requires multiple measurement of each individual. Only if the latter alternative is true is local optimality of foraging behavior a possible conclusion. We stress the need for data in this regard, as the prior beliefs that differences in foraging activity among individuals are 'likely' or 'unlikely' amount to answering the question of the local optimality of this trait. Milinski's study is exemplary in many ways but with its lack of analyses concerning the possible differences among the traits of individuals it shares a deficiency with almost all other tests of optimality models that makes a test of local optimality impossible (see also Ref. 23).

The test of adaptationism

The results obtained in the analyses of *Sphex ichneumoneus* and *Nasonia vitripennis* are mixed in regard to supporting adaptationism. Yet, any present claim about the validity of adaptationism is weak since adaptationism cannot be assessed by examining the way a single specific model conforms to a single dataset[4,5,11]. It is only by assembling the results of such focused investigations of many traits that adaptationism can be assessed in a reasonable way. This test need not engender an endless 'debate'. If, say, 45 out of 50 studies lead to the conclusion that the trait in question is locally optimal, one could conclude in our opinion that adaptationism is correct.

The significance of optimality models

We wish to promote a valid assessment of adaptationism. We are also motivated by the belief that optimality models are too important to be applied inexactly and to have unsubstantiated conclusions drawn about their explanatory power. Optimality models and the test of adaptationism deserve better.

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Advances in marine conservation: the role of marine protected areas

M. Tundi Agardy

The world's oceans are now attracting the serious attention of conservationists. Paradoxically, as the value of marine biological diversity is recognized, the ecosystems that harbor this diversity are fast becoming degraded. New thinking about how to conserve coastal areas has resulted in protected-area models that incorporate principles of landscape ecology, adaptive and ecosystem management, and zoning in protected-area plans.

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Though most people continue to perceive oceans as monochromatic, homogenous, resilient, vast – and therefore limitless – new notions about marine systems have surfaced recently. Most of the world's biological diversity at higher levels of taxa is found in the sea; indeed, 32 of 33 known phyla are marine – 15 exclusively so. Habitat diversity, ranging from distinctive and well-known coral reefs to the obscure and bizarre non-photosynthesis-based hydrothermal vent systems, is unparalleled. Marine productivity is highly variable, exhibiting extensive patchiness even within a particular habitat type, and in some areas carbon fixing rates exceed the most productive terrestrial systems. Yet, even as we gain more insight into the complex and heterogeneous world of the seas, the signs of destructive human impact are visible everywhere. What we once thought limitless, isn't; what we once thought as resilient seems less so.

Conservationists have only focused their attention on marine issues in recent times; therefore, marine conservation lags several decades behind the land-based conservation movement. There are many obstacles impeding successful conservation of marine systems, some of which are detailed later in this essay. The fluid nature of the environment and the nebulous character of ecological boundaries underlie these difficulties, and have made it necessary for conservation biologists to develop new models. Truly effective marine conservation will require that we give up our traditional preoccupation with conserving structure (by erecting fencing around the fragments of systems that we feel have a structure worth protecting) and instead direct ourselves towards safeguarding the critical ecological processes that are responsible for maintaining that valuable structure. Though such a functional approach is not unique to marine conservation, it is the only feasible option for relieving some of the pressures that a burgeoning coastal population and ever-increasing marine resource-use bring to bear on the seas.

Is this a real departure from the status quo or merely new light shed on an old way of thinking? The flurry of recent papers on marine ecophysiology and on functionally based approaches to conservation suggest the former[1–3]. Take, for instance, the scenario of protecting an estuary – that vital organ of the marine system that is so rich in ecological services and productivity. In the old days, a government agency charged with protecting such an estuary might have outlined the embayment on a map, fenced off its land margin and posted signs alerting visitors and potential users of its protected status. Today the conservation effort would extend far beyond the boundaries of the bay itself by looking

at critical linkages in nutrient cycling, migration of species and system dependencies on other habitats in the watershed and out at sea[4]. And while the garrison reserve of yore would slowly become degraded by impacts from a distance, the functionally based conservation scheme stands a chance of safeguarding that vital ecology for the future.

Today's marine protected areas (MPAs) are a decided departure from past practice and its umbilical link to terrestrial park planning. Marine protected areas are no longer established as amusement parks for recreational use or as shaded areas on a map with little thought given to how that area might be used most wisely. Coastal planning and MPA management are becoming sophisticated initiatives employing new models and new tools. The new generation of marine protected areas is now largely represented by multiple use reserves accommodating many different stakeholders, each with their own set of objectives[5]. Administrators are finding that different uses can indeed be accommodated without adverse impacts on ecosystem function, as long as planning is both science-based and establishes clear, detailed objectives *a priori*.

Nonetheless, the survival and efficacy of MPAs is inevitably linked to the larger matrix in which they are planned and carried out. No MPA is an island; the extensive linkages and amorphous nature of boundaries make context all the more important. Sadly, if we allow the world outside MPAs to continue to decline in response to myriad, chronic impacts, even the most well-designed and executed protected areas have no future. Yet MPAs serve as valuable anchors for the large-scale conservation of the biosphere, and as such they secure the future of marine conservation.

Marine protected areas as a vital tool for science-based conservation

The potential benefits that MPAs can confer are varied. The common thread running through all MPA benefits is their provision of physically definable testing grounds for some of the newest and most exciting concepts in conservation biology, resource economics and management.

Arguably, the most important role MPAs serve is as a starting point for exploring and delimiting functional linkages in coastal systems[6], metaphorically moving us away from being quacks to being effective physicians. Ecological studies that provide the basis for marine protected area work facilitate the determination of appropriate boundaries for management units and a specific framework for applying ecological principles for the purposes of management. Ecosystem management, seen by many as 'the joke at the party that everyone laughs at but no one gets', can be field tested in the context of MPAs. For those with a more terrestrial orientation, ecosystem management implies using ecosystem science as a basis for management decisions that aim to maximize production of a commodity. For those with a marine background, ecosystem management typically means looking at the functional linkages between the target ecosystem and habitats or ecological communities outside in order to define functionally viable management units[7]. Both these interpretations of ecosystem management need a geographic context in which to be tested[8], and MPAs provide the ideal venue for doing so.

Marine protected areas allow us to invoke the 'precautionary principle' – a term that like ecosystem management has lost some of its intrinsic value as it becomes popular political jargon without stringent definition. In science-based conservation, the precautionary principle is what drives managers to err on the side of conservatism when scientific uncertainty looms[9]. Central to the idea of the precautionary principle is the notion that actions that produce irreversible change to ecosystems (extinctions and the permanent restructuring of food webs, for instance) must be avoided at all costs. Recognizing that the general status and condition of coastal and nearshore areas will undoubtedly decline and that scientific knowledge about marine and coastal ecosystem functions is far from complete, MPAs provide a physical area in which to apply the precautionary principle and buffer against unforeseen yet potentially disastrous management mistakes.

Marine protected areas also establish frameworks for applying the idea of 'adaptive management'. Adaptive management is also a nebulous term[10], but fisheries science has provided us with some rigorous definitions of precisely what is meant by it[11]. Two conditions must apply for resource management to be adaptive: (1) an explicit feedback loop between science and management must be maintained, so that management can be maximally flexible and responsive to both environmental and social changes; (2) management measures must provide a setting for experimental manipulation of regulations so that their efficacy can be objectively tested. As clearly recognizable entities, MPAs can firmly establish such management–science links and provide a laboratory for experimental testing. This is all the more necessary in marine systems, where managers must deal with largely stochastic systems characterized by enormous uncertainties[12,13]. Marine protected areas also provide a framework for reconciling potentially contrasting goals advocated by different user groups, such as protecting property rights, establishing scientific research sites, maximising economic development and practising effective, cost-efficient enforcement.

Some MPAs act as nodes in networks of monitoring sites designed to try and evaluate the general state of the marine environment and specific conditions of nearshore ecosystems. Such monitoring and evaluation allows estimates of potential productivity of renewable resources and is thus a major component in determining sustainable levels of use. Marine protected area monitoring networks also provide means to assess global change and field test theoretical models of global scale processes. Certain areas within MPAs, such as strictly protected core areas, also serve as necessary controls against which the rate of environmental deterioration can be gauged.

As we gain more understanding of marine systems and their productivity, we reinforce intuitive beliefs that the management of our impacts on ecological function must not be taken one-by-one. Cumulative impacts stretch over time and across space to collectively impair function and undermine resilience. Establishing conservation measures that protect against the suite of anthropogenic impacts is notoriously difficult, and even the most idealistic among us recognize that triage is sometimes necessary. Since not all components of coastal and marine systems can be protected, human and financial resources should be targeted at those areas that harbor the most important ecological functions or those that are most threatened by direct and indirect human activity[14]. In this context, MPAs allow establishment of systems of non-extractive zones or harvest refugia, in order to protect seed banks or sources of recruits and critical ecological processes that are currently being impaired or are likely to be impaired in the short term future[15,16]. There is increasing evidence that such refugia not only protect marine organisms *in situ* but that they can serve to increase productivity in a wider area[17].

Marine protected areas also provide a means to protect critical habitats or areas of high concentration of endangered species. If MPAs exist in the public consciousness, it is this for which they are known. However, the days of using protected areas solely to safeguard a single species, or an especially sensitive community of organisms, are numbered.

Nowadays, MPAs often use species protection as a starting point for establishing a more comprehensive and ecologically realistic system of management[18].

Marine protected areas and the human component

It may be doing conservation a disservice to separate the role that MPAs play in science-based management and the role they play in accommodating human needs, since the latter is a critical component of the former. Yet, modern MPAs are much more than laboratories for evaluating how scientifically rigorous our management measures are – they are often the only starting point for creating fora to resolve use conflicts and establish a basis for responsible use and responsible attitudes[19]. Marine protected areas in this context are publicly recognizable spaces which allow users to become actively involved in planning (rather than being the recipient of management regimes imposed from outside) and in management – including undertaking enforcement of regulations – through partnerships between regulatory agencies and user groups[20,21]. Marine protected areas thus provide the sociological anchor for averting the 'tragedy of the commons'[22] and fostering a sense of stewardship for ocean resource and ocean space among the people who most rely on healthy, intact coastal systems.

Additionally, MPAs can act as a means to preserve traditional uses that have survived as sustainable over long periods of human history. As eloquently stated by McNeely[23], local societies have ebbed and flowed as their wisdom was tested against the criterion of sustainability – those that were able to develop the wisdom, technology and knowledge to live within the limits of their environment were able to survive. By delimiting an area for the purposes of conservation, MPAs provide precise locales in which traditional and sustainable practices can be maintained by local and indigenous peoples[24].

One dilemma facing coastal conservationists is having to deal with the debasement of coastal communities who live on marginal lands, have little or no political voice, and realize few of the benefits of national scale economic development. In such areas, MPAs provide a means to empower local stakeholders and raise the profile of their coastal conservation needs. Marine protected areas can help advertise the potential value of coastal resources and space to political entities and development agencies[25] by facilitating economic valuation of such areas, creating venues for ecotourism or nature-based tourism, and demonstrating how development and conservation can be integrated at the local level[26].

If MPAs are ideal why aren't they surfacing everywhere?

Attention is increasingly being given to marine systems, yet the decisions to initiate MPA projects are often taken hesitantly. And severing the umbilical cord from the terrestrial parks model is harder than one might think. Many conservationists now working in the coastal margins come from academic backgrounds or field training that is based on terrestrial planning and management. Major differences in the dynamics and scales of terrestrial and marine systems have been elucidated[27], yet many conservationists choose to ignore those differences rather than rise to the challenge of creating new paradigms. Our strong reliance on terrestrial models must be abandoned in favor of a vigorous, independent growth of ideas more fitting to ocean systems.

Public perception may also hinder the application of innovative new ideas. Marine protected areas are still viewed as marine parks – off limits to local users, benefiting only temporary visitors. Shedding the old reputation of protected areas as being elitist unaffordable luxuries is difficult, especially in the eyes of user groups like fishermen and local communities in the developing world, for whom words like 'park' and 'reserve' have deeply ingrained negative connotations. Marine protected areas suffer because their benefits are hard to quantify and are often slow to be realized. We live in a world that craves instant gratification, and the mutually dependent functions of resource renewal, sustainability of ecosystem function and long-term socioeconomic welfare of coastal peoples is not always linked in people's minds. It is for this reason that clearly stated and specific management objectives, against which progress can be quantitatively measured, constitute the core of MPAs.

Establishing the new generation of MPAs is risk-laden. Frameworks for management in these MPAs must thus be sufficiently responsive and flexible to allow for change as better scientific information is gathered or conditions (environmental or social) change. Despite this, MPA planning must be done within the limits of a resource-management community that is typically risk-averse. Getting administrators and government agencies to 'buy in' to new models for marine conservation, especially those that recognize large scientific uncertainties and put more of management in the hands of the users, requires patience and compromise. At the same time, we stand at a critical juncture with respect to the future of marine biological diversity and ocean health. We can't afford to be patient and plodding much longer.

Navigating the future

A recent editorial in *Conservation Biology*[28] suggested that in order for conservation to be effective on landscape scales an integrated four-pronged effort was necessary. The four components are the preservation of critical habitats, protection of threatened species, mitigation of cumulative environmental degradation, and determining levels of sustainable use for renewable resources. Marine protected areas provide a rare opportunity to utilize this multi-disciplinary approach and make conservation in the marine realm effective.

Selection of sites in which to implement MPAs will continue to be based largely on criteria relating to needs: for instance, how threatened are resources, ecosystem processes and lifestyles? Yet the best MPAs of the future are likely to be those that use forward-looking, flexible management to accomodate myriad needs and expectations – making opportunity criteria additionally important in decisions regarding where and when to establish MPAs.

With all the visionary new concepts in conservation biology and resource management currently afloat, even the most conservative scientists agree that field-testing ideas is a prerequisite to embracing them (or, for that matter, tossing them blithely aside). Marine protected areas that are appropriate to the geographic scales of coastal and marine ecosystems, that contain management units grounded in ecology, and that allow multiple uses by establishing zoning to protect that which is most critical, most sensitive or most amenable to monitoring and evaluation, can be the anchor to evaluate new ideas. In many cases, MPAs provide a unique opportunity to force definitions of vague concepts, field test them, evaluate their potential objectively and demonstrate their usefulness. Unique because our history of tinkering with the oceans is so far brief, and we haven't had the time yet to establish entrenched bureaucracies and rigid paradigms. This is an opportunity we must not waste. Successful MPAs not only resolve local management issues but can also provide salient examples of how we should be managing our impacts on our seas at regional and even global scales. It is probably no exaggeration that the future of the earth's nearshore areas, to the extent that we have some role to play in deciding that future, rests firmly

on the shoulders of the new generation of MPAs.

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Primate socioecology

Juvenile Primates: Life History, Development and Behavior

edited by M.E. Pereira and L.A. Fairbanks

Oxford University Press, 1993.
$65.00/£50.00 hbk (xvi + 428 pages)
ISBN 0 19 507206 5

Lemur Social Systems and Their Ecological Basis

edited by P. Kappeler and J. Ganzhorn

Plenum Press, 1993.
$79.50 hbk (viii + 274 pages)
ISBN 0 306 44576 X

Juvenile Primates is the first book on primates that focuses specifically on juveniles. It will be a necessary and useful reference for any future studies of primate development. The two editors are to be praised for their effort to assemble a large body of information concerning this relatively neglected area of primatology and for the care and clarity with which they introduced and connected all of the material. They are also to be commended for successfully encouraging their contributors to present new data and ideas and not simply to review previously published material.

The book's best part is perhaps its life history and comparative approach. In Part I, the distinctive features of primate development – delayed somatic growth and maturation, vulnerability to malnourishment and predation – are analysed in a broad mammalian perspective (a perspective that should be adopted more often by primatologists). The juvenile period has been extensively studied only in a few species of cercopithecine monkeys and apes, and some chapters in Part II provide important quantitative information on juvenile socioecology in some lesser-known species. The development of social relationships, in particular the process of dominance rank acquisition in macaques and vervet monkeys, is one of the aspects of juvenile behavior that has been most accurately studied in the past three decades. Most of the chapters in Parts III and IV emphasize the implications of juvenile behavior for adult roles, but only one of them (Chapter 17, by Chapais and Gauthier) examines the relationship between juvenility and infancy. This book, however, would have been an appropriate context to present or review some of the recent research on early influences on exploratory and risk-taking behavior[1,2,3]. Similarly, other aspects of primate behavioral development, such as vocal communication[4,5], deserved a mention. Among the chapters on human juveniles, Chapter 21 by Blurton-Jones focuses on parental reproductive strategies in hunter-gatherers and does not fit well with the theme of the book. *Juvenile Primates* is, however, an excellent book that can be recommended to all biologists and anthropologists who are interested in the study of animal and human behavior from an ecological and evolutionary perspective.

Lemur Social Systems contains the proceedings of a symposium held at the 1992 Conference of the International Primatological Society. Its 17 chapters span a wide range of topics. Among other things, the book contains useful, though in some cases very preliminary, information concerning the ecology of some little-known species of Malagasy lemurs (chapters by Sterling, Colquhoun and Rigamonti); a review of predation on lemurs and of some experiments on lemur antipredator responses (chapters by Goodman *et al.* and Macedonia); the comparison of habitat use and food selection between pairs of sympatric or closely related species (chapters by Ganzhorn, Overdorff, and Meyers and Wright); and some interesting essays on lemur social evolution (chapters by Sauther and Sussman, Kappeler, and van Schaik and Kappeler).

Given the proliferation of research on lemurs in the past two decades, a book on lemur socioecology is certainly timely and it will be a useful reference for future research and conservation of these primates. This book, however, will be difficult to read for researchers and students who are not lemur specialists. While many different species of Malagasy lemurs are discussed, very few photographs are provided to help the reader visually identify these species. The information provided in different chapters is poorly integrated, in part because the editors' input is minimal. For instance, the book has a short preface but the chapters are not organized into sections and there is no synthetic or conclusive chapter. Even for the best-known species, the ring-tailed lemur, there seem to be some discrepancies between information reported from different field sites and from natural and semi-natural conditions, and disagreement over their territorial organization, the functional significance of female dominance, and the role of infanticide versus resource competition in shaping the species' social organization. Therefore, it would have been helpful to synthesize and discuss critically these discrepancies and opposing views rather than leaving the burden entirely on the reader. Although the field studies reported in this book expand our knowledge of lemur ecology, a full understanding of lemur social evolution will require more-detailed information on the