

Mutualism between ecologists and ethologists?

Judith Bronstein's¹ review of the conditionality of mutualism between species induced a strong sense of déjà vu. I do not say that pejoratively, but rather to highlight that, ignorant as I am of ecology, the ideas that she wrote about were nevertheless very familiar to me from my own discipline of animal social relationships, where they are perhaps most explicit in the literature on cooperation between individuals within species. Ecologists interested in mutualism and ethologists working on cooperation are apparently grappling with very similar problems. Social ethologists too are investigating how outcomes depend on the immediate situation²⁻⁴, and could, I suspect, gain insight from ecologists' studies where the contributions of the partners are often so

measurably different. And it looks as if ecologists might not yet have got as far as ethologists in applying game theory in general, and developments of Prisoners' Dilemma models in particular, to the analysis of conditional outcomes^{5,6}. And yet Bronstein did not refer to our literature, and we far too rarely refer to hers.

If I am correct, and the two disciplines have much to say to one another, is their lack of contact yet another instance of jargon preventing discourse? Have I ignored 'mutualism' between species simply because I study 'cooperation' between individuals? Or is there indeed a fundamental difference in the questions, the approach and the understanding that makes cross-disciplinary intercourse unhelpful? Ronald Noë's and Peter Hammerstein's⁷ application of market analysis (which models conditionality in potential mutually beneficial relationships) to both intraspecific cooperation and interspecific mutualism (and courtship) suggests not. That being the case, the

disciplines' usual ignorance of each other's work is a great pity.

A.H. Harcourt

Dept of Anthropology, University of California, Davis, CA 95616-8522, USA

References

- 1 Bronstein, J.L. (1994) *Trends Ecol. Evol.* 9, 214-217
- 2 Noë, R. (1990) *Behaviour* 113, 117-170
- 3 Külling, D. and Miliński, M. (1992) *Anim. Behav.* 44, 949-955
- 4 Chapais, B. (1988) *Behaviour* 104, 41-59
- 5 Dugatkin, L.A., Mesterton-Gibbons, M. and Houston, A.I. (1992) *Trends Ecol. Evol.* 7, 202-205
- 6 Boyd, R. (1992) in *Coalitions and Alliances in Humans and Other Animals* (Harcourt, A.H. and de Waal, F.B.M., eds), pp. 473-489, Oxford University Press
- 7 Noë, R. and Hammerstein, P. *Behav. Ecol. Sociobiol.* (in press)

Shyness and boldness in humans and other animals

David Sloan Wilson

Anne B. Clark

Kristine Coleman

Ted Dearstyne

The shy-bold continuum is a fundamental axis of behavioral variation in humans and at least some other species, but its taxonomic distribution and evolutionary implications are unknown. Models of optimal risk, density- or frequency-dependent selection, and phenotypic plasticity can provide a theoretical framework for understanding shyness and boldness as a product of natural selection. We sketch this framework and review the few empirical studies of shyness and boldness in natural populations. The study of shyness and boldness adds an interesting new dimension to behavioral ecology by focusing on the nature of continuous behavioral variation that exists within the familiar categories of age, sex and size.

David Sloan Wilson, Anne Clark, Kristine Coleman and Ted Dearstyne are at the Dept of Biological Sciences, Binghamton University, Binghamton, NY 13902-6000, USA.

viduals seem to thrive on risk and novelty while others shrink from the same situations. Psychologists regard the shy-bold continuum as a fundamental axis of human behavioral variation, having complex physiological and hormonal underpinnings. Individual differences along the continuum appear early in life, are phenotypically stable in at least some individuals, and are partially heritable^{1,2}.

Why do humans vary in their propensity to take risks? Does similar variation exist in other species? Although the shy-bold continuum has been studied in captive primates²⁻⁴ and a few other species in the laboratory (including cats⁵, rats⁶, canids⁷ and quail, *Coturnix coturnix japonica*⁸), almost nothing is known about its taxonomic distribution or its consequences in natural populations⁹. Our purpose in this article is to explore the concepts of shyness and boldness from the perspective of behavioral ecology. Models of optimal risk-taking strategies, frequency-dependent selection and phenotypic plasticity can provide a theoretical framework for understanding shyness and boldness in humans and other species. In addition, the study of shyness and boldness adds an interesting new dimension to behavioral ecology. When behavioral ecologists study individual differences, they tend to focus on discrete categories of behavior, such as alternative reproductive strategies, and discrete categories of individuals, such as sex, age or size. In contrast, shyness-boldness is a be-

havioral continuum that cuts across the categories of age, sex and size, although these categories may differ in their average degree of shyness and boldness. Can behavioral ecologists explain the shape of adaptive phenotypic distributions (e.g. bimodal versus unimodal) and the nature of individual differences within the familiar categories of age, sex and size?

The natural history of shyness and boldness

Before sketching a theoretical framework, we will review what little is known about shyness and boldness in natural populations; its ecological consequences, proximate mechanisms and correlations with other traits such as social dominance.

Does a shy-bold continuum exist in natural populations?

Almost everyone who observes animals is impressed by the behavioral differences that exist among individuals, even within the categories of age, sex and size. A few behavioral ecologists have actually studied these differences by systematically exposing individuals to a variety of stimuli and noting their response. Factor analysis is often used to identify major axes of behavioral variation, much as in studies of human personality. As with humans, one of the major axes can be interpreted as a shy-bold continuum in taxa as diverse as mammals¹⁰, fish¹¹, cephalopods¹² and crustaceans¹³.

Child psychologists often measure shyness and boldness in children by noting their response to a novel object. Similar techniques can be applied in the field to nonhuman species. We used unbaited wire minnow traps as a novel object in our studies of juvenile pumpkinseed sunfish (*Lepomis gibbosus*)¹⁴. The

The behavioral continuum from shyness to boldness is familiar to all of us from our personal interactions. Some indi-

traps were immediately surrounded by a cluster of fish that, in anthropomorphic terms, could only be described as curious. After ten minutes, the traps were removed and the fish in the immediate vicinity that had not entered were collected with a seine net. The two groups were then studied in the laboratory or marked and released back into the pond for field observations. If a shy–bold continuum existed in juvenile pumpkinseeds, the trapped and seined groups were expected to differ behaviorally. The possibility of differences caused by the trapping method itself was excluded by an additional experiment that subjected trapped fish to the experience of being seined¹⁴. The two groups differed in the time required to acclimate to the laboratory, their diets prior to capture, their parasite fauna, and their behavior in the field.

To summarize, even the small number of studies that exist suggest that a shy–bold continuum is likely to be common in natural populations and widely distributed taxonomically. However, more-sophisticated comparisons across taxa and environments are needed to address the conceptually oriented questions outlined below. It is especially important to identify species in which shyness–boldness is not a major axis of behavioral variation, since the evolutionary forces that maintain the shy–bold continuum are not expected to operate in all species.

What are the ecological consequences of shyness and boldness?

Since the shy–bold continuum has been explicitly identified in few species, it is not surprising that the consequences for survival and reproduction are virtually unstudied. Bold pumpkinseed sunfish forage at a greater rate and in a riskier fashion, although so far we have been unable to measure a detectable difference in growth rate or survival¹⁴. In pioneering field research on marmots (*Marmota flaviventris*), Armitage and Svendsen^{10,15} identified three axes of behavioral variation that they termed 'approach', 'avoidance' and 'sociability' and that correlated with dispersal and reproductive success. They interpreted these individual differences as adaptations to physical and social environments that vary greatly in time and space. Their research suggests that the shy–bold continuum is not the only important axis of behavioral variation in animals. Five axes are usually suggested for humans¹⁶. The approach that we are suggesting for shyness and boldness can also be applied to other behavioral continua that cut across the familiar categories of age, size and sex.

Even humans, who are so well studied in other respects, have seldom been

monitored outside the laboratory to see how shyness and boldness function in every day life. Using longitudinal data from the Berkeley Guidance study, which monitored the lives of several hundred individuals over many years, Caspi *et al.*¹⁷ examined the phenotypic stability and the apparent consequences of shyness and boldness in individuals from late childhood through middle age. Shy men were more likely to delay entry into marriage, parenthood and stable careers and were less likely to attain occupational stability and achievement. Shy women were more likely to follow a conventional pattern of marriage and childrearing than bold women, and by midlife their husbands had a higher occupational status. Thus, at least according to prevailing social standards, there appeared to be a net benefit for boldness in men and shyness in women, but these net benefits almost certainly disguise situation-specific costs and benefits within each sex. For example, the tendency of bold women to enter the workforce would probably be a net economic advantage today, even if it was a net disadvantage in the 1950s. Clearly, there is a great need for long-term field studies on humans in ancestral and modern environments, in addition to research on other species.

What are the proximate determinants of shyness and boldness?

Psychologists and behavioral ecologists alike seem most eager to demonstrate a heritable component to individual behavioral differences. There can be little doubt that shyness and boldness is partially heritable, but this should not distract us from the larger and more important question of how genetic differences and environmental inputs interact to produce adaptive phenotypes². One point to stress is that 'phenotypic plasticity' is not equivalent to 'state' on the state-trait continuum. In the European minnow (*Phoxinus phoxinus*), brief exposure to a model pike at the age of two months heightened the response to predators 24 months later¹⁸. Three-spined sticklebacks (*Gasterosteus aculeatus*) from lakes with and without predators differed in their degree of boldness, even when they were raised in the laboratory, but these differences were actually reversed when the male parent was removed. Adult males chased their own young more vigorously in lakes with predators, which acted as an environmental 'signal' that altered the response of their phenotypically plastic offspring towards predators later in life¹⁹.

Even highly reversible 'states' can appear as 'traits' in environments that reinforce individual differences. In our studies of pumpkinseeds¹⁴, shy and bold

individuals were phenotypically stable for as long as we observed them in the field. When trapped and seined juveniles were brought into the laboratory and housed individually in sections of aquaria, the trapped fish began feeding on artificial food an average of five days sooner than the seined fish, once again illustrating impressive phenotypic differences between the two groups. After both groups were acclimated to the laboratory, however, we were unable to demonstrate any differences in a battery of novel object and novel environment experiments. It seems that the natural environment acts to create and maintain individual differences in phenotypically plastic individuals and that several weeks of ecological and social isolation causes the phenotypes to converge. These patterns of phenotypic plasticity are more difficult to study than simple genetic polymorphisms but they are equally important and interesting from the adaptationist perspective.

What is the relationship between the shyness/boldness and social dominance?

Are shy individuals simply the losers in social competition? Even the small amount of data that exists suggests otherwise. In pumpkinseeds, dominance interactions are common in aquaria but rare in natural populations. Nevertheless, a strong shy–bold continuum exists and individuals can even be ranked linearly along the continuum by recording the relative shyness/boldness of pairs of fish observed together: if A is bolder than B and B is bolder than C, A also tends to be bolder than C when they are observed together. There is no relationship between rank on the shy–bold continuum and common determinants of social rank such as body size or sex. Thus, shyness–boldness appears to be an axis of behavioral variation in its own right and not a simple consequence of social dominance. Even in species that exhibit a strong correlation between boldness and social dominance, it is possible that bold individuals become dominant rather than dominant individuals becoming bold. Huntingford *et al.*²⁰ showed that the familiar relationship between body size and dominance did not exist in very young Atlantic salmon (*Salmo salar*). Rather, individuals differed in their behavioral propensities, with some individuals becoming larger as the result of their ability to dominate the others.

To summarize, there can be little doubt that the shy–bold continuum is an important axis of behavioral variation in many species that deserves the attention of behavioral ecologists. In fact, the shy–bold continuum creates methodological problems that should be taken seriously by all behavioral ecologists.

even those that are not interested in shyness and boldness *per se*. Almost by definition, shy individuals are a relatively invisible segment of the population that will be under-represented by most sampling techniques and behaviorally inhibited in the face of most observation techniques. The shyer pumpkinseeds in our study populations evade capture even by a seine and must be identified by natural markings. They are recorded less often during censuses. In one pair of adult pumpkinseeds that often forage together in our study population, the shyer member never fed during focal observations, even though the bolder member of the pair fed often. When the bold fish was experimentally removed from the population, the shy fish spent three days under a submerged tree stump and did not emerge in our presence until its bold associate was returned! Other adults are so shy that we know them only as hazy figures in the distance. Although these behavioral differences are fascinating to study, they are a nuisance from the standpoint of sampling and observational methods.

A theoretical framework

Optimization models, norms of reaction and differences between populations

For the purpose of this discussion we will equate shyness and boldness with a propensity to take risks. Organisms are frequently faced with a trade-off between acquiring benefits (e.g. food or mates) and protecting themselves from dangers (e.g. predators or intraspecific aggressors). Taking risks can be adaptive if the expected benefits are sufficiently great, with the optimal degree of risk depending on the situation²¹. For example, hungry guppies (*Poecilia reticulata*) forage in a way that increases their feeding rate but also increases their vulnerability to predators²². Their need for food evidently increases the degree of risk that is warranted to acquire food.

Optimization models make it clear that individuals should be flexible in their propensity to take risks. To function adaptively they must have a 'norm of reaction'²³ within which the acceptable degree of risk-taking is tailored to the environmental conditions. Species that experience different environmental conditions, however, can be expected to evolve different norms of reaction, as can local populations within species^{24,25}. As one example, small fish species in lakes that contain effective predators often differ in their innate patterns of boldness from the same species in lakes that lack predators²⁶.

Density-dependence, frequency-dependence and differences within populations

The profound variation in boldness that exists within a single population is more difficult to explain with optimization models. By definition, risk-averse (shy) and risk-prone (bold) individuals display very different norms of reaction to the range of environmental conditions that they encounter. How can such differences coexist if there is an optimal degree of risk-taking for any particular situation? Why isn't there a single optimal norm of reaction? As for other adaptive polymorphisms, density- and frequency-dependent selection can be invoked to explain the coexistence of shy and bold individuals within populations (Box 1). The ingredients of this model – activities that vary in their degree of risk and whose benefits depend on the number of individuals performing the activities – are sufficiently common to suggest that a shy–bold continuum might exist in many taxonomically diverse species. Equally importantly, the shy–bold continuum should be absent in at least some species, since the conditions for its evolution are not completely general. For example, a single optimal norm of reaction may be favored in species that are chronically maintained at low num-

bers by predators and seldom experience the negative effects of their own density.

Domain specificity of shyness and boldness

One important implication of the model outlined in Box 1 is that shyness and boldness can be domain-specific. It is easy to imagine the ingredients of the model operating with respect to predation risk, for example, but not with respect to intraspecific social interactions. In some bird species, socially dominant individuals allow subordinates to explore the physical environment, displacing them when they have found food²⁸. In other bird species, all individuals must forage for themselves regardless of their social status. We might expect the correlation between boldness in social interactions and boldness in exploration of the physical environment to differ between these two kinds of species. More generally, shyness and boldness may be domain-general because of physiological and hormonal constraints, but from the adaptive standpoint we should expect them to be domain-specific. Empirical studies should therefore attempt to measure shyness and boldness across a variety of domains.

Genetic polymorphisms and phenotypic plasticity: the evolution of proximate mechanisms

When psychologists say that a behavior has a 'biological' or a 'genetic' basis, they usually mean that the behavior is genetically predisposed and relatively inflexible – a 'trait' as opposed to a 'state'²⁹. Unfortunately, these terms are misleading and do not adequately describe the range of possibilities. Adaptive individual differences at the phenotypic level can be caused directly by underlying genetic differences or by mechanisms of phenotypic plasticity that allow single genotypes to achieve multiple forms^{23,30,31}. Mechanisms of phenotypic plasticity are themselves diverse in the period of the life cycle in which they operate, their reversibility and the particular environmental stimuli that trigger phenotypic change (e.g. personal experiences versus observing mother's response to events²⁻⁴). To the extent that these mechanisms have evolved by natural selection, they have as much a 'biological', 'genetic' basis as genetic polymorphisms. In addition, mechanisms of phenotypic plasticity can span the full range from 'states' to 'traits', depending on how early in life they operate and the degree to which they are reversed by subsequent environmental input.

Evolutionary models that predict the proximate determinants of the phenotype can help guide expectations about the causes of shyness and boldness in humans

Box 1. How density- and frequency-dependent selection might favor an innate shy–bold continuum within a single population

Imagine that we sequentially introduce individuals that have the same norm of reaction into an environment that offers both a safe and a dangerous habitat. The first individuals will wisely remain within the safe habitat. As additional individuals are added, however, the safe habitat will become increasingly crowded. At some point, the benefits of entering the dangerous-but-empty habitat will outweigh the benefits of entering the safe-but-crowded habitat. Thus, if population density exceeds this critical point, some individuals will exist in each habitat despite the fact that all individuals have the same norm of reaction.

Now consider a mutation that increases fitness within the dangerous habitat. The mutant form may still prefer the safe habitat if it is sufficiently empty, but it will decide to enter the dangerous habitat sooner than the original form and will reside entirely in the dangerous habitat if the population is sufficiently dense. Mutations that increase fitness in the safe habitat will similarly become restricted to the safe habitat. In this fashion, risk-averse and risk-prone 'specialists' with different skills and correspondingly different norms of reaction can evolve within a single population and also within categories of age, sex and size. A similar scenario can be constructed for safe and risky behaviors within a single habitat.

These models are similar to Rosenzweig's 'isoleg' model²⁷ that results in the evolution of habitat specialists.

and other animals³². One interesting possibility is that a mixture of inflexible and phenotypically plastic genotypes will be maintained within a single population (Box 2). In other words, natural selection might promote not only individual differences at the phenotypic level, but also at the level of proximate determinants of the phenotypes. There are actually some data to support this conjecture for shyness and boldness in humans. Kagan *et al.*²⁹ showed that children at the extremes of the shy–bold continuum are phenotypically more stable than individuals in the middle of the continuum. They speculate that what appears to be a continuum at the phenotypic level is not a continuum at the mechanistic level, but rather a mixture of inflexibly shy and bold individuals occupying the extremes and phenotypically plastic individuals occupying the middle range.

One advantage of studying shyness and boldness across a wide range of taxa is to discover how similar phenotypes are caused by diverse mechanisms. The density- and frequency-dependent processes outlined in Boxes 1 and 2 almost certainly operate in all major vertebrate and invertebrate taxa, yet the physiological systems that orchestrate shyness and boldness in insects or crustaceans, for example, are presumably different from the adreno-cortical response system that underlies this axis in mammals^{2,29,34,35}. Comparative studies can help to partition shyness and boldness into its adaptive aspects that are common to all taxa, and its particular forms that are unique to specific underlying mechanisms.

We have reviewed only a few of the theoretical models in behavioral ecology that can be applied to the study of shyness and boldness. It may turn out that our specific scenarios are inappropriate and must be amended or replaced by others. The important goal is to explain both behavior and its proximate mechanisms as a product of natural selection. Adaptationist thinking, which has produced such insights in other areas of animal behavior, should be used as a guide to explore the shy–bold continuum. To this end we suggest some specific testable hypotheses that emerge from the models outlined above.

The fitness of shy and bold individuals is density- and frequency-dependent. For some species, shy and bold individuals can be identified in natural populations and used to assemble experimental populations in which the density and frequency of shy and bold individuals are varied. If the model outlined in Box 1 is appropriate in its simple form, shy individuals should have the highest fitness in populations that consist mostly of bold individ-

Box 2. A model that predicts a mixture of innate and phenotypically plastic determinants of shyness and boldness within a single population

Assume that shyness and boldness are indeed 'strategies' that are maintained by frequency-dependent selection. Suppose further that 'innately' shy and bold individuals that are produced by phenotypically inflexible genotypes are superior to facultatively shy and bold individuals produced by phenotypically plastic genotypes. In other words, an individual who can become shy or bold depending on the situation will not be quite as successful as individuals who are predisposed from birth to be shy or bold. These assumptions are reasonable, given the complex physiological and hormonal basis of shyness and boldness.

In a constant environment, the innately (= specialist) shy and bold individuals will simply replace the facultative (= generalist) form. If the opportunities for risk-prone and risk-averse individuals are temporally variable, however, natural selection will promote a mixture of innate and facultative forms, whose relative proportions will depend on the magnitude of temporal variation. Even though the facultative form is inferior to the innate forms, it more easily switches to utilize the under-exploited opportunities. See Ref. 33 for technical details.

uals and vice versa, but only if population density is sufficiently high.

Phenotypic stability is density- and frequency-dependent. The first hypothesis assumes that individual differences are relatively inflexible, such that altering frequency and density will result in fitness differences. If shyness and boldness are easily modified, however, individuals can respond to changes in frequency and density by altering their phenotypes. Thus, when the phenotypic distribution is experimentally shifted towards one end of the continuum, we should observe at least some individuals shifting their phenotypes to re-establish the original distribution.

Innate shyness and boldness is superior to facultative shyness and boldness. The model outlined in Box 2 assumes that phenotypically plastic genotypes are 'jacks of all trades and masters of none'. If so, they should be inferior in competition with genotypes that are predisposed to be shy and bold. If imbalances are created in the phenotypic distribution of shy and bold individuals, however, phenotypically plastic genotypes should be the first to shift and benefit from the opportunities that are in greatest supply.

Conclusion

Psychologists who study shyness and boldness have a thorough appreciation of biology when it comes to genetic and physiological mechanisms. However, their work has not been consistently informed by an appreciation of natural selection, which molds phenotypes and their proximate controls in most species. Adaptationist thinking does not always produce the right answers³⁶ but it provides a useful conceptual framework for guiding empirical research. We hope that this framework will be increasingly applied to the study of shyness and boldness in humans and other animals.

Acknowledgements

We thank the many colleagues who responded to our requests for ideas, references and data during the preparation of this article.

References

- 1 Kagan, J. (1989) *Am. Psych.* 44, 668–674
- 2 Suomi, S.J. (1991) in *Plasticity of Development* (Brauth, S.E., Hall, W.S. and Dooling, R.J., eds), pp. 27–56, MIT Press
- 3 Fairbanks, L. and McGuire, M.T. (1993) *Am. J. Primatol.* 30, 119–129
- 4 Stevenson-Hinde, J., Stillwell-Barnes, R. and Zung, M. (1980) *Primates* 21, 498–509
- 5 Feaver, J., Mendl, M. and Bateson, P. (1986) *Anim. Behav.* 34, 1016–1025
- 6 Blanchard, R.J., Flannelly, K.J. and Blanchard, D.C. (1986) *J. Comp. Psychol.* 100, 101–107
- 7 MacDonald, K. (1983) *J. Comp. Psychol.* 97, 99–106
- 8 Jones, R.B., Mills, A.D. and Faure, J. (1991) *J. Comp. Psychol.* 105, 15–24
- 9 Clark, A.B. and Ehlinger, T.J. (1987) in *Perspectives in Ethology* (Bateson, P.P.G. and Klopfer, P.H., eds), pp. 1–47, Plenum
- 10 Armitage, K.B. (1986) *Ecology* 67, 1186–1193
- 11 Huntingford, F. and Giles, N. (1987) *Ethology* 74, 205–210
- 12 Mather, J. and Anderson, R.C. (1993) *J. Comp. Psychol.* 107, 336–340
- 13 Caldwell, R.L. (1986) in *Deception: Perspectives on Human and Nonhuman Deceit* (Mitchell, R.W. and Thompson, N.S., eds), pp. 129–146, State University of New York Press
- 14 Wilson, D.S., Coleman, K., Clark, A.B. and Biederman, L. (1993) *J. Comp. Psychol.* 107, 250–260
- 15 Svendsen, G. (1974) *Ecology* 55, 760–771
- 16 Buss, D.M. (1991) *Annu. Rev. Psychol.* 42, 459–491
- 17 Caspi, A., Elder, G.H.J. and Bem, D. (1988) *J. Dev. Psychol.* 24, 824–831
- 18 Magurran, A.E. (1990) *Anim. Behav.* 39, 834–842
- 19 Tulley, J.J. and Huntingford, F.A. (1987) *Anim. Behav.* 35, 1570–1572
- 20 Huntingford, F.A., Metcalfe, N.B., Thorpe, J.E., Graham, W.D. and Adams, C.E. (1990) *J. Fish. Biol.* 36, 877–881
- 21 Lima, S.L. and Dill, L.M. (1990) *Can. J. Zool.* 68, 619–640
- 22 Godin, J.-J. and Smith, S.A. (1988) *Nature* 333, 69–71
- 23 Stearns, S.C. (1989) *BioScience* 39, 436–445
- 24 Clarke, A.S., Mason, W.A. and Moberg, G.P. (1988) *Am. J. Primatol.* 14, 37–52
- 25 Clarke, A.S. and Boinski, S. *Am. J. Primatol.* (in press)
- 26 Giles, N. and Huntingford, F.A. (1984) *Anim. Behav.* 32, 264–275
- 27 Rosenzweig, M.L. (1991) *Am. Nat.* 137S, S5–S28

- 28 Barnard, C.J. (1984) *Producers and Scroungers: Strategies of Exploitation and Parasitism*, Chapman & Hall
- 29 Kagan, J., Reznick, J.S. and Snidman, N. (1988) *Science* 240, 167-171
- 30 Thompson, J.D. (1991) *Trends Ecol. Evol.* 6, 246-249
- 31 Newman, R.A. (1992) *BioScience* 42, 671-678
- 32 Fagen, R. (1987) *Evol. Ecol.* 1, 263-271
- 33 Wilson, D.S. and Yoshimura, J. *Am. Nat.* (in press)
- 34 Sapolsky, R.M. (1993) *Recent Prog. Horm. Res.* 48, 437-467
- 35 Sapolsky, R.M. (1990) *Biol. Psychiatry* 28, 862-878
- 36 Orzack, S.H. and Sober, E. (1994) *Am. Nat.* 143, 361-380

Conserving biological diversity in the sea

Global Marine Biological Diversity: A Strategy for Building Conservation into Decision Making

edited by Elliot A. Norse

Island Press, 1993.

\$50.00 hbk, \$27.50 pbk

(xxxii + 383 pages)

ISBN 1 55963 255 0/1 55963 256 9

Publications on conservation, biodiversity and ecosystem management have proliferated enormously in recent years, as can be seen in the lengthy bibliographies of *Global Biodiversity Strategy*¹ and its new companion volume, *Global Marine Biological Diversity*. Conserving biological diversity has coalesced as a dominant theme for decision making in response to the growing list of detrimental environmental effects associated with expanding human populations and short-term planning. Tropical rainforests, in particular, have captured considerable attention, fueled by graphic satellite and ground-level photography of clear-cutting and fires. Such habitat loss and degradation, coupled with biologists' limited cataloguing of species², raise the disturbing prospect that human activities are reducing biological diversity faster than it can be described and understood. Marine systems may lack the war-zone imagery of forests, but issues of conserving habitats and biological diversity are as pressing at sea as on land³.

As is the case in rainforests, new species are continually discovered in the sea (e.g. Refs 4-8). These species descriptions sometimes result in the establishment of higher taxa. For example, the discovery of coral-line sponges in caves and the deep fore-reef

of Jamaica led to the erection of a new family (Sclerospongiae⁹). In addition, the first chemosynthetic communities were only recently discovered at deep-sea hydrothermal vents, and the description of more than 200 new species has led to the naming of 23 new families. These discoveries of species, higher taxa and a previously unknown ecosystem underscore the urgency of incorporating conservation and management of marine resources into decision making, as suggested in *Global Marine Biological Diversity*.

Set against this need to acknowledge how seriously human activities affect the ocean, this book suggests that our understanding of how to conserve and manage marine resources and ecosystems is two decades behind our knowledge of terrestrial systems. A scan of articles in the past 24 years of *Annual Review of Ecology and Systematics* and seven years of *Conservation Biology* reveals only a small proportion of papers covering marine diversity, conservation and management. Both *Global Marine Biological Diversity* and Thorne-Miller and Catena¹⁰ note the characteristics of marine systems and organisms that differ fundamentally from their terrestrial counterparts and thus require special consideration by both scientists and decision makers. Recent workshops on ecosystem management, however, suggest a continuing focus on land-based issues, with little attention to the unique features of marine organisms and ecosystems. These two recent books on marine biological diversity may help counter this 'terracentrism'.

Few editors are willing to tackle more than 100 contributions, and Norse's effort undoubtedly expanded the scope and detail of *Global Marine Biological Diversity*. However, the book suffers from redundancy and uneven coverage. The science coverage is more extensive than that of Thorne-Miller and Catena, yet its recommendations are less comprehensive and more tentatively expressed than the objectives and actions presented in *Global Biodiversity Strategy*. Individuals concerned about conserving marine biological diversity should consider all three of these books and derive the best elements of each.

Brian D. Keller

The Ecological Society of America,
2010 Massachusetts Avenue, NW,
Suite 420, Washington, DC 20036, USA

References

- 1 WRI/IUCN/UNEP (1992) *Global Biodiversity Strategy*, World Resources Institute, The World Conservation Union, and United Nations Environment Programme
- 2 Wilson, E.O. (1988) in *Biodiversity* (Wilson, E.O. and Peter, F.M., eds), pp. 3-18, National Academy Press
- 3 Ray, G.C. and Grassle, J.F. (1991) *BioScience* 41, 453-457

- 4 Knowlton, N. and Keller, B.D. (1985) *Bull. Mar. Sci.* 37, 893-904
- 5 Knowlton, N., Weil, E., Weigt, L.A. and Guzman, H.M. (1992) *Science* 255, 330-333
- 6 Knowlton, N. (1993) *Annu. Rev. Ecol. Syst.* 24, 189-216
- 7 Sebens, K.P. (1994) *Am. Zool.* 34, 115-133
- 8 Allen, G.R. and Robertson, D.R. (1992) *Rev. Fr. Aquariol. Herpetol.* 19, 37-40; 47-52; 53-56
- 9 Hartman, W.D. and Goreau, T.F. (1970) *Symp. Zool. Soc. London* 25, 205-243
- 10 Thorne-Miller, B. and Catena, J. (1991) *The Living Ocean: Understanding and Protecting Marine Biodiversity*, Island Press

Ecology and environmental education: case studies and policies from around the world

Ecology in Education

edited by M. Hale

Cambridge University Press, 1993.

£29.95/\$49.95 hbk (xvi + 191 pages)

ISBN 0 521 43346 0

What can ecologists contribute to the field of environmental education? In some circles, ecologists are viewed as more rigorous scientists than the individuals who generally produce environmental education curricula. Ecologists are therefore able to lend a degree of scientific rigor to what has been seen as a 'touchy-feely' or 'media-hype' approach to teaching about the environment. In the US, ecologists have been able to capitalize on their scientific legitimacy, and acquire funding from science education agencies for environmental education programs. These programs address societal concerns about both the state of science education and the deteriorating environment. This approach is exemplified by efforts of members of the Ecological Society of America, who have established a set of criteria (drawing heavily from recent thought in science education) by which to evaluate environmental education curricula.

This is one of a number of approaches described in *Ecology in Education*. At the other end of the spectrum is the view that environmental education has been coopted by the 'technocratic rationality of empirical/analytic science'. The argument here is that by emphasizing ecological and other scientific concepts, as well as by a top-down approach to teacher education which limits teachers' creative input into the curriculum, environmental education has missed