Vol. 126, No. 2 The American Naturalist August 1985

NOTES AND COMMENTS

THE INFLUENCE OF SIZE AND PHYLOGENY ON LIFE HISTORY VARIATION IN REPTILES: A RESPONSE TO STEARNS

In a recent paper, Stearns (1984) concluded that reptilian life history traits are strongly influenced by size and phylogeny. Stearns analyzed data from 61 lizard and snake species that included the following traits: average snout-vent length of adult females, clutch size, age at maturity, mode of reproduction, and number of broods per year. These data were subjected to a correlation analysis, a two-level (order and family) nested ANOVA, and a principal-components analysis to determine the effects of size and phylogeny on the patterns of covariation in those traits. There are numerous problems with his data set (Stearns 1984, appendix). These range from the misspelling of scientific names to more-serious errors involving the extraction of data from the literature. Vitt and Seigel (1985) discussed these errors in detail, pointing out that the validity of Stearns' conclusion is impossible to determine given so many errors. In this note, I discuss some major problems with Stearns' analysis, in particular his use of the covariates "size" and "phylogeny." These comments, although specifically directed toward Stearns' article, are of general application to analyses of life history traits.

In life history studies, the best overall measure of body size is weight (mass). It explains more variation in life history traits than any other single measure and is directly coupled with the physiology of the animal (Western 1979; Lindstedt and Calder 1981; Western and Ssemakula 1982). Because of this, it has been referred to as the "axis of similitude" or a species' "first-order strategy" (Western 1979). Unlike body length, the weight of an organism is not dependent on its shape and allows a comparison between animals with different body plans. Stearns' choice of length as a measure of body size in reptiles was thus unfortunate owing to the enormous variability in body shape of these organisms. In snakes, the difference is more than twofold between the weight of a typical 1-m-long colubrid (*Coluber constrictor*, 296 g; Fitch 1963) and a 1-m viperid (*Crotalus horridus*, 700 g; Gibbons 1972). In lizards, a 60-mm *Ophisaurus attenuatus* weighs 1 g (Fitch 1970), whereas a 60-mm *Holbrookia maculata* weighs 6 g (Gennaro 1974), and a 60-mm *Moloch horridus* weighs over 10 g (Pianka and Pianka 1970). Even within the Iguanidae, similar differences in weight for identical lengths are seen between the genera *Anolis* and *Sceloporus*. Although length data are much more abundant

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than weight data in the literature, length is clearly a poor measure of body size among reptile species.

The other covariate Stearns considers is "phylogeny." Although this term is not defined, it apparently encompasses all variation in life history traits that is not accounted for by length. Thus, any ecological differences that may exist among the groups are included. For example, a tropical skink, *Emoia atrocostata*, reaches sexual maturity in 9 mo (Stearns' appendix), yet a similar-sized temperate skink, *Eumeces fasciatus*, requires 24 mo to reach sexual maturity. Animals living in colder climates typically have a shorter growing season and hence take longer to reach sexual maturity. The difference between the two species in age at sexual maturity may be entirely a result of their geographic location rather than a consequence of their phylogenetic history. This argument applies equally to differences in the number of broods per year in these two species (3 and 1, respectively). A similar problem is encountered at the familial level when tropical representatives are used for one family and temperate representatives for another, as in the Agamidae and Anguidae, respectively (see Stearns' appendix).

It may indeed be difficult or impossible to determine accurately the effects of phylogeny on life history traits. In order to totally eliminate all environmental factors that may be responsible for differences, one would have to compare only species living together in the same microhabitat with identical behaviors and ecologies. It is doubtful that such species exist. A less objective but more practical way to examine the effects of phylogeny on life history traits is to compare convergent groups. One example is the case of the New World and Old World natricine snakes. Both groups have radiated into a variety of aquatic niches. The New World species are viviparous, however, whereas the Old World species are oviparous, except for one (Fitch 1970). The mode of reproduction therefore appears to be a lineage-associated trait. An example of a lineage-associated trait in lizards is clutch size in the iguanid genus *Anolis* (200+ species): the clutch size of all species in this genus is one. Clutch size among species in other iguanid genera, however, is usually variable and rarely as low as one (Fitch 1970).

Such patterns can only suggest a lineage-associated effect. A more careful examination of environmental or ecological factors may provide a better explanation for the life history differences. For instance, in the last example, *Anolis* differs from most other iguanids by being predominantly arboreal. Most likely, it is selectively advantageous for a slender arboreal lizard to carry only one egg at a time rather than a heavy clutch. But not all *Anolis* are slender arboreal lizards. This genus has radiated into a variety of ecological situations, with some species being almost entirely terrestrial. Since even those species have a clutch size of one, it is likely that clutch size in this group was fixed in the early stages of the adaptive radiation. The method of analysis employed by Stearns (1983, 1984), although objective, does not take into account the multitude of environmental and ecological variables that influence life history traits. Lineage-associated traits do exist, but they can be identified only by a careful examination of each particular case.

The question that Stearns is asking is vital to the understanding of life history variation: what are the important covariates of life history traits? These variables must be taken into account before most theories of life history evolution can be tested properly. A large body of literature on life history allometry (Blueweiss et al. 1978; Kaplan and Salthe 1979; Leutenegger 1979; Western and Ssemakula 1982; and references therein) has already answered this question for many groups: body size (weight) is the single most important covariate of life history traits. The extent of its influence on traits in other groups and the identification of other covariates are problems that now need attention. Our knowledge of reptiles lags behind that for other groups in this respect primarily because body-weight data are not available for most species. It is hoped that more researchers will include this important datum in their papers so that future analyses of reptilian life history traits will have a strong data base.

ACKNOWLEDGMENTS

I thank J. Coyne, D. Gill, H. Greene, C. Hass, R. Highton, and two anonymous reviewers for their helpful comments. This research was supported in part by a National Science Foundation grant (BSR 83-07115) to R. Highton.

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Submitted March 15, 1984; Revised October 9, 1984; Accepted October 23, 1984