Females	Highland Females
Olive-sided Flycatcher, *Nuttallornis borealis*	1.31	1.72, 1.96		
Steller Jay, *Cyanocitta stelleri*	0.80–1.14 (0.91)	0.89–1.12 (1.01)	0.82–0.92 (0.88)	0.87–1.02 (0.94)
Pigmy Nuthatch, *Sitta pygmaea*	1.15–1.35 (1.24)	1.52–1.79 (1.64)	1.18–1.32 (1.24)	
Brown Creeper, *Certhia familiaris*	1.22	1.20, 1.86		
Orange-crowned Warbler, *Vermivora celata*	1.35	1.76		
Yellowthroat, *Geothlypis trichas*	1.03–1.26 (1.14)	1.39		
Spotted Towhee, *Pipilo erythrophthalmus*	0.83–0.93 (0.87)	1.26	0.73–0.85 (0.77)	1.11
Oregon Junco, *Junco oreganus*	1.04–1.19 (1.14)	1.13–1.57 (1.42)	1.00–1.16 (1.09)	
Chipping Sparrow, *Spizella passerina*	1.22–1.31 (1.27)	1.43		
White-crowned Sparrow, *Zonotrichia leucophrys*	0.83	1.33		
Fox Sparrow, *Passerella iliaca*	0.84–0.97 (0.92)	1.08–1.62 (1.28)	0.70–0.93 (0.81)	0.97, 1.25
Song Sparrow, *Melospiza melodia*	1.06–1.28 (1.19)		0.95–1.08 (1.02)	1.34

Hartman (1954), in a report on cardiac and pectoral muscles of trochilids, states: "In a series of 300 species and subspecies of birds which I have collected, only 12 possessed hearts 1.5 per cent or more of the body weight. From the activity of hummingbirds, the relatively greater size of the hearts [their ratios ranging from 1.74 to about 2.40] might be expected." Although this thought on hummingbirds is certainly justified by Hartman's quantitative information, the first statement, which applies presumably to a large

proportion of passerine species, leads us to suspect that very few, if any, of his specimens were obtained at high altitudes. The data on hummingbirds are well presented (*ibid.*), but the heart-ratio values are not separated according to sex. It would be interesting to know whether male hummingbirds resemble male passerines in having relatively larger hearts than do females. Hartman's trochilid species, excepting the Ruby-throated Hummingbird (*Archilochus colubris*), were obtained in Panama, presumably at relatively low elevations. If, however, certain of his species are represented by both mountain and lowland specimens, it would seem desirable to re-examine the data because of the possibility of altitudinal differences comparable to those indicated for passerines.

Further analysis of variation of heart ratio in birds in relation to altitude, sex, activity, and other matters will be made at a later time. It is sufficient to say at present that in both intra- and interspecific comparisons, both altitudinal and sexual differences provide variables to be reckoned with. Too, in making analyses, one should distinguish nicely between intra- and interspecific variation. To illustrate: in twelve male *Sitta pygmaea*, from 200 to 600 feet in central coastal California, the heart ratios averaged 1.24 (1.15–1.35); in ten male Brown-headed Nuthatches (*Sitta pusilla*), a closely related species taken at approximately 350 feet in Georgia, the ratio averaged 1.56 (1.42—1.68). Similarly, in seven female *pygmaea* the ratio was 1.24 (1.18—1.32); in five female *pusilla* it was 1.47 (1.38—1.56). Whether or not these samples are segregated by sex, there is no overlap between even the extreme heart ratios in these two species of *Sitta*. Curiously, the species *pusilla*, living in a generally warmer climate, has the significantly larger heart (body size in the two compared populations being almost identical). Hence factors influencing such a ratio difference might well relate to intrinsic biological characteristics of the species more than to effects of the physical environment.

Conceivably, measurements of heart ratios of birds will in time be helpful to the taxonomist, not only in the matter of describing and defining closely related species but also in the matter of identification of high-altitude or, perhaps, high-latitude subspecies taken in migration or on wintering areas. It seems probable that such measurements will also be useful to avian physiologists, as has been suggested by Odum (1941:315).

Summary

Evidence from twelve species of passerine birds points to higher heart ratios in high-altitude populations. Such variation in relative heart size, which might be expected on physiological grounds, lends support to earlier findings of Rensch (1931) based on three tropical species. Both altitudinal and sexual differences contribute importantly to variation in heart ratio in

birds as illustrated by passerines, and these variables among others ought to be considered in the analysis of heart-ratio data.

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