Towards a behavioral ecology of ecological landscapes

2 authors, including:

associate with humans may differ, and ecological differences related to the stricter commensalism of *domesticus* than that of *musculus*[2] have been used to explain various genetical observations[3,4]. Moreover, several authors have proposed that the high rates of chromosomal evolution in mammals may be better understood if social structure and behaviour are taken into account[5]. Although house mice are an ideal model to study mate discriminatory behaviour owing to their well-studied chemical communication systems[6], attempts to document behavioural differences between the two subspecies and between standard and robertsonian mice remain very limited.

Nachman and Searle[1] do not consider that habitat diversification may be involved in chromosomal change. Colonization of man-made structures by house mice from natural habitats involves increased population densities leading to changes from a largely territorial to a hierarchical social structure[7]. Chromosomal divergence may or may not have occurred during this process of adaptation to the commensal habitat. Support for

this idea lies in the fact that certain physiological traits are known to differentiate commensal from wild-ranging mice[8] and that almost all chromosomal races of the house mouse are commensal[9]. Additionally, adaptation to a novel niche such as the commensal one may involve transient phases of disequilibrium. Environmental stress and disequilibrium have been shown in some cases to generate high chromosomal mutation[10] or recombination[11] rates. Such events can lead to rapid evolutionary changes, which might have been the case for the house mouse.

The point I wish to stress is that chromosomal evolution in house mice presents not only a challenge for mouse geneticists[1], but also an ideal opportunity for behavioural ecologists and geneticists to work together. Comparative studies between standard, robertsonian, chromosomal hybrid populations and between the two subspecies are unavoidable. The areas that deserve particular attention are: population dynamics, ecophysiology, behavioural characterization and mate discriminating capacities.

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References
1 Nachman, M.W. and Searle, J.B. (1995) *Trends Ecol. Evol.* 10, 397–402
2 Sage, R.D. (1981) in *The Mouse in Biomedical Research* (Foster, H.L., Small, J.D. and Fox, J.G., eds), pp. 39–90, Academic Press
3 Boursot, P. *et al.* (1984) *C. R. Acad. Sci.* 299, 365–370
4 Vanlerberghe, F. *et al.* (1988) *Genet. Res.* 52, 185–193
5 Wilson, A.C. *et al.* (1975) *Proc. Natl Acad. Sci. USA* 72, 5061–5065
6 Sage, R.D., Atchley, W.R. and Capanna, E. (1993) *Syst. Biol.* 42, 523–561
7 Boursot, P. *et al.* (1993) *Annu. Rev. Ecol. Syst.* 24, 119–152
8 Ganem, G. (1991) *Comp. Biochem. Physiol.* 99(A), 531–536
9 Ganem, G. (1993) *Mammalia* 57, 349–357
10 Parsons, P.A. (1987) *Evol. Biol.* 21, 311–347
11 Parsons, P.A. (1993) *Am. Nat.* 142, S5–S20

Towards a behavioral ecology of ecological landscapes

Steven L. Lima
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Recent developments in landscape-level ecological modeling rest upon poorly understood behavioral phenomena. Surprisingly, these phenomena include animal movement and habitat selection, two areas with a long history of study in behavioral ecology. A major problem in applying traditional behavioral ecology to landscape-level ecological problems is that ecologists and behaviorists work at very different spatial scales. Thus a behavioral ecology of ecological landscapes would strive to overcome this inopportune differential in spatial scales. Such a landscape-conscious behavioral undertaking would not only establish more firmly the link between behavior and ecological systems, but also catalyze the study of basic biological phenomena of interest to behaviorists and ecologists alike.

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The studies of behavioral ecology and landscape-level ecological processes are poised for a productive union. Animal ecologists have identified animal movement, dispersal and habitat selection as particularly important determinants of the dynamics and spatial distribution of populations in heterogeneous landscapes[1–9]. Behavioral ecologists have long been interested in animal decision making regarding movement[10,11], dispersal[4,12] and habitat selection[13]. So why are most ecologists and behaviorists largely unaware of this impending union? The answer, in a word, is scale. Ecologists and behaviorists are usually working and thinking at vastly different

spatial scales. As a result, well-established research programs in each realm have unfortunately few points of contact.

Our goal is, therefore, to encourage the development of a behavioral ecology of ecological landscapes. Such a 'landscape-conscious' behavioral undertaking would revolve around understanding, at the scale of ecological landscapes, the sort of information available to an animal as it moves through its environment, and how this information is used in selecting a patch or habitat. We organize our discussion around behaviorally explicit ecological models that address population dynamics and spatial distribution across heterogeneous land-

scapes. Our discussion has several recurrent themes. One theme is the aforementioned issue of spatial scale. We will not specify a precise scale under consideration, as the spatial scale of ecological landscapes versus local movement, and so on, will undoubtedly depend upon the species and phenomenon under study. A second theme concerns an informational continuum in which model animals are bestowed with considerable knowledge about their landscape in some situations, whereas in others they are allowed very little knowledge. A third theme concerns a 'standard of plausibility' in the application of behavioral concepts in landscape-level ecological modeling, which reflects the current lack of empirical, landscape-oriented behavioral information.

Movement and dispersal
Information-based approaches

Information-based approaches to modeling movement/dispersal endow an animal with some information about its landscape, and the ability to use that information in a decision-making process. Such approaches usually specify a goal and some sort of stopping rule, typically reflecting a process of habitat selection (see below). In aggregate, these information-based approaches deal with a range of spatial scales and vastly different degrees of informational availability and behavioral abilities.

At one extreme on the informational continuum are theoretical studies assuming that animals disperse in random directions for a random distance, and then settle in the nearest detectable habitat patches[9]. Related models allow the animal to detect

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Box 1. Perceptual range and its implications

The notion of a perceptual range of some sort appears in many landscape-explicit ecological models[3,5,9,14-19]. However, few theoretical studies have systematically investigated the effects of changing perceptual abilities on the dynamics of populations in heterogeneous landscapes. Those that have done so demonstrate the potential importance of perceptual range as a determinant of population dynamics[3,9] (but see Refs 17,18).

At the level of behavioral decision making, we envision the link between perceptual range and landscape-level ecological processes as being mediated through the elevated risk of mortality experienced by dispersing animals[14,29]. An animal with a low perceptual range can expect a relatively high risk of mortality, as it will spend more time searching for a suitable habitat patch than would an animal with a high perceptual range. Thus, dispersal-limiting ecological phenomena that occur at the boundary of landscape elements (e.g. forest fragments), such as edge hardness[11] and neighborhood effects[30], may be accentuated for low-perceptual-range species; animals may be unwilling to accept the risk of leaving their home patch if they do not perceive any other suitable habitat (see also Ref. 31). Perceptual range may therefore act as a determinant of landscape connectivity[22]. For similar reasons, perceptual range may also be a determinant of landscape-level ecological processes such as landscape complementation and supplementation[30], or the spatial scale at which an animal interacts with a given landscape[32].

The potential importance of perceptual range is eclipsed by the almost complete lack of empirical data on perceptual ranges. Questions as simple as 'from what distance can animal x detect landscape element y' have very few answers in the behavioral literature. This is particularly true for vertebrates. It is probable that birds can detect landscape features at great distances. This may also be the case for many large terrestrial mammals. We suspect, however, that empirical investigations of perceptual range might yield some surprising results. For instance, pond slider turtles (*Trachemys scripta*) seem able to detect the presence of ponds at least 300 m away, based upon polarized light[33]. In contrast, we have found recently that the small forest mammal *Peromyscus leucopus* is unable to locate forested habitat only 30 m away (Zollner and Lima, unpublished). The insect literature provides some exceptions to this dearth of studies on perceptual range[34]. Overall, most insects have only a very limited ability to detect habitat patches visually. However, habitat patches may be detected chemically at a distance of several meters, depending upon weather conditions[34].

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suitable habitat during dispersal itself[14,15]. These models effectively allow the animal very little information about the landscape through which it moves, and are typically concerned with dispersal (see Ref. 12) and relatively large-scale population dynamics (e.g. metapopulations).

At the other extreme on the informational continuum are studies attributing considerable cognitive abilities to animals. Using significant powers of spatial memory and learning, such animals move through their landscape in an attempt to travel as efficiently as possible. This is exemplified by modeling approaches that use artificial intelligence[16]. These sorts of models deal mainly with relatively small (local) spatial scales, such as movement within a home range. These models have more in common with studies of foraging theory than with models of population dynamics.

Intermediate in the informational continuum are theoretical studies intermediate in spatial scale (often dealing with local population dynamics). Animals modeled are typically given knowledge only about their nearby landscape; they have no information about the greater landscape. Rules of movement usually reflect an assumption regarding the motivations of the animals under study. Model animals typically move in the direction of greatest detectable resource abundance[3,17] or disperse in the direction of the best detectable living-site[5,18].

All information-based modeling approaches to movement and dispersal have at least three things in common, regardless of spatial scale or informational availability. First, all such modeling approaches share an entity that we refer to as an animal's perceptual range. We define perceptual range as the distance from which a particular landscape element can be perceived as such (or detected) by a given animal. An animal's perceptual range represents its informational window onto the greater landscape. In most models, an animal has knowledge about only that portion of the landscape within its perceptual range, and thus all movement decisions are predicated on the animal's perceptual range. The importance of perceptual range is not fully appreciated in the theoretical or empirical literature (Box 1).

A second point of commonality is that the mechanics or rules of animal movement are often imposed on a model animal without considering their efficacy relative to other rules. A rarely posed question, outside of the 'small-scale' foraging literature[10], is just how an animal should move through its landscape such that its fitness is maximized. The question of the optimal mechanics of dispersal through an ecological landscape is interesting, as a dispersing animal may have relatively little information about the distribution or number of potential living-sites/habitats in the greater landscape. Dusenbery[19] adapted existing search theory in considering the question of optimal searching behavior with respect to a uniform distribution of patches across a landscape. He found that a straight path of movement will maximize the likelihood of an encounter with a patch. Recent work by Duvall *et al.*[20], however, suggests that a degree of sinuosity in travel paths will maximize encounters with patches when the latter are clumped in distribution.

A third point of commonality among information-based approaches to animal movement is an almost complete reliance on a standard of plausibility in specifying behavior. Such a standard is inevitable given the lack of (landscape-level) empirical information with which to assess the validity of most postulated rules of movement. This lack of information holds regardless of the spatial scale under consideration. We would not argue that the prevailing standard is an unreasonable one, but the field must move beyond mere plausibility regarding behavioral issues in ecological modeling.

We note here that the above considerations apply mainly to spatially explicit ecological models[2]. It is difficult to specify realistic animal movement in non-spatially explicit models (but see Ref. 6). Typically, such modeling approaches assume that animals choose patches at random, and that all patches are equally accessible and detectable from all others.

Information-free movement

Ironically, some of the more notable applications of behavioral concepts to landscape-level ecological questions effectively

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Box 2. Conspecific attraction

One way to ensure the choice of suitable habitat is to settle where conspecifics have already established themselves. Animals using such a rule of thumb in choosing habitat patches would exhibit conspecific attraction[27,31]. Such a behavioral rule of thumb could act to lower metapopulation viability, since empty but otherwise suitable habitat patches would go unoccupied[27]. A theoretical confirmation of this effect provides a tantalizing glimpse of the importance of conspecific attraction in population dynamics[35].

There are several unaddressed issues surrounding the idea of conspecific attraction. One issue concerns the extent to which the greater landscape determines the attractiveness of conspecifics in a given habitat patch: the decision not to settle in a sparsely populated patch should depend on the probability of locating a better patch in the greater landscape. We expect that animals facing limited perceptual ranges and risky dispersal would exhibit a relatively low degree of conspecific attraction in patch selection. Another issue concerns the logical possibility that animals might use a decline in conspecifics as a signal of a decline in habitat quality. Such a behavioral rule might lead to the active abandonment of occupied patches during (local) population declines (see also Ref. 31). These resulting 'pseudo-extinctions' could greatly complicate empirical assessments of population extinction risks. A further issue concerns the degree to which conspecifics make a patch more detectable rather than more attractive *per se*; making such a distinction might have interesting theoretical consequences.

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rule out information and its use in adaptive decision making. These applications are based upon random walks and diffusion processes, and draw upon a substantial empirical base of information[7,8,21]. Such approaches assume that animals have no knowledge of the general landscape or their immediate surroundings, and that they gain no information while moving across a landscape. Furthermore, these animals do not make strategic 'decisions' regarding their movements, nor do they have a goal towards which they are moving (but see Ref. 8). It is perhaps no surprise that the random-walk/diffusion approach is strongly biased towards arthropods[7,8,21], a group not normally considered to possess higher cognitive abilities. This approach may not be readily applicable to vertebrate systems[3], but may nonetheless provide a useful starting point in assessing the effects of complex movement behavior on ecological systems. Overall, the random-walk/diffusion approach can be seen as the ultimate expression of 'behavioral minimalism' in landscape-level ecological analyses (see below).

Corridors

Some modeling approaches, dealing mostly with metapopulation dynamics[22–24], specify interpatch movement via fixed corridors. An important unanswered behavioral question here is whether corridors are perceived (i.e. sought out) as travel routes to distant patches, or merely landscape elements that animals enter passively. This is not a trivial distinction. For instance, animals with corridor-based strategies of movement or dispersal might be able to determine which corridors will facilitate safe movement between patches, and which are dead ends or of low quality. A network of corridors might function more as an ecological trap than as a facilitator of dispersal for animals lacking corridor-based

strategies for movement (see also Refs 24,25). Some recent studies show that animals will move along corridors[23], but the above behavioral distinction is largely impossible to make at present.

Habitat selection

Nowhere is the 'spatial scale differential' between behavioral ecology and landscape-level ecology more apparent than in the area of habitat selection. Behavioral ecologists have produced a variety of studies on habitat selection motivated by the ideal free distribution (IFD) model of habitat or patch selection[13]. Such studies deal with very small spatial scales, and very high degrees of informational availability. Typically, each animal has much information on both the location and quality of resource patches (habitats). Indeed, in experimental studies of habitat selection within the IFD paradigm, all animals can typically view all patches simultaneously.

The process of habitat selection relevant to landscape-oriented ecologists is vastly different. At large spatial scales, animals may face great uncertainty as to not only the location of patches, but also the number of such patches in the local or regional landscape, and the number of animals occupying those patches. They might also be unable to assess quickly the quality of the patches that they do locate. There have been learning-based attempts to incorporate informational uncertainty into the IFD paradigm of habitat selection[26], but at an effectively small spatial scale. Furthermore, opportunities for learning would appear to be minimal at a very large spatial scale. Such learning requires the repeated abandonment and location of potentially widely spaced patches, which might be too risky to attempt.

The present situation is thus an unhappy one in which behavioral ecology can provide relatively little guidance to land-

scape-level ecological studies. Therefore, a standard of plausibility must inevitably be applied to behavioral issues surrounding habitat selection on a large spatial scale. In models at the scale of metapopulations, a rule of 'choose the nearest detectable habitat patch' is often used[9,15]. This is certainly a plausible rule. It presumes, however, a landscape with no inherent interpatch variability. The question of variation in patch quality and its influence on patch choice (or immigration) is rarely considered at the metapopulation scale. An exception involves the role of conspecific attraction as an influence on patch selection and overall metapopulation viability[27]. In fact, conspecific attraction, and its influence on animal decision making, is one of the few behavioral issues to have received much attention in the context of ecological landscapes (Box 2).

This issue of variation in habitat quality plays a more conspicuous role in some simulation models of habitat selection at an 'intermediate' spatial scale. This is most prominent in recent source–sink models of population dynamics, in which animals are assumed to choose the best living-site from among the sites they have sampled[6]. This is indeed a plausible behavioral rule, but there is little evidence that any such rule exists. Plausible rules of movement determined by resource gradients in other simulation models[17,18] constitute another (implicit) form of habitat selection in a heterogeneous landscape.

Behavioral minimalism

'Behavioral minimalism' is apparent in every behaviorally oriented model of landscape-level ecological processes. Behavioral minimalism dictates a focus on only those few behavioral traits that are likely to be important to the question under study. This approach is essential if landscape-level (spatially explicit) ecological models are to retain a reasonable degree of tractability[1]. Such reasoning is clear in Turchin's[8] justification for the use of the most extreme form of behavioral minimalism in ecological modeling: random walks. He states that the assumption of random movement 'does not imply that animals move truly at random…each organism may be…reacting to environmental cues in accordance with some internal behavioral rules. However,…we do not care to know [these rules] in their totality,…since a complete model would have an enormous number of parameters, and would require an accurate representation of all environmental microcues. The stochastic element in the [random walk] model represents all those factors affecting movement that are either purely stochastic, or effectively so because we do not know the cues underlying them'. While we share this basic sentiment, we

believe that there is ample justification for a more behaviorally sophisticated approach to behavioral minimalism.

A major challenge for behavioral ecologists will be the development of a judicious behavioral minimalism for landscape-level ecological modeling. There are several important and unanswered questions about behavioral minimalism. For instance, at what spatial scale (for the animal in question) should one be concerned with things like exploratory behavior, spatial memory, cognitive maps, or conspecific attraction? How much of an impact do relatively sophisticated behavioral rules have on predictions regarding overall population dynamics or viability? At present, we venture to speculate that behavioral minimalism is not only necessary, but increasingly acceptable as one increases the spatial scale of the ecological analysis. For better or worse, however, it is clear that the trend towards increasing behavioral minimalism with increasing spatial scale is already well established in landscape-level ecological models. This holds in treatments of both animal movement/dispersal and habitat selection.

The future

A behavioral ecology of ecological landscapes must be based on something more concrete than a standard of plausibility. We clearly must develop an empirical base of knowledge regarding the many behavioral issues discussed above. We know remarkably little about the sorts of information available to animals at the scale of ecological landscapes, and we know even less about how such information is used in decisions regarding movement and patch/habitat selection. Not only are we uninformed about the mechanics of landscape navigation or habitat selection, but also we largely lack information on the basic natural history of such phenomena[2]. This overall lack of behavioral information may ultimately limit the development of spatially explicit, individual-based population models[2].

A behavioral ecology of landscapes must also have a strong theoretical underpinning. An interplay between theoretical and empirical studies has fostered great progress in 'traditional' behavioral ecology, and the same interplay should be sought at the scale of ecological landscapes. Two areas particularly worthy of theoretical attention concern search behavior and habitat selection. At the level of ecological landscapes, both of these behavioral processes will be characterized by much more behavioral uncertainty and inherent risk than those typically examined by behavioral ecologists. It should also be profitable to apply the basics of optimality/game theory to the question of habitat selection

and rules of movement at various spatial scales. In this regard, we suspect that game-theoretical models would suggest behavioral decision making that is more conservative than that postulated in many landscape-level models (Box 3).

An impediment to an optimality-based (or adaptationist) approach to theory may be the evolutionary novelty of human-altered landscapes. For instance, forest animals in many parts of the world presently live in an environment more fragmented than that in which they evolved[28]. Such animals might thus be using search tactics or rules of habitat selection that are inappropriate in their now fragmented environment. Nevertheless, modeling the situation in which these animals evolved might give us some insight into the rules they may be using, even if those rules are maladaptive.

There is clearly much to be done, and working at large spatial scales will undoubtedly pose several challenges to behavioral ecologists. Nevertheless, we believe that the attempt will be rewarding.

Acknowledgements

References

1 Wiens, J.A. et al. (1993) **Ecological mechanisms and landscape ecology**, Oikos 66, 369–380

2 Dunning, J.B., Jr et al. (1995) **Spatially explicit population models: current forms and future uses**, Ecol. Appl. 5, 3–11

3 Turner, M.G. et al. (1993) **A landscape simulation model of winter foraging by large ungulates**, Ecol. Model. 69, 163–184

4 Hansson, L. (1991) **Dispersal and connectivity in metapopulations**, Biol. J. Linn. Soc. 42, 89–103

5 Pulliam, H.R., Dunning, J.B., Jr and Liu, J. (1992) **Population dynamics in complex landscapes: a case study**, Ecol. Appl. 2, 165–177

6 Danielson, B.J. (1991) **Communities on a landscape: the influence of habitat heterogeneity on the interactions between species**, Am. Nat. 138, 1105–1120

7 Kareiva, P. (1990) **Population dynamics in spatially complex environments: theory and data**, Philos. Trans. R. Soc. London Ser. B 330, 175–190

8 Turchin, P. (1991) **Translating foraging movements in heterogeneous environments into spatial distribution of foragers**, Ecology 72, 1253–1266

9 Fahrig, L. (1988) **A general model of populations in patchy habitats**, Appl. Math. Comput. 27, 53–66

10 Bell, W.J. (1991) Searching Behaviour: the Behavioural Ecology of Finding Resources, Chapman & Hall

11 Stamps, J.A., Buechner, M. and Krishnan, V.V. (1987) **The effects of edge permeability and habitat geometry on emigration from patches of habitat**, Am. Nat. 129, 533–552

12 Johnson, M.L. and Gaines, M.S. (1990) **Evolution of dispersal: theoretical models and empirical tests using birds and mammals**, Annu. Rev. Ecol. Syst. 21, 449–480

13 Milinski, M. and Parker, G.A. (1991) **Competition for resources**, in Behavioural Ecology: an Evolutionary Approach (3rd edn) (Krebs, J.R. and Davies, N.B., eds), pp. 137–168, Blackwell

14 Doak, D.F., Marino, P.C. and Kareiva, P.M. (1992) **Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation**, Theor. Pop. Biol. 41, 315–336

15 Adler, F.R. and Nuernberger, B. (1994) **Persistence in patchy irregular landscapes**, Theor. Pop. Biol. 45, 41–75

16 Saarenmaa, H. et al. (1988) **An artificial intelligence modeling approach to simulating animal/habitat interactions**, Ecol. Model. 44, 125–141

17 Turner, M.G. et al. (1994) **Simulating winter interactions among ungulates, vegetation, and fire in northern yellowstone park**, Ecol. Appl. 4, 472–496

18 Liu, J., Dunning, J.B., Jr and Pulliam, H.R. (1995) **Population effects of a forest management plan on Bachman's sparrows (Aimophila aestivalis): linking a spatially explicit model with GIS**, Conserv. Biol. 9, 62–75

19 Dusenbery, D.B. (1989) **Ranging strategies**, J. Theor. Biol. 136, 309–316

20 Duvall, D., Chiszar, D. and Mintzer, R.A. (1994) **Plane geometry for naive searchers: some results of the simulation Rattlesnake©**, Am. Zool. 34, 78A

21 Johnson, A.R. et al. (1992) **Animal movements and population dynamics in heterogeneous landscapes**, Land. Ecol. 7, 63–75

22 Merriam, G. (1991) **Corridors and connectivity: animal populations in heterogeneous environments**, in Nature Conservation 2: The Role of Corridors (Saunders, D.A. and Hobbs, R.J., eds), pp. 133–142, Surrey Beatty

23 Saunders, D.A. and Hobbs, R.J. (1991) **The role of corridors in conservation: what do we know and where do we go?** in Nature Conservation 2: The Role of Corridors (Saunders, D.A. and Hobbs, R.J., eds), Surrey Beatty

24 Heinen, K. and Merriam, G. (1990) **The elements of connectivity where corridor quality is variable**, Land. Ecol. 4, 157–170

25 Soule, M.E. and Gilpin, M.E. (1991) **The theory of wildlife corridor capability**, in Nature Conservation 2: The Role of Corridors (Saunders, D.A. and Hobbs, R.J., eds), pp. 3–8, Surrey Beatty

26 Bernstein, C., Kacelnik, A. and Krebs, J.R. (1991) **Individual decisions and the distribution of predators in a patchy**

environment. II. The influence of travel costs and structure of the environment, *J. Anim. Ecol.* 60, 205–225

27 Smith, A.T. and Peacock, M.M. (1990) **Conspecific attraction and the determination of metapopulation colonization rates**, *Conserv. Biol.* 4, 320–323

28 Robinson, S.K. *et al.* (1995) **Regional forest fragmentation and the nesting success of migratory birds**, *Science* 267, 1987–1990

29 Hanski, I. and Zhang, D-Y. (1993) **Migration, metapopulation dynamics and fugitive co-existence**, *J. Theor. Biol.* 163, 491–504

30 Dunning, J.B., Jr, Danielson, B.J. and Pulliam, H.R. (1992) **Ecological processes that affect populations in complex landscapes**, *Oikos* 65, 169–175

31 Reed, J.M. and Dobson, A.P. (1993) **Behavioural constraints and conservation biology: conspecific attraction and recruitment**, *Trends Ecol. Evol.* 8, 253–256

32 Wiens, J.A. *et al.* (1995) **Fractal patterns of insect movement in microlandscape mosaics**, *Ecology* 76, 663–666

33 Yeomans, S.R. (1995) **Water-finding in adult turtles: random search or oriented behaviour?** *Anim. Behav.* 49, 977–987

34 Nottingham, S.F. (1988) **Host-plant finding for oviposition by adult cabbage root fly**, *Delia radicum*, *J. Insect Physiol.* 34, 227–234

35 Ray, C., Gilpin, M. and Smith, A.T. (1991) **The effect of conspecific attraction on metapopulation dynamics**, *Biol. J. Linn. Soc.* 42, 123–134

The economic value of the Earth's resources

Graciela Chichilnisky

Economics is the driving force of today's widespread environmental destruction. Markets undervalue the earth's resources and compound their overuse. Since World War II the world has used resources voraciously. The situation can be described as the industrial countries overconsuming resources, which are overextracted and exported by developing countries and traded at prices that are lower than the social costs. Resource-intensive patterns of growth and trade are inefficient for the world economy, and lead to tragic maldistribution of the Earth's riches. They should be replaced by knowledge-intensive patterns of growth. Information technology and the environmental agenda are two of the most important trends in the world economy. Together they can lead to growth that is intrinsically compatible with the environment.

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What is the economic value of the Earth's resources? The question is classical and has more than one answer. Market economies value goods and services by their market prices. These are the prices that clear markets, equating supply with demand. They simultaneously reflect costs of production and consumer preferences.

Under ideal circumstances market prices lead to efficient patterns of resource allocation, which cannot be improved so as to make everyone better off. These are valuable properties, buttressed by theory and by some economic evidence. Yet there is increasing unease today about the pricing of resources. Physical scientists question economic wisdom, and the matter has become the subject of popular debate[1].

Part of the problem is the lack of organized markets. The problem is acute in the case of water and air. There are no organized markets, and therefore no market prices, for either. In some cases, users pay for water, but the price is divorced from competitive markets, and therefore from efficiency. In the case of air, a further difficulty emerges: one individual cannot easily choose air quality independently from others. For such goods, called 'public goods', standard markets do not work well. Efficiency is lost. The problem of pricing resources is pervasive. In practice, many scarce and valuable resources have zero prices. For example the achievement of cleaner water and air have zero economic value in all systems of economic accounting used today.

Faulty prices compromise the evaluation of economic progress. For example, we burn fossil fuels to produce industrial output. This output has an economic value, but clean air does not. Therefore, burning fossil fuels has an unequivocally positive economic value, and counts as economic progress even as it pollutes the air and can cause climate change. A similar situation emerges with respect to the world's forests: the destruction of a forest in order to extract its wood or to grow agricultural products has an unequivocally positive value, and is counted as economic progress all over the world. In a world increasingly concerned with the survival of its forests and with its clean air and water, this vision of economic progress defies common sense. It is now under close scrutiny.

It has been pointed out that markets for environmental assets may never emerge, and that, even if they do, they may not act efficiently[2–4]. Wider notions of economic value are being proposed by some, including myself, in an attempt to reconcile equity and efficiency, as well as to balance the weight given to the present and the future[2–5]. This article cannot, and will not, cover all the issues, important as they are. It will discuss basic needs and environmental markets. As an organizing theme, I will propose that we must now focus on the choice between two, fundamentally different, patterns of growth: resource-intensive and knowledge-intensive. One works and the other doesn't. Economic progress is not doing more with more: it is doing more with less.

Before suggesting solutions, however, one should understand the nature of the problem: what is driving our unease? Why is the question of economic valuation of the Earth's resources now timely and somewhat controversial? What is the source of the problem? To answer these questions a brief review of the situation is required.

The global environment today

Human beings, or their close genetic relatives, have lived on Earth for several million years. Yet only recently has human activity reached levels at which it can affect natural processes such as the concentration of gases (CFC, CO_2) in the atmosphere of the planet, the stability of the global climate, and the complex web of species that constitutes life on earth. There is no consensus about the magnitude of these impacts, but it is widely agreed that, for the first time in recorded history, economic activity has reached levels at which it can alter the planet's atmosphere and endanger its biodiversity[6–8].

At the June 1992 Earth Summit in Rio de Janeiro, 150 countries chose three areas in which concerted international action is urgently needed – Biodiversity, Climate Change, and Sustainable Development –