SHORT COMMUNICATIONS

ESTIMATION OF THE DURATION OF BIRD MOLT

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In estimating the duration of bird molt, it is common to sample the molting population at intervals and assign a score which represents the degree to which a bird has molted (Pimm, Condor 75:386–391, 1973). This process is one of a large set where some estimate of duration is of interest, and the problems described below may be general ones. The purpose of this paper is to draw attention to a potential pitfall in the estimation of the duration of molt from regression analyses using molt score data.

In regression analyses one seeks to predict one variable (the dependent variable, 'Y') from another variable (the independent variable, 'X') on which the first variable usually depends. Though it would seem that molt depends on date and not vice versa, one faces the paradox that treating time as the dependent variable and molt score as the independent variable is the more reasonable procedure. The reason is simple but does not appear to have been appreciated or explicitly stated in the literature. This interchange of variables can drastically alter the estimates of duration and the biological interpretation of one's results. If only one bird were followed through time, then regression using score as the dependent variable is appropriate. Usually a whole population is measured, with individuals starting and finishing molt at different times. The resultant scatter of points is usually shaped like a parallelogram (fig. 1). Regressions using *score* as the dependent variable produce lines from one corner of the scatter to the other; this does not indicate the molt duration of the individual bird, but rather some function of this and the time over which birds commence molt. If *time* is used as the dependent variable the regression line correctly estimates the duration of molt, and the variance about this line is a measure of the variability of starting (and finishing) dates.

As an example, I shall consider the recent paper by Green and Summers (Bird Study 22:9–17, 1975). Two populations were considered, the first from Scoresbyland, the second from work by Stresemann and Stresemann (Beitrage zur Vogelkunde 16:386–392, 1971). Using time as the dependent variable, one obtains estimates of 28 and 45 days respectively; using molt score as the dependent variable one obtains estimates of 38 and 67 days. The differences are obvious and marked. With score as the dependent variable one would expect longer "durations" of molt from more heterogeneous samples since these would be expected to be more variable in starting dates. Care should be taken in comparing rates of molt since most authors are not specific about how they obtained these estimates.

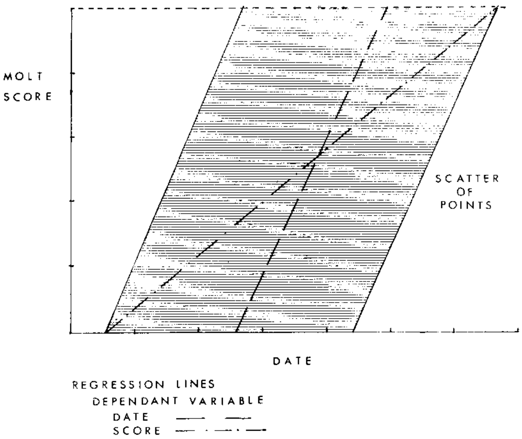

FIGURE 1. Estimation of duration of molt from molt score data: note that the axes should be reversed for a correct estimation of the duration of molt.

The rate of molt may not be linear. Fitting curvilinear models with time as the dependent variable is easy; a serious problem even with linear models is that the scatter may not be parallelogram-shaped because of late starting birds molting faster, or because birds might leave the population with incomplete molt (Pimm 1973). In these circumstances regression techniques are inapplicable though duration of molt of those birds which remain in the population might be obtained from retrap data.

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MORE ON CHICKEN-TURKEY-PHEASANT RESEMBLANCES

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In a recent paper, Nolan et al. (1975) discussed a supposed contrast between results of studies at the protein level and evidence at the organismal level regarding the degree of resemblance among three species—the Domestic Chicken (*Gallus gallus*), the Domestic Turkey (*Meleagris gallopavo*), and the Ring-necked Pheasant (*Phasianus colchicus*). While the authors indicated that studies in the last 20 years make it less certain that the turkey is as distant from the chicken as once thought, they stated that "There seems to be unanimous agreement among ornithologists that the turkey shows less overall resemblance (at the supramolecular or organismal level) to the chicken than the pheasant does." While a number of classifications maintain the turkey in the family Meleagrididae or the subfamily Meleagridinae (of

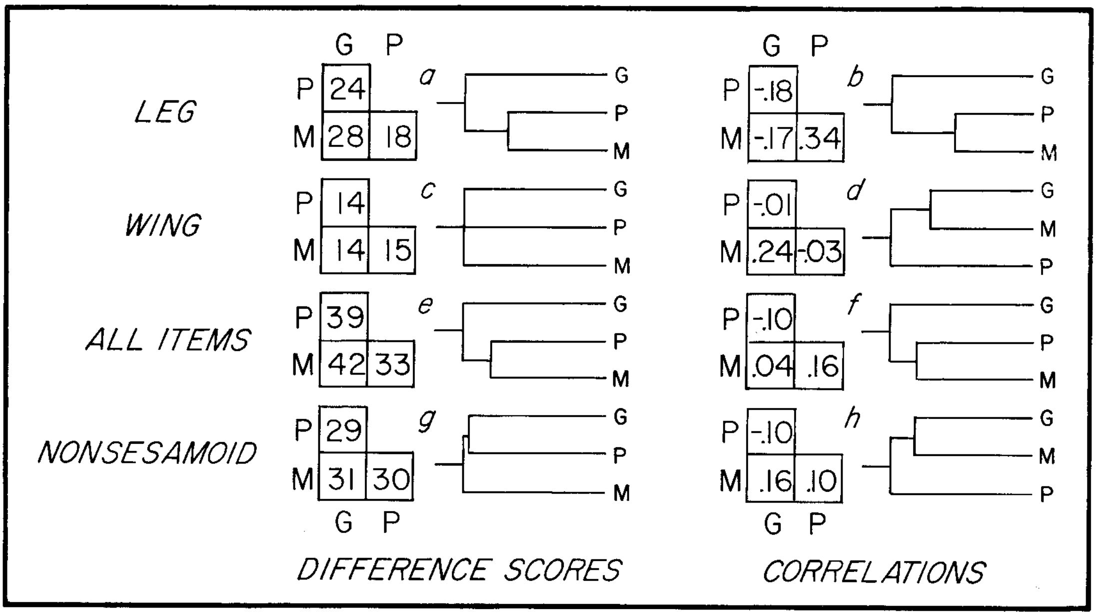

FIGURE 1. Scores of difference and correlations beween *Gallus* (G), *Phasianus* (P), and *Meleagris* (M), based on characters from leg muscles (a,b), wing muscles (c,d), both sets combined (e,f), and both sets minus the sesamoid characters (g,h). Values from Hudson et al. (1966). For scores of difference, low values indicate similarity. Correlations can range from –1 to 1, with high values indicating similarity.

Phasianidae), we think, based on the data available in the literature, that it is incorrect to assume that these treatments reflect accurately resemblance at the supramolecular or organismal level.

Recent authors (Brodkorb 1964, Hudson et al. 1966, Storer 1971, Sibley and Ahlquist 1972) appear to have constructed what they consider to be phylogenetic classifications; such classifications purport to show resemblance (often restricted to the patristic portion of phenetic similarity), as well as the branching sequences in evolution or cladistic relationship (see Mayr 1969). Thus, if one wishes to compare protein resemblance with morphologic resemblance (or that based on another character set), the appropriate comparison is not with proposed phylogenetic classifications, but rather with the resemblance values that were computed or determined in these studies—values that indicate phenetic similarity based on morphology (or other character type). Below we briefly re-evaluate and add some information on morphologic similarity for these three species, to see if the conclusions of Nolan et al. (1975) are warranted.

The most extensive quantitative data available on morphologic similarity of the three forms are those of Hudson and coworkers on the pelvic (1959) and pectoral (1964) limb musculature. These data were reanalyzed (Hudson et al. 1966) using a weighted difference score and the product-moment correlation coefficient as measures of resemblance. Their results for the three genera considered here are summarized in figure 1, which also includes phenograms we constructed using the unweighted pair-group method with arithmetic averages (Sneath and Sokal 1973).

For leg scores, *Phasianus* and *Meleagris* are most similar (figs. 1a and b). Wing score differences (fig. 1c) indicate that the three species are about equally different, although *Gallus* and *Meleagris* are most similar if one uses correlations (fig. 1d) to assess resemblance. *Phasianus* and *Meleagris* are more similar considering all characters (figs. 1e and f). If weighted score differences are computed based on only the nonsesamoid items (i.e., muscle characters excluding those for sesamoids), then chickens and pheasants are most alike (fig. 1g). However, applying correlations to these data results in *Gallus* and *Meleagris* showing the greatest phenetic affinity (fig. 1h). These results from morphologic data do not show any clearcut separation of one form from the other two and certainly do not suggest that *Meleagris* is substantially different from *Gallus* and *Phasianus*.

Nolan et al. (1975) made only the chicken-pheasant and chicken-turkey comparisons. Considering only these two combinations, the weighted scores from Hudson et al. (1966) show the chicken and pheasant to be most alike in three of four comparisons; *Meleagris* and *Phasianus* are equally similar to *Gallus* in the fourth. However, when correlations are applied to their information, *Meleagris* is always more similar to *Gallus* than is *Phasianus*. Thus, the biochemical results are not particularly surprising, given the morphologic findings of Hudson et al. (1966) for muscles.

In order to evaluate phenetic similarities based on skeletal dimensions, we measured 10 domestic *G. gallus*, 10 wild *P. colchicus*, and 4 wild *M. gallopavo* skeletons (all adult individuals) from the collections of the Museum of Natural History at the University of Kansas. The measurements taken were the 51 outlined by Schnell (1970) and are from all parts of the body. We analyzed the logarithms of measurements, as well as relative values (i.e., measurements divided by sternum length and measurements divided by humerus length). Data were standardized and similarities between species were assessed using average distance and product-moment correlation coefficients (Sneath and Sokal 1973). Species were clustered by the unweighted pair-group method with arithmetic averages, and the results are given in figure 2.

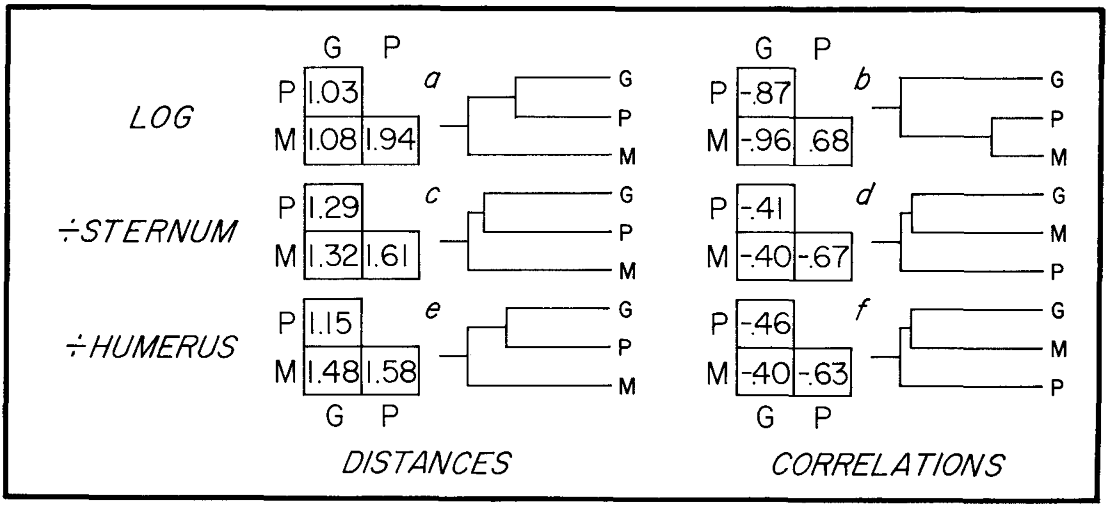

FIGURE 2. Average distances and correlations between *Gallus* (G), *Phasianus* (P), and *Meleagris* (M) based on 51 skeletal dimensions. Data were analyzed with logs (a,b) and as relative measurements—dividing measurements by sternum length (c,d) or by humerus length (e,f). For distances, low values indicate similarities; correlations can range from −1 to 1, with high values indicating similarity.

All three distance phenograms (figs. 2a, c, and e) show that on the average *Gallus* and *Phasianus* are most similar. However, the results are different if one uses correlations to assess similarity. For the phenogram based on the logarithms of measurements (fig. 2b), *Phasianus* and *Meleagris* are most alike, whereas the phenograms based on relative dimensions (figs. 2d and f) indicate that *Gallus* and *Meleagris* are the most similar species.

Considering only the chicken-pheasant and chicken-turkey distances (figs. 2a, c, and e), *Gallus* and *Phasianus* are always most alike. However, in two of the three comparisons (logs of measurements and measurements divided by sternum), the distances are very similar. For correlations (figs. 2b, d, and f), *Gallus* is closer to *Phasianus* than to *Meleagris* when analyzing the logs of measurements. *Gallus* is more closely associated with *Meleagris* than with *Phasianus* in the correlation analyses based on relative measures (figs. 2d and f), although the values are nearly the same. These results for skeletal dimensions, just as those for muscles, are mixed and do not support the idea that morphologically there is a substantially greater difference between chickens and pheasants than between chickens and turkeys.

Nolan et al. (1975) in their summary as well as title, indicated that their findings were at variance with expectations based on the prevailing system of classification and that there was an inconsistency between protein resemblance and "taxonomic resemblance." However, it seems likely, based on the literature they cited, that the retention of Meleagrididae or Meleagridinae reflects a basic nomenclatural conservatism—which results from investigators being reluctant to discard the taxon designation (see for example Sibley 1960)—rather than differences of turkeys from phasianids.

From a broad systematic viewpoint, the biologically interesting question involves the comparison and possible explanation of similarities and differences based on different character sets rather than comparisons with prevailing sets of names. Certainly, it would be appropriate to compare protein results against what would be expected based on a cladistic or phenetic tree showing the relationships between species, but a series of names is usually a poor way of representing such affinities (as seems evident for this case). Just as Selander (1971) cautioned that the systematic and taxonomic aspects of the "species problem" must be carefully distinguished and separated, one must show equal care in separating the two when dealing with affinities above the species level.

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SIMILARITY OF A TYRANT-FLYCATCHER AND A SILKY-FLYCATCHER: NOT ALL CHARACTER CONVERGENCE IS COMPETITIVE MIMICRY

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The standard example of convergent appearance in birds, Eastern Meadowlarks (*Sturnella magna*) of the New World and Yellow-throated Longclaws (*Macronyx croceus*) of Africa, has been widely used in text-books (for example, R. E. Ricklefs, Ecology, Chiron Press, Newton, Mass., 1973: p. 342). The Crested Black-tyrant (*Knipolegus lophotes*), a tyrant-flycatcher of open scrub and dry areas in eastern South America, is equally convergent to the unrelated Phainopepla (*Phainopepla nitens*) of open scrub and dry areas of western North America, but the resemblance does not seem to have been noted before.

Both species are crested, glossy-black, slender and upright birds with red eyes, with large white patches flashing at the bases of primaries in flight. Both flit from high in one small tree or bush to another in rather open areas, capturing insects in the air at times and eating small fruits at other times. The Black-tyrants I have seen do well in scrubby pastures, in scattered trees around ranch houses, and in semi-open "cerrado" vegetation from Caparaó to Furnas in the eastern part of the state of Minas Gerais, Brazil, but are less common in wetter deforested regions in the state of São Paulo. Small groups, pairs or single birds wander through such areas, much as do Phainopeplas in Arizona. Their mainly highland black relatives, *Knipolegus aterrimus* and *K. cyanirostris*, are progressively less like Phainopeplas.

Since there are few characters to point out in nearly-black birds, the resemblance of *K. lophotes* to *P. nitens* is unlikely to supplant the meadowlark-longclaw example in textbooks. However, the convergence brings up the point that various types of habitat-induced convergences of characters are common phenomena: unrelated grassland birds are often streaked; black and white patterns are common in forest-edge birds; seed-eaters have thick bills and insect-eaters thin bills, etc. There are also many other types of character convergence, some of them called "mimicry."

Cody (1973. Ann. Rev. Syst. Ecol. 4: 189–211), however, restricted the term "character convergence" to one type of convergence in appearance: that seen where different species become more alike in competitively excluding each other in zones of overlap. However, his "character convergence" is not sufficently unambiguous to describe this type of convergence, which has all the characteristics of the types of character convergence normally called "mimicry." I suggest that what Cody called "character convergence" is best referred to as "convergent character displacement" (Grant, Biol. J. Linn. Soc. London 4:39–68, 1972) or, more specifically, as "competitive mimicry." This is in line with previous ornithological use of "aggressive mimicry" (Willis, Condor 65: 313–317, 1963) and "social mimicry" (Moynihan, Evolution 122: 315–331, 1968). Cody, indeed, compared his phenomenon directly with what otherwise is in danger of becoming "Moynihanian mimicry."

Moynihan and Cody were separately led to use the term "character convergence" in attempts to contrast first social mimicry and then competitive mimicry with "character displacement" (Brown and Wilson, Syst. Zool. 5: 48–64, 1956). In character displacement, one or more organisms evolve away from or toward each other in morphological characters in and near a zone of overlap (Grant, 1972). The term is reasonably appropriate and descriptive (though various types of mimicry and the phenomenon of predator-selected aspect diversity also seem character displacement), but divergent character displacement is only one type of "character divergence" —which includes simple adaptive radiation in allopatry or otherwise. Character convergence, being more or less the opposite of character divergence, should not be used as the opposite of "character displacement." Grant (1972) used "character release" instead, a reasonable suggestion.

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