

7 Natural History and Evolutionary Biology

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1. Introduction

Natural history has had profound and diverse influences on the life sciences. It was a cornerstone in the origins of modern evolutionary biology, and many of us began our careers as weekend naturalists, equipped only with curiosity and a spiral notebook. There are signs, however, that natural history has fallen from grace in the last decades of the Twentieth Century. It has even been called boring, muddled, uninspiring, old-fashioned, and of no value in itself. Nevertheless, most speakers in the symposium upon which this volume is based called for more "basic natural history data." This prompted me to pose several questions from the floor, and I am grateful to the editors for an opportunity to discuss these problems in the following essay.

Natural history focuses attention on organisms, on where they are and what they do in their environments, and is approximately synonymous with autecology plus descriptive ethology. It includes normal behavioral repertoires ("ethograms") and changes in external and internal states, insofar as these pertain to what organisms do. Natural history includes things like the chronology of reproductive events, clutch size, and ecdysis, but typically does not encompass fine details of hormonal cycles and other physiological phenomena.

I will argue that natural history provides an interpretive context for addressing both broader and narrower questions, sometimes in serendipitous and unexpected ways. It is the "idea and induction" part of "the" scientific method, the essential prelude to formulating hypotheses as well as the raw material for testing them. In all of these

attributes, good natural history is exactly analogous to descriptive anatomy and alpha systematics. This is not a novel viewpoint (e.g., Schmidt, 1946; Wilson, 1973), but it deserves further emphasis and explication. I will draw examples that pertain to the evolutionary morphology and foraging ecology of lower vertebrates, but the implications extend to other organisms and topics. Strong et al. (1984) make a cogent plea for the role of natural history in formulating community studies.

2. What's **Wrong** with Natural History?

The reasons for recent disinterest in and condescension toward natural history perhaps include strict adherence to Popperian concepts of what constitutes science, without regard for the origins of theory; the widespread appeal of reductionism and a certain "technophilia" that have accompanied the rise of molecular biology (cf. Platt, 1964); and powerful, institutionalized pressures to deliver fast results (Tinkle, 1979). Negative attitudes undoubtedly also reflect the fact that natural history sometimes does fall short, in that the information given is so incomplete as to be of little value for broader purposes. This is true of many accounts of snake diets (e.g., Greene and Oliver, 1965), which consist of only taxonomic lists of prey, with no mention of relative prey size, sex, and other variables. As a result, such data are of little value in the recent surge of emphasis on the feeding biology of these animals (Pough, 1983).

That natural history is viewed as old fashioned and of limited value, even by some evolutionary biologists, is in contrast to attitudes toward anatomy. Old, beautifully illustrated, descriptive accounts of morphology continue to be used frequently and even held in reverence by some modern workers. Perhaps a key difference is that structure is usually the most salient and constant aspect of an animal's phenotype. Thus, regardless of one's theoretical orientation (Wake, 1982), the immediate aim for comparative anatomy always has been straightforward: describe carefully and fully everything that can be seen. This has been accomplished by dedicated, skillful workers, and it has benefited from an aesthetic appeal as well. Natural history has not sustained a comparable aura among evolutionary biologists, and much of it has been done anecdotally, seemingly as an afterthought and under the naive assumption that no special training, perspective, or effort was necessary.

Another reason for the differential treatment of anatomy and natural history might be that functional and evolutionary morphologists are increasingly disposed toward an approach to the study of structure that is both holistic and truly comparative (Gans, 1975; Lauder, 1982; Wake, 1982; Chapter 2), thereby enhancing the potential value of extensive, strictly descriptive work. By contrast, conceptual advances in the "outdoor branches" of organismal and population biology seem to have been accompanied by a narrowing of focus. Ecologists and ethologists increasingly seem to concentrate on studying clutch size, mating system, or some other restricted subset of an animal's biology, and to ignore or treat naively holistic and historical considerations (e.g., Clutton-Brock and Harvey, 1984; there are notable exceptions, e.g., Huey and Pianka, 1981; Janzen, 1983; Chapter 6).

Peters' (1980) eloquent and thought-provoking essay presented a sharp dichotomy between natural history and ecology that epitomizes the problems addressed herein. He portrayed natural history as art, a "contemplative and reflective activity," sometimes deeply satisfying but always of value solely to the individual observer. For Peters (1982), science is prediction; only as such is it worth doing as a professional activity, and only as such can it grapple with the pressing environmental issues of the day. Or, as a colleague once told me, "If you're not doing an experiment every moment, you're wasting time."

I have some sympathy for Peters' skepticism, but his position is incomplete. All predictive hypotheses inevitably arise inductively, either from logical consideration of observations or from some form of imagination. One might sit by the fire and wait until the ring structure of benzene appears as an image of a snake among the flames (as did Kekule [Dobzhansky et al., 1977]), but the combination of careful empiricism and a well-prepared mind seems like a good bet, too. High quality, publicly recorded natural history *is* data-in-waiting, simultaneously able to provoke theory and confront any number of previously unforeseen predictions.

Whatever the reasons for current attitudes, they have practical consequences. Natural history courses are conspicuously absent in some quarters and viewed as pointless anachronisms in others. There is no National Science Foundation panel that explicitly accommodates autecology and descriptive ethology, despite the fact that reliable, broadly representative natural history data will always be essential for testing important theories in ecology and systematic biology. As recently as 1983, the reviewer's instructions for ecological papers submitted to *Herpetologica* implied that manuscripts which simply described the life of a previously unstudied organism were not

acceptable. Instead, publishable papers were to address broader issues, despite the fact that this journal routinely includes alpha taxonomic work.

3. What's Good about Natural History?

The concept of adaptation includes differential performance of different phenotypes under natural conditions (Chapters 2 and 10). Behavior thus serves as a functional couple between the structural features of an organism and its environment, and must be a component in the complete evolutionary analysis of form. My ongoing studies of feeding in California snakes (Greene, 1986) underscore this point, by demonstrating ways in which intrinsically identical prey can confront different predators with very different tasks.

The western whiptail lizard (*Cnemidophorus tigris*, Teiidae) forages diurnally by moving from bush to bush, and remains in a shallow, tight-fitting burrow at night. This common species is important in the diets of several desert snakes. The sidewinder (*Crotalus cerastes*, Viperidae) lacks rostral specializations for burrowing, possesses immobilizing and tissue destructive venom, and apparently catches relatively large *C. tigris* by striking them from under bushes during the day. The longnosed snake (*Rhinocheilus lecontei*, Colubridae) is a powerful constrictor, has a pointed rostral scale that presumably facilitates digging, is nocturnally active, and probably subdues sleeping whiptails in their burrows. The coachwhip (*Masticophis flagellum*, Colubridae) is a slender, diurnal snake with physiological specializations that permit unusually fast movements, and catches relatively small, active lizards by chasing them. Simply knowing that *C. tigris* is a major diet item for each of these species would mask the significant differences in how each species interacts with its prey, and thereby confound the analysis of putative feeding adaptations.

An anecdote from recent field studies of large, tropical vipers also illustrates a way in which simple observations can yield unexpected rewards. For several weeks in the summer of 1984, I watched daily a gravid female fer de lance (*Bothrops asper*) at Finca La Selva, in northeastern Costa Rica. This 2.2 kg animal confined her activities to an area of a few square meters in a treefall gap, basking in the open for several hours every day and resting at night in a tight coil among nearby fallen branches. She did not feed during the time that I watched her, and no standing water was available in the immediate environment. However, the integument of this species has a peculiar, beautiful

texture (the local name, *terciopelo*, means velvet) and rain water always formed large, standing beads on her back. On several occasions the snake inclined her head against her coils and drank water droplets, once for over ten minutes. It might well be that water-holding properties constitute a major biological role for the skin in some tropical snakes, as is the case for certain desert lizards (Gans et al., 1982, for *Moloch horridus*) and snakes (Louw, 1972, for *Bills peringucyi*). However, in the absence of field observations, a laboratory morphologist asking evolutionary questions about reptile skin in moist habitats probably could not have even considered this possibility (cf. Smith et al., 1982).

Natural history also sets realistic boundaries on theory. We don't need theory that applies to things that don't occur, but we do need to know what a global theory must encompass or how to restrict and subdivide it. Most foraging theory has been predicated on the assumption that organisms have "a fairly clear statistical expectation of the resources [they] will come upon" (page 59 in MacArthur, 1972), and that search and handling costs are sufficiently similar that they can be manipulated relative to each other. Given this fact, it probably is not surprising that many successful studies, in terms of data matching theoretical predictions, have come from predators feeding very frequently on abundant, small prey (cf. Krebs et al., 1983).

Other studies on tropical snakes at La Selva suggest that if a truly general foraging theory is possible, it must encompass a greater range of possibilities than previously considered. By using radiotelemetry, I estimated foraging rates in the bushmaster, *Lachesis muta*, a 2-4 kg, 2-3 m long viper (Greene and Santana, 1983). A female slept during the day and hunted in an alert posture every night. She used three sites for 3-15 days and traveled a total of ca. 50 meters in a 35 day period. On the 15th night at the third site (24th day of observation), she caught a rodent weighing at least 50% of her body weight. Judging from observations on captive vipers, immobilization and ingestion would have required no more than a few dozen minutes. The snake then rested for nine days before changing sites. More limited observations of other bushmasters were similar, and also indicated that hunting sites were frequently within one meter of a palm tree (*Welfia georgii*), the fruits of which are an important food for the rodents upon which *Lachesis* feeds. Using our movement and diet data, some reasonable assumptions, and standard metabolic equations, C. R. Peterson (personal communication) has calculated that an adult bushmaster needs only approximately six typical meals per year to support the energetic costs of maintenance and foraging movements.

The feeding dynamics of these large snakes present a stark contrast to those of small to medium size *endotherms*, animals that have large daily energy requirements (cf. Carpenter et al., 1983; Congdon and Tinkle, 1982), feed frequently, and make foraging decisions on a scale of seconds or minutes (Krebs et al., 1983). If bushmasters make decisions at all, they might do so on a scale of days or weeks! Given the apparently large disparity between search and handling costs in snakes (Godley, 1981; Greene, 1984), a bushmaster should probably try for any prey that it encounters, within certain functionally constrained limits (e.g., several species of rodents within a broad size range, but not birds).

We still do not know enough about the array of existing feeding *biologies* to state whether a continuum exists between *hummingbirds* and *bushmasters*, or if these animals represent two or more clusters of phenomena. Although textbooks present generalizations about foraging styles in diverse animals, there are actually exceedingly few careful, direct observations of hunting and its consequences in wild animals (cf. Carpenter et al., 1983; Table 14 in Curio, 1976; Greene, 1982). This is particularly true for species other than large mammals and birds in open habitats, although there are impressive exceptions (e.g., Pianka, 1982, for varanid lizards; Spencer and Zielenski, 1983, for pine martens).

4. What is the Future of Natural History?

The above examples present a dilemma. Thorough, satisfying answers to important questions in evolutionary biology will ultimately require detailed, autecological inventories for a wide spectrum of organisms. But who will do this work, and who will pay for it? My impression is that descriptive accounts accumulate usually as anecdotes or as side effects of long-term studies on more narrow topics, themselves subject to attitudinal and economic constraints (Tinkle, 1979). I surmise that broad, detailed, explicitly organism-centered studies are relatively rare today, at least in part because they are not "trendy," they usually require long-term efforts, their relevance to evolutionary biology is not appreciated universally, and there are very few direct avenues of support for them.

Good natural history is a source of timeless, priceless information for the biological sciences. It inspires theory as well as provides crucial data for answers to comprehensive, synthetic problems in ecology, ethology, evolution, and conservation biology. Despite this fact, natural

history costs relatively little compared to the resultant benefits. It is too important to be left only to chance observations, unprepared minds, and ancillary benefits of other studies.

Natural history should be encouraged to flourish, and I will close with some suggestions:

(i) Theoreticians and laboratory workers should cultivate a respect for and communication with natural historians. The hubris and obscure, in-group jargon that characterize some literature are only self-serving, and discourage others from contributing to the empirical refinement of theory.

(ii) Systematic biologists should recognize that comparative natural history is an essential component of the complete study of morphological evolution. In the wake of recent criticism of "naive adaptationism" (e.g., Gould and Lewontin, 1979), it is important to stress that wild organisms *do* have surroundings. To ignore this fact as a matter of approach is to pursue, at least tacitly, an historical theory that is devoid of environmental context.

(iii) Journals that focus on particular groups of organisms should encourage the publication of high quality natural history papers, as an investment in the future testing of theories. Specialty journals should consider the example of the *Journal of Ecology* and publish regularly a small number of excellent, autecological studies.

(iv) Granting agencies should face up to the high, intrinsic, lasting value and low relative costs of good natural history studies. They should seek ways to insure the overt support of *high quality* work with explicit *potential* importance (rather than immediate answers) for general questions.

(v) Theoreticians have made tremendous contributions to evolutionary biology, often causing us to seek out things in nature that we never dreamed existed. It must be emphasized that I am not denying the importance of theoretical and experimental work, that I am not making excuses for sloppy natural history, and I do not advocate that ill-conceived studies should receive public support. Natural historians should eschew "field boot chauvinism" (Colwell, 1983) and strive to be well informed on new techniques and theory. For field observations to be useful maximally to others, and thereby have value beyond the immediate satisfaction of the *observer*, they must be sufficiently precise, accurate, and detailed to chronicle interesting phenomena (cf. Drummond, 1981). To do otherwise in today's world of shrinking habitats and spreading extinctions is a disservice to science and the organisms that we study.

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