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Organisms in nature as a central focus for biology

Harry W. Greene

Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853-2701, USA

Theories summarize science, tell us what to measure when we test hypotheses, and help us study nature better. Nevertheless, organisms themselves embody genetics, development, morphology, physiology and behavior, and they are the units of populations, communities and ecosystems. Biologists seek to understand organisms, their diversification and environmental relationships – not theories and experiments *per se* – and discoveries of new organisms and new facts about organisms reset the research cycles of hypothesis testing that underlie conceptually progressive science. I argue here that recent disagreements about the fate of natural history are thus more apparent than real and should not distract us from addressing important issues. The conservation of biodiversity requires factual knowledge of particular organisms, yet we know little or nothing about most species, and organismal diversity is often poorly represented in biological education. Accordingly, I urge those who are especially concerned with teaching and conservation to seek increased financial and curricular support for descriptive natural history, which is so fundamental to many of the applied facets of biology.

Twenty years ago, I sat through a symposium on predator–prey interactions, becoming increasingly frustrated as speaker after speaker appealed for 'more empirical data' to test the theories on which their talks were focused. In the open discussion that followed, I asked, 'But who will do that work, and who will pay for it?' Then, in response to what I hoped were sympathetic chuckles from the audience, I facetiously added, 'Does anyone know the program director for natural history at the US National Science Foundation?' The organizers of the symposium invited me to contribute an essay to the subsequent volume [1], in which I argued that natural history, defined for my purpose as descriptive ecology and ethology, is central to modern evolutionary and environmental biology yet is under appreciated and under funded. I was careful to stress reciprocal relationships among the growth of robust theory, experimentation and accurate natural history, and I explicitly decried 'field boot chauvinism' [2].

Fast-forward to 2002 and another symposium, organized by past president Peter R. Grant for the annual meeting of the American Society of Naturalists (http://www.amnat.org). Current president Johanna Schmidt set the tone of the meeting by encouraging a dual agenda of increasing emphasis on genomics and conceptual integration, through the study of organisms themselves. Several participants in the Grant symposium addressed the enduring value of natural history, particularly its importance in environmental conservation, whereas Stevan J. Arnold responded from the floor that, rather than worthy of revival in an outmoded format, natural history has been appropriately encompassed and transformed within modern evolutionary biology [3]. These disparate views reverberated throughout the meeting, as well as in subsequent correspondence and conversations, and soon Arnold [4] and Paul K. Dayton [5], a speaker in the Grant symposium, published eloquent but radically different position papers, unaware of each other's written arguments (see Boxes 1–3 for the literary flavor of this spirited controversy).

The meaning and fate of natural history are inevitably in some sense personal, because organisms in their environments are at the heart of a personal aesthetic, the emotional core of why many of us became scientists. The substance of 21st-century biology and its role in broader world affairs are also at issue, and the contradictory perspectives that I highlight here help bring these underlying themes into sharp relief. I aim to provoke further discussion and, because the debate encompasses some important questions for academic biologists, especially those who are concerned with education and conservation, to seek some resolution.

A view from the kelp beds and beyond

Dayton [5] assayed the state of marine biology and bemoaned the dearth of the information that we need to slow or even reverse environmental degradation. Using examples from the intertidal, near shore, benthos and open ocean, he underscored how problems of scale, absence of knowledge about organisms and failure of existing theories thwart our abilities to solve ecological predicaments. Photographs illustrating human impact accompanied his essay, of which the most dramatic show a Tasmanian seamount, the former site of a species-rich coral community, which was devastated by commercial fishing and now looks like vacant lunar expanse. Dayton documented an urgent need for natural history in confronting the plight of marine ecosystems and surely his manifesto would move anyone who cares about the fate of life on Earth.

Numerous others have commented on the plight of what they typically called 'natural history' (e.g. [6–10])

Corresponding author: Harry W. Greene (hwg5@cornell.edu).

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and, similar to Dayton, those writers have been especially concerned with the discovery of facts about organisms in nature: their distributions and microhabitats, activity patterns, interactions with other organisms, life histories and so forth. As background for the present discussion, I emphasize four reasons why we need descriptive ecological and ethological research:

(i) Organisms themselves embody genetics, development, morphology, physiology and behavior, and they are the fundamental components of populations, communities and ecosystems. An understanding of organisms in nature is thus integral to studies at both lower and higher levels in the hierarchy of biological complexity [11–13]; accordingly, researchers focused on questions at a particular level will require information about their study organisms that might have been gathered, even primarily so, for different purposes. Future studies of the giant antennal interneurons of amblypygids, for example, can now be informed by the first long-term field studies of these predatory arthropods [14]. Until recently, one might have at least claimed that an understanding of diverse organisms was irrelevant to biochemistry and molecular biology, whereas the most exciting frontiers in these disciplines now involve integration and reciprocal illumination, from genomics and the ontogeny of myriad phenotypes to communities, ecosystems, conservation, agriculture and biomedical sciences [13,15–19].

(ii) Discoveries of new organisms and new facts about organisms often reset the research cycles of hypothesis testing and theory refinement that underlie good progressive science [20,21]. By way of examples, first, the biotas of deep-sea hydrothermal vents illustrate previously unimagined biochemical, physiological and morphological diversity, the exploration of which sparked a wide array of new research programs [22]. Second, prominent reviews have confidently proclaimed that snakes are 'the least social of all the reptiles' [23] and that 'obviously reptiles are unlikely to teach us much about the hormonal control of parental care' [24], yet recent field and laboratory studies reveal that pitvipers (Crotalinae) are appropriate for mechanistic research on maternal attendance, sibling recognition and family structure in vertebrates [25,26].

(iii) Organisms themselves (what they look like, where they live and what they do) provoke widespread human curiosity, including that of conceptually focused biologists and of the public who, in large measure, financially support scientific research [27,28].

(iv) As Dayton [5] and others [29–33] have discussed in detail, descriptive ecological and behavioral data underlie many aspects of conservation, management and nature appreciation.

Natural history by any other name

Arnold [4] singled out essays by Noss [6], Futuyma [34] and me [30] as exemplary of a 'distinctive genre' that claims 'naturalists are dying off and that natural history is unappreciated and disappearing.' Instead, he asserted that a historical perspective demonstrates that natural history flourishes today as modern evolutionary biology, behavioral ecology, and other intellectual descendants of the age of European exploration and Enlightment; for Arnold, echoing Farber [35], a search for order in nature has always been the defining feature of natural history, one that has persisted from Linnaeus and Charles Darwin through Robert H. MacArthur, Edward O. Wilson, and beyond (Box 1). Arnold believes that naturalists are all around us and that the 'vitality of the naturalist's tradition depends on new ideas and new tools from other disciplines.' Accordingly, he portrayed the views of Noss, Futuyma and me as 'narrow, non-historical,' 'stereotyped,' focused on 'natural history *sensu stricto*' and he 'reserve[s] special admiration for naturalists who excel both in the field and at the blackboard.'

Arnold emphasized recurrent tensions between theorists and empiricists in ecology and evolutionary biology, and he believes that defenders of natural history *sensu stricto* are excessively critical of the former. In this regard, Noss [6] and others (e.g. [7]) indeed can be read as denigrating theory, but Futuyma, Dayton and I are staunch supporters of conceptual unification in biology (Box 2 and [1]). Moreover, Arnold, with whom I have enjoyed chasing desert lizards and catching gartersnakes,

Box 1. What's in a name?

Definitions of 'natural history' and 'naturalist' have shaped the debate about whether either of them is endangered, as exemplified by these contrasting commentaries by two distinguished evolutionary biologists.

'I think of a scientific naturalist as a person with a deep and broad familiarity with one or more groups of organisms or ecological communities, who can draw on… systematics, distribution, life histories, behavior, and perhaps physiology and morphology to inspire ideas, to evaluate hypotheses, to intelligently design research with an awareness of organisms' special peculiarities… a person who is inexhaustibly fascinated by biological diversity, and who does not view organisms merely as models, or vehicles for theory, but, rather, as the reason for biological investigation… the thing in itself, that excites our admiration and our desire for knowledge, understanding, and preservation.' (Douglas J. Futuyma [34], in his past presidential address to the American Society of Naturalists.)

'Naturalists who worry about the fate of natural history have recently produced a distinctive genre of essays… Among the claims… are… that naturalists are dying off and that natural history is underappreciated and disappearing. I think these notions are wrong, born of a narrow, non-historical view of naturalists and natural history… [instead] natural history is a vigorous, blossoming enterprise. I arrived at this view by adopting the perspective of historians of science… [of] natural history as a lineage that includes descendants…. Commentators on the current plight of 'natural history' usually take a narrow view of the naturalist's tradition… Greene (1994 [30]) adopts this more stereotyped vision when he focuses on descriptive ecology and ethology as the building blocks of natural history… How can we reconcile these narrow, sometimes pejorative views of 'natural history' with a 250-year-old naturalist's tradition that includes the development of Darwinism and other major concepts as well as the incorporation of experimentation and model building? Why do we take a narrow view of 'natural history'? As new disciplines split off from natural history, the genealogical trunk kept the original name, but in time the trunk was whittled down to a remnant… The meaning of the term 'natural history' continues to contract… Within a few decades, in this narrow view, 'natural history' will be a small sliver-like remnant, a vacant scientific profession.' (Stevan J. Arnold [4], in an invited essay for the 50th anniversary of *Animal Behaviour*, reproduced, with permission, from [4])

Box 2. Theories and concepts versus empirical knowledge

Facts and generalizations are at the heart of science, but prominent biologists differ as to whether either component deserves primacy in terms of financial support and education.

'Much of the best empirical work on organisms tests and is guided by theory… [but] surely the purpose of theories and conceptualizations is *not merely to exist in themselves, as monuments to our ingenuity and insight but to organize the myriad details of the natural world as well*… the glory of biology - its mark of distinction, its inexhaustible appeal - is the diversity of its subjects, the variety of organisms that 'age cannot wither, nor customs stale.' The theories that appear in our journals hardly begin to capture, and certainly cannot predict, the richness of biology found in a textbook of invertebrate zoology, or entomology, or botany. Our theories, mutable and usually ephemeral, should be viewed as vessels for the abiding information on the real properties of real organisms; and our vessels are as meaningless, if they are empty, as a catalog system is for a library that lacks books.' (Douglas J. Futuyma [34], emphasis in original.)

'Will the next generation of conservation biologists be nothing but a bunch of computer nerds with no firsthand knowledge of natural history? …I am not suggesting that mathematics, statistics, and computer literacy are irrelevant… but they are arguably less central to our discipline than ecological and organismic courses.' (Reed F. Noss [6], in an editor's essay for *Conservation Biology*.)

'Far too few of my college courses had any outdoor action… either the 'laboratory' involves labwork (blades and flasks and splay-pinned worms), or 'field exercises' are just a sideline, a necessity for collecting data to be wisked away indoors and onto disk for numerical analysis… organisms only supply the numbers to fuel the statistical engines.' (John M. Aguiar [7], in one of many sympathetic responses to Noss' [6] essay.)

'Great naturalists are remembered for their concepts rather than for their fieldwork and collections. Natural history lives and breathes because of the concepts it has produced… concepts are the triumphs of natural history, the essence of the discipline and its descendants… Observation, discovery, experimentation, models and simulation are all subservient to concept building… history does not support the idea that the field worker armed with just a notebook is the only true naturalist.' (Stevan J. Arnold [4]; reproduced, with permission, from [4])

'…testing theory remains the cornerstone of science… A commonly seen trap [however] is that hypotheses are based on inappropriate simplifications and assumptions contradict natural history… that the bad assumptions can be mensurate and precise, esthetically pleasing, and appear heuristically useful, but the tests might be irrelevant or make the right predictions for the wrong reasons… arguably the most important message from this essay is that current ecological model systems do not generalize very well.' (Paul K. Dayton [5], in an invited essay on marine conservation for *American Naturalist*.)

epitomizes that unusual admirable combination of talented naturalist and accomplished theoretician. The dispute among us thus looks to be a red herring, an emotional but largely inconsequential misunderstanding that has perhaps been fueled in part by fuzzy, interchangeable use of the words 'theory,' 'models' and 'concept building' on the one hand and 'natural history,' 'organism-focused' and 'empiricism' on the other.

I happily embrace Arnold's view that natural history encompasses the whole of modern organismal, environmental and evolutionary biology, but there remain two points of contention. First, he concluded that 'observation, discovery, experimentation, models and simulation are all subservient to concept building,' and he regards finding order in nature as the ultimate prize. I believe instead that carefully recorded observations, from late Pleistocene murals of courtship behavior by extinct cave lions *Panthera spelaeus* [36,37] to DNA sequence data for copperheads *Agkistrodon contortrix* [38], are at least as much the enduring core of biology as those conceptual frameworks in which they were assembled. Second, Arnold expressed no concerns for the empirical and educational aspects of natural history *senso stricto*, whereas Noss, Futuyma, Dayton and I perceive an overemphasis on hypothesis testing and concept building as the defining criteria for allocating resources in biology, to the detriment of exploratory field research and organism-focused course offerings.

Why we all need to get along

Whatever the words 'natural history' mean, I am worried primarily about our ignorance of the ecology and behavior of most extant organisms, a knowledge gap that is so large that, for most species, even in the best-studied regions on Earth, we cannot specify the most basic aspects of their biology. Among endless possible examples, there is a giant desert centipede *Scolopendra heros*, common in the southwestern USA, often mentioned in popular works, and at 10–12 g weighing more than many vertebrates, about which we know almost nothing in terms of its feeding and reproduction in nature [39]. The fang-like forcipules and venom of scolopendromorph centipedes can inflict a painful bite on humans, yet several species of small, poorly known colubrid snakes *Tantilla* spp. subdue these noxious arthropods with impunity [40], so an understanding of the biochemistry of their interactions might well yield breakthroughs in molecular ecology, neurobiology and medicine.

Futuyma, Dayton and I are particularly concerned that we lack sufficient empirical reference points to move reliably among scales of time, space and biological organization, and that science therefore cannot adequately address environmental dilemmas (Box 3). We are emphatically not criticizing the vital work of theoreticians, but rather seeking more balance in research support and training. I readily grant that all biologists, including those of us whose work is primarily descriptive, gather data in the context of concepts; I also acknowledge that youthful curiosity entails mentally organizing our findings, that, even as children, we seek order in nature. Nevertheless, scientists who gather data in the service of specific hypotheses and conceptual disciplines often ignore other organismal attributes, as a matter of efficiency if nothing else. That some brilliant theoreticians are inspired by nature is not helpful either in the sense of providing the descriptive building blocks of biology [41], unless their field observations are archived and accessible for use by others. All of that said, biology generally, and conservation science in particular, would profit from a massive phenotypic equivalent of the widely popular genomics initiatives: we need accurate quantitative accounts that are representative of physiological, morphological, behavioral and ecological variation across the full panoply of biological diversity. These factual inventories will be most widely useful if they are designed, conducted and prioritized within the conceptual frameworks of ecology, evolution and conservation, but their

Box 3. What is at stake?

Attitudes toward natural history – about what, if anything, needs fixing? – might hinge on the relative importance afforded to education and conservation as motivating goals for science.

'If equations and simulations, as well as field experiments and observations from blinds, are all legitimate parts of natural history, why do we hear our colleagues disparage each others activities? Why are there conflicts within the natural history community, sensu lato? Where does the tension come from? …It is the defenders of natural history sensu stricto who feel that their backs are against the wall.' (Stevan J. Arnold [4]; reproduced, with permission, from [4])

'Only ~31% of the respondents to the questionnaire felt they had as much access to training in organismal diversity and natural history *as they would like*… many students… are emerging from graduate school with little knowledge of organisms beyond the species they did their dissertation on, often a system suggested by their adviser… I do not at all disparage theory or conceptual progress. I am not suggesting that one kind of knowledge is more important than another. I only urge balance, and I believe we should be concerned about the prospective growth of purely factual knowledge of organisms. We need it, and we do not have enough of it.' (Douglas J. Futuyma [34], emphasis added.)

'While society is concerned about the rapidly declining quality of the biosphere, most anthropogenic stresses are protected through rabid political resistance to conservation in favor of short-term economic gain. Representative natural areas are almost impossible to find, and few endangered species show signs of recovering, even with millions of conservation dollars spent on their behalf. A sad commentary is that our ability to respond and defend natural systems has been eroded within academe by scientific elitism against natural history and systematics… very few students are being trained… and our ability to identify any of the species in extremely important habitats, such as the continental shelf ecosystems, which include perhaps hundreds of thousands of species, will be lost with the retirements of the aging experts. This loss means that we will not perceive any but the most massive changes… the most insidious result of the loss of respect for 'old-fashioned' natural history… [might be that] very few students are offered the opportunity of observing nature and accumulating the background natural history essential to the ecological understanding necessary to ask relevant questions.' (Paul K. Dayton [5].)

worthiness for financial support need not be contingent on immediate hypothesis testing.

Of those who think 'natural history *sensu* stricto' is not in trouble or not worth worrying about, I ask are descriptive facts of organisms in nature unimportant or do we already have enough of them? If the factual gaps in our knowledge do need to be filled, as widely and as rapidly as possible, who will do that work and who will pay for it? How and where will young scientists train to identify and study organisms in the field? In their editorial response to my earlier plea for more natural history [1], Feder and Lauder [42] opined that little would be forthcoming because of a lack of precise field instrumentation, the inaccessibility of many predator–prey interactions, and the 'discomfort of field work.' The intervening two decades have seen remote temperature data loggers that are smaller than some coins, we now have telemetry devices for beetles, and can anyone imagine a cell or molecular biologist saying that we will not make progress understanding microtubule assembly or *cis*-regulatory elements because laboratory benches are uncomfortable? The real impediments to natural history *sensu stricto* were then and still are more pervasive, sometimes subtle and sometimes not; they include excessive technophilia, a dearth of funding for discovery and descriptive research, the power of grant overhead monies in shaping academic programs, elitism on the part of some biologists, a shortage of journals that publish organismally focused studies and the widespread eclipse of biological diversity itself in high school and undergraduate curricula [1,5,28,43–45].

We need to work together as a community of truly integrative modern biologists to redress our ignorance of the lives of most species and I believe that there are grounds for optimism. A conceptual unification of molecular, organismal, evolutionary and environmental biology is well underway (e.g. [15,18,33,46,47]), such that the central importance of studying organismal diversity is increasingly appreciated, and web-based initiatives provide easy access to an ever increasing array of natural history archives [e.g. Global Biodiversity Information Facility (http://www.gbif.org/), Museum of Vertebrate Zoology (http://www.mip.berkeley.edu/mvz/), Caterpillars, Pupae, Butterflies & Moths of the ACG (http://janzen.sas.upenn.edu/), The Parasite Database (http://brooksweb.zoo.utoronto.ca/index.html/) and EthoBank (http://www.Indiana.edu/~ethobank/)].

Governments will probably never underwrite the exploration of biodiversity on a scale even remotely as large as the ~US$15 billion that the USA budgets each year for space research – after all, the US National Aeronautics and Space Administration spent US$30 million for one toilet on a space shuttle, three times as much as the annual budget for systematic biology at the National Science Foundation. In the face of such lopsided priorities, perhaps the best hopes for funding studies of organisms in their environments lie instead with the private sector, and we need to inspire that support, to promote more widely the importance of nuts-and-bolts natural history. Those who can reach out to larger constituencies, including foundations and individual philanthropists, should seek financial backing for the central role of descriptive organismal biology, especially if it will be done in a naturalistic context and with regard to broader human concerns.

Our ignorance of the lives of organisms in nature entails complex problems on a global scale, but, for many of us, the best places to start seeking solutions might be within local educational institutions. People will care more about, pay more for, and even sacrifice on behalf of things that they understand, so we need to establish biological diversity, ecology, behavior and conservation as among the core components of scientific literacy. Ask your colleagues, for example, if they can explain with a straight face why introductory courses must encompass Taq polymerase, *HOX* genes, endoplasmic reticulum and serotonin inhibitors but not also liverworts, angiosperms, onychophorans and tetrapods. Ask them to justify explicitly the requirement that all students earning biology degrees take a genetics course with a fly laboratory but not that they also gain sustained first-hand exposure to the study of organisms in nature? As the global human population climbs steadily past the six billion mark and our environmental crisis deepens, we must vigorously address these serious issues.

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References

1 Greene, H.W. (1986) Natural history and evolutionary biology. In *Predator–Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates* (Feder, M.E. and Lauder, G.V. eds), pp. 99–108, University of Chicago Press
2 Colwell, R.K. (1983) Review of R.M. May (ed.). Theoretical ecology: principles and applications. *Auk* 100, 261–262
3 Ruvinksy, J. (2002) Metersticks and microarrays. *Trends Ecol. Evol.* 17, 496–497
4 Arnold, S.J. (2003) Too much natural history, or too little? *Anim. Behav.* 65, 1065–1068
5 Dayton, P.K. (2003) The importance of the natural sciences to conservation. *Am. Nat.* 162, 1–13
6 Noss, R.F. (1996) The naturalists are dying off. *Conserv. Biol.* 10, 1–3
7 Aguiar, J.M. (1996) Are the naturalists dying off? *Conserv. Biol.* 10, 924–925
8 Schmidt, K.P. (1946) The new systematics, the new anatomy, and the new natural history. *Copeia* 1946, 57–63
9 Bates, M. (1950) *The Nature of Natural History*, Charles Scribner's Sons
10 Iltis, H.H. (1988) Serendipity in the exploration of biodiversity: what good are weedy tomatoes? In *Biodiversity* (Wilson, E.O. ed.), pp. 98–105, National Academy Press
11 Bartholomew, G.A. (1964) The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. *Symp. Soc. Exp. Biol.* 18, 7–29
12 Bartholomew, G.A. (1986) The role of natural history in contemporary biology. *Bioscience* 36, 324–329
13 Gilbert, S.F. and Sarkar, S. (2000) Embracing complexity: organicism for the 21st century. *Dev. Dynam.* 219, 1–9
14 Hebets, E.A. (2002) Relating the unique sensory system of amblypygids to the ecology and behavior of *Phrynus parvulus* from Costa Rica (Arachnida, Amblypygi). *Can. J. Zool.* 80, 286–295
15 Carroll, S.B. *et al*. (2001) *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*, Blackwell Scientific
16 Mandoli, D.F. and Olmstead, R. (2000) The importance of emerging model systems in plant biology. *J. Plant Growth Regul.* 19, 249–252
17 Kafatos, F.C. and Eisner, T. (2004) Unification in the century of biology. *Science* 303, 1257
18 Stearns, S.C. and Magwene, P. (2003) The naturalist in a world of genomics. *Am. Nat.* 161, 171–180
19 Freudenstein, J.V. *et al*. (2003) From basepairs to birdsongs: phylogenetic data in the age of genomics. *Cladistics* 19, 333–347
20 West-Eberhard, M.J. (2001) The importance of taxon-centered research in biology. In *Anuran Communication* (Ryan, M.J. ed.), pp. 3–7, Smithsonian Institution Press
21 Greene, H.W. and McDiarmid, R.W. (2005) Wallace and Savage: heroes, theories, and venomous snake mimicry. In *Ecology and Evolution in the Tropics: A Herpetological Perspective* (Donnelly, M.A. *et al*., eds), pp. 190–208, University of Chicago Press
22 Jollivet, D. (1996) Specific and genetic diversity in deep-sea hydrothermal vents: an overview. *Biodiv. Conserv.* 5, 1619–1653
23 Wilson, E.O. (1975) *Sociobiology: The New Synthesis*, Harvard University Press
24 Moore, M.C. and Lindzey, J. (1992) The physiological basis of sexual behavior in male reptiles. In *Biology of the Reptilia* (Gans, C. *et al*., eds), pp. 70–113, University of Chicago Press
25 Greene, H.W. (2003) Parental care in vipers. In *Biology of the Vipers* (Schuett, G. *et al*., eds), pp. 179–205, Eagle Mountain Publishing
26 Clark, R.W. (2004) Kin recognition in rattlesnakes. *Proc. R. Soc. Lond. Ser. B* 271(Suppl. 4), S243–S245
27 Wilcove, D. and Eisner, T. (2000) The impending extinction of natural history. *Chron. Higher Ed. Sept.* 15, B24
28 Gladfelter, E.H. (2002) *Agazzis' Legacy: Scientists' Reflections on the Value of Field Experience*, Oxford University Press
29 Caughley, G. (1994) Directions in conservation biology. *J. Anim. Ecol.* 63, 215–244
30 Greene, H.W. (1994) Systematics and natural history, foundations for understanding and conserving biodiversity. *Am. Zool.* 34, 48–56
31 Caro, T. ed. (1998) *Behavioral Ecology and Conservation*, Oxford University Press
32 Greene, H.W. (1999) Natural history and behavioural homology. In *Homology* (Bock, G.R. and Cardew, G. eds), pp. 173–188, John Wiley & Sons
33 Brooks, D.R. and McLennan, D.A. (2002) *The Nature of Diversity: An Evolutionary Voyage of Discovery*, University of Chicago Press
34 Futuyma, D.J. (1998) Wherefore and whither the naturalist? *Am. Nat.* 151, 1–6
35 Farber, P.L. (2000) *Finding Order in Nature: The Naturalist Tradition from Linnaeus to E.O. Wilson*, Johns Hopkins University Press
36 Packer, C.J. and Clottes, J. (2000) When lions ruled France. *Nat. Hist.* 109, 52–57
37 Yamaguchi, N. *et al*. (2004) Evolution of the mane and group-living in the lion (*Panthera leo*): a review. *J. Zool.* 263, 329–342
38 Parkinson, C.L. *et al*. (2000) Phylogeography of the pitviper clade *Agkistrodon*: historical ecology, species status, and conservation of cantils. *Mol. Ecol.* 9, 411–420
39 Shelley, R.M. (2002) A synopsis of the North American centipedes of the order Scolopendromorpha (Chilopoda). *Mem. Virg. Mus. Nat. Hist* 5, 1–108
40 Greene, H.W. (1997) *Snakes: The Evolution of Mystery in Nature*, University of California Press
41 Hughes, D. (2002) The value of a broad mind: some natural history meanderings of Bill Hamilton. *Ethol. Ecol. Evol* 14, 83–89
42 Feder, M.E. and Lauder, G.V. eds (1986) *Predator–Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*, University of Chicago Press
43 Tinkle, D.W. (1979) Long-term field studies. *Bioscience* 29, 717
44 Bonnett, X. *et al*. (2002) Taxonomic chauvinism. *Trends Ecol. Evol.* 17, 1–3
45 Vogel, S. (1998) Academically correct biological science. *Am. Sci.* 86, 504–506
46 Wake, M.H. (2000) Integrative biology as a framework for education and training. *Biol. Int.* 39, 14–18
47 West-Eberhard, M.J. (2003) *Development Plasticity and Evolution*, Oxford University Press