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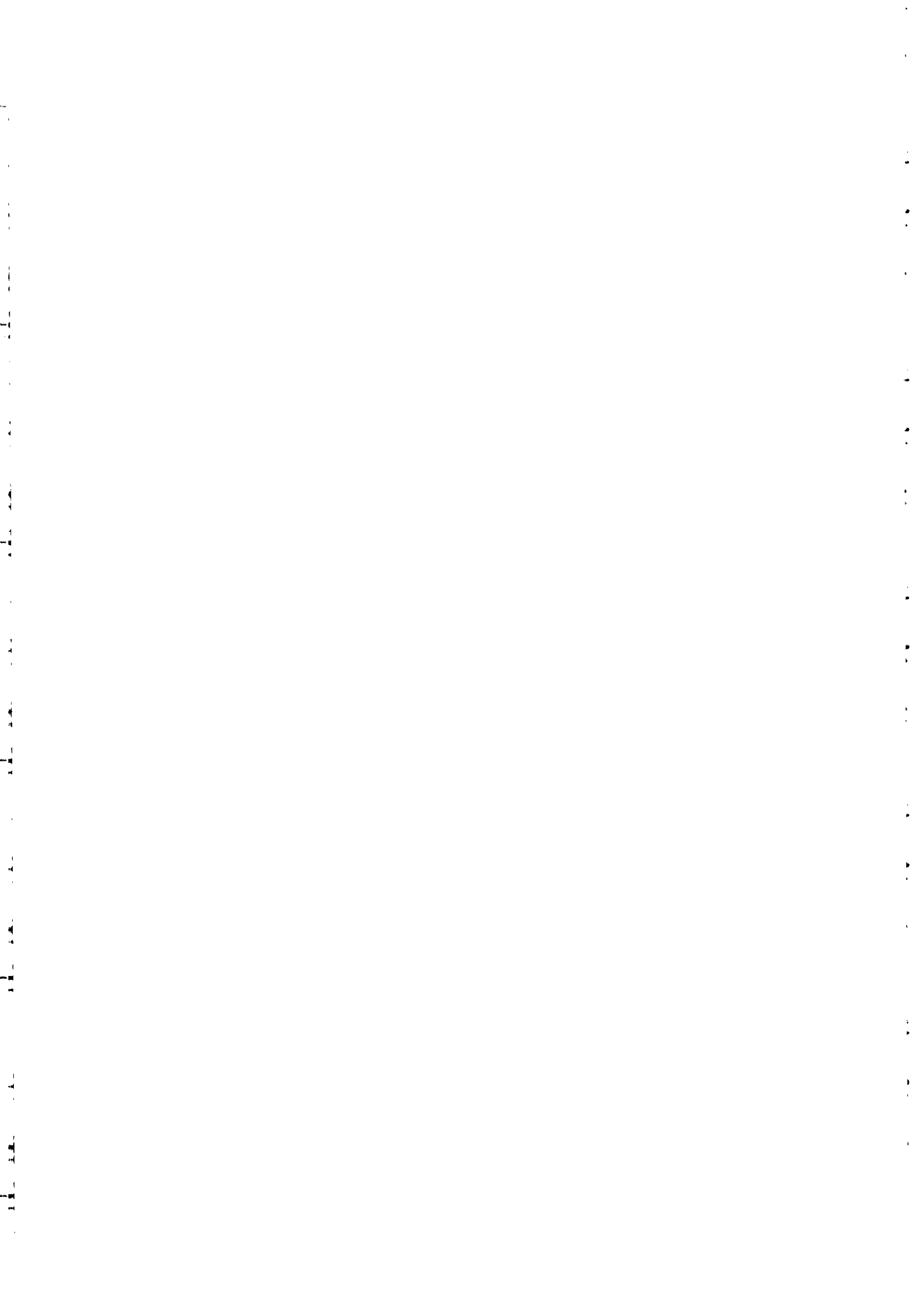
**"Fifth Course on Mathematical Ecology  
including and introduction to Ecological Economics"**

**28 February - 24 March 2000**

**PRINCIPLES OF CONSERVATION BIOLOGY**

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Outline for talks at ICTP's  
*Fifth Course on Mathematical Ecology*  
Trieste, 6-10 March, 2000

Three talks:

- I) Monday, March 6, 1:30 pm: *Biodiversity status and trends. Why conserve biodiversity?*
- II) Tuesday, March 7, 2:30 pm: *Principles of conservation biology.*
- III) Wednesday, March 8, 10:30 am: In situ and ex situ approaches to the conservation of biodiversity.

I) Biodiversity status and trends. Why conserve biodiversity?

1) **What is biodiversity?**

Classic definition of biodiversity, following biological levels of organization: genes, individuals, populations, species, communities/ecosystems, biomes.

Begin with definition of species—basic unit of diversity measurement. Highlight that definition of species is not equally clear for all taxa.

Move up and down the hierarchy of the levels of organization to illustrate the other components of biodiversity: 1) from species “downward”: populations, individuals and genes; 2) from species “upward”: communities/ecosystems and biomes.

References:

- Harper, J. L. and D. L. Hawksworth (1994) Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London B* 345: 5-12.
- Jenkins, M. (1992) Species diversity: an introduction. In: WCMC, Ed. *Global Biodiversity: Status of the Earth's Living Resources*, pp: 40-46. World Conservation Monitoring Centre (WCMC), Chapman and Hall.

2) **Global biodiversity patterns**

Maps of 1) latitudinal distribution of biodiversity and 2) megadiverse countries.

Origin of the term "hot spots". Megadiversity countries: seventeen of the world's countries (out of ~200) include between 60-70% of described species.

The paradox of biodiversity conservation: more resources where there are fewer species: 1) scientists per country (participants in UNEP's global biodiversity assessment), 2) per-capita GDP.

Discuss the idea that it is not only distribution but also abundance that matters. Most species are rare. Seven forms of rarity.

#### References:

- Adams, J. M. (1989) Species diversity and productivity of trees. *Plants Today* 2: 183-187.
- Myers, N. (1988) Threatened biotas: "hot spots" in tropical forests. *The Environmentalist* 8(3): 187-208.
- Rabinowitz, D., S. Cairns and T. Dillon (1986) Seven forms of rarity and their frequency in the flora of the British isles. In: M. E. Soulé, Ed. *Conservation Biology: the Science of Scarcity and Diversity*, pp: 182-204. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

### **3) How many species are there?**

Classic estimates and controversy by Erwin, May and others.

#### References:

- May, R. M. (1990) How many species? *Philosophical Transactions of the Royal Society of London B* 330: 293-304.
- Pimm, S. L., G. J. Russell, J. L. Gittleman and T. M. Brooks (1995) The future of biodiversity. *Science* 269: 347-350.

### **4) Extinction rates past and present**

Background extinction rates. Evidence from the fossil record. Extinction is part of the Earth's evolutionary history, but rates have changes. Contrast with current extinction rates. Present range of estimates—including the most extreme ones.

Current rates associated to impact of human activities. Examples: 1) earth from space, 2) habitat destruction rates; photographs of mahogany harvesting, deforestation in Amazonia. Rates of habitat conversion.

## References:

- May, R. M., J. H. Lawton and N. E. Stork (1995) Assessing extinction rates. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 1-24. Oxford University Press.
- Jablonski, D. (1995) Extinctions in the fossil record. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 25-44. Oxford University Press.
- Bibby, C. J. (1994) Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London B* 344: 35-40.

## **5) What are we loosing?**

Direct (e.g. biotechnology) and indirect (e.g. ecosystem services, ecotourism) benefits from biodiversity. Biophilia. Aspirin example from Lovejoy in *Biodiversity II*.

Direct use of biodiversity: bioprospecting. International legal framework provided by the Convention of Biological Diversity. Property rights, benefit sharing and technology transfer.

The value of biodiversity in pharmaceutical research. Costs and benefits of drugs derived from natural products. The random sampling approach vs. the ethnobiological research approach. Case studies: Costa Rica's INBIO and Shaman Pharmaceuticals.

Bioprospecting in the Third World: making the First World healthier? Outline research agendas for major pharmaceutical companies. Turning bioprospecting into a truly equitable enterprise.

## References:

- Carlson, T. J., R. Cooper, S. R. King and E. J. Rozhon (1997) Modern science and traditional healing. *Royal Society of Chemistry Special Publication* 200: 84-95.
- Carlson, T. J., M. M. Iwu, S. R. King, C. Obialor and A. Ozioko (1997) Medicinal plant research in Nigeria: an approach for compliance with the Convention on Biological Diversity. *Diversity* 13(1): 29-33.
- King, S. R., T. J. Carlson and K. Moran (1996) Biological diversity, indigenous knowledge, drug discovery, and intellectual property rights. In: S. Brush and D. Stabinsky, Eds., *Valuing Local Knowledge: Indigenous People and Intellectual Property Rights*, pp: 167-185. Island Press.
- Simpson, R. D., R. A. Sedjo and J. W. Reid (1996) Valuing biodiversity for use in pharmaceutical research. *Journal of Political Economy* 104(1): 163-185.
- DiMasi, J. A., R. W. Hansen, H. G. Grabowsky and L. Lasagna (1991) Cost of innovation in the pharmaceutical industry. *Journal of Health Economics* 10: 107-142.

## II) Principles of conservation biology.

### 1) Definition of conservation biology

Conservation biology is one of the fastest-growing fields of modern scientific research. It is an applied discipline that integrates principles of natural and social sciences with the objective of achieving the long-term persistence of biodiversity on Earth. The current global biodiversity crisis is the driving force behind the discipline's rapid growth, but its origins and practice are older. Formal recognition of conservation biology as an academic field dates back to the 1960s; since then, it has gradually acquired a character of its own which differentiates it from the many other disciplines it continues to borrow from, including: ecology, genetics, population biology, sociology, economics, and policy.

### 2) Conservation biology as a crisis discipline

Because conservation biology has grown in response to the extinction crisis, much of the attention of conservation biologists has focussed on dealing with problems of small, threatened populations. Genetics and population ecology have played a prominent role. Outline Caughley's "small population" and "declining populations" paradigms..

Restoration ecology, the cost of putting it back together.

Preventative conservation: the wave of the future?

### 3) Using biogeographic and natural history data for planning wild species conservation

Conceptual framework for using quantitative methods of conservation biology for large-scale (e.g. sub-national, national, regional) species conservation planning exercises. Three fundamental, consecutive questions provide structure to the process: 1) What to conserve?, 2) Where to conserve?, and 3) How to conserve?

The first question is answered using biological indicators, which help define the target of conservation action; for example: identify centers of endemism or areas of high diversity, monitor changes in habitat quality, or locate foci of human disturbance.

Once the target is established, the second question is approached using gap analysis in conjunction with algorithms for the optimal selection of nature reserve networks. This approach is aimed at maximizing the number of species included in protected area systems, while minimizing the amount of land needed to do so. Reserve selection algorithms.

The third question refers to the design of management plans either for single (or groups of) protected areas or individual (or groups of) species. An integration of the techniques of population viability analysis with the principles of adaptive management of natural resources allows for contrasting different management options, by weighing their benefits (e.g. reduced risk of extinction) against their costs (e.g. resources required to implement each option) over time.

### References:

#### *Bioindicators:*

Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution* 13(7): 275-280.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss and M. A. Sanjayan (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7(4): 796-808.

Pearson, D. L. and F. Cassola (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* 6(3): 376-391.

Rodríguez, J. P., D. L. Pearson and R. Barrera R. (1998) A test for the adequacy of bioindicator taxa: Are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? *Biological Conservation* 83(1): 69-76.

#### *Keystone and umbrella species:*

Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83(3): 247-257.

#### *PVA:*

Possingham, H. P., D. B. Lindenmayer and T. W. Norton (1993) A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* 1: 39-45.

#### *GAP analysis:*

Scott, J. M. and B. Csuti (1997) Gap analysis for biodiversity survey and maintenance. In: M. L. Reaka-Kudla, D. E. Wilson and E. O. Wilson, Eds., *Biodiversity II: Understanding and Protecting our Natural Resources*, pp: 321-340. Joseph Henry Press, Washington, D.C., U.S.A.

*Reserve selection algorithms:*

Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Kiestler, B. Downs, R. Hamilton, M. Huso and K. Sahr (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80: 83-97.

### III) In situ and ex situ approaches to the conservation of biodiversity.

#### 1) Major threats to biodiversity

A few famous cases of extinct species: 1) the dodo, 2) passenger pigeon. Large population sizes are not necessarily enough.

Threatened species of the world, by taxonomic group.

Species' threats are not uniformly distributed, maps of 1) extinct species of the world, 2) hotspots of endangered species in the US.

Evolving threats for endangered species. Most extinct species due to overexploitation; most threatened species due to habitat destruction (Endangered Species Handbook).

Example from Venezuela to illustrate evolving threats.

Causes of threat in the US.

#### References:

Dobson, A. P., J. P. Rodríguez, W. M. Roberts and D. S. Wilcove (1997) Geographical distribution of endangered species in the United States. *Science* 275: 550-553.  
Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos (1998) Quantifying threats to imperiled species in the United States. *BioScience* 48(8): 607-615.

#### 2) Classifying endangered species

History of Red Data Books and red Lists. Evolution of endangered species classification systems. The 1994 IUCN Red List Criteria—assessing extinction risk. The difference between risk assessment and priority setting: national/regional conservation planning.



## References:

Mace, G. M. (1995) Classification of threatened species and its role in conservation planning. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 197-213. Oxford University Press.

### **3) What are we doing to conserve biodiversity?**

Present definition of *in situ* and *ex situ* approaches (based on glossary in UNEP's *Global Biodiversity Assessment*). Emphasize that habitat conservation is the ultimate purpose.

Conservation not only limited to wild species. Brief introduction to germoplasm banks and botanical gardens. Value of domestic animal breeds.

### **4) Nature reserve design and management**

Theory of island biogeography. Single large or several small (SLOSS) debate. Pros and cons of ecological corridors.

Ecotourism and charges for ecosystem services as mechanisms for funding protected areas; achieving self-sufficiency.

Nature reserves alone are not enough. Most protected areas are too small for long-term survival of large carnivores (Newmark's analysis of parks in the US and Tanzania). many species require habitat in private lands. Need to think more broadly—integrated large-scale management. Habitat Conservation Planning in the US.

## References:

Wilcox, B. A. (1980) Insular ecology and conservation. In: M. E. Soulé and B. A. Wilcox, Eds., *Conservation Biology: an Evolutionary-ecological Perspective*, pp: 95-118. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

Margules, C., A. J. Higgs and R. W. Rafe (1982) Modern biogeographic theory: are there any lessons for nature reserve design? *Biological Conservation* **24**: 115-128.

Newmark, W. D. (1987) A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* **325**: 430-432.

Simberloff, D., J. A. Farr, J. Cox and D. W. Mehlman (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**(4): 493-504.

Aengst, P., J. Anderson, J. Chamberlin, C. Grunewald, S. Loucks, E. Wheatley and S. Yaffee (1997) Introduction to habitat conservation planning. *Endangered Species UPDATE* **14**(7&8): 5-9.

## 5) Captive breeding for endangered species

Zoos and botanical gardens as a conservation tool. The evolution of zoos from collections of animals to conservation centers. Examples of species who have been saved by captive breeding. Problems with captive breeding: genetic, behavioral/social (e.g. adaptation to captivity), cost, lack of interinstitutional continuity and coordination. The value of captive breeding as an educational tool and for fundraising for wild population conservation.

### References:

- Mench, J. A. and M. D. Kreger (1996) Ethical and welfare issues associated with keeping wild mammals in captivity. In: D. G. Kleiman, M. E. Allen, K. V. Thompson, S. Lumpkin and H. Harris, Eds., *Wild Mammals in Captivity: Principles and Techniques*, pp: 5-15. University of Chicago Press, Chicago, USA.
- Wiese, R. J. and M. Hutchins (1994) The role of zoos and aquariums in amphibian and reptilian conservation. In: J. B. Murphy, K. Adler and J. T. Collins, Eds., *Captive Management and Conservation of Amphibians and Reptiles*, pp: 37-45. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA.
- Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone and B. Miller (1996) Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10(2): 338-348.

## 6) Reintroductions and translocations

When are reintroductions appropriate? Reintroductions as the last front in conservation action. The Margarita parrot: an example of a successful reintroduction; cost of each parrot.

### References:

- Kleiman, D. G. (1996) Reintroduction Programs. In: D. G. Kleiman, M. E. Allen, K. V. Thompson, S. Lumpkin and H. Harris, Eds., *Wild Mammals in Captivity: Principles and Techniques*, pp: 297-305. University of Chicago Press, Chicago, USA.
- Sanz, V. and A. Grajal (1998) Successful reintroduction of captive-raised yellow-shouldered amazon parrots on Margarita island, Venezuela. *Conservation Biology* 12(2): 430-441.
- Griffith, B., J. M. Scott, J. W. Carpenter and C. Reed (1989) Translocations as a species conservation tool: status and strategy. *Science* 245: 477-480.

## 7) Additional bibliography

### 1) General reference

UNEP (1995) *Global Biodiversity Assessment*. United Nations Environment Programme, Cambridge University Press, Cambridge, UK.

WCMC (1992) *Global Biodiversity: Status of the Earth's Living Resources*. World Conservation Monitoring Centre, Chapman and Hall, London, UK.

Worldwatch Institute's *State of the World* annual reports

World Resources Institute's *World Resources* annual reports

### 2) Some recent textbooks

Caughley, G. and A. Gunn (1996) *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge, Massachusetts, USA.

Dobson, A. P. (1996) *Conservation and Biodiversity*. Scientific American Library, New York, USA.

Hunter, M. L. (1996) *Fundamentals of conservation biology*. Blackwell Science, Cambridge, Massachusetts, USA.

Meffe, G. K. and C. R. Carroll, Eds. (1997) *Principles of Conservation Biology*. Principles of Conservation Biology. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Primack, R. B. (1995) *A Primer of Conservation Biology*. Sinauer Associates Inc., Sunderland, Massachusetts, U.S.A.

- 27 Sarich, V.M. (1993) Mammalian systematics: twenty-five years among their albumins and transferrins, in *Mammal Phylogeny: Placentals* (Szalay, F.S., Novacek, M.J. and McKenna, M.C., eds), pp. 103–114. Springer-Verlag
- 28 Lavergne, A. et al. (1996) Interordinal mammalian relationships: evidence for paenungulate monophyly is provided by complete mitochondrial 12S rRNA sequences, *Mol. Phylog. Evol.* 6, 245–258
- 29 de Jong, W.W., Leunissen, J.A.M. and Wistow, G.J. (1993) Eye lens crystallins and the phylogeny of placental orders: evidence for a macroscelid–paenungulate clade? in *Mammal Phylogeny: Placentals* (Szalay, F.S., Novacek, M.J. and McKenna, M.C., eds), pp. 5–12. Springer-Verlag
- 30 Douzery, E. and Catzeflis, F.M. (1995) Molecular evolution of the mitochondrial 12S rRNA in Ungulata (Mammalia), *J. Mol. Evol.* 41, 622–636
- 31 Lecointre, G. et al. (1993) Species sampling has a major impact on phylogenetic inference, *Mol. Phylog. Evol.* 2, 205–224
- 32 Philippe, H. and Douzery, E. (1994) The pitfalls of molecular phylogeny based on four species, as illustrated by the Cetacea/Artiodactyla relationships, *J. Mammal. Evol.* 2, 133–152
- 33 Naylor, G.J.P. and Brown, W.M. (1997) Structural biology and phylogenetic estimation, *Nature* 388, 527–528
- 34 Cao, Y. et al. (1994) Phylogenetic relationships among eutherian orders estimated from inferred sequences of mitochondrial proteins: instability of a tree based on a single gene, *J. Mol. Evol.* 39, 519–527
- 35 Zardoya, R. and Meyer, A. (1996) Phylogenetic performance of mitochondrial protein-coding genes in resolving relationships among vertebrates, *Mol. Biol. Evol.* 13, 933–942
- 36 Russo, C.A.M., Takezaki, N. and Nei, M. (1996) Efficiencies of different genes and different tree-building methods in recovering a known vertebrate phylogeny, *Mol. Biol. Evol.* 13, 525–536
- 37 Swofford, D.L. et al. (1996) Phylogenetic inference, in *Molecular Systematics* (2nd edn) (Hillis, D.M., Moritz, C. and Mable, B.K., eds), pp. 407–492. Sinauer
- 38 Shimamura, M. et al. (1997) Molecular evidence from retroposons that whales form a clade within even-toed ungulates, *Nature* 388, 666–670
- 39 Hedges, S.B. and Maxson, L.R. (1996) Molecules and morphology in amniote phylogeny, *Mol. Phylog. Evol.* 6, 312–314
- 40 Lockett, W.P. and Hartenberger, J.L. (1993) Monophyly or polyphyly of the order Rodentia: possible conflict between morphological and molecular interpretations, *J. Mammal. Evol.* 1, 127–147
- 41 Milinkovitch, M.C. and Thewissen, J.G.M. (1997) Even-toed fingerprints on whale ancestry, *Nature* 388, 622–624
- 42 Hartenberger, J.L. (1986) Hypothèse paléontologique sur l'origine des Macroscelidea (Mammalia), *C. R. Acad. Sci. Ser. II* 302, 247–249
- 43 Butler, P.M. (1995) Fossil Macroscelidea, *Mamm. Rev.* 25, 3–14
- 44 Woodall, P.F. (1995) The penis of elephant shrews (Mammalia: Macroscelidea), *J. Zool.* 237, 399–410
- 45 Hedges, S.B. et al. (1996) Continental breakup and the ordinal diversification of birds and mammals, *Nature* 381, 226–229
- 46 McKenna, M.C. and Bell, S.K. (1997) *Classification of Mammals Above the Species Level*, Columbia University Press
- 47 Simpson, G.G. (1945) The principles of classification and a classification of mammals, *Bull. Am. Mus. Nat. Hist.* 85, 1–350

## Biodiversity hotspots

Walter V. Reid

The study of the distribution of species, which has long been a central focus of ecology and biogeography, is taking on new urgency as evidence of the global biodiversity crisis mounts. The question of what geographical regions to protect in order to maintain the most biological diversity is central to the design of effective conservation programs. For a field of study with a lineage that includes Andrewartha and Birch's (1954) *Distribution and Abundance of Animals*<sup>1</sup> and Wallace's (1876) *The Geographical Distribution of Animals*<sup>2</sup>, the answer to this question would seem to be readily at hand. However, the question is proving challenging. Indeed, recent studies are revealing surprising patterns that challenge long-held biogeographical assumptions.

The term 'biodiversity hotspot' was coined by Norman Myers<sup>3,4</sup> in the late 1980s in two papers that identified 18 geographical regions as conservation priorities because they contained large numbers of endemic species found in relatively small areas that were facing significant threats of habitat loss. It was reasoned that protecting hotspots, defined in this manner, should prevent the extinction of a larger number

**Hotspots of biodiversity – areas particularly rich in species, rare species, threatened species, or some combination of these attributes – are increasingly being delineated to help set priorities for conservation. Only recently have we begun to test key assumptions that determine how useful a hotspot approach can be for conservation planning. The evidence suggests that although at large geographic scales hotspots do provide useful information for conservation planning, at smaller scales their value may be more limited.**

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of species than would protecting areas of a similar size elsewhere. This definition of a hotspot continues to be used in many studies today<sup>5,6</sup>. More generally, however, the term hotspot is now applied to a geographical area that ranks particularly high on one or more axes of species richness, levels of endemism, numbers of rare or threatened species, and intensity of threat.

The term biodiversity hotspot is now most commonly used with reference to regions of high species richness. For example, the GAP analysis program being carried out in the United States uses hotspots to identify gaps in the existing network of protected areas<sup>7,8</sup>. This analysis begins by mapping hotspots of species richness, then

determines which species are already well-conserved in existing protected areas, then maps the pattern of species richness for the remaining species, and, using various selection algorithms, chooses the minimum set of grid cells that encompass the unprotected species.

Alternatively, hotspots of species rarity or endemism – regions rich in species with restricted distribution ranges – have been used to help set priorities for bird conservation<sup>9,10</sup>.

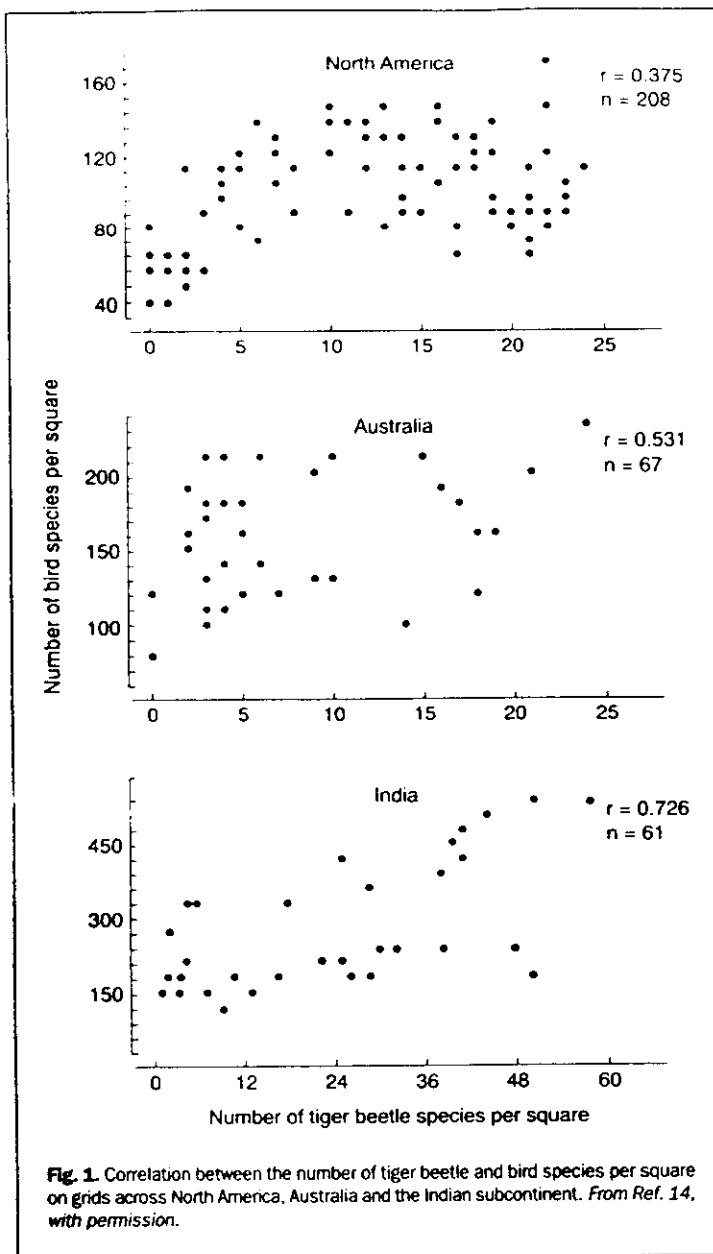


Fig. 1. Correlation between the number of tiger beetle and bird species per square on grids across North America, Australia and the Indian subcontinent. From Ref. 14, with permission.

For example, the International Council for Bird Preservation (ICBP), now known as BirdLife International, mapped the distribution of land bird species with range sizes less than 50 000 km<sup>2</sup> and subsequently identified 221 areas that contained at least two restricted-range species. These areas accounted for 95% of all restricted-range birds<sup>9</sup>.

Other studies have defined hotspots based on both species richness and endemism. Megadiversity countries, for example, are nations that either have extremely high species richness of plants and vertebrates (e.g. Brazil, Colombia and Indonesia) or are relatively less species rich but have extremely high levels of endemism (e.g. Madagascar and Australia)<sup>11</sup>. Finally, hotspots have also been defined as regions with the largest number of threatened species, independent of the overall species richness or endemism of the region<sup>12,13</sup>.

Intensive research is currently focused on two aspects of the analysis of biodiversity hotspots that are key to its value for setting conservation priorities. First, because species distribution data for most taxa are limited or unavailable,

the use of a hotspot approach in setting priorities rests on the assumption that patterns of diversity among relatively well-studied 'indicator' groups, such as birds, mammals and plants, are good predictors of patterns of diversity in less-studied groups. Second, the research aims to determine the optimal method of analysis for using hotspot information in setting conservation priorities.

#### Overcoming data constraints

Do geographic regions that rank high on a scale of species richness, endemism or threat in well-known taxa also rank high for other taxa? At coarse-grained geographic scales, diversity patterns do correspond across taxa, as shown by the pattern of increased species richness at lower latitudes found in many taxonomic groups. Species richness of tiger beetles (Cicindelidae), for example, is positively correlated with measures of bird and butterfly diversity across North America, Australia and the Indian subcontinent<sup>14</sup> (Fig. 1), although when the effect of latitude is removed the correlations are much weaker<sup>15</sup>. Similarly, correspondence of patterns of endemism across taxonomic groups would be expected at global or continental scales because of the common trend of species range size to decrease as one moves from higher to lower latitudes<sup>16</sup>.

At finer scales of resolution, however, the correspondence of patterns of species richness and endemism across taxonomic groups breaks down<sup>17</sup>. Little concordance is found among the most species-rich regions in the USA for mammals, birds, reptiles, amphibians, tiger beetles and trees<sup>15</sup>. Similarly, if the regions highest in species-richness (the top 5% of 10 km grid squares) in the UK are identified for five different taxonomic groups (butterflies, dragonflies, liverworts, aquatic plants and breeding birds), the maximum overlap of diversity hotspots between groups is only 34% (between butterflies and dragonflies)<sup>18</sup>. In South Africa, a similar approach examining overlap in richness and endemism hotspots among fish, frogs, tortoises, snakes, birds and mammals found substantial overlap for species richness hotspots between some groups (e.g. frogs and birds, 72%; frogs and mammals, 62%) but low overlap for many other combinations (e.g. tortoise diversity hotspots showed less than 10% overlap with other groups)<sup>19</sup>. For endemism hotspots, the maximum overlap was only 44% (between frogs and mammals), and for 12 out of 15 combinations of species the overlap was 25% or less (Table 1).

If patterns of species richness and endemism do not correspond across taxa at finer scales of resolution, we would not expect hotspots of threatened or endangered species in different taxonomic groups to correspond either, which is indeed the case. For example, there is relatively little overlap among areas (counties) in the USA containing the highest numbers of federally listed endangered species in different taxa (molluscs, birds, fish, mammals, arthropods, herptiles)<sup>13</sup> (Fig. 2).

There is a good explanation for the weak correspondence between patterns of richness and endemism at fine scales of geographic resolution, and this explanation suggests that weaker correspondence would also be expected for more fine-grained taxonomic scales (e.g. genera as opposed to classes). Fine-scale geographic samples and fine-scale taxonomic groups are likely to contain species that share narrower habitat requirements; thus, areas of high richness or endemism for those samples are less likely to correspond across taxonomic groups. Amphibian diversity patterns are less likely to correspond to diversity in gymnosperms, for example, than vertebrate diversity patterns would be expected to correspond to vascular plant diversity. It is not

surprising, therefore, that studies are showing that at fine scales of resolution hotspots of certain taxa do not reflect hotspots of other taxa. For indicator taxa to be useful in setting priorities, a careful balance needs to be struck between the geographic and taxonomic scale of resolution, and the type of conservation question being addressed.

#### Higher-taxon diversity as a surrogate for species diversity

Instead of relying on indicator taxa to reflect distribution patterns in lesser-known taxa, other studies have examined the potential value of other surrogate measures of species richness or endemism, including vegetation classes, land classes, environmental variables (e.g. precipitation and net primary productivity) and richness at higher taxonomic levels. A number of these surrogates have been shown to have useful predictive power, but higher taxon-diversity appears to be most closely correlated to patterns of species diversity<sup>20</sup>. Most of this research has focused on patterns of species richness.

At both coarse and fine geographic scales, richness of genera and families have proved to be relatively good predictors of species richness<sup>21,22</sup>. For example, at a continental scale (using 611 000 km<sup>2</sup> grid cells), 99% of the variation in bird species richness in North America can be explained by genus richness, and 91% of variation by family richness<sup>20</sup>. Similarly, at a fine scale in 35 forest reserves ranging in size from 18–30 000 ha in Sri Lanka, 96% of woody-plant species richness can be explained by genus richness, and 86% of variation by family richness<sup>22</sup>.

Can higher-taxon richness patterns be combined to create even better surrogates for overall species diversity? The challenge here is to determine how best to weight numbers of genera or families in different taxa, because higher taxonomic groups may be defined in different ways, particularly where the taxa are distantly related. In one coarse-grained (global) study examining different methods for combining family richness in plants, reptiles, amphibians and mammals (absolute number of families; proportional family richness; and proportional family richness weighted for total species richness in each group), all three methods gave fairly similar results<sup>23</sup>. At other scales of analysis or using other taxonomic groups, however, the different methods would be expected to produce different patterns. Which method to use depends on the objective of the analysis and the availability of data (e.g. good estimates of total species richness might not be available for some taxa).

Patterns of higher taxon richness can therefore serve as surrogates for species richness. It remains to be seen whether this same correspondence holds for patterns of endemism. The utility of this surrogate measure for conservation planning hinges on the seemingly reasonable but untested assumption that if only a partial survey of a region has been undertaken, the cumulative list of higher taxa encountered will converge on the total number of taxa more rapidly than will the cumulative list of species.

**Table 1. The proportional overlap of (a) hotspots (above diagonal), cold spots (below diagonal), and (b) endemic species hotspots, among six vertebrate taxa in greater South Africa<sup>a,19</sup>**

	Fish	Frogs	Tortoises	Snakes	Birds	Mammals
<b>(a) Hotspots and coldspots</b>						
Fish	–	0.35 (31)	0.00 (5)	0.35 (31)	0.48 (31)	0.36 (28)
Frogs	0.24 (110)	–	0.00 (9)	0.49 (47)	0.72 (47)	0.62 (47)
Tortoises	0.54 (98)	0.61 (128)	–	0.10 (10)	0.00 (12)	0.08 (12)
Snakes	0.19 (118)	0.25 (153)	0.62 (133)	–	0.59 (61)	0.42 (59)
Birds	0.67 (3)	1.00 (2)	0.88 (32)	0.47 (19)	–	0.47 (68)
Mammals	0.19 (144)	0.22 (172)	0.65 (155)	0.34 (177)	0.41 (39)	–
<b>(b) Endemic hotspots</b>						
Fish	–	0.00 (21)	0.00 (7)	0.14 (14)	0.18 (22)	0.19 (16)
Frogs		–	0.20 (10)	0.25 (24)	0.42 (33)	0.44 (18)
Tortoises			–	0.00 (10)	0.20 (15)	0.22 (9)
Snakes				–	0.24 (25)	0.16 (19)
Birds					–	0.40 (20)
Mammals						–

<sup>a</sup>Numbers in parentheses are total possible overlaps.

#### Setting conservation priorities

##### Setting global priorities

Biodiversity hotspot analysis was originally used to identify large regions, typically the size of an entire nation, that deserved conservation attention, such as Madagascar, Northern Borneo, or the Philippines. The 18 global hotspots defined by Norman Myers have since been used by the MacArthur Foundation to target its grantmaking. Organizations including the World Wide Fund for Nature-India and Conservation International also set priorities among countries or regions using Myers' rankings.

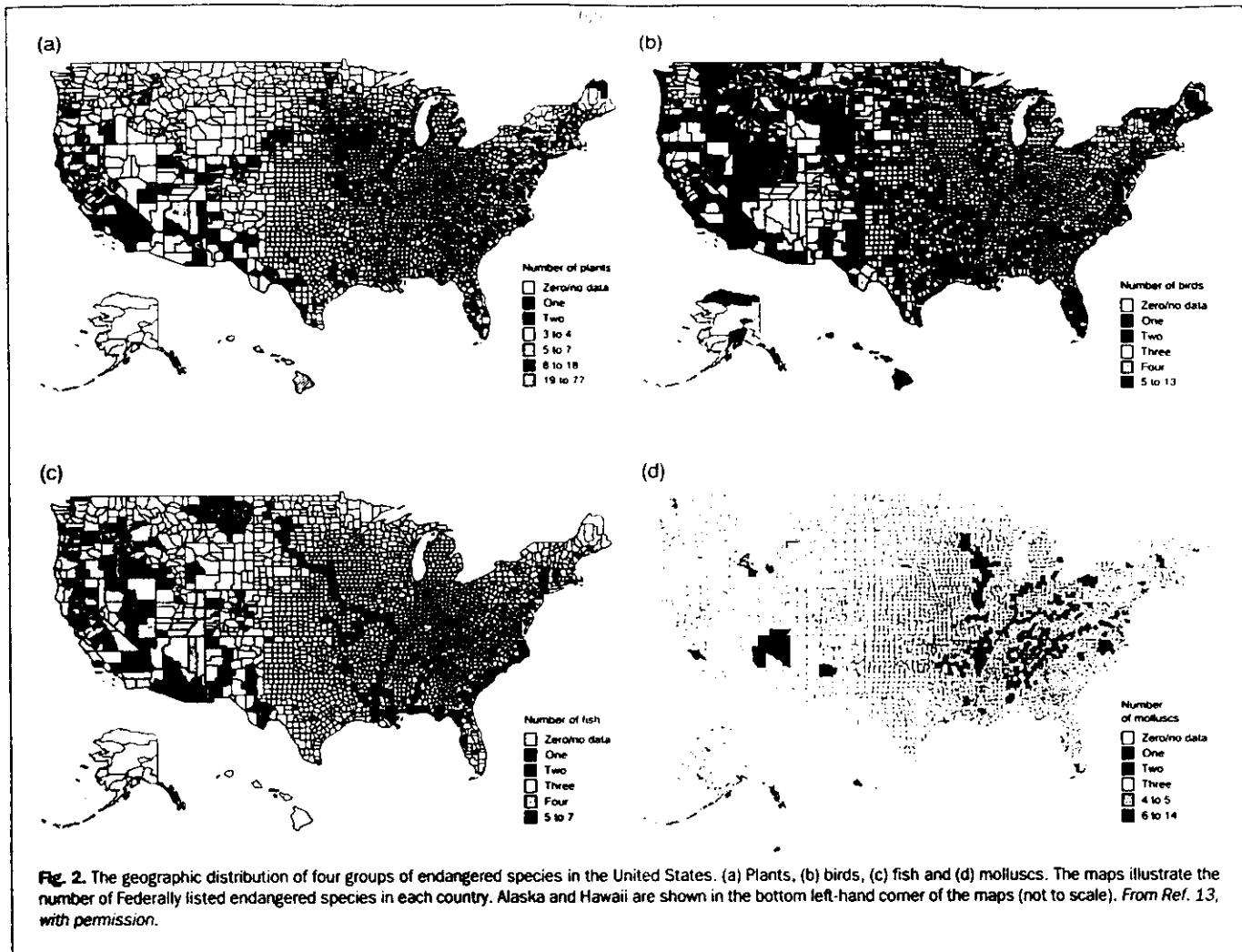
The studies discussed here provide reasonable support for the utility of hotspots that are defined by using species richness and endemism at a global or continental scale of analysis. At this coarse scale, patterns of richness and endemism tend to correspond reasonably well across taxa. By its nature, a continental or global hotspot analysis tends to identify regions with relatively small overlap in species composition – Madagascar is unlikely to share many species with Borneo, for example.

##### Using hotspots to guide conservation decisions

At more fine-grained geographic scales, which tend to be the scales at which conservation and development decisions are made, the application of hotspot analysis is more challenging<sup>19,24,25</sup>. To begin with, the poor correspondence between species hotspots in different taxa implies that priorities determined on the basis of either richness or endemism in a few taxonomic groups cannot be relied upon to capture similar patterns in other groups.

Just as important, the choice of method for defining a hotspot – whether it is based on richness, endemism, threat or a combination of these factors – significantly influences which regions or sites are identified as conservation priorities.

Site selection algorithms based on identifying hotspots of species richness tend to be the least efficient in maximizing the protection of species diversity. This is because hotspots of species richness do not often include relatively rare species – hotspots that are ranked highest for richness often contain overlapping sets of common species, while failing to capture rarer species. In the UK, 43% of rare bird species do not occur in the top 5% of species richness hotspots<sup>18</sup>. In South Africa, the top 5% of richness hotspots for fish only include 66% of the total diversity of fish species<sup>19</sup>.



**Fig. 2.** The geographic distribution of four groups of endangered species in the United States. (a) Plants, (b) birds, (c) fish and (d) molluscs. The maps illustrate the number of Federally listed endangered species in each country. Alaska and Hawaii are shown in the bottom left-hand corner of the maps (not to scale). From Ref. 13, with permission.

The failure of species richness hotspots to capture rare species is scale dependent. As the size of the sample unit increases, an increasing number of rare species will be found in richness hotspots because the sample unit will 'need' rare species to be unusually species rich. This has been suggested as one explanation for why nearly twice as many hotspots of bird species richness in Australia (defined using 100-km<sup>2</sup> grid cells) hold at least one rare bird species compared with hotspots in the UK (defined using 10-km<sup>2</sup> grid cells)<sup>26</sup>. Similarly, although endemism or rarity and species richness are only weakly correlated at national scales<sup>27</sup>, at a continental scale, patterns of richness and endemism coincide<sup>28</sup>.

A more efficient method for site selection relies on choosing hotspots of rarity or endemism – sites that are richest in species with the most restricted ranges<sup>24</sup>. Because sites that contain species with narrow distributions must be included in a protected area network in order to cover all species, the high priority that rarity-based algorithms give these sites tends to reduce the number of total sites needed.

A still more efficient mechanism for maximizing the number of species protected in a given land area is to use methods of complementarity, where the species content of existing reserves is identified and then further sites are selected in a stepwise fashion to add areas that contribute the greatest number of new species<sup>24,25,29</sup>. These selection algorithms are most efficient (i.e. capture all species in the smallest number of sites) when they begin with sites containing species found nowhere else (and, therefore, which often

have relatively low species richness) rather than with the most species-rich locations.

Finally, the most efficient site selection is achieved using a maximal-covering-location model which uses integer linear programming methods to choose simultaneously the optimal set of sites<sup>24,30</sup>. Such methods, however, are prohibitive for large datasets and also fail to provide information on the best sequence for adding new sites to an existing reserve network so as to provide the greatest marginal gain with each new site<sup>31</sup>.

Comparisons among site selection algorithms tend to be based on the algorithms' efficiency in capturing all species in a given region. Using this criterion of complete species coverage, hotspots of richness or endemism prove to be a less efficient means of setting conservation priorities than approaches using complementarity. However, in the real world of conservation decision-making, a more relevant question to ask often is: given the ability to protect only a small number of sites, what proportion of overall diversity is captured in priority areas that are identified on the basis of the various methodologies? Where the number of sites is limited, richness-based approaches perform relatively well<sup>24</sup>.

The utility of richness- or endemism-based hotspots for conservation decision-making can also be enhanced by combining hotspot analysis with an attempt to protect representative samples of ecosystems. The World Conservation Union, for example, has recommended a minimum conservation goal of protecting 10% of every biogeographic region.

This objective helps to reduce the potential overlap in species composition if only a limited number of protected areas are to be established. For example, if we were to identify the top two hotspots of species richness in a region encompassing two biogeographic regions, both hotspots could fall within a single region and the overlap in species composition could be quite high. If, instead, the top hotspot in each region was selected – that is, representative samples of the ecosystems were chosen – then overlap in species lists would decrease, and the total number of species protected could increase. When only richness or endemism hotspots are used in the analysis, protection of representative samples using this method helps to increase the complementarity of site selection. World Wildlife Fund-USA, for example, recently identified 232 conservation priorities by first stratifying data into major habitat types and biogeographic realms and then examining species richness and endemism (and other factors) to identify relatively rich ecoregions within each group<sup>32</sup>.

No matter which approach to priority setting is used, however, if the areas conserved capture the diversity of the indicator taxa only and not that of the more poorly-known taxa, then the use of the method for conserving biodiversity is questionable. Recent studies, demonstrating the failure of hotspots of richness and endemism to correspond across different taxa, seem to undermine the utility of hotspots in priority setting. However, on closer examination the message of these studies is not so bleak: these same studies lend support to the hypothesis that a set of areas in which one major taxon is well represented can also represent diversity in unrelated taxa.

For example, in the UK, a recent study found that the greatest overlap in hotspots among five taxonomic groups was only 34%. However, if it were possible to protect every hotspot designated for birds (that is, the top 5% of grid cells with the most species of birds), then 87% of birds, 100% of butterfly species and over 90% of dragonflies, liverworts and aquatic plants would be encompassed<sup>18</sup>. Similarly, it appears that a set of areas in Oregon, USA, which completely represents one major taxon does a good job of representing diversity in others<sup>24</sup>. This result is not surprising. Any site selection approach, whether it is based on richness, rarity or complementarity, that captures most of the diversity in one taxon is likely to include a diversity of habitats and, therefore, capture a substantial amount of the diversity of other taxa as well. This is the case even if the areas of high richness or endemism do not correspond.

### How hot are hotspots?

One of the most important lessons that we are learning from the study of diversity hotspots is that the extent of the biodiversity crisis is often highly localized. Although hotspots do not always correspond across taxa, a substantial fraction of species diversity can be found in very small regions and most threatened species can be found in smaller regions still. Rarity hotspots covering just 5% of the UK represent 98% of British species of breeding birds<sup>25</sup>. Richness hotspots in the UK covering a similar area encompass 91% of butterflies, 92% of dragonflies, 95% of liverworts, 96% of aquatic plants and 87% of breeding birds<sup>18</sup>. Within the coterminous US, more than 50% of endangered species of plants, birds, fish and molluscs are found in less than 2% of the land area<sup>13</sup>. This is not to say that these hotspots are sufficiently large to maintain viable populations of all the species found in them, but it does re-affirm the emphasis that conservation strategies place on protected areas: significant species diversity can be encompassed in relatively small fractions of the landscape.

Hotspot analysis is one of a set of different tools now available to help set priorities for conservation planning. Different methods of analysis of hotspot information have different strengths depending on the conservation goal being pursued<sup>33</sup> and the availability of data. For example, the analytic method chosen to maximize the number of surviving species would not be the best approach for maximizing the genetic or taxonomic diversity of surviving species<sup>34</sup> or maintaining critical ecosystem functions. Although the utility of a hotspot approach to setting conservation priorities is probably greatest at relatively coarse spatial scales, a hotspot analysis can be useful at finer scales, particularly if used in combination with other analytical methods.

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# Terrestrial Arthropod Assemblages: Their Use in Conservation Planning

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**Abstract:** *Arthropods, the most diverse component of terrestrial ecosystems, occupy a tremendous variety of functional niches and microhabitats across a wide array of spatial and temporal scales. We propose that conservation biologists should take advantage of terrestrial arthropod diversity as a rich data source for conservation planning and management. For reserve selection and design, documentation of the microgeography of selected arthropod taxa can delineate distinct biogeographic zones, areas of endemism, community types, and centers of evolutionary radiation to improve the spatial resolution of conservation planning. For man-*

Asociaciones de artrópodos terrestres: Su uso en la planificación conservacionista

**Resumen:** *Los artrópodos, el componente más diverso de los ecosistemas terrestres, ocupa una tremenda variedad de nichos funcionales y microhábitats a lo largo de una amplio espectro de escalas espaciales y temporales. Nosotros proponemos que los biólogos de conservación deberían aprovechar la diversidad de los artrópodos terrestres como una rica fuente para el planeamiento y manejo conservacionista. La documentación de la microgeografía de ciertos taxones de artrópodos puede delinear zonas biogeográficas precisas, áreas de endemismo, tipos de comunidades, y centros de radiación evolutiva para mejorar la resolución espacial en el planeamiento conservacionista destinado a la selección y*

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agement of natural areas, monitoring of terrestrial arthropod indicators can provide early warnings of ecological changes, and can be used to assay the effects of further fragmentation on natural areas that no longer support vertebrate indicator species. Many arthropod indicators respond to environmental changes more rapidly than do vertebrate indicators, which may exhibit population responses that do not become evident until too late for proactive management. Not all arthropod taxa are equally effective as indicators for conservation planning, and the qualities of indicators can differ for purposes of inventory versus monitoring. Assemblages of arthropod taxa used as biogeographic probes in inventories should exhibit relatively high species diversity, high endemism, and encompass the geographic range of interest. For monitoring purposes, indicator assemblages should exhibit varying sensitivity to environmental perturbations and a diversity of life-history and ecological preferences.

## Introduction

Whether measured by species, individuals, or biomass (Erwin 1982, 1988, 1991c; Wilson 1985, 1988; Stork 1988; Gaston 1991a, 1991b), arthropods dominate terrestrial ecosystems. Despite increased awareness of their importance to global conservation planning (Wilson 1988), relatively little attention has been devoted to the inventory and monitoring of terrestrial arthropods (Dourojeanni 1990; di Castri et al. 1992). The diversity and abundance of terrestrial arthropods can provide a rich base of information to aid efforts in the conservation of biodiversity and the planning and management of nature reserves (Pyle et al. 1981; Collins & Thomas 1991; Murphy 1992; Pearson & Cassola 1992). This paper, the synthesis of a workshop held in June 1991 is intended to encourage conservation biologists to develop methods for tapping this rich data source to improve inventory and monitoring for conservation planning.

## Inventory and Monitoring: Definitions

Inventory and monitoring, two essential and interrelated activities necessary for scientific conservation planning, differ in their objectives and hence in the types of indicators useful to each activity. Inventory programs document the spatial distribution of biological elements—populations, species, guilds, communities, and ecosystems. For conservation planning, such information can be used (1) to select and design reserves (Usher 1986; Noss 1987; Scott et al. 1987; Margules et al. 1988; Margules & Stein 1989; McKenzie et al. 1989); (2) to assess the potential for sustainable use of natural

diseño de reservas. En cuanto al manejo de áreas naturales, el monitoreo de artrópodos terrestres puede proveer de avisos tempranos sobre cambios ecológicos y puede ser usado para investigar los efectos de la fragmentación subsecuente de áreas naturales que ya no mantienen especies de vertebrados indicadoras. Muchos artrópodos indicadores responden a los cambios ambientales mas rápidamente que vertebrados indicadores, los cuales pueden exhibir respuestas poblacionales que sólo se hacen evidentes cuando ya es muy tarde para el manejo proteccionista. No todos los taxones de artrópodos son igualmente efectivos como indicadores para el planeamiento conservacionista, y las calidades de los indicadores pueden variar dependiendo si su uso es con fines de inventario o de monitoreo. Las asociaciones de artrópodos usados como sondas en inventarios deberian exhibir diversidades especificas relativamente altas, alto endemismo y deberian abarcar el rango geográfico de interés. Si son usados con propósitos de monitoreo, las asociaciones de indicadores deberian exhibir diferentes sensibilidades a las perturbaciones ambientales, y diversidad en cuanto a historias de vida y preferencias ecológicas.

resources (Eisner 1991; Plotkin & Famolare 1992); (3) to strengthen the case for habitat conservation by documenting the distribution of threatened or endangered species (see Thomas et al. 1990; Reinthal & Stiassny 1991); and (4) to provide the basis for selecting indicator species or assemblages for ecological monitoring (Noss 1990; Spellerberg 1991; Kremen 1992).

In contrast, the goals of monitoring programs are to assess changes in ecosystem structure, composition, and function in response to natural factors, human disturbances, or management activities over time (Noss 1990; Spellerberg 1991). A challenge in monitoring is to separate variation in baseline conditions due to natural fluctuations from variation due to human disturbances. This challenge is met in part by monitoring control plots in "pristine" habitats, as well as plots subject to disturbance. The response of indicators to known environmental perturbations, including management activities, can then be used to suggest better management practices (Holling 1978; Murphy & Noon 1991).

In the conservation context, neither inventory nor monitoring programs can be exhaustive. Such programs must therefore rely on indicator species or indicator assemblages; that is, suites of species that respond readily to environmental change in ways that are easily measured or observed. Increasing attention is now being directed to the use of indicator species assemblages (Verner et al. 1986; Landres et al. 1988; Noss 1990; Karr 1991), which tend to improve both resolution and scale of inventory and monitoring programs (Kremen 1992, 1994). Use of species assemblages is especially appropriate for terrestrial arthropods, since many of their most valuable attributes as biological probes result from their extraordinary morphological and functional diver-

sity. For example, a monitoring program that includes assemblages of terrestrial arthropods representing a diversity of taxa and/or functional groups automatically broadens the scope of the environmental factors that can be perceived.

Indicator assemblages useful for reserve selection and design should allow planners to identify biogeographic zones, areas of endemism, evolutionary centers of radiation (Erwin 1991*b*), patterns of geographic replacement, and community types. Indicator assemblages appropriate for monitoring must be sensitive to anthropogenic disturbance and should be able to provide an early warning of ecological change. Given these different objectives, indicator assemblages to be used in inventory are not always the best ones for monitoring purposes, and vice versa.

### Terrestrial Arthropods as Indicators for Inventory and Monitoring

Terrestrial arthropods have been referred to as "the little things that run the world" (Wilson 1988); they occupy the widest possible diversity of ecosystems, microhabitats, and niches, and they play many key ecological roles (Collins & Thomas 1991). Values of terrestrial vertebrate indicators have already been recognized and are generally accepted (Vejner et al. 1986; Landres et al. 1988). In this discussion, we frequently compare terrestrial arthropods and vertebrates—not to insist that terrestrial arthropods universally serve as "better" indicators, but to illustrate circumstances in which their use might be particularly advantageous.

Terrestrial arthropods make up 93% of the total animal biomass in one hectare of Amazonian rain forest (Wilson 1987), a fact reflecting their ecological importance. In tropical and temperate settings, insect herbivores exert comparable or greater grazing pressures on plants than do their vertebrate counterparts (Broadhead 1958; Janzen 1981; Thornton 1985). Arthropod spatial and temporal distributions span the ranges occupied by many vertebrate and plant species, but they also include finer-grained patch sizes and geographic distributions, more complex seasonal and successional sequences, and patch dynamics with more rapid turnover (Shelford 1907; Callan 1964; Waloff 1968; Price 1973; Lawton 1978; Southwood 1978; Erwin & Scott 1980; Schoener 1986; Scott & Epstein 1986; Gaston & Lawton 1988; Wolda 1988; Usher & Jefferson 1991). Terrestrial arthropods exhibit a great range of body sizes, vagilities, and growth rates (Borror & DeLong 1971; Walker 1975; Duellman & Trued 1986; Tyrrell & Tyrrell 1990; M. J. Kaliszewski & D. Wagner, personal communication), and they span a great variety of ecological niches and distributional, population, and dispersal traits. In short, the diversity of arthropods provides a potentially wide

array of biogeographical and ecological probes for use in virtually any inventory or monitoring challenge.

Statistical rigor in inventory and monitoring programs is feasible for many terrestrial arthropod species, given the high diversity of species and their tendency to exhibit large population sizes. Terrestrial arthropods can be easier and less costly to survey than vertebrates. Passive survey methods can reliably sample large numbers of individuals over short time periods, and specimens can be processed in a fraction of the time necessary to handle equivalent numbers of vertebrate specimens. Fewer societal and ecological considerations constrain the collection of terrestrial arthropods during the course of inventory or monitoring studies. For these reasons, terrestrial arthropod species have been the preferred subjects of many basic and applied ecological studies, including some studies that would have been impossible to investigate using other taxa—for instance, Simberloff and Wilson's (1969) extirpation of the entomofauna of mangrove islands to test island biogeographic theory.

Reference collections of terrestrial arthropods can be maintained indefinitely and inexpensively for future and retrospective studies (for example, for molecular genetics); extensive holdings already exist in public and private collections. Terrestrial arthropods, rich in external morphological characteristics, are amenable to rapid species sorting, construction of taxonomic keys (Hammond 1990), and phylogenetic analysis. Phylogenetic systematics in turn can be valuable in assessing global conservation priorities (Humphries et al. 1991) and for detecting centers of radiation where speciation is occurring congruently in distinct lineages (Erwin 1991*b*). Although certain terrestrial arthropods (including some families of Lepidoptera, Coleoptera, Hymenoptera, and Odonata) are taxonomically well known in many geographic areas, the systematics of many other groups are poorly known. Terrestrial arthropods, nonetheless, can be used successfully for inventory or monitoring purposes if individuals can be accurately sorted to morphospecies. Increasingly, entomologists interested in applying their work to conservation and land management issues are taking this approach (Klein 1989; Andersen 1991; Erwin 1991*a*; Kremen 1992, 1994; McIver et al. 1992; Moldenke in press). In fact, in poorly surveyed regions such as many tropical moist forests, sorting to morphospecies for some arthropod taxa may be quicker and more reliable than for many plants and some vertebrates, a real advantage for inventory studies.

Training local assistants in the preparation and recognition of morphospecies is no more difficult or time consuming for terrestrial arthropod taxa than for vertebrate or plant taxa, provided appropriate target groups of terrestrial arthropods are chosen (groups in which morphospecies can be readily recognized) and training

is limited in taxonomic scope. Because specimens of terrestrial arthropods are generally collected (rather than observations alone being recorded), more opportunities exist for experts to supervise parataxonomists and ensure the accuracy of data collection.

### Inventory of Arthropods

Because an explicit goal in establishing networks of reserves is to maximize protection of biotic diversity, it is logical to utilize the most diverse biotic elements as indicators in the assessment of land areas for their conservation value. Many terrestrial arthropod taxa not only are diverse but include suites of species that are endemic to highly localized areas and specific microhabitats (O'Neill 1967; Fellows & Heed 1972; Kaneshiro et al. 1973; Turner & Broadhead 1974; Freitag 1979; Savage 1982; Pearson & Cassola 1992). Erwin (1983), for instance, found that 83% of beetle species collected in four types of forest in the Brazilian Amazon were restricted to a single forest type. Inventories of such taxa could result in enhanced biogeographic resolution of communities, habitats, ecotones, and biotypes, as well as areas of endemism and centers of diversity (Kremen 1994), and thus could provide effective tools for conservation planning (Brown 1991; Greenslade & New 1991; see also Ryti 1992), particularly for determining reserve boundaries or identifying small reserves to capture unique remnant communities. For example, in temperate-zone grasslands, Erhardt and Thomas (1991) used their detailed understanding of the microhabitat requirements (microclimate, fine-scale habitat structure, and host-plant needs) of an assemblage of diurnal Lepidoptera to identify the minority of grassland sites that had histories of continuous traditional management over the past 3500–4000 years, arguing that a similar inventory of plant species would not be equally revealing. Such grasslands now constitute an important and diminishing biotic resource in Britain and continental Europe.

Conserving the habitats of charismatic megavertebrates that require large land areas for population persistence has been an effective strategy that also affords protection for organisms with lesser habitat requirements (Murphy & Wilcox 1986). Increasingly, however, invertebrates, other smaller animals, and plants that are able to persist in small habitat patches are becoming the umbrella species for the protection and management of tiny, remnant natural areas (Main 1987; Murphy et al. 1990; Samways 1990; Wilson 1991; Murphy 1992; Pearson & Cassola 1992; The Wilds and IUCN/SSC Captive Breeding Specialist Group 1992). Protection of the Oregon silverspot butterfly (*Speyeria zerene hippolyta*) under the Endangered Species Act, for example, will

ensure the conservation of several highly threatened native coastal grassland communities in Oregon (McIver et al. 1989). In the developed world, where few large natural areas remain to be protected, inventory of the terrestrial arthropod fauna of such patches is a critical priority to aid in establishing the potential conservation value of these areas, as well as legal mechanisms for their protection (Murphy 1991).

The inventory of arthropods can also contribute to assessments of the economic value of natural areas. Prospecting for unusual organic compounds used by arthropods for defense, communication, and reproduction may reveal lucrative new chemicals for medicine or industry and can result in benefits for conservation (Eisner 1991; Roberts 1992). Taxa likely to display such characteristics (such as spiders and certain beetle families) can be selected as the target assemblages for "chemical prospecting" inventories.

### Inventory Strategies

To represent the biological diversity and ecological complexity present within a region, a conservation inventory (an inventory conducted for conservation planning) should strive to include a number of higher taxa with differing ecological functions, habitat and niche specializations, and distributional characteristics (di Castri et al. 1992). We therefore advocate that such inventories include several vertebrate, plant, and terrestrial arthropod taxa, at a minimum. Strategies for conducting terrestrial arthropod surveys within the context of team-conducted inventories are presented below. All taxa to be selected for inventories should be readily observed or collected, amenable to random and reproducible sampling, and relatively well-known taxonomically and/or ecologically.

In the first method, Coddington et al. (1991) stress reconciling the differences in taxonomic sampling practiced by traditional museum collectors and by community ecologists. Museum collectors efficiently generate relatively complete species lists at sites but rarely gather quantitative data on relative abundances. In contrast, community ecologists often concentrate on obtaining relative abundance estimates to the detriment of species lists. Using spiders as an example, Coddington et al. demonstrate that it is possible to do both, simply by developing time-limited sampling methods based on taxon-specific collecting procedures that can be replicated between sites. Quantitative between-site comparisons can then be drawn from data on relative abundances, community composition, and species diversity, and then can be used to aid in prioritizing sites for conservation planning.

In related work, Lamas et al. (1991) discuss the ad-

vantages and disadvantages of sampling with an intended bias to maximize the number of species collected, rather than sampling at random. This method can work only for taxa in which species can be readily recognized at the time of sampling (such as butterflies), such that species previously collected can be ignored or released. Such a protocol allows a much higher proportion of the focal taxon to be collected at a site in a shorter time period, without over-collecting the fauna or gathering a huge number of specimens that will then be expensive to process and curate.

A final method, target taxon analysis (Kremen 1994), is based on the concept of inventorying only "biogeographically informative" taxonomic assemblages that are likely to represent environmental patterns or the distributional patterns of species in other unrelated assemblages. Kremen hypothesized that taxonomic assemblages resulting from evolutionary radiations within a region will be biogeographically informative. Such taxa (usually of low taxonomic rank, such as genera or tribes, to be of relevance to regional conservation planning) can be preselected on the basis of their high species richness and endemism within a region. Assemblages with these characteristics frequently occur among terrestrial arthropods, especially in the tropics, and many groups are well-characterized enough for such target groups to be selected.

By focusing on a number of such narrowly-defined taxa representing a diversity of higher taxa, the time and cost devoted to sampling, sorting, and training are greatly reduced. Target taxon analysis lends itself to team survey work and, in fact, depends upon it. The following steps are recommended:

- (1) Five to ten higher taxa that are relatively well-characterized (a preliminary regional species list would be sufficient) are chosen—for example, bats, birds, frogs, certain families of vascular plants, butterflies, carabid (ground) beetles, dragonflies, wasps and bees, and dung beetles (see also Brown 1991; Sutton & Collins 1991). Each higher taxon chosen should include one or more low-ranking taxa with high diversity and endemism for testing as a target taxon.
- (2) For each taxon, specialists will select a target assemblage using the selection criteria (species-rich, high endemism), to the extent possible given available knowledge. When known, additional criteria should be used to select those taxon whose member species are collectively well distributed and abundant and display high *beta* or *gamma* diversity (Kremen 1994).
- (3) Using standard ecological sampling design (as in Coddington et al. 1991), the information value of target assemblages can be tested in a limited in-

ventory across an obvious environmental gradient or dispersal barrier. Correlations can then be analyzed (1) between target taxa and environmental gradients, and (2) between the distributions of different taxonomic assemblages. The strength of resulting correlations provides the basis for accepting or rejecting target assemblages as biogeographic indicators.

- (4) Once target assemblages are chosen, the team can conduct larger-scale inventories of the entire region, including all major habitat types and environmental gradients. The information can then be used to identify areas of endemism (Brown 1982, 1991; Fa 1989; Cracraft 1991), to select a minimum number of sites by complementarity to represent the full range of species or habitat types (Margules et al. 1988), or to perform "gap analysis" (Scott et al. 1987). Alternatively, the relationship between distributional and environmental data can be used to predict the full range of a species or species assemblage, and the predicted ranges can then be used to select reserves or to evaluate protection afforded by existing reserve networks (Margules & Stein 1989; McKenzie et al. 1989).

### Monitoring of Arthropod Indicator Assemblages

An effective monitoring program will utilize a variety of indicators to assess environmental responses at population, species, community, and ecosystem levels of organization (Noss 1990). Monitoring of terrestrial arthropods can fit into this scheme across a continuum from populations to communities. Indicator assemblages of arthropods might be chosen taxonomically (that is, by monitoring the presence/absence or relative abundance of all members of a taxonomic group or groups over time) or functionally (by monitoring sets of species representing different ecological roles in their habitats).

To reiterate, the advantage of considering arthropod indicators, either individual species or groups of species, as candidates for monitoring is that their tremendous ecological diversity provides a wide choice for designing appropriate assessment programs. The sensitivity of many terrestrial arthropod populations to environmental impact, including fragmentation, disturbance, habitat modification, ecological disruption, climate change, and chemical pollution, makes them potentially informative for scientifically based reserve design and management. For example, most previous studies of habitat fragmentation have focused on birds (see Diamond 1975; Thomas et al. 1990; Blake 1991; Newmark 1991) and other vertebrates (Burgess & Sharpe 1981; Shaffer 1981; Harris 1984; Newmark 1985, 1987;

Cutler 1991) and have shown the tremendous and far-reaching impact of fragmentation on the maintenance of ecological diversity and stability. It is far less widely recognized that habitat fragmentation also exerts considerable influence on terrestrial arthropod populations; those studies that do exist have shown striking area and isolation effects, particularly for species with limited dispersal capabilities. Turin and den Boer (1988) found that, over the past century, the most sedentary carabid beetle species no longer occupy many localities in which they were formerly found in the Netherlands, a pattern attributable to habitat fragmentation (see also den Boer 1990). Heathland spiders in Great Britain were also found to be restricted to the largest habitat patches, having disappeared from smaller patches (Hopkins & Webb 1984). Klein (1989) found that dung- and carrion-eating beetles of Brazilian rain forests would not cross even narrow clear-cut barriers (less than 350 m wide); species richness and abundances declined significantly in this group in response to decreasing patch area just several years after isolation. In the same study area, in patches isolated since 1980, forest-restricted butterflies of the subfamilies Morphinae, Brassolinae, Theclinae, and Riodininae showed dramatic declines in species richness with area (Brown 1991). Selected terrestrial arthropods thus can demonstrate strong responses to habitat fragmentation, and therefore can be effective indicators that will provide early warnings of the ecological consequences of fragmentation.

Monitoring the distributional and functional responses of terrestrial arthropods to fragmentation may also permit detection of ecological change at an appropriately fine spatial scale to permit improved reserve design and management. The reactions of terrestrial arthropods to microenvironmental gradients (such as temperature, humidity and wind) make them highly responsive both to edge effects (Brown 1991) and to the size of forest clearings (Shure & Phillips 1991). Fragmentation and habitat destruction influence not only the distribution and abundance of terrestrial arthropods (Desender & Turin 1989) but also their ecological functions. Jennersten (1988) demonstrated a disruption in insect pollinator services due to fragmentation, and Klein (1989) showed that dung decomposition in small, isolated patches of tropical moist forest declined with lowered diversity and abundance of dung-feeding beetles. Minimization of dysfunctions resulting from edge and area effects are of critical concern in reserve design and management (Noss 1983; Harris 1984), and further studies of area and edge impact on functional linkages are needed for a variety of taxa.

The ecological health of certain microhabitats may be best monitored using highly specific assemblages of terrestrial arthropods. For example, the terrestrial arthropod fauna of Pacific Northwest old-growth forest floors is comprised of highly characteristic assemblages

adapted to the narrow temperature and moisture ranges of these environments (McIver et al. 1990; Moldenke & Lattin 1990; Parsons et al. 1991; Lattin & Moldenke 1992). These assemblages include numerous species of oribatid mites, harvestmen, millipedes, centipedes, springtails, beetles, flies, wasps, crickets, and isopods. Many of the species inhabiting understory microhabitats are relatively sedentary (wingless or flightless). The dispersal of understory species is therefore limited by both distance and inhospitable terrain; consequently these assemblages are likely to be strongly affected by alteration of old-growth and mature forest environments (Moldenke & Lattin 1990; Olson 1992). Since many of these species are involved in litter decomposition and nutrient recycling, disruptions in the structure of these communities will have important functional implications for old-growth ecosystems.

One goal of the management of natural areas is to maintain the ecological stability and diversity found in "pristine" ecosystems. Gilbert (1980) noted the importance of "mobile-links"—species that pollinate or disperse the seeds of a wide variety of plants—in maintaining diversity and suggested that autecological and monitoring studies of representative mobile-link species be conducted. Mobile-link species, many of which are insects, support "keystone mutualist" plant species, which in turn provide critical resources (such as fruits, nectar, leaves, secondary chemical compounds, sites for mating and predator avoidance, and so forth) used by a wide variety of other organisms (Janzen 1981; Bawa 1990). The monitoring of mobile-link species would complement studies of two other functional groups critical to the maintenance of community diversity and stability: top predators (Terborgh 1988) and keystone-mutualist plants (Gilbert 1980; Terborgh 1986).

Paradoxically, these mobile-link species may include some of the more generalized taxa among terrestrial arthropods. A well-studied group of mobile links are the neotropical euglossine bees. Single species of euglossine bees can link plant species from all stages and strata of forests into systems of indirect mutualism. Many euglossine species rely on early successional patches and the plants that they support for larval food, and they are the obligate pollinators of plants restricted to late-successional forests. Females may travel long distances when foraging for pollen and thus may be critical to the reproductive success of plants that exist in low densities (Dobson 1966; Janzen 1971; Gilbert 1980). Monitoring euglossine populations thus indirectly allows assessment of the health of interacting habitat patches within ecosystems. Euglossines are easy to inventory and monitor because they are attracted to chemical scents, can be readily identified without collecting, and can be individually marked for population studies.

Many terrestrial arthropods have rapid population growth rates and short generation times, and therefore

can exhibit rapid responses to fluctuating environmental conditions (including local and regional changes in abundance, patch extinction and colonization, and range expansions and contractions—see Pollard 1979; Murphy & Weiss 1988a, 1988b, 1991; Murphy et al. 1990; Colwell & Naeem 1993). When such changes can be shown to be correlated across taxa, to be causally connected or strongly correlated with known environmental changes, or to occur as persistent population lows, highs, or extinctions, these changes may be recognized as early warnings of human-influenced ecosystem change. For example, declines in the abundance of temperate diurnal Lepidoptera species have heralded alterations in habitat structure well before those changes have become evident in populations of their host plants (Erhardt & Thomas 1991; Thomas 1991). The challenge in separating natural population fluctuations from those produced by anthropogenic perturbation holds for any indicator species, particularly when species demonstrate nonequilibrium population dynamics; recent analysis of available time-series data (Turchin & Taylor 1992) suggests that both insect and vertebrate populations "exhibit a similar spectrum of population dynamics," ranging from no obvious regulation of population density to complex endogenous dynamics (damped oscillations, limit cycles, etc.).

The sensitivity of population growth rates and development of many arthropods to temperature, humidity, and rainfall (Wolda 1988), and the reliance of arthropod populations on narrowly defined microclimate niches (Dobkin 1985; Weiss et al. 1987, 1988; Erhardt & Thomas 1991; Murphy & Weiss 1988b; Britten et al. 1994) may make arthropods especially effective indicators of local and regional climate change (see Ehrlich et al. 1972; Murphy & Weiss 1992; see also Fajer 1989; Fajer et al. 1989; Dennis & Shreeve 1991; Britten et al. 1994). Fossil records of arthropod communities have been used to reconstruct climatic history (Atkinson et al. 1987).

Understanding the natural population dynamics of terrestrial arthropods has already proved important for managing arthropod pests in agroecosystems, such as the catastrophic cottony-cushion-scale outbreak in California in 1946, when DDT killed the natural enemy, vedalia beetles, of this citrus pest—see Anlow and Rosset (1990). Controlling agricultural disease vectors will become increasingly important as pest populations change in response to pesticide campaigns, climate change, and declines in the populations of their natural enemies (Schowalter 1985, 1989; Morris et al. 1991). When the environmental impact caused by pesticides is monitored, nonpest arthropods are natural subjects (Bracker & Bider 1982) because they are often the first organisms to be affected by phenomena that can later have severe consequences for rare mammals and birds, species at high trophic levels that may then require in-

tensive and costly recovery programs (for example, the peregrine falcon, Anderson & Hickey 1972; Cade 1988; Nisbet 1988). For example, honey bees are highly susceptible to DDT, dieldrin, carbaryl, malathion, and methyl parathion, and bee poisoning can be easily monitored by collecting dead bees at commercial hives (Johansen 1977).

Despite their relative merits, there has been little experience in utilizing terrestrial arthropod species or assemblages as indicators for inventory or monitoring related to conservation planning and management (but see Murphy et al. 1990; Brown 1991; Pearson & Cassola 1992). Instead, traditional management indicator species have been large vertebrates (Landres et al. 1988). The methodologies for utilizing terrestrial arthropod assemblages thus have yet to be fully developed and tested, and their constraints have not been identified.

### Monitoring Strategy

To capitalize on the diversity of arthropods and their inherent potential for rapid ecological change, the goal is to select indicators that respond to human impact long before changes ramify through complex networks of ecological interactions to affect higher trophic levels and/or more long-lived organisms. Terrestrial arthropod assemblages could be selected to represent (1) a diversity of higher taxa; (2) a diversity of higher taxa and functional groups; or (3) a diversity of functional groups within the same higher taxon.

If monitoring is to be conducted to assess the effects of a suspected or known environmental impact, then the assemblages should comprise species responsive to the direct or indirect effects of that impact. The monitoring system will be potentially more sensitive if radically different functional elements can also be incorporated or metrics integrated from different taxonomic groups or levels of ecological organization (see the Index of Biological Integrity, Karr 1991). For example, in response to forest thinning (the proposed management strategy for the federal forest matrix outside of Habitat Conservation Areas in the Pacific Northwest), terrestrial arthropod populations might be expected to decline due to desiccation stresses, temperature increases, and wider ranges of variation for these factors (Majid & Jusoff 1987; Uhl & Kaufman 1990; Olson 1992). One might monitor the impact of such changes using assemblages of decomposers in the leaf litter and of predatory insects in the understory or canopy. The leaf-litter assemblage is composed of a high percentage of stenotopic species and will be highly responsive to changes in microclimate induced by the reduction of canopy cover. While the predaceous understory and canopy insects may be less narrowly adapted (Olson 1992) and therefore less responsive to the direct impact on microclimate, they



may respond indirectly to alterations in the densities of their prey populations. The sensitivity of these two assemblages can be tested in field trials (see also Kremen 1992).

If monitoring is instead more generalized (assessment of the status of biodiversity or "ecological health"), then a strategy that maximizes the representation of diverse higher taxa and functional groups would be preferred. Again, selection of indicator assemblages that are likely to respond in different ways to the same stress improves the sensitivity and robustness (Karr 1991) of monitoring, particularly in situations in which the relative importance of different effects is not known.

Monitoring of terrestrial arthropod assemblages could be conducted by (1) measuring the presence or absence of member species; (2) characterizing community structure by functional groups; (3) measuring the relative abundance of member species; or (4) carrying out population or autecological studies of member species. These techniques represent a gradient from least to most costly and difficult to implement. The second method, characterizing community structure by functional groups, potentially represents an efficient means of measuring biological responses to environmental changes using terrestrial arthropods. For example, the faunal assemblages of old-growth forests of the Pacific Northwest are distinct and contain predictable proportions of functional groups, including many herbivores, predators, and detritivores (Mispagel & Rose 1978; Voegtlin 1982; Schowalter et al. 1988; Schowalter 1990); in contrast, younger forests and monocultures are dominated by sap-sucking herbivores and a much less diverse array of predators (Schowalter 1989). Similar community shifts are observed in eastern deciduous forests with respect to natural or human-generated succession, leading to the conclusion that functional linkages are being altered in predictable ways in these different forest types (Schowalter 1989, 1990). Environmental impact could thus be reliably assessed by monitoring the functional structure of communities over time.

The functional approach integrates a huge amount of data (the responses of many, differently adapted organisms, see also Karr 1991) but is comparatively easy to implement because it relies on cataloging individuals or morphospecies by function rather than by taxonomic identity. For certain taxa (for example, Scarabeidae), functional groupings can be readily assigned using morphological characteristics (for example, mouthparts) in combination with knowledge of the functional biology of higher taxa. Keys to the functional groups found within higher taxa can then be generated by specialists for use in assessment programs. Such methods would be particularly applicable in the tropics, where taxonomic identifications are frequently not feasible due to lack of knowledge of the diverse terrestrial arthropod fauna.

## Conclusions

Terrestrial arthropods, because of their diversity of species and functional roles; wide range of body sizes, vagilities, and distributional characteristics; and propensity for rapid growth and evolutionary rates, offer certain exceptional characteristics as indicator groups for conservation inventory and monitoring programs. The unparalleled diversity of arthropods provides a rich data source that can improve the spatial resolution of biological inventories and hence the planning of natural-areas networks. Their capacity for exhibiting rapid responses to environmental change over both ecological and microevolutionary time makes them potential early warning indicators of environmental change.

To date, this rich data source remains largely untapped. In contrast, substantial experience exists in using aquatic arthropod communities for monitoring of water quality (Berkman et al. 1986; Karr 1991) and classification of aquatic habitats (Savage 1982; Johnson & Wiederholm 1989; Johnson et al. 1993). Some of this experience could be translated to terrestrial systems. An effort is needed on the part of conservation biologists, terrestrial arthropod ecologists, and systematists both to apply current knowledge and to develop new methodologies using terrestrial arthropods as indicators for conservation inventory and monitoring.

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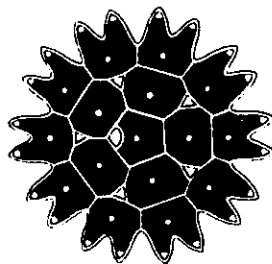
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# World-Wide Species Richness Patterns of Tiger Beetles (Coleoptera: Cicindelidae): Indicator Taxon for Biodiversity and Conservation Studies\*

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**Abstract:** *The family of tiger beetles (Cicindelidae) is an appropriate indicator taxon for determining regional patterns of biodiversity because (1) its taxonomy is stabilized; (2) its biology and general life history are well understood; (3) individuals are readily observed and manipulated in the field; (4) the family occurs world-wide and in a broad range of habitat types; (5) each species tends to be specialized within a narrow habitat; (6) patterns of species richness are highly correlated with those of other vertebrate and invertebrate taxa; and (7) the taxon includes species of potential economic importance. Logistical advantages provide some of the strongest arguments for selecting tiger beetles as an appropriate indicator taxon. Species numbers of tiger beetles are relatively well known for 129 countries. Eight countries alone account for more than half the world total of 2028 known species. Species numbers are also indicated for eleven biogeographical zones of the world. For gridded squares across North America, the Indian subcontinent, and Australia, species richness of tiger beetles, birds, and butterflies shows significant positive correlations. However, tiger beetle species numbers can be reliably determined within fifty hours on a single site, compared to months or years for birds or butterflies, and the advantage of using tiger beetles in conservation biology is evident.*

**Resumen:** *La familia de los escarabajos tigre (Cicindelidae) constituye un taxon indicador apropiado para determinar patrones regionales de biodiversidad porque (1) su taxonomía es estable; (2) su biología e historia natural son bien conocidas; (3) los individuos son fácilmente observables y manipulables en el campo; (4) la familia tiene una amplia distribución mundial, así como un gran variedad de hábitats; (5) cada especie tiende a especializarse dentro de un hábitat restringido; (6) los patrones de riqueza de especies están altamente correlacionados con los de otros taxones de vertebrados e invertebrados; y (7) el taxon incluye especies de potencial importancia económica. Las ventajas logísticas de los escarabajos tigre proporcionan una de las evidencias más sólidas para considerarlos un taxon indicador apropiado. El número de especies de escarabajos tigre es bien conocido en 129 países. Ocho de estos países contienen más de la mitad de las 2028 especies conocidas en el mundo. También se indica el número de especies para once zonas biogeográficas del mundo. Mediante el estudio de cuadrículas de muestreo situadas en Norte América, el Subcontinente Indio y Australia, que ilustran la riqueza de especies de escarabajos tigre, aves y mariposas, se observa una correlación positiva significativa. Sin embargo, el número de especies de escarabajos tigre puede determinarse confiablemente mediante unas cincuenta horas de muestreo en un solo sitio, en comparación con los meses o años que se necesitan para aves o mariposas, pro lo que la ventaja de utilizar los escarabajos tigre en conservación biológica es obvia.*

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## Introduction

Biodiversity as a focus for conservation has received increasing attention (Wilson 1988; Noss 1990; Ehrlich & Wilson 1991). To test for pertinent patterns of biodiversity, various protocols and levels of study have been proposed that include ecological communities (Hunter et al. 1988), cladistic classifications (Vane-Wright et al. 1991), a hierarchical composite of different levels of organization (Noss 1990), as well as groups of taxonomically related species (Wilson 1988).

Although severe time and funding limits are problems for many research projects, the addition of political, sociological, and cultural pressures make conservation biology a "crisis discipline," for which risk analysis is a major consideration in designing programs (Maguire 1991). A common approach to resolving these problems has been to use indicator taxa as test organisms. The use of indicator taxa in conservation efforts from pollution control to biodiversity has been the focus of considerable attention (Landres et al. 1988).

No single species or taxon can be expected to represent or indicate patterns for all other species and taxa. There are, however, some logistical and biological criteria that maximize the usefulness of a taxon as an indicator (Noss 1990), including the following: (1) its taxonomy is well-known and stable so that populations can be reliably defined; (2) its biology and life history are well understood—limiting resources, enemies, physical tolerances, and all stages of the life cycle can be incorporated into hypotheses and experimental design; (3) individuals are readily observed in the field, and studies are facilitated by uncomplicated observations and manipulations such that inexperienced students and non-professionals can be trained easily to help conduct studies; (4) the taxon occurs across a broad geographical range and number of habitat types to permit broad experimental design and comparisons; (5) each population or species tends to be specialized within a narrow habitat and thus sensitive to habitat degradation and regeneration; (6) patterns observed in the indicator taxon are reflected in other related and unrelated taxa, and (7) the taxon includes species that have potential economic importance so that scientists and politicians, especially in Third World countries where pure or basic science is frequently considered a luxury, can be convinced that this taxon is worth dedicating local personnel and resources for studies.

The preponderance of studies using indicator taxa has relied on vertebrates, especially those "species of high public interest" (United States Department of Interior [USDI] 1980). Vertebrates, however, tend to be relatively long-lived and have low rates of population increase, long generation times, and comparatively low habitat specificity (Murphy et al. 1990), all of which tax time and finances for proper investigation. More re-

cently there has been an effort to overcome these problems by using arthropod species, especially insects, instead of vertebrates as indicators (Pyle et al. 1981; Collins & Morris 1985; Rosenberg et al. 1986; Morris & Rispin 1988; Murphy & Weiss 1988; Samways 1988, 1989, 1990a,b; Viejo et al. 1989; Webb 1989; den Boer 1990; Rushton et al. 1990; Thomas 1991).

In addition to displaying the general criteria for indicator taxa, insects are appropriate because of rising rates of human-caused extinction (Wilson 1988). Insects represent more than 80% of the several million animal species now extant in the world, and extinction is probably more significant in terms of absolute numbers for insects than for any other group of organisms in the world.

The family of tiger beetles (Coleoptera: Cicindelidae) is a potentially ideal indicator taxon. Their taxonomy is well known. All are predaceous on small arthropods, and they share similar larval and adult body forms around the world. Adults are generally diurnal and found primarily on soil surfaces. Larvae are easy to raise in the laboratory and are relatively easy to find and observe in the field (Palmer 1978; Knisley & Pearson 1984; Shivashankar et al. 1988). A journal, *Cicindela*, published since 1969, is the result of efforts by both amateurs and professionals to document basic natural history, distribution, and identification of tiger beetles world-wide.

The hypothesis of this paper is that tiger beetles are an ideal bioindicator taxon. The tests will be comparisons of the characteristics of tiger beetles to each of the seven criteria proposed for an ideal indicator taxon. In addition to establishing the strengths and weaknesses of tiger beetles as indicators, this procedure can be used as a gauge against which to judge the usefulness of other potential indicator taxa.

## Methods and Materials

### Stable Taxonomy

To quantify the concept of "stable," we chose five relatively recent and broad taxonomic revisions of tiger beetles and calculated the percent of species/subspecies names that had been eliminated through synonymy from those in original or previous studies. The monographs selected were revisions of (1) the genus *Cicindela* (sensu lato) from Australia (Freitag 1979), (2) the family Cicindelidae on the island of New Guinea (Cassola 1987), (3) the family Cicindelidae on the island of Sumatra (Wiesner 1986), (4) the genus *Cicindela* (s. l.) on the Indian subcontinent (Acciavatti & Pearson 1989), and (5) the family Cicindelidae on the Indonesian island of Sulawesi (Cassola 1991).

### Biology and Life History

Although it is difficult to quantitatively establish which taxa have well-known biology and natural history, the



breadth of studies on tiger beetle adults and larvae from around the world would serve as an indication of the level of this knowledge.

#### Field Observations and Experimentation

To illustrate how readily and accurately tiger beetles can be surveyed, we chose seven sites for which there are at least five years of exhaustive studies of tiger beetles (three tropical forest sites: La Selva, Heredia, Costa Rica; Pakitza—Manu National Park, Madre de Dios, Perú; Tambopata, Madre de Dios, Perú; a desert grassland-pond edge habitat near Willcox, Arizona, U.S.A.; a salt marsh—ocean beach area near Puerto Peñasco, Sonora, Mexico; and an open forest and a riparian habitat near Bangalore, Karnataka, India). These sites include a wide range of habitats that represent the most simple to the most complex and heterogeneous habitats in which tiger beetles occur naturally. We have studied these beetles intensively during the period of greatest activity, the early rainy season, at each of these sites (Pearson & Mury 1979; Pearson 1980, 1984; Ganeshaiah & Belavadi 1986). We determined the number of species of tiger beetles found within the first cumulative 50 hours of field studies during periods in which tiger beetles could be expected to be active, in moist substrate with warm, sunny periods. Then we determined the number of additional species found in the subsequent 200 to 5000 hours of field work conducted during the season of tiger beetle activity.

To establish how readily untrained personnel can learn to accurately observe and survey these beetles in the field, the first author worked with biology and entomology students who had no previous experience with tiger beetles. As a part of conservation workshops in India, Perú, Bolivia, Ecuador and Brazil, these students were taken to a field site in which the first author had recently determined the number of species of tiger beetles. For 2–4 hours the students were shown the microhabitats in which tiger beetle adults occurred, their flight patterns, foraging behavior, and general natural history. Each of the students then went on the site alone. They were asked to collect as many of the tiger beetle species as they could find in two hours. Their collection was then compared to the number of species predetermined by the first author.

#### Breadth of Habitats and Geographical Range for the Family

As an indication of how widely the family of tiger beetles ranges geographically and over habitat types, we used published habitat data. As an indication of the geographical range of the family, we used regional and local publications together with our own unpublished records from around the world to determine the total number of species now known world-wide as well as the number of species known for each of as many countries

of the world as possible. As an additional comparison that helped control for differences in the size of countries, we calculated the number of km<sup>2</sup> per species for each country. Low numbers indicate high diversity of species (wide range of habitats and biogeographic influences) and high numbers indicate low diversity of species (few habitats, extreme habitat types, and in a few cases perhaps insufficient field work). We also calculated how many of these species were endemic to each country.

Although seldom of biological significance, the number of species within political boundaries not only indicates the world-wide distribution of the family, but it can also be a significant parameter for making conservation decisions. In addition, the number of species that are restricted to the confines of political boundaries can be useful information for convincing nonbiologist decision makers of conservation priorities that involve their political units. To show one way in which these species number data could be useful in developing a list of priority areas for conservation, we ranked in descending order the 75 countries with endemic species. By distinguishing nonendemic species shared between these countries and then calculating a cumulative total number of species, we determined the countries exhibiting the greatest endemism as well as contributing the most to global tiger beetle species diversity (Collins & Morris 1985).

Of more biological significance, an understanding of distributions of species numbers within biogeographic regions and habitat types also has broad implications for basic and conservation research. Identifying patterns of biodiversity and their causes can provide insight into species co-occurrence and the evolution of community structure (Ricklefs 1987) as well as provide a preliminary basis upon which priority areas for conservation can be determined (Kuliopulos 1990). Using published data and specimens in private and public collections, we determined the total number of species occurring in each of eleven biogeographical zones of the world (Nearctic, including most of Mexico; Neotropics; Palearctic, including Africa north of the Sahara; Ethiopian; Madagascar; Indian subcontinent; China, including Mongolia, Korea and Japan; Indomalaysia; New Zealand; Papua-Oceania; and Australia). From our knowledge of the history of tiger beetle study as well as the diversity of likely tiger beetle habitats yet unstudied in each area, we estimated how many more undescribed species are likely present in each zone. We also judged how reliable is the number of species now known from each biogeographical area.

#### Habitat Specialization of Species

To establish the degree of habitat specialization of tiger beetle species, we used data from ecological studies that

quantified habitat use among tiger beetle species. We also determined the percent of habitat specialists versus generalists as reported in broader natural history, systematic, and ecological publications on tiger beetles from Australia (Freitag 1979), southeast Perú (Pearson 1984), southwestern U.S.A. (Knisley & Pearson 1984), and the Indian subcontinent (Acciavatti & Pearson 1989).

#### Biological Patterns Correlated with Other Taxa

Previous studies in tropical, semi-tropical, and temperate areas indicate that a square 275 km on a side is an area within which one or two intensive collections of tiger beetles is likely to be representative of the entire square (Pearson & Ghorpade 1989). We gridded North America south of the near-surface permafrost line (evidently because larval tiger beetles cannot overwinter in this soil, tiger beetles are absent north of this line) and the Indian subcontinent into squares 275 km on a side. Because tiger beetle faunas from Australia are less well known, we increased the size of the squares to 350 km on a side. Using regional publications, taxonomic revisions, and private field notes, we determined the total number of tiger beetle species within each of these squares. To better visualize patterns of species richness at a continental level, we produced isoclines by connecting the approximate center of squares in the grid that had similar numbers of species.

To test the generality of these patterns of diversity, we compared the number of tiger beetle species to the total number of terrestrial (nonaquatic and nonmarine) breeding bird species (Pizzey 1980; Ali & Ripley 1987; National Geographic Society 1987) and also, for Australia and North America, the number of breeding butterfly species (Common & Waterhouse 1982; Scott 1986) known from each of these squares. We calculated correlation coefficients between pairs of taxa for each continental area.

#### Potential Economic Importance

Although normally not considered of great economic importance, as predators tiger beetles in some habitats

could be preadapted to help control pest species of arthropods.

## Results

### Stable Taxonomy

The total number of species of tiger beetles in the world now stands at 2028, including some as of yet unpublished names. Among the five systematic revisions analyzed for species name stability, a total of 406 species names (with some duplication of species between Sumatra, Sulawesi, and India and between Australia and New Guinea), or 20.3% of the world's tiger beetle fauna, are represented (Table 1). Of these 406 species, only 11 (2.4%) were lost through synonymy.

The number of new species described in each of these revisions also indirectly affects the interpretation of these quantifications of stability. Because no authority has yet had the chance to consider the newly described species for synonymy, the number of newly described species in each revision is pertinent (Table 1).

As a frame of reference, birds are among the most taxonomically stable groups at the species level. Revisions from even the most poorly-studied regions, such as South America (Ridgely & Tudor 1989), seldom have more than 2% loss of species through synonymy.

### Biology and Life History

A preliminary list of articles dealing with tiger beetles has been published in two parts (Larochelle 1980*a,b*). Of these 909 papers, over 85% include some life history or biology of larvae or adult beetles. A more recent review (Pearson 1988) summarizes the extensive biology known for species of this family.

### Field Observations and Experimentation

The first cumulative 50 hours of collecting, including the biologically and physically complex rain forest field stations, revealed 78–93% of the tiger beetle fauna for each of the seven sites (Table 2). In the additional 200 to 5000 hours of survey work during times of potential beetle activity, only two to five species were added, and

Table 1. The number and percent of synonymized species and the number of newly described species in five regional systematic revisions of tiger beetles.

	Number of species considered	Names synonymized		Number of newly described species
		Number	% of total	
Australia (Freitag 1979)	29	8	21.6	4
Sumatra (Wiesner 1986)	65	1	1.5	0
New Guinea (Cassola 1987)	99	1	1.0	24
Indian subcontinent (Acciavatti & Pearson 1989)	151	1	0.6	24
Sulawesi (Cassola 1991)	82	0	0	26

Table 2. The number of species of tiger beetles found within the first 50 hours of effort, and the number of additional species found in subsequent hours of search at seven field sites.

	Number of species within first 50 h (% of total)	Number of species added subsequently (total additional hours)
Puerto Peñasco, Sonora, Mexico	7 (88)	1 (> 200)
La Selva, Heredia, Costa Rica	7 (78)	2 (> 1000)
Pakitza (Manu), Madre de Dios, Perú	20 (80)	5 (> 200)
Tambopata, Madre de Dios, Perú	27 (93)	2 (> 500)
Willcox, Arizona, U.S.A.	20 (95)	1 (> 5000)
Bangalore, Karnataka, India (scrub forest)	9 (100)	0 (> 1000)
Bangalore, Karnataka, India (riparian)	10 (83)	2 (> 500)

these tended to be rare species at the limit of their geographical range (*Cicindela wickhami* W. Horn near Willcox, Arizona) or arboreal species (*Ctenostoma* and *Iresia* on the Neotropical forest sites) that are most readily collected with special techniques such as beating foliage and fogging the canopy with insecticide.

In addition, the time to train student assistants adequately to observe and collect tiger beetle specimens is much less than that for other taxa. To adequately train a novice student to observe and identify birds in these Amazonian forests would take several years; for butterflies it would take several months. In the conservation workshops, 80% of the students were trained within 4 hours to find at least 90% of the species of tiger beetles on the study site.

#### Breadth of Habitats and Geographical Range for the Family

In a world-wide study of habitat type and chemical defense, 83 species were examined. They occurred from alpine meadows to desert grasslands to tropical rain forests (Pearson et al. 1988).

By geographical region, the number of species is greatest in the Neotropics, Ethiopian, and Indomalaysia areas (Fig. 1). The total number of tiger beetle species

and the number of species whose range is completely restricted to that country are listed for 129 countries (Table 3). By political boundaries, Madagascar has the greatest number of endemic species (174), and Indonesia has the highest total number of species (219). India, with 193 species, has the second highest total number in the world, but with a land area of 3,287,590 km<sup>2</sup> it has 5.6 times the area of Madagascar (587,041 km<sup>2</sup>) and 1.7 times the area of Indonesia (1,904,569 km<sup>2</sup>). Brazil is third in both total number of species and number of endemic species.

The seven countries with the highest amounts of endemic species contain a total of 1014 species (Table 4), half the described species in the world. If the next nine countries are included, 75% of all the species in the world are represented. The 40 highest countries together contain more than 95% of all the described species in the world, and a minimum of 75 countries together contain the whole world's tiger beetle fauna.

Comparison to a similar study on swallow-tailed butterflies (Papilionidae) (Collins & Morris 1985) shows that seven of the top ten countries for endemic species are shared by tiger beetles, and five of the top ten countries for total number of species are shared.

#### Habitat Specialization of Species

Studies of tiger beetle habitat use in Japan (Hori 1982), India (Ganeshaiah & Belavadi 1986), and the U.S. (Shelton 1912; Willis 1967; Knisley 1984; Schultz & Hadley 1987) all indicate relatively narrow adaptation by adults and larvae. Mechanisms for these adaptations include morphology (Pearson & Mury 1979; Schultz & Hadley 1987), physiology (Hadley et al. 1990), and behavior (Knisley & Pearson 1981; Pearson & Lederhouse 1987).

Of 151 species of the genus *Cicindela* (s. l.) on the Indian subcontinent, only one species, *C. flavomaculata* Hope, tends to occur in several distinct habitat types (Acciavatti & Pearson 1989). Of the 20 species in the Sulphur Springs Valley of southeastern Arizona, U.S.A., only one species, *C. nigrocoerulea* Leconte, regularly occurs in more than one distinct habitat type (Knisley & Pearson 1984). Of the 29 species in the

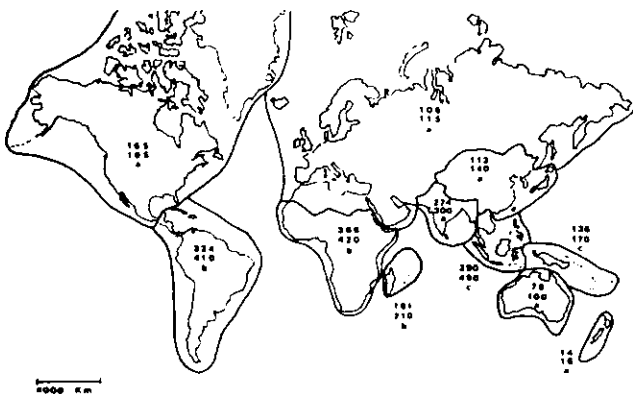


Figure 1. Number of described tiger beetle species (top number), estimated total number eventually to be described, and the assessment of precision of estimate (a = excellent; b = good; c = poor) for each of 11 biogeographical areas.

Table 3. Total number of tiger beetle species known from within the political boundaries of selected countries, the number of species endemic to each country, and the ratio of surface area to total number of species.

	Total number of species	Number of endemic species	% Endemic	Area (Km <sup>2</sup> )	Km <sup>2</sup> /species
<b>NEARCTIC</b>					
Canada	29	0	0	9,976,140	344,004
Mexico	116	57	49	1,972,550	17,004
U.S.A.	111	45	40	9,372,610	84,438
<b>NEOTROPICAL</b>					
Argentina	64	11	17	2,780,090	43,438
Bolivia	86	21	24	1,098,580	12,774
Brazil	184	97	51	8,511,970	46,260
Chile	6	1	17	756,630	126,105
Colombia	42	7	16	1,138,910	27,116
Costa Rica	38	1	3	51,100	1344
Cuba	11	4	36	110,920	10,084
Ecuador (with Galapagos Is.)	74	19	26	283,560	3831
El Salvador	17	1	6	21,041	1296
Guatemala	23	1	4	108,890	4734
Guyanas (Fr. Guiana, Guyana, & Suriname)	29	5	17	448,793	15,476
Hispaniola (Haiti and Dominican Rep.)	9	3	33	76,190	8465
Honduras	7	1	14	112,088	16,012
Jamaica	4	0	0	10,990	2747
Nicaragua	24	0	0	139,000	5791
Panama	28	4	14	75,650	2702
Paraguay	38	3	8	406,750	10,703
Peru	79	14	18	1,285,215	16,268
Trinidad & Tobago	4	1	25	5128	1282
Uruguay	17	0	0	177,510	10,441
Venezuela	51	8	16	912,050	17,883
<b>PALAEARCTIC</b>					
Afghanistan	19	0	0	649,970	34,208
Albania	5	0	0	28,750	5749
Algeria	15	1	7	2,381,740	158,782
Austria	9	0	0	83,850	9317
Bulgaria	11	0	0	110,910	10,082
Cyprus	7	0	0	9250	1321
Denmark	4	0	0	43,070	10,767
Egypt	9	0	0	1,002,000	111,333
Finland	4	0	0	337,030	84,257
France	15	0	0	543,990	36,266
Germany	6	0	0	356,130	59,355
Great Britain	5	0	0	244,030	48,806
Greece	14	0	0	131,940	9424
Holland	6	0	0	36,150	6025
Hungary	7	0	0	93,030	13,290
Iran	30	5	17	1,648,000	54,933
Iraq	11	0	0	438,446	39,859
Israel	9	0	0	20,770	2307
Italy	17	1	6	301,250	17,720
Lybia	6	1	17	1,759,540	293,256
Malta	4	0	0	315	79
Mongolia	23	2	9	1,565,000	68,043
Morocco	14	3	21	458,730	32,766
Norway	4	0	0	324,220	81,055
Poland	7	0	0	311,730	44,532
Portugal	10	0	0	92,020	9202
Romania	10	0	0	237,500	23,750
Saudi Arabia	9	0	0	2,153,170	239,241
Spain	16	1	6	504,750	31,546
Syria	10	0	0	185,180	18,518

Table 3. Continued.

	Total number of species	Number of endemic species	% Endemic	Area (Km <sup>2</sup> )	Km <sup>2</sup> /species
Sweden	4	0	0	442,750	110,687
Switzerland	7	0	0	41,290	5899
Tunisia	14	1	7	163,610	11,686
Turkey	25	4	16	779,450	31,178
U.S.S.R.	49	4	8	22,274,900	454,590
Yemen	10	1	10	482,680	48,268
Yugoslavia	9	0	0	255,800	28,422
ETHIOPIAN					
Angola	69	23	33	1,246,700	18,068
Benin	14	0	0	112,620	8044
Botswana	27	1	3	600,370	22,235
Burkina Faso	11	0	0	274,200	24,927
Burundi	6	0	0	27,830	4638
Cameroon	43	5	12	470,200	10,934
Cent. African Republic	46	3	6	622,980	13,543
Chad	16	0	0	1,284,000	80,250
Congo	27	0	0	342,000	12,666
Ethiopia	51	8	16	1,221,900	23,958
Gabon	11	0	0	267,670	24,333
Gambia	13	0	0	11,290	868
Ghana	12	0	0	238,540	19,878
Guinea	20	0	0	245,860	12,292
Guinea Bissau	34	0	0	36,120	1062
Guinea (Equatorial)	9	0	0	28,050	3116
Kenya	53	9	16	582,640	10,993
Ivory Coast	21	1	5	322,460	15,355
Liberia	10	0	0	111,370	11,136
Malawi	36	0	0	118,480	3291
Mali	16	1	6	1,240,140	77,508
Mauritania	13	0	0	1,030,700	79,284
Mozambique	47	7	15	799,380	17,008
Namibia	31	2	6	824,280	26,589
Niger	10	0	0	1,267,000	126,700
Nigeria	24	0	0	923,770	38,490
Senegal	33	0	0	196,190	5945
Sierra Leone	25	0	0	71,740	2870
Somalia	31	12	39	637,660	20,570
South Africa	94	40	43	1,221,040	12,990
Sudan	32	0	0	2,505,810	78,306
Tanzania	68	8	12	939,700	13,819
Togo	24	1	4	56,600	2358
Uganda	33	0	0	235,880	7147
Zaire	134	27	20	2,344,880	17,499
Zambia	53	2	4	746,250	14,080
Zimbabwe	53	4	8	389,300	7345
MADAGASCAR					
Comores Is.	2	0	0	2170	1085
Madagascar, Glorieuses & Juan de Nova Is.	176	174	99	587,040	3335
Mauritius Is.	3	2	67	1860	621
Reunion Is.	4	3	75	2512	628
Seychelles Is.	1	0	0	410	410
ORIENTAL-AUSTRALIAN					
Australia	81	72	88	7,617,930	94,048
Bangladesh	53	2	4	133,910	2527
Bhutan	22	0	0	47,000	2136
Burma (Myanmar)	93	12	12	657,740	7072
Cambodia	33	0	0	176,520	5349
China (PRC)	94	16	17	9,326,410	99,217
Fiji	2	1	50	18,270	9136

Table 3. Continued.

	Total number of species	Number of endemic species	% Endemic	Area (Km <sup>2</sup> )	Km <sup>2</sup> /species
India (with Andaman & Nicobar Is.)	193	82	42	3,287,590	17,034
Indonesia					
Irian Jaya	53	22	42	410,650	7748
Java	45	8	18	132,200	2937
Kalimantan	42	2	5	534,890	12,735
Sulawesi	81	58	72	159,000	1962
Sumatra	67	8	12	472,610	7053
Other	25	5	20	195,219	7808
Japan	22	4	18	372,540	16,933
Korea (N. & S.)	15	0	0	219,360	14,624
Laos	59	3	5	230,800	3912
Malaysia					
Peninsular	47	3	6	327,810	6974
Borneo	73	19	26	198,210	2715
Nepal	64	4	6	140,800	2200
New Caledonia	17	16	94	17,400	1023
New Zealand	14	14	100	269,060	19,218
Pakistan	33	1	3	796,100	24,124
Papua New Guinea	72	45	62	451,710	6273
Philippines	94	74	79	298,170	3172
Solomon Islands	20	11	55	27,540	1377
Sri Lanka	55	32	58	64,740	1177
Taiwan	26	9	35	36,180	1391
Thailand	102	20	19	511,770	5017
Vanuatu	3	0	0	12,190	4060
Vietnam	93	25	27	325,360	3498
Western Samoa	2	1	50	2840	1421

Tambopata Reserved Zone, Madre de Dios, Perú, only one species, *Odontochella annulicornis* Brullé, occurs in more than one forest habitat type (Pearson 1984). Of 29 species of the genus *Cicindela* (s. l.) in Australia, two species, *C. mastersi* Castelnau and *C. semicineta* Brullé, occur over several habitat types (Freitag 1979).

#### Biological Patterns Correlated with Other Taxa

The number of species of birds, butterflies, and tiger beetles found within each square are indicated on the respective grids (Figs. 2, 3, 4, 5). Isoclines connecting squares of similar tiger beetle species numbers on the gridded maps for North America (Fig. 6), the Indian subcontinent (Fig. 7), and Australia (Fig. 8) emphasize areas of high and low species richness (Myers 1990).

Correlations by grid squares within each continental area resulted in a significant ( $p < 0.01$ ) relation between tiger beetle and breeding bird species numbers in North America, the Indian subcontinent, and Australia (Fig. 9). For North America and Australia the correlations between tiger beetle and butterfly species numbers (Fig. 10) as well as between butterfly and bird species numbers (Fig. 11) were also all significant ( $p < 0.01$ ).

#### Potential Economic Importance

There is a growing interest in these natural predators as controls of certain crop pests (Hudson et al. 1988, Pearson 1988). Preliminary studies in India and Perú indicate that some species common in rice paddies may prove to be effective controls of rice pests (A. Marmol of the Universidad Nacional de la Amazonia Peruana, Iquitos; and G. K. Veeresh of the University of Agricultural Sciences, Bangalore, personal communication).

#### Discussion

Insects as models or indicators for conservation biology have many advantages over other taxa (Rosenberg et al. 1986; Wilson 1988; Forney & Gilpin 1989; Samways 1989; Viejo et al. 1989; Lockwood & DeBrey 1990). Because of their well-known biology and systematics and their aesthetic qualities, butterflies have served as the most widely-used insect group for conservation studies (Pyle et al. 1981; Collins & Morris 1985; Brown 1991; Thomas 1991). To answer some questions, however, alternative insect taxa such as tiger beetles may be more appropriate.

Our study indicates that even with increasing quantification and analysis of criteria, an indicator taxon is

**Table 4.** Analysis of critical tiger beetle faunas of the world (after Collins and Morris 1985). A = country (total number of species); B = number of endemic species; C = nonendemic species not occurring in previous countries; D = newly accountable species; E = cumulative species number.

A	B	C	D	E
1. Madagascar (176)	174	2	176	176
2. Indonesia (217)	103	114	217	393
3. Brazil (184)	97	87	184	577
4. India (193)	82	88	170	747
5. Philippines (94)	74	2	76	823
6. Australia (81)	72	4	76	899
7. Mexico (116)	57	58	115	1014
8. U.S.A. (111)	45	24	69	1083
9. Papua New Guinea (72)	45	1	46	1129
10. South Africa (94)	40	52	92	1221
11. Sri Lanka (55)	32	0	32	1253
12. Zaire (134)	27	90	117	1370
13. Vietnam (93)	25	29	54	1424
14. Angola (69)	23	8	31	1455
15. Malaysia (95)	22	3	25	1480
16. Bolivia (86)	21	21	42	1522
17. Thailand (102)	20	15	35	1557
18. Ecuador (74)	19	19	38	1595
19. China (94)	16	31	47	1642
20. New Caledonia (17)	16	0	16	1658
21. Perú (79)	14	1	15	1673
22. New Zealand (14)	14	0	14	1687
23. Somalia (31)	12	11	23	1710
24. Burma (Myanmar) (93)	12	2	14	1724
25. Argentina (64)	11	8	19	1743
26. Solomon Islands (20)	11	0	11	1754
27. Kenya (53)	9	7	16	1770
28. Taiwan (26)	9	2	11	1781
29. Venezuela (51)	8	12	20	1801
30. Tanzania (68)	8	11	19	1820
31. Ethiopia (51)	8	4	12	1832
32. Mozambique (47)	7	9	16	1848
33. Colombia (42)	7	1	8	1856
34. Iran (30)	5	17	22	1878
35. Cameroon (43)	5	6	11	1889
36. Guyanas (29)	5	0	5	1894
37. U.S.S.R. (C.I.S.) (49)	4	10	14	1908
38. Panamá (28)	4	4	8	1916
39. Turkey (25)	4	4	8	1924
40. Zimbabwe (53)	4	2	6	1930
41. Cuba (11)	4	2	6	1936
42. Japan (22)	4	1	5	1941
43. Nepal (64)	4	0	4	1945
44. Morocco (14)	3	4	7	1952
45. Central African Republic (46)	3	2	5	1957
46. Laos (59)	3	0	3	1960
47. Paraguay (38)	3	0	3	1963
48. Hispaniola (9)	3	0	3	1966
49. Réunion Island (4)	3	0	3	1969
50. Namibia (31)	2	3	5	1974
51. Zambia (53)	2	0	2	1976
52. Bangladesh (53)	2	0	2	1978
53. Mongolia (23)	2	0	2	1980
54. Mauritius Island (3)	2	0	2	1982
55. Costa Rica (38)	1	8	9	1991
56. Ivory Coast (21)	1	2	3	1994
57. Italy (17)	1	2	3	1997
58. Spain (16)	1	2	3	2000
59. Algeria (15)	1	2	3	2003

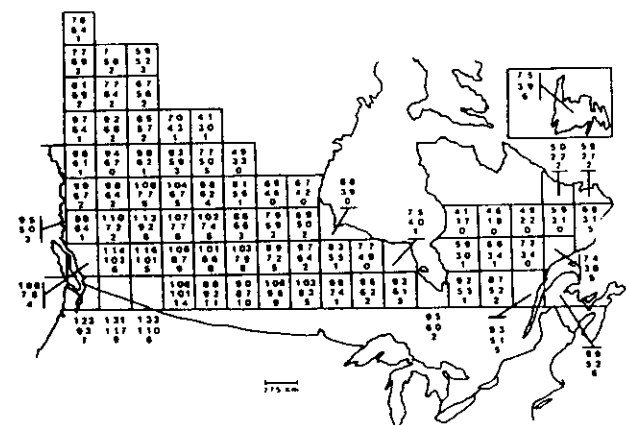
**Table 4.** Continued.

A	B	C	D	E
60. Togo (24)	1	1	2	2005
61. Tunisia (14)	1	1	2	2007
62. Fiji (2)	1	1	2	2009
63. Pakistan (33)	1	0	1	2010
64. Guatemala (23)	1	0	1	2011
65. Botswana (27)	1	0	1	2012
66. Mali (16)	1	0	1	2013
67. El Salvador (17)	1	0	1	2014
68. Yemen (10)	1	0	1	2015
69. Honduras (7)	1	0	1	2016
70. Chile (6)	1	0	1	2017
71. Lybia (6)	1	0	1	2018
72. Trinidad & Tobago (4)	1	0	1	2019
73. Western Samoa (2)	1	0	1	2020
74. Guinea-Bissau (34)	0	3	3	2023
75. Uganda (33)	0	1	1	2024

Four species of unknown origin (*Odontocheila iodopleuroides* Mandl, *Langea fleutiauxi* W. Horn, *Trichotaenia africana* Cassola, and *Cicindela javeti* Chaudoir) are not included in this table.

ultimately selected on the basis of compromise. For instance, compared to the numbers of butterfly and bird species per grid square, the small numbers of tiger beetle species is likely to result in some loss of detail in constructing patterns of species richness, especially at higher latitudes. Also, in the correlations between tiger beetle, butterfly, and bird species, the comparisons using butterflies did not reach an asymptote as rapidly as those using tiger beetles. On the basis of these two criteria, butterflies could logically be judged a more appropriate indicator taxon.

At the Tambopata site in Madre de Dios, Perú, however, it took less than 50 hours of observation to find 93% of the tiger beetle fauna (29 species). In the same area, it took nearly a thousand hours of work to find



**Figure 2.** Total number of breeding (nonmarine, nonaquatic) bird (top number), butterfly (middle number), and tiger beetle species (bottom number) occurring within each square (275 km per side) on a grid across northern North America.

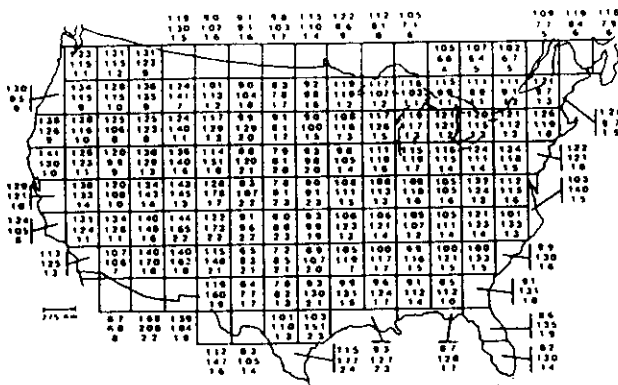


Figure 3. Total number of breeding (nonmarine, nonaquatic) bird (top number), butterfly (middle number), and tiger beetle species (bottom number) occurring within each square (275 km per side) on a grid across southern North America.

90% of the butterfly species (over 1200 species and still rising significantly with subsequent visits, even after more than ten years of collecting) (Lamas 1981, 1983). Even when the focus of the survey was narrowed to families within the order of Lepidoptera at Tambopata (Lamas 1984), the time to find a significant percent of the fauna was extensive. Likewise, the bird list of more than 560 species for this area is one that necessitated at least several years of work in different seasons of the year to approach 90% (T. A. Parker, III, personal communication). In terms of risk analysis, when time limits

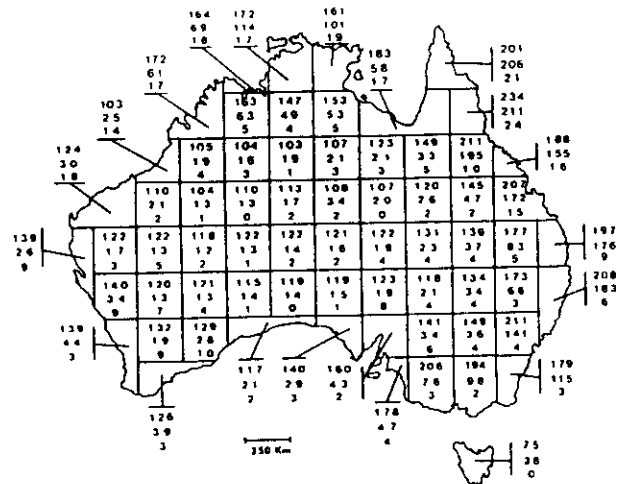


Figure 5. Total number of breeding (nonmarine, nonaquatic) bird (top number), butterfly (middle number), and tiger beetle species (bottom number) occurring within each square (350 km per side) on a grid across Australia.

are severe the advantages of working with tiger beetles offset the disadvantages.

In addition, the habitat specialization of these tiger beetle species and their presence in the predator trophic level make it likely that they are highly susceptible to habitat changes. Paradoxically, this specialization also makes possible the survival of viable populations in remnant patches of undisturbed habitat. Species

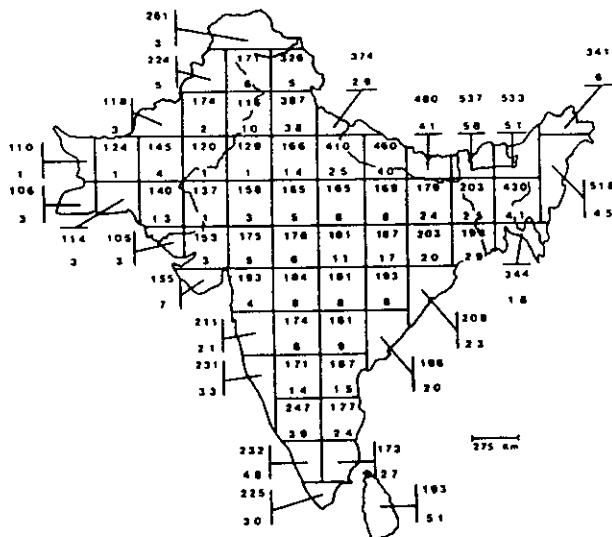


Figure 4. Total number of breeding (nonmarine, nonaquatic) bird (top number) and tiger beetle species (bottom number) occurring within each square (275 km per side) on a grid across the Indian subcontinent.

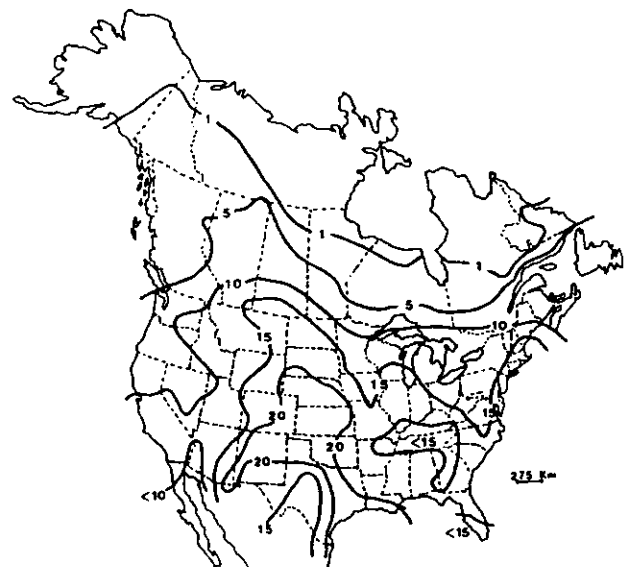


Figure 6. Isoclines connecting approximate centers of squares with similar numbers of tiger beetle species in North America.



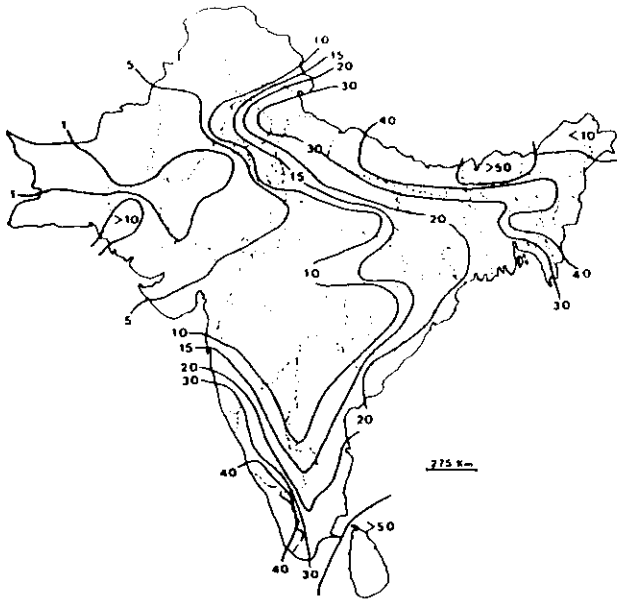


Figure 7. Isoclines connecting approximate centers of squares with similar numbers of tiger beetle species on the Indian subcontinent.

in west Texas, U.S.A. (Gage 1988), along the northeastern seaboard of the United States (Knisley et al. 1987), and in Italy (Cassola 1972) occur in areas of undisturbed remnant habitat as small as a few hectares. In many parts of Amazonia, in which only small patches of original forest remain, many bird (Bierregaard & Lovejoy 1989) and butterfly (Lovejoy et al. 1984) species are no longer able to maintain viable populations. Insects like tiger beetles are likely to maintain viable popula-

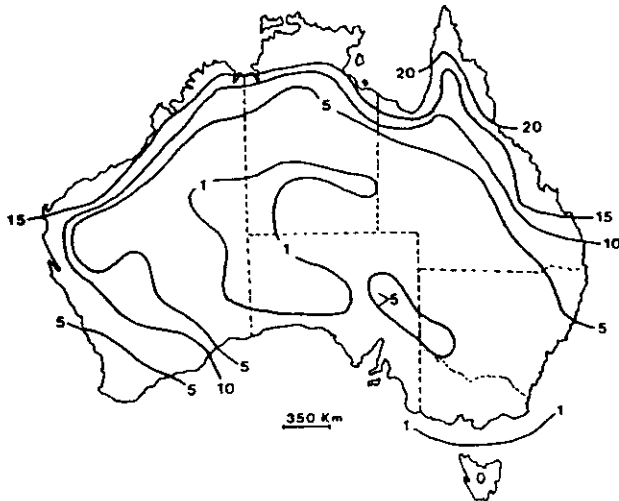


Figure 8. Isoclines connecting approximate centers of squares with similar numbers of tiger beetle species in Australia.

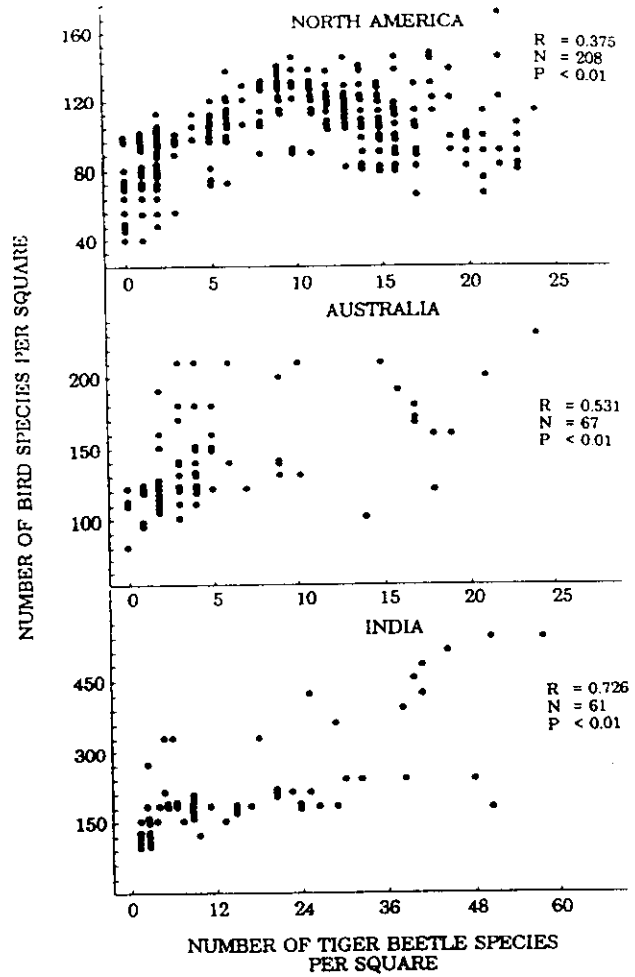


Figure 9. Correlation between the number of tiger beetle and bird species per square on grids across North America, Australia, and the Indian subcontinent.

tions in much smaller patches of remnant forests. They lend themselves as an indicator taxon for studies undertaken to understand the general distribution and dynamics of recent historical distribution in the face of the disappearance of a large proportion of habitat and populations (Murphy et al. 1990).

Apart from regional studies of biodiversity, tiger beetles may also be of use as an indicator taxon for studies of unique and threatened habitats. Because of extensive historical collections and records that document the presence and decline of many species associated with changes in habitat and human impact (Nagano 1982; Desender & Turin 1989), studies of tiger beetles may function significantly in at least two ways to enhance this area of conservation biology. First, the U.S. Fish and Wildlife Service is considering several endemic species of tiger beetles in Florida, Maryland, Texas, and Idaho as

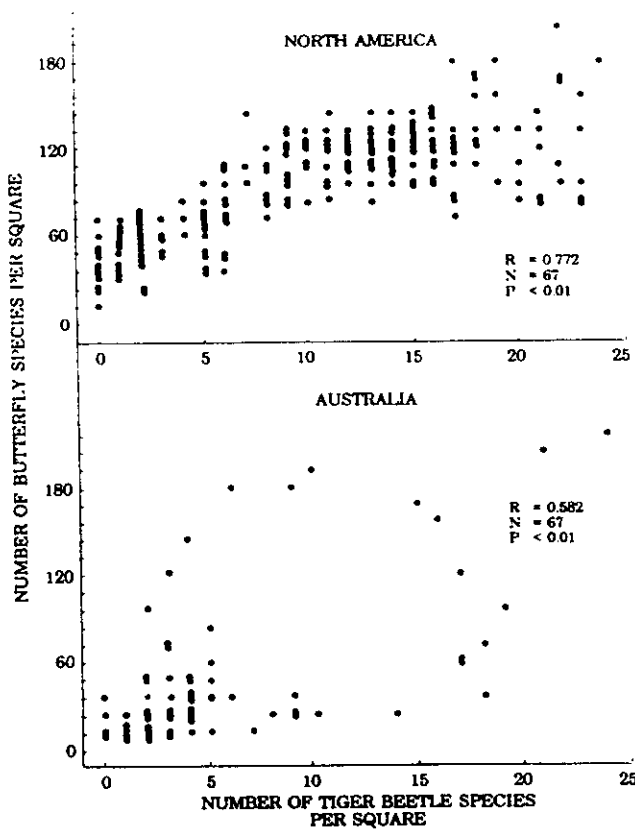


Figure 10. Correlation between the number of tiger beetle and butterfly species per square on grids across North America and Australia.

endangered species and has already declared two species, *C. dorsalis dorsalis* Say and *C. puritana* G. Horn, as threatened (Federal Register 1990). This status will in turn bring protection to other invertebrate and vertebrate species associated with the habitats of these endemic tiger beetles.

Second, several groups of insects have been used to document long term (20–100 years) changes in habitats (Turin & den Boer 1988; van Swazay 1990; Dennis & Shreeve 1991). In many areas the uncomplicated monitoring of common tiger beetle species over long periods makes them a useful indicator of the disappearance of species, which can in turn be associated with human impact and the rate of habitat degradation (Wilson 1970; Cassola 1974, 1983; Knisley 1979; Shook 1981; Nagano 1982; Schultz 1988; Tanner 1988; Desender & Turin 1989).

It is in evaluations of biodiversity, however, that tiger beetles reach some of their highest potential as an indicator taxon. Politicians and scientists largely agree that priority areas for conservation must be identified, especially in tropical forests, if preservation and rational economic use of many areas throughout the world are to be accomplished (Vane-Wright et al. 1991). Recently in

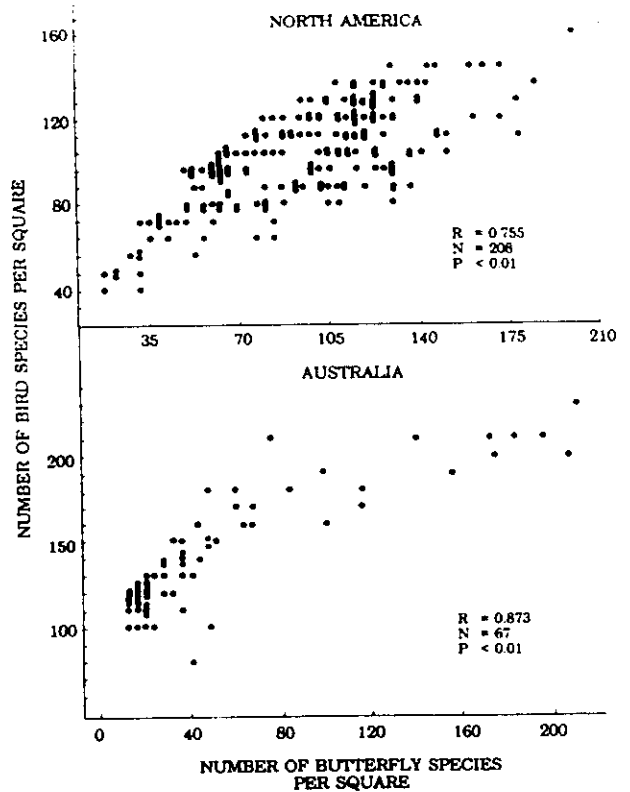


Figure 11. Correlation between the number of butterfly and bird species per square on grids across North America and Australia.

Manaus, Brazil, a meeting of many of the active biological researchers in the Amazon sought to establish the relatively simple distribution of pockets of high and low species numbers for various plant and animal taxa across the basin. Using these data, an initial list of priority areas for conservation could be established, with those areas exhibiting high species numbers across many taxa of the highest priority. Some accord was reached (Kuliopulos 1990), but for most taxa, high diversity was often associated with the presence of a biological field station. It is unclear whether many of the intervening areas with relatively low species numbers actually had few species or were simply understudied.

To determine valid patterns of species richness for taxa such as birds or butterflies across the Amazon Basin would take decades. Tiger beetles, on the other hand, could yield such patterns in five years (Pearson 1992). Applying the quadrate squares, 275 km per side, used for North America and the Indian subcontinent, one or two intensive collections within each of about 70 squares would be the minimum effort needed (McKenzie et al. 1989; Owen & Owen 1990). These patterns of species richness together with phylogenetic (Wiley 1981), biogeographical (Haffer 1969; Endler 1977; Cracraft 1986), and ecological studies (Holloway & Jar-

dine 1968; Pearson 1986; Brown 1988) could then be used to distinguish historical centers of evolution and speciation as the highest priority for conservation (Erwin 1991) in a relatively short time.

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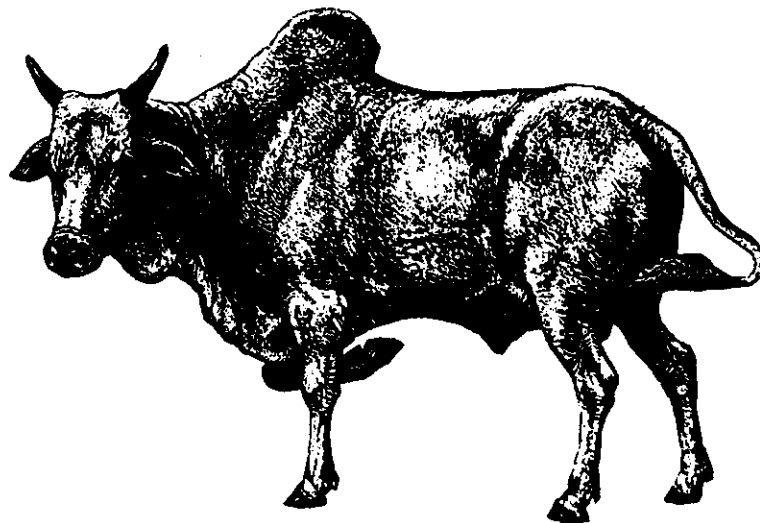
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# A TEST FOR THE ADEQUACY OF BIOINDICATOR TAXA: ARE TIGER BEETLES (COLEOPTERA: CICINDELIDAE) APPROPRIATE INDICATORS FOR MONITORING THE DEGRADATION OF TROPICAL FORESTS IN VENEZUELA?

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## Abstract

Indicator species can be a valuable tool for conservation research. Their use has been divided in two categories: inventory studies and monitoring studies. Tiger beetles (Coleoptera: Cicindelidae) have been identified as appropriate indicators for inventory studies. Here we test their value as potential bioindicators for monitoring habitat degradation in Venezuela. We analyze the general habitat associations of 47 of the 51 species of this insect family known to occur in Venezuela. We also analyze the assemblage patterns of forest-floor dwelling species associated with contiguous forest patches of primary and secondary forest in two sites. At the family level, tiger beetles occupy most of the major habitat types of Venezuela, but individual species tend to be restricted to one or two habitats. Forest-floor species assemblages change significantly with the degree of forest disturbance, and each stage of disturbance is characterized by a particular subset of species. Species associated with intermediate levels of disturbance show larger habitat breadth than those located at the extremes of the spectrum. The results of this study provide evidence that supports the use of tiger beetles as bioindicators for monitoring the degradation and regeneration of tropical forests. © 1997 Elsevier Science Ltd

**Keywords:** Bioindicators, Cicindelidae, Coleoptera, habitat quality, tiger beetles, tropical forests, Venezuela.

## INTRODUCTION

The potential use of indicator species for conservation research can be divided in two basic categories (Kremen *et al.*, 1993; Pearson, 1994). First, *monitoring studies*

evaluate changes in habitats or ecosystems over time, such as successional stage or habitat degeneration. In this context, the choice of an indicator will be served best by a taxon that is sensitive to environmental change. On the other hand, *inventory studies* record distributional patterns of taxa or ecological units over geographical space, often with the purpose of identifying areas for establishing nature reserves. Here, the choice of indicators should favor taxa whose distribution or abundance correlate, for example, with areas of high endemism or high species diversity (Erwin, 1991).

However, the vast majority of studies that rely on bioindicators have used taxa with little or no initial assessment of their adequacy as indicators. Many of these studies have focused on taxa that are either of high public concern (such as endangered species) or have been coincidentally the object of previous studies by the scientists intending to use indicators (Pearson, 1994).

For this reason, a series of criteria has been proposed for the objective selection of an indicator taxon (Noss, 1990; Pearson & Cassola, 1992; Pearson, 1994). These criteria are:

1. taxonomically well known and stable, so that populations can be readily defined;
2. biology and natural history well understood — limiting resources, enemies, physical tolerances, and all stages of the life cycle available to readily incorporate into hypotheses and experimental design;
3. populations readily surveyed and manipulated such that tests are logistically simple and inexperienced students and non-professionals can be trained easily to help conduct studies;
4. at higher taxonomic levels (order, family, tribe, genus), occurrence over a broad geographic range and breadth of habitat types, so that results will be broadly applicable;

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5. at lower taxonomic levels (species, subspecies), specialization of each population within a narrow habitat is likely to make them sensitive to habitat change;
6. some evidence that patterns observed in the indicator taxon are reflected in other related and unrelated taxa; and
7. potential economic importance.

On a global scale, tiger beetles (Coleoptera: Cicindelidae) meet most of these criteria. Their taxonomy is stable, with a level of synonymy in current revisions of around 2.4% (Pearson & Cassola, 1992). Their biology and life history have been the object of numerous studies (Larochele, 1980a,b; Pearson, 1988). In tropical forest sites, it takes approximately 4 h to train an inexperienced student or assistant to find at least 90% of the species present (Pearson & Cassola, 1992). They have a worldwide distribution (except Tasmania, Antarctica and some remote oceanic islands) which covers a variety of habitats ranging from alpine meadows to desert grasslands and tropical rain forests (Pearson, 1988; Pearson *et al.*, 1988). Each species rarely occurs in more than one or a very few habitat types (Pearson, 1984; Knisley & Pearson, 1984; Acciavatti & Pearson, 1989). The number of species of tiger beetles is often correlated with that of other groups (Pearson & Cassola, 1992), and there is a growing interest in these natural predators as controls of certain crop pests (Hudson *et al.*, 1988).

In this paper we aim to examine whether tiger beetles — promising as bioindicators on a global scale — are useful for monitoring habitat degradation on the more local scale of tropical forests in Venezuela. Since the tiger beetle fauna of Venezuela occupies a relatively complex array of habitats and biogeographical regions, any procedural and biological generalizations we establish here should also have applications in other parts of the world.

The tiger beetles of Venezuela are already known to meet the first three criteria listed above: their taxonomy and natural history are well-known and their populations are readily easy to study (Rodríguez *et al.*, 1994). In this paper we will establish whether they meet the fourth and fifth criteria of the list: do they occupy most habitat types as a family, and are they habitat specialists at the species level?

## METHODS

### Habitat specificity

We built a database of tiger beetle collection records in Venezuela. Specimens are held in the museums of the Instituto de Zoología Agrícola (Universidad Central de Venezuela — MIZA), the Museo de Biología UCV (Universidad Central de Venezuela), the Museo de Biología LUZ (La Universidad del Zulia), and the private

collections of J. M. Ayala, C. Bordón, D. W. Brzoska, F. Cassola, J. Camacho, Ronald L. Huber, J. Hutchings, M. Kriz, M. Quiroz, the Romero Family, C. J. Rosales, W. D. Sumlin III, J. Wiesner and K. Werner. For each specimen, we recorded the species, date and location of collection.

To simplify the procedure for future use by non-specialists and to stabilize replication using other potential bioindicator taxa, habitat types were assumed equivalent to previously established major vegetation types. Therefore, we followed Huber and Alarcon's (1988) Map of the Vegetation of Venezuela, which classifies the plant communities of the country into 12 major groups: coastal vegetation (CO), savannas (SA), shrubs and bushes (SB), spiny forests (SF), deciduous forests (DF), semi-deciduous forests (SDF), evergreen forests (EF), riparian forests (RF), cloud forests (CF), páramo vegetation (PV), tepui vegetation (TV), and disturbed habitat (DH). We used this last category to include habitats that have been degraded as a consequence of human activities and cannot be assigned to one of the previous vegetation types. It also is a convenient category for all agricultural lands (which have been the object of many insect collections).

Each of the sites from which tiger beetles had been recorded was located on Huber and Alarcon's (1988) map, and the corresponding habitat type was determined. This procedure allowed us to build a frequency distribution of specimens of each species across the 12 major habitat types of the country. Microhabitat descriptions, such as "sandy river beach", would undoubtedly have more accurately described habitat use by some tiger beetle species; however, we felt this would undermine our aim of developing a system appropriate for non-specialists, using existing habitat maps and label data.

To quantify the degree of habitat specificity for each species, we adapted Bulla's (1994) diversity index as measure of habitat breadth ( $H$ ). We used data on the relative frequency of each species in each habitat type (Table 1) to calculate  $H$ , consequently expressing habitat breadth in terms of utilization of the available habitat spectrum. Species restricted to one habitat type have minimum habitat breadth, and are thus characterized by a value of  $H$  equal to zero. If a species is evenly distributed across all habitat types,  $H$  would be equal to the total number of habitats.

### Indicators of habitat quality in tropical forests

#### Study sites

Two study sites were selected to evaluate the use of tiger beetles as indicators of habitat quality in tropical forests:

1. The Imataca Forest Reserve (2,873,250 ha), is located in the northeastern portion of Bolívar state and contiguous areas in Delta Amacuro (06°00'–



Table 1. Relative abundances (%) and habitat breadth (*H*) of the tiger beetles of Venezuela across the major habitat types of the country

Species	n	Vegetation types										Habitat Breadth
		CO	SA	SB	SF	DF	SDF	EF	RF	CF	DH	
<i>Ctenostoma brevicorne</i>	16	—	—	—	—	6.2	—	—	—	93.8	—	0.70
<i>Ctenostoma ebeninum</i>	2	—	—	—	—	—	50.0	—	50.0	—	—	1.11
<i>Ctenostoma succinctum</i>	6	—	—	—	—	16.7	—	33.3	—	50.0	—	2.22
<i>Ctenostoma chaudiiri</i>	1	—	—	100.0	—	—	—	—	—	—	—	0.00
<i>Ctenostoma metallicum</i>	33	—	—	3.0	—	3.0	—	3.0	—	91.0	—	1.00
<i>Aniara sepulchralis</i>	49	4.1	8.1	—	—	4.1	24.5	24.5	—	—	34.7	4.04
<i>Megacephala (Phaeoxantha) aequinoctialis</i>	42	—	—	—	—	—	9.5	21.5	69.0	—	—	2.17
<i>Megacephala (Phaeoxantha) klugi</i>	64	—	—	—	—	—	—	—	100.0	—	—	0.00
<i>Megacephala (Tetracha) affinis</i>	307	0.6	2.9	2.3	—	16.0	8.5	8.1	14.6	2.0	45.0	4.94
<i>Megacephala (Tetracha) sp. A</i>	12	—	—	25.0	8.3	8.3	—	8.3	8.3	—	41.8	4.80
<i>Megacephala (Tetracha) ensenada</i>	5	60.0	—	—	40.0	—	—	—	—	—	—	1.11
<i>Megacephala (Tetracha) angusticollis</i>	4	—	—	—	—	—	—	—	75.0	—	25.0	1.11
<i>Megacephala (Tetracha) fulgida</i>	154	11.8	0.6	—	—	0.6	52.6	—	4.5	—	29.9	2.86
<i>Megacephala (Tetracha) klagesi</i>	4	—	—	—	—	—	—	25.0	75.0	—	—	1.11
<i>Megacephala (Tetracha) lucordairei</i>	248	—	1.7	—	0.4	5.2	2.8	3.2	5.7	0.8	80.2	2.18
<i>Megacephala (Tetracha) sobrina</i>	356	58.4	2.2	—	1.2	4.2	6.8	1.4	25.0	—	0.8	2.93
<i>Oxycheila chestertoni</i>	12	—	—	—	—	—	—	50.0	—	—	50.0	1.11
<i>Pseudoxycheila bipustulata</i>	206	—	—	—	—	—	0.5	22.8	1.0	74.7	1.0	1.39
<i>Cheiloxia binotata</i>	3	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Iresia mniszehi</i>	1	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Iresia surinamensis</i>	1	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Iresia sp. n. 1</i>	1	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Iresia sp. n. 2</i>	1	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Odontocheila cayennensis</i>	121	—	0.8	2.5	—	2.5	24.8	63.6	5.8	—	—	2.40
<i>Odontocheila margineguttata</i>	278	—	—	2.5	—	4.7	39.3	42.4	0.7	—	10.4	3.10
<i>Odontocheila ignita</i>	1	—	—	—	—	—	100.0	—	—	—	—	0.00
<i>Odontocheila chrysis</i>	10	—	—	—	—	—	70.0	20.0	10.0	—	—	2.22
<i>Odontocheila angulipennis</i>	17	—	—	—	—	—	17.6	76.5	5.9	—	—	1.77
<i>Odontocheila luridipes</i>	2	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Odontocheila confusa</i>	3	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Odontocheila scapularis</i>	4	—	—	—	—	—	—	25.0	75.0	—	—	1.11
<i>Pentacomia (Pentacomia) egregia</i>	1	—	—	—	—	—	—	100.0	—	—	—	0.00
<i>Pentacomia (Mesochila) discrepans</i>	2	—	—	—	—	—	100.0	—	—	—	—	0.00
<i>Pentacomia (Poecilochila) lacordairei</i>	31	—	—	3.2	—	6.5	38.7	48.4	3.2	—	—	2.54
<i>Pentacomia (Poecilochila) ventralis</i>	59	—	1.7	—	—	—	5.1	1.7	47.4	1.7	42.4	2.24
<i>Cicindela (Cicindelidia) favergeri</i>	40	—	—	—	7.5	7.5	42.5	7.5	12.5	—	22.5	4.72
<i>Cicindela (Cicindelidia) trifasciata</i>	16	87.5	—	—	—	—	12.5	—	—	—	—	1.11
<i>Cicindela (Opilidia) graphiptera</i>	365	92.1	—	0.5	1.1	1.4	3.5	—	1.1	—	0.3	0.86
<i>Cicindela (Habrosclimorpha) auraria</i>	133	89.5	—	—	9.0	—	—	1.5	—	—	—	1.17
<i>Cicindela (Plectographa) suturalis</i>	96	2.1	8.3	—	—	—	7.3	33.3	42.8	1.0	5.2	3.77
<i>Cicindela (Brasiella) argentata</i>	75	—	2.7	1.3	—	2.7	25.3	54.7	13.3	—	—	2.97
<i>Cicindela (Brasiella) venustula</i>	573	0.7	5.2	0.9	—	39.3	25.3	5.4	8.2	0.5	14.5	4.55
<i>Cicindela (Brasiella) misella</i>	171	—	4.7	12.9	2.9	12.9	22.2	9.9	27.5	0.6	6.4	6.06
<i>Cicindela (Brasiella) nebulosa</i>	76	—	19.7	—	—	5.3	26.3	19.7	6.6	—	22.4	4.66
<i>Cicindela (Brasiella) wiesneri</i>	4	50.0	—	—	—	25.0	—	—	—	—	25.0	2.22
<i>Cicindela (Brasiella) venezuelensis</i>	1	—	—	—	—	—	100.0	—	—	—	—	0.00
<i>Cicindela (Brasiella) jolyi</i>	3	—	—	—	—	—	—	100.0	—	—	—	0.00
Total	3610	19.7	2.5	1.5	0.9	10.1	16.2	13.8	12.7	6.0	16.6	6.73

Species in bold face were also included in the field study, see Table 2.

n. Number of specimens, other abbreviations in the text.

08°28' N, 60°14'–62°29' W). Annual precipitation varies between 1560 and 2330 mm and mean annual temperature is 26°C. This reserve is currently under exploitation, mainly through selective logging of high-value species. Originally, the entire area was covered by evergreen tropical rainforest (Huber & Alarcón, 1988) but, as a consequence of exploitation, many areas have been disturbed. We conducted our study in three contrasting habitats: *primary forest* which represents the condition previous to exploitation, *disturbed forest* where most of the large trees have been removed and the remaining vegetation has been severely disturbed by the extraction process, and *semi-disturbed forest* which represents an intermediate point along the disturbance gradient.

- Guatopo National Park (122,464 ha) is located between Guárico and Miranda states, less than 50 km south of the city of Caracas (09°57'–10°14' N, 66°15'–66°43' W). It is characterized by an altitudinal gradient that affects the existing vegetation types: the northern section of the park is dominated by evergreen forests and the southern section has more deciduous and semi-deciduous vegetation (Huber & Alarcón, 1988). Annual precipitation varies from 1455 mm in the more humid areas to 1180 mm in the drier areas, while the mean annual temperature is close to 25°C throughout the park. In Guatopo, we also focused on three habitats. The first one is an evergreen forest located in the humid part of the park. The second habitat, located a few kilometers away from the first, has a similar topography but the vegetation had been logged and severely modified

by human settlements that existed prior to the time of the park's creation in 1958. The third habitat is located in the drier portion of the park and is dominated by deciduous vegetation. We designated these three habitats as *primary forest*, *secondary forest*, and *dry forest*, respectively.

#### Relative densities of tiger beetles

In each of the three selected habitats of the two study sites we located existing trails through the forest and established 300–500 m transects along them. These transects were surveyed between 09:00 h and 17:00 h, the time of day when adult tiger beetles show maximum activity (Pearson, 1988). Relative abundances were estimated by capturing individuals with sweep nets as they ran along the trail or flew to the nearby understory vegetation. A habitat was considered adequately surveyed when increasing the sampling effort did not result in the addition of new species. In accordance to previous studies in similar habitats (Pearson & Cassola, 1992), the minimum sampling effort was established at 300 person/minutes of effort.

Surveys were carried out between June and July 1991. Adult tiger beetle abundances are highly seasonal, and their populations respond quickly to the initiation of the rainy season (Pearson & Derr, 1986; Pearson, 1988; Rodriguez *et al.*, 1994). Visits to field sites were therefore designed to coincide with times of maximum activity and abundance. To verify the timing of field visits, tiger beetle abundances were monitored in Guatopo from March to July 1991. Adult tiger beetles were not seen until May and their abundance was highest approximately 1 month after the onset of the rainy season (Fig. 1).

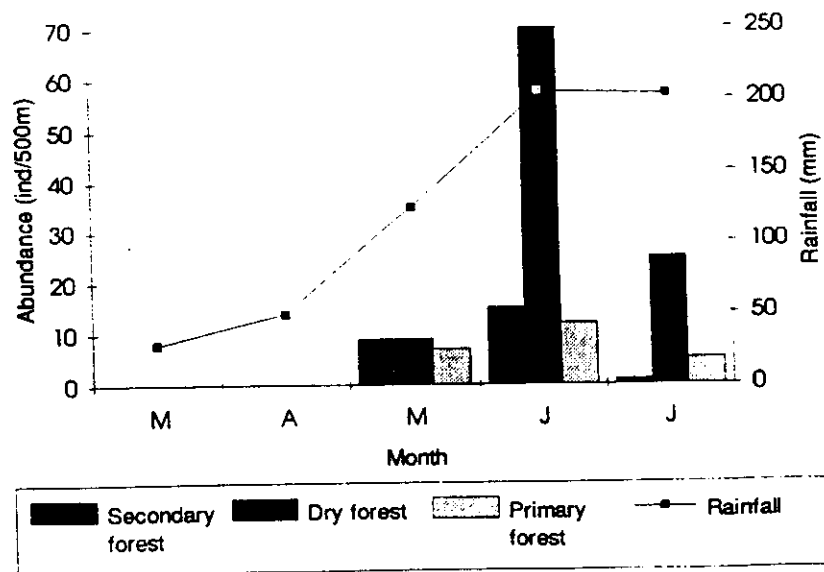


Fig. 1. Total monthly tiger beetle abundances (number of individuals per 500 m of trail) in the three habitat types of Guatopo (average monthly rainfall data was obtained from the Meteorological Service, Ministry of the Environment and Renewable Natural Resources, Caracas).

## RESULTS

**Habitat specificity**

Our review of entomological collections produced a database of 3610 specimens belonging to 47 species and collected over a period of almost 100 years. Although 51 species are known from Venezuela (Rodríguez *et al.*, 1994), it was not possible to obtain precise collection sites (and therefore habitat type) for four of these species, and they were, therefore, excluded from further analyses. Of the 12 habitat types considered, tiger beetles were found in all but two of them: *páramo* (high alpine) vegetation and *tepui* (table mountain) vegetation. Tiger beetles tend to be absent from habitats at extremely high latitudes and altitudes because their fossorial larvae cannot survive in soil that is too cold. Similarly, because the larvae must be able to move vertically in their tunnels to escape desiccation or temperature extremes (Hadley *et al.*, 1990), shallow soil substrates over impervious bed rock or frost-prone areas tend to have few or no tiger beetle species present (Pearson, 1988). In fact, the mean collection altitude of the specimens of all of the species recorded for Venezuela is below 2000 m (Rodríguez *et al.*, 1994). Therefore, their absence in the *páramos*, a habitat that occurs over 3500 m and is characterized by low mean annual temperature, is not unexpected. Their absence from *tepuis* (also known as table mountains) may be explained by generally shallow soils over bed rock that make impossible adequate movement of larvae to escape desiccation and temperature extremes.

Tiger beetle species were recorded in all of the remaining ten habitat types (Table 1), but not all habitats were equally species-rich: humid, warm forests (semi-deciduous forest, evergreen forest and riparian forest) contained more species than any other habitat type (Fig. 2). However, this could be partially a conse-

quence of the size of each habitat, as the number of species per habitat is correlated to its area ( $r=0.675$ ,  $R^2=0.455$ ,  $p<0.05$ ). At the species level, each species tends to concentrate in one or a few habitats (Fig. 3).

**Indicators of habitat quality in tropical forests**

Five species of tiger beetles were found in Imataca and two in Guatopo (Table 2); of these, *Odontocheila cayennensis* and *Pentacomia lacordairei* were restricted to primary forest, while *Pentacomia ventralis* was only found in disturbed forest. *Cicindela venustula* was absent from primary forest, and *Odontocheila marginoguttata* was present in all sampled habitats. In other words, each habitat type had a characteristic tiger beetle assemblage that differed in species present and species abundances. Prior to being disturbed, all forest types within each study site (except the dry forest in Guatopo) were equivalent (Huber & Alarcón, 1988). Therefore, the differences in species composition is associated with disturbance level.

In Imataca (Fig. 4), primary forests are characterized by the presence of *O. cayennensis*, *P. lacordairei* and *O. marginoguttata*, in relatively equal abundance. Following a disturbance, *O. cayennensis* and *P. lacordairei* disappear, while *C. venustula* is added to the species assemblage. As the degree of disturbance increases, the density of *O. marginoguttata* decreases, and *P. ventralis* appears. Although Fig. 4 provides only qualitative evidence, these results are in accordance with studies in other South American countries in which these species also occur (Pearson 1984; Pearson & Huber 1995; Nuñez *et al.*, 1994). A similar pattern was also observed in Guatopo (Table 2); *O. cayennensis* was present only in primary forest.

Interestingly, species at both ends of the disturbance spectrum have smaller habitat breadths than those in intermediate positions (Fig. 5). In ecological communities

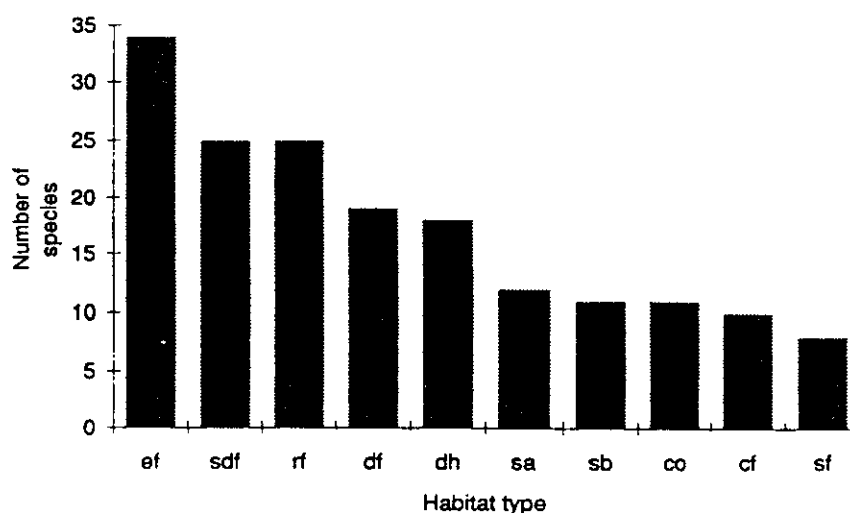


Fig. 2. Number of species of tiger beetles registered in each of the major habitat types of Venezuela (ef, evergreen forests; sdf, semi-deciduous forests; rf, riparian forests; df, deciduous forests; dh, disturbed habitat; sa, savannas; sb, shrubs and bushes; co, coastal vegetation; cf, cloud forests; sf, spiny forests).

Table 2. Tiger beetle abundances (number of individuals/500 m of trail) in each of the sampled habitats

Species	Habitat (forest type)					
	Imataca			Guatopo		
	Primary	Semi-disturbed	Disturbed	Primary	Secondary	Dry
<i>Cicindela venustula</i> <sup>a</sup>	0	19	11	—	—	—
<i>Odontocheila margineguttata</i>	17	13	4	29	24	61
<i>Odontocheila cayennensis</i>	11	0	0	11	0	0
<i>Pentacomia lacordairei</i> <sup>a</sup>	12	0	0	—	—	—
<i>Pentacomia ventralis</i> <sup>a</sup>	0	0	1	—	—	—

$\chi^2$  test,  $p < 0.05$ .

<sup>a</sup>Species collected only in Imataca.

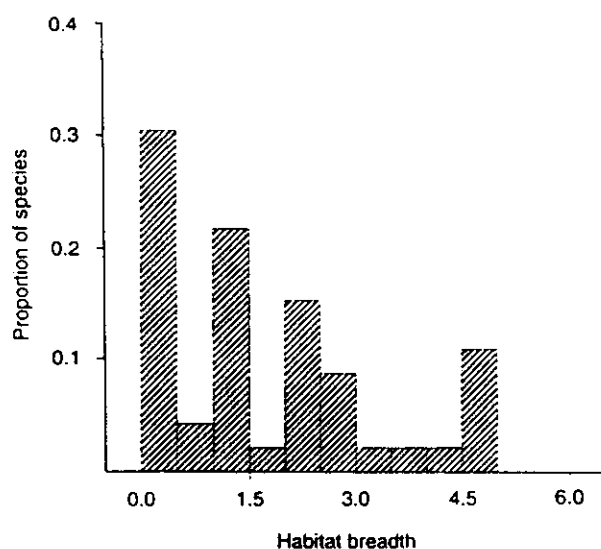


Fig. 3. Distribution of habitat breadths (from Table 1) for the tiger beetles of Venezuela.

that are periodically perturbed, diversity is often higher at intermediate levels of disturbance (Connell, 1978). Therefore, it is not surprising that the species we found associated with intermediate disturbance, have larger habitat breadths. Species of primary and highly disturbed habitat may have evolved adaptations to their narrower microclimatic conditions.

## DISCUSSION

Historically, studies with indicator taxa have focused primarily on vertebrates. However, their relatively long generation times, low population growth rates and comparatively low habitat specificity, make them sub-optimal (though certainly charismatic) indicator species (Pyle *et al.*, 1981; Rosenberg *et al.*, 1986; Murphy & Weiss, 1988; Samways, 1989, 1990a,b; Kremen, 1992, 1994). Insects suffer none of these drawbacks, and have therefore received increased recent attention as possible indicators. The family of tiger beetles (Cicindelidae) has been identified as one of the better indicators for

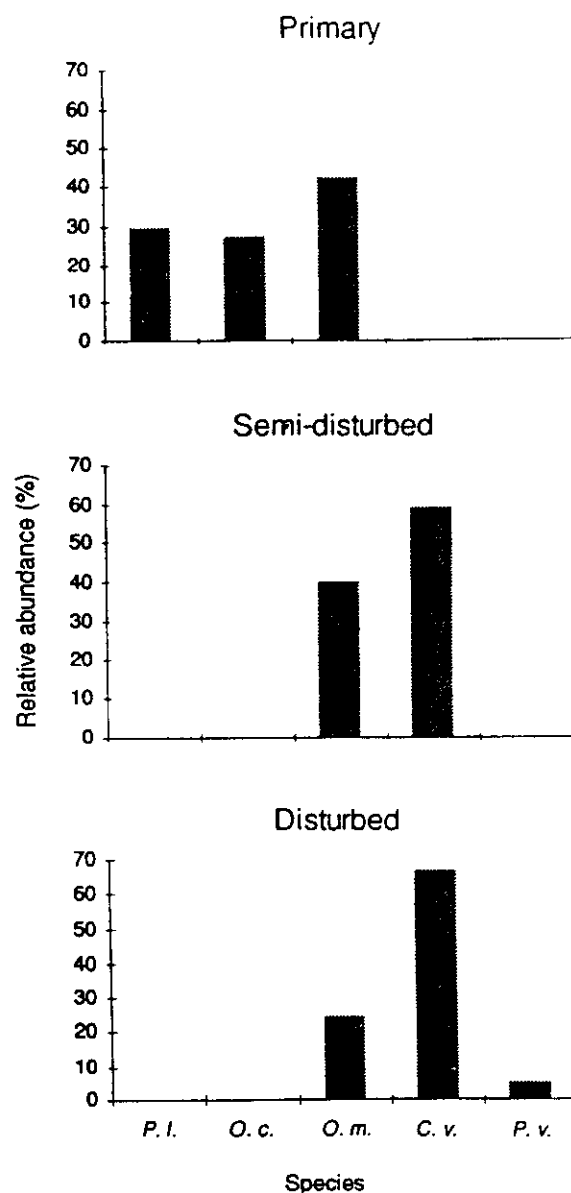


Fig. 4. Replacement sequence of tiger beetle species along the analyzed tropical forest disturbance gradient (P.l., *Pentacomia lacordairei*; O.c., *Odontocheila cayennensis*; O.m., *Odontocheila margineguttata*; C.v., *Cicindela venustula*; P.v., *Pentacomia ventralis*).

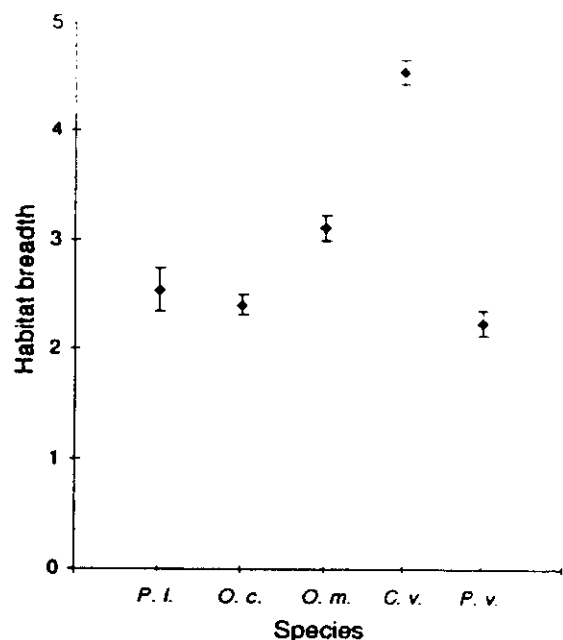


Fig. 5. Habitat breadths for the tiger beetle species on which the field study was focused (from Table 1). The vertical lines indicate a 95% confidence interval for the diversity index (abbreviations are the same as in Fig. 4).

inventory studies (Pearson & Cassola, 1992; Pearson, 1994), and has been proposed as a candidate for the identification of areas of conservation concern in Amazonia (Pearson, 1992).

Our study suggests that tiger beetles are appropriate indicators for monitoring studies as well. Although we relied heavily on museum collections and based our conclusions on data gathered over a long period, by a large number of collectors, and employing a great variety of collecting techniques, our results unambiguously indicate that tiger beetles have a broad range of habitat types. At the same time, our data reveal characteristic habitat specialization at the species level (Table 1). At a finer scale, represented by our analysis of relative abundance of ground-dwelling species in tropical forests, the pattern also holds (Table 2, Fig. 4). More importantly, the results of both field and museum specimen data analysis are consistent. Species that occur in humid forest types according to the museum collection sites were located in our field studies only in undisturbed forest habitats (e.g. *O. cayennensis* and *P. lacordairei*). Those species that were more widespread according to museum data also occupied a larger number of habitats in the field studies (e.g. *C. venustula* and *O. marginoguttata*).

Field studies of tiger beetle species throughout the world show consistent habitat specialization (Pearson, 1988; Acciavatti & Pearson, 1989; Pearson & Juliano, 1991). The reason for this pattern of narrow habitat use is most likely due to physiological adaptations of the larvae and limited dispersal capacity of the adults (Mury Meyer, 1987; Knisley & Juliano, 1988; Hadley et

al., 1990; Shivashankar & Pearson, 1994). Larval stages occur in a narrower range of microhabitats than adults, and appear to tolerate less variation of many physical factors, especially soil moisture, soil composition and temperature (Shelford, 1908, 1912; Knisley & Pearson, 1981; Hori, 1982; Knisley, 1984, 1987). Female choice of oviposition site contributes to habitat specialization as well, as it is highly specific to soil type (Willis, 1967; Knisley, 1987).

Among the consequences of habitat conversion from closed canopy to secondary and agricultural forests is the change in microclimatic conditions (Murcia, 1995). In particular, soil humidity decreases and air temperature increases (Lovejoy et al., 1986; Murcia, 1995). Tiger beetle larvae are sensitive to these changes; during hot, dry periods, larval tiger beetles plug their burrows and become inactive (Willis, 1967; Knisley, 1987). If soil desiccation reaches extreme levels, larvae leave their burrows and relocate (Shelford, 1908). Our observed changes in species assemblages and abundances most likely reflect these changes in microclimatic conditions as disturbance increases. Future studies of tiger beetles as monitoring indicators, therefore, should focus on the precise determination of the ecological correlates of larval survival for each species involved.

#### ACKNOWLEDGEMENTS

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## FLAGSHIPS, UMBRELLAS, AND KEYSTONES: IS SINGLE-SPECIES MANAGEMENT PASSÉ IN THE LANDSCAPE ERA?

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### Abstract

*Because it is so difficult to monitor and manage every aspect of biodiversity, several shortcuts have been proposed whereby we monitor and/or protect single species. The indicator species concept is problematic because there is no consensus on what the indicator is supposed to indicate and because it is difficult to know which is the best indicator species even when we agree on what it should indicate. The umbrella species (a species that needs such large tracts of habitat that saving it will automatically save many other species) seems like a better approach, although often whether many other species will really fall under the umbrella is a matter of faith rather than research. Intensive management of an indicator or an umbrella species (for example, by transplant or supplemental feeding) is a contradiction in terms because the rest of the community to be indicated or protected does not receive such treatment. A flagship species, normally a charismatic large vertebrate, is one that can be used to anchor a conservation campaign because it arouses public interest and sympathy, but a flagship need not be a good indicator or umbrella. And conservation of flagship species is often very expensive. Further, management regimes of two flagship species can conflict. Ecosystem management, often on a landscape scale, is a proposed solution to problems of single-species management. Keep the ecosystem healthy, according to this view, and component species will all thrive. However, conservationists have concerns about ecosystem management. First, it is variously defined, and many definitions emphasize the commodities ecosystems provide for humans rather than how humans can protect ecosystems. Second, the term 'ecosystem health' is ill-defined and associated with an outmoded, superorganismic view of the ecosystem. Third, ecosystem management seems focused on processes and so would appear to permit losses of species so long as they did not greatly affect processes like nutrient-cycling. Fourth, ecosystem management is often implemented by adaptive management. This may make it difficult to study the underlying mechanisms driving an ecosystem and to know when an entirely new management approach is*

*needed. Thus, some conservationists see ecosystem management as a Trojan horse that would allow continued environmental destruction in the name of modern resource management.*

*The recognition that some ecosystems have keystone species whose activities govern the well-being of many other species suggests an approach that may unite the best features of single-species and ecosystem management. If we can identify keystone species and the mechanisms that cause them to have such wide-ranging impacts, we would almost certainly derive information on the functioning of the entire ecosystem that would be useful in its management. Some keystone species themselves may be appropriate targets for management, but, even when they are not, our understanding of the ecosystem will be greatly increased. Keystone species may not be a panacea, however. We do not yet know how many ecosystems have keystone species, and the experiments that lead to their identification are often very difficult. © 1998 Published by Elsevier Science Ltd. All rights reserved*

**Keywords:** adaptive management, ecosystem health, ecosystem management, endangered species, flagship species, indicator species, keystone species, landscape ecology, umbrella species.

### INTRODUCTION

In an era of burgeoning conservation needs and tightening budgets, an increasingly loud claim is that the scope of conservation management must be expanded to achieve economies of scale and efficiency. According to this view, managing populations of particular species of interest will lead us to fall further and further behind in meeting the challenge of preserving biodiversity, as more and more species fall below a threshold of imperilment and funding in no way keeps pace with their individual needs. The only way to deal with this challenge is then seen to be to manage at least entire ecosystems, if not whole landscapes, by unified methods designed to save all their inhabitants at one time.

However, the precise objectives of such methods have not often been articulated beyond vague aims to 'preserve the environment' or to 'maintain biodiversity', and it is not always clear exactly how management of such high-level entities as ecosystems will supersede management of their component species. This paper attempts to understand the specific goals of management at the ecosystem level and higher, and also to compare proposed procedures to those of traditional management focused on individual populations and species.

The examples used to elucidate these matters will be primarily North American, largely because of the author's familiarity with conservation on that continent. A large fraction of the discussion relates to management actions aimed at satisfying the Endangered Species Act (1973) of the United States. This legislation has become the major vehicle for protecting biodiversity in the United States (Mann and Plummer, 1995). It is reactive, rather than proactive, and explicitly targets species and populations, in that it specifically provides protection for species (and, in certain instances, some populations rather than entire species) that are already felt to be doomed to extinction if new action is not taken to redress their decline. However, often the Act has been invoked to save entire ecosystems because, under some circumstances, it provides for protection of the habitat of an endangered species, and that habitat includes the biotic as well as the abiotic habitat. Thus, a recent interpretation by the Supreme Court says that the Act can prevent habitat destruction (Baker, 1995) if such destruction 'harms' endangered species or populations. The Endangered Species Act also mandates that, in addition to calling a halt to most activities causing the decline of an endangered species, a management plan must be produced that will rehabilitate the species by bringing its population size above the threshold of endangerment. These management plans have become the testing ground for various ideas on how and at what level to conserve nature in the United States.

#### Indicator, umbrella, and flagship species

Because monitoring and managing all aspects of biodiversity that might interest us (including species richness and composition, physical structure, and processes) are so difficult, a variety of shortcuts have been proposed whereby attention is focused on one or a few species.

The most venerable of these approaches is that of the indicator species. Managers use indicators for two different reasons—first because their presence and fluctuations are believed (or hoped) to reflect those of other species in the community, and second because they are believed to reflect chemical and/or physical changes in the environment (Landres *et al.*, 1988). However, there is no reason why a species particularly sensitive to chemical pollution, for example, need necessarily reflect the status of a large number of other species, so I will restrict my consideration to the first type of indicator species.

Criteria for choosing such indicator species are very controversial (Landres *et al.*, 1988), at least partly because of confusion over what the indicator should indicate. Generally, we want an indicator to indicate the 'health' of the system, but different persons view different things as constituting health. For example, whether species richness alone, independently of species' identities, contributes to the functional health of a community or ecosystem is hotly debated and currently under intensive study (Baskin, 1994; Tilman and Downing, 1994). For some persons, species richness itself is ecosystem health—the tacit goal of all conservation should be species richness, and, *ipso facto*, a rich community is a healthy one. For still others, structural diversity and aspects of function (like nutrient cycles) are the *sine qua non* of health, independently of species richness or composition. The *reductio ad absurdum* of this confusion of goals is the proposition (Noss, 1990) that we should monitor virtually *everything* as indicators—a large group of species, dominance-diversity curves, canopy height diversity, percent cover, nutrient cycling and predation rates, etc. The problem is that this full set of indicators leaves nothing to be indicated, as opposed to measured directly. Of course the absence of resources to do all this measurement was the *raison d'être* for indicator species in the first place!

Even if we concede at the outset that all we want the indicator species to indicate is the presence and population trends of a group of other species in a community of interest, it is not so obvious how to choose the best species for this purpose. At the very least, we would need a pilot study measuring co-occurrence patterns and correlations of population fluctuations, plus ease of monitoring, for all species in the group. To my knowledge, such a pilot study has never been attempted. The scale of observation would also be important for an indicator (Meffe and Carroll, 1994; Weaver, 1995). Species like the large vertebrates discussed below might be excellent indicators for other species that require massive, continuous tracts of habitat, but they may not do very well in a landscape fragmented into small patches, so long as the habitat of the patches was appropriate.

*Faute de mieux*, often vertebrate species are chosen as indicators simply because they are so charismatic that a manager feels obliged to monitor them anyway and nourishes the vague hope that such a 'flagship species' (see below) will fortuitously reflect the health of the entire system. For example, the US Forest Service is mandated to use 'management indicator species' to assess the impacts of any proposed management procedure on the system as a whole and chose the northern spotted owl *Strix occidentalis caurina* to serve this role for the Pacific Northwest region. The specific grounds were that the owl (1) was on the threatened species list for Oregon, (2) is a species of special interest (because it is an attractive bird that typifies a beautiful forest type),



concern, much less is known about their biology, so the impact of the management plan cannot be guessed with much assurance.

The Florida panther *Felis concolor coryi* is the quintessential 'flagship species' (Shrader-Frechette and McCoy, 1993)—a species that has become a symbol and leading element of an entire conservation campaign. The panther is identified with Florida (Shrader-Frechette and McCoy, 1993) and has been used as a poster-animal in both public and private campaigns for broader conservation objectives. A disjunct subspecies of the widely ranging cougar, it is slightly distinctive morphologically and is gravely threatened. Some 40 individuals remain, restricted to undeveloped areas of south Florida, among the regions of the US undergoing the most rapid development and habitat destruction. The main problems for the panther are the dramatic decline in its favoured prey animal, the white-tailed deer *Odocoileus virginianus*, owing to habitat destruction (Shrader-Frechette and McCoy, 1993) and the fragmented nature of remaining panther habitat, which causes individuals to cross highways, incurring substantial mortality. It would be no trivial matter to sequester land sufficient for an increased population, as male home ranges average 550 km<sup>2</sup> and female home ranges 300 km<sup>2</sup> (Cox *et al.*, 1994), and land in Florida is very expensive. In fact, although Florida has by far the largest state fund in the US for purchase of conservation lands, the budget could easily be exhausted simply by purchases of potential panther habitat.

However, Florida has numerous other threatened taxa, including 51 other mammal, bird, reptile, and amphibian species and subspecies (Shrader-Frechette and McCoy, 1993). Of course, panther habitat could serve double-duty. Areas proposed specifically for panther conservation have at least 24 of these 51 taxa, plus 29 threatened plant species and subspecies (Cox *et al.*, 1994). Other species may be even better umbrellas. For example, proposed conservation areas for the Florida black bear *Ursus americanus floridanus* include more threatened vertebrates and many threatened plants (Cox *et al.*, 1994). Of course, to evaluate the relative merits of potential umbrella species and to determine how many of them are needed, we would need a full analysis of the costs of the proposed purchases, the likelihoods of survival of each species in the umbrella, etc. At least the latter aspect of the analysis would be extremely difficult. No method incorporating all the potential threats to species survival can currently be used with much confidence.

The panther is so charismatic that thousands of Floridians pay \$66 annually to have an automobile license plate with its picture. These funds go towards conservation, as do others generated in various private appeals featuring the panther. On the other hand, the attempt to preserve the panther at both state and federal levels has been enormously expensive, ca \$1.4 million (J. Cox, pers. comm.) in addition to land-acquisition costs

for the new, 12 000 ha Panther National Wildlife Refuge. Costs have included a journal (*Coryi*) devoted solely to this animal, extensive field management projects, and field and laboratory studies. Are the benefits generated by the panther conservation program worth the costs? Could the funds devoted to it have greater conservation benefit if spent otherwise? No significant research treats these questions.

An irony is that the panther may not survive long even with this expenditure, at least not without successful translocation to other regions of Florida (Shrader-Frechette and McCoy, 1993; Cox *et al.*, 1994). In fact, some might argue that the very procedure that has now been adopted to forestall a decline from hypothesized inbreeding depression will eliminate the Florida panther quickly—at least eliminate it as *Felis concolor coryi*. After the discovery that one of the two populations already contains genes from escaped captive Central or South American cats (O'Brien *et al.*, 1990), the federal government and state have now embarked on a plan to import and release individuals of another *F. concolor* subspecies from Texas to increase effective population size (Dold, 1995).

#### **But what happens when the flagship sinks or there is no flagship?**

That the Florida panther might disappear or evolve into another species leads us to question from yet another direction the wisdom of hinging an overall conservation strategy on a single charismatic threatened flagship species. Suppose the population disappears? Will public emotional investment in this species turn to despair and disenchantment with conservation in general? Would not the money have been better spent on a combination of conservation projects to preserve other species and educational programs to teach the lay public about the importance and inherent attractiveness of the myriad less dramatic species that dominate any ecosystem?

Worse, suppose a region has no threatened species, charismatic or mundane, to begin with? This is precisely the situation in the Alaskan rain forest, such as the huge (6 812 000 ha) Tongass National Forest in Alaska. Although parts of this region are revered for spectacular vistas as well as large populations of dramatic animals (such as the grizzly bear, *Ursus arctos*), no one forest-dwelling species qualifies for protection under the Endangered Species Act. The United States has no law that specifically protects communities or ecosystems. Thus, the Endangered Species Act has been pressed into service for this purpose because it protects the 'critical habitat' of listed species, and the habitat can be construed as the biotic habitat, such as old-growth trees for the spotted owl, as well as the physical context. It is widely recognized that this approach will not suffice for all communities and ecosystems, as exemplified by the Tongass case, and that what is needed is some sort of 'Endangered Communities Act' or 'Endangered Ecosystems Act' (e.g. Hunt, 1989; Meffe and Carroll, 1994).

implementation and management, the processes themselves often seem to have become the valued elements. For example, among US federal agencies, many list maintenance of processes or functions as either the first goal of ecosystem management or the only goal. And an attempted consensus document (Keystone Center, 1993) produced by representatives of many government agencies and private organizations listed maintaining processes as the first aspect of ecosystem management. This focus on processes is seen as a Trojan horse by some conservation biologists, as will be discussed below.

The emphasis on processes automatically leads to a broad spatial scale with a focus on landscapes. One definition of landscape ecology (Golley, 1993) is "the study of how land patterns influence processes". Of course, landscape ecology also answers a growing interest in large-scale phenomena, while it is quite clear that at least some single-species management can be conducted without considering the structure and dynamics of the landscape. Thus, ecosystem management, though not simply the management version of landscape ecology, is very closely related to the latter discipline.

Another feature shared by many definitions of ecosystem management is that it is holistic, a trait seen as clearly distinguishing it from single-species management. This feature might seem trivial—after all, holists study systems as systems. However, it is important to realize that holists are committed to the view that it is impossible to understand the components of a system *except* as parts of the system. Thus, they would argue that insightful, effective single-species management is not only expensive and inefficient, but is impossible, because the species exists only as part of the ecosystem.

Yet another aspect of ecosystem management in most definitions is that humans are part of the ecosystem, or at least of most ecosystems. There are two subtle consequences of this view.

First, although this point is rarely articulated in scientific publications, this conception of ecosystem management casts into doubt the very idea of excluding humans from selected areas, as somehow antithetical to the nature of an ecosystem. Of course, this is an extreme view (which is probably why it is rarely written down), but the implication is clear that such restricted areas should play at best a limited role in conservation. The title of a recent exposition of ecosystem management for forests (Shepard, 1994) says it all: "Modern forest management: it's about opening up, not locking up".

Second, humans use resources, and such resource use is conceived as a natural process not inherently dangerous to ecosystem health. Biologists and environmentalists, if they advocate ecosystem management at all, tend to see its key goal as maintaining biodiversity (e.g. Meffe and Carroll, 1994). In short, humans should manage ecosystems to protect other species and communities. However, many people, especially in management agencies, have a very different focus (e.g. Overbay, 1992; Jensen and Everett, 1993), namely the goods and

services that ecosystems provide to humans (Grumbine, 1994). In other words, humans should manage ecosystems primarily in response to human resource needs. The Forest Service and some other US agencies have in the past attempted to resolve this conflict by the philosophy of 'multiple use', at least since the Multiple Use Sustained-Yield Act of 1960 (Kessler *et al.*, 1992). The assumption was that the managed land could serve all purposes, although in practice the human resource needs were greatly emphasized. But this was only an assumption. Now that there is public pressure to pay more attention to protection of other species and communities, the validity of the entire multiple-use framework is in question (Wagner, 1994). It may well be that ecosystem management, at least in some ecosystems or large parts of them, will have to serve one or the other goal almost exclusively. It is important to state explicitly that multiple use may not be possible (Grumbine, 1994).

A final feature common to many conceptions of ecosystem management (e.g. Kessler *et al.*, 1992; Everett *et al.*, 1993) is that adaptive management (Walters, 1986; Walters and Holling, 1990) will be the scientific basis for it. Adaptive management is essentially project-as-experiment, and the key aspect that seems to attract many adherents in ecosystem management circles is that management goals and methods are changed in the course of the project. The aegis for adaptive management is that the effects of a procedure are very uncertain because mechanistic understanding of a system is rather poor (Walters and Holling, 1990). This state of affairs certainly obtains for many components of proposed plans for managing ecosystems. Adaptive management has had some successes, as, for example, in some fisheries in which simply adjusting yearly limits in accord with the catch has prevented overfishing, without any detailed understanding of the mechanisms of the underlying population dynamics (Policansky, 1986).

A contentious aspect of adaptive management is whether the changing procedures and goals really permit improved mechanistic understanding of the system. Walters and Holling (1990) contend that adaptive management leads to scientific understanding, but their defense of the proposition that this understanding *is* scientific, even if it is not the customary analytical type of scientific knowledge, suggests the contention is controversial. Is an 'experiment' for a short enough time to be considered adaptive (in the ecosystem-management sense of subject to modification in the course of the project) really a scientific experiment? And is there adequate replication and control, especially if the project is at an ecosystem or landscape scale? Many studies in ecology are called 'experimental' that do not really qualify for this status (Underwood, 1990). The importance of this problem for conservation is that the term 'experiment' has a scientific cachet and may suggest a kind of rigor that is, in fact, absent from a management scheme. Wiens (1992) has pointed to a distressing lack

noted above, can now be seen as associated with a problematic criterion for assessing management success.

Even determining the health status of an individual organism is difficult. Determining, at least to the satisfaction of all parties, whether an ecosystem is healthy is hopeless. We have seen that different people have different definitions of health and different conceptions of ecosystems, and that even the physical boundaries of an ecosystem are often in doubt. Truly, ecosystem health is not a workable goal.

Further, the integral relationship of adaptive management to many conceptions of ecosystem management is worrisome to conservationists. There are two problems. First, the possible absence of a clear criterion for rejection of a hypothesis and the continually changing management practices may make it impossible to proceed by normal scientific means to study the underlying mechanisms of the system and thus to conceive of entirely new ways to manage it or its component species. Second, the focus is on the entire ecosystem rather than on individual species. This fact suggests that ecosystem management would not nurture the sorts of experiments and observations on single species that have often provided great insight into not only their own biology but the structure and function of entire systems (examples given below).

Finally, it is often said that single-species management 'doesn't work' (see, for example, Cushman, 1995; Mann and Plummer, 1995), as witness the fact that several listed species managed under the US Endangered Species Act have nonetheless disappeared. Some of these species, at the time of listing, were almost certainly already extinct (McMillan and Wilcove, 1994). Others that had substantial populations when listed, such as the dusky seaside sparrow *Ammodramus maritimus nigrescens*, were grossly mismanaged, and non-biological factors, such as lax law enforcement, led to their demise (Walters, 1992). It was not the inability of biologists to know enough science to save these species that doomed them. Rather, the knowledge was there or could have been gathered, but economical, political, or social concerns came to dominate the programs.

#### Keystone species management

A slightly different orientation to single-species management might be more effective than the alternatives discussed above. The concept of the keystone species () suggests that, at least in many ecosystems, certain species have impacts on many others, often far beyond what might have been expected from a consideration of their biomass or abundance. Paine originally studied a starfish that selectively preyed on a species that would otherwise have been competitively dominant. The starfish thereby prevented that dominance and allowed numerous other species to coexist. The definition of 'keystone' has been expanded (see Bond, 1993; Menge *et al.*, 1994), and species not near the top of foodwebs have also been seen as keystones. For example, Gilbert,

(1980) termed 'keystone mutualists' plant species that support many animal species whose activities may themselves support many other species. And species may serve as keystones by virtue of how they change the physical structure of the environment, as do beavers *Castor canadensis* with their dams (Naiman *et al.*, 1986; Pollock *et al.*, 1995). Many species provide shelter for numerous other species. In the longleaf pine forest, gopher tortoise *Gopherus polyphemus* burrows are home to 332 other species (Jackson and Milstrey, 1989), some of which use this microhabitat obligatorily, while the holes that red-cockaded woodpecker clans laboriously excavate in longleaf trees are the only such holes present and are used by at least 22 other species (Harlow and Lennartz, 1983), including the fox squirrel as noted above.

The expansion of the keystone species concept has led some researchers to criticize it as so fuzzy that it is impossible to say what is and what is not a keystone species; they go so far as to charge that it is dangerous to apply the concept to management (Mills *et al.*, 1993). However, to discard the idea would be to throw the baby out with the bathwater (deMaynadier and Hunter, 1994). It seems more reasonable to refine it. A recent such effort (Power *et al.*, 1996) aims to quantify the criteria for designation as a keystone species and attempts to separate the concept from that of the 'ecological dominant', or species whose great biomass and abundance make it crucial for an entire community and allow it often to constitute the physical structure of the community.

Power *et al.* (1996) are pessimistic about the prospects for concocting a list of attributes that would *a priori* identify a keystone species inexpensively and efficiently. I agree. It is telling that much of the literature on keystone species is experimental in either the narrow sense of controlled manipulation (e.g. Paine, 1969) or the broader sense of some 'natural experiment' without strict control and replication, like an introduction of a species (Simberloff, 1991) or a removal of one (e.g. rabbit *Oryctolagus cuniculus*, Harper, 1969; American chestnut *Castanea dentata*, references in Simberloff, 1997; and beaver *Castor canadensis*, references in Naiman *et al.*, 1986; Hackney and Adams, 1992; Pollock *et al.*, 1995). In the latter cases, it is more difficult to draw inferences, but before-and-after comparisons or spatial comparisons between sites where the event occurred and those where it did not can often be quite suggestive.

Understanding the role of keystone species certainly requires inspired natural history (Paine, 1995), and there is no real shortcut for obtaining sufficient insight into the dynamics of an ecosystem. However, because a keystone species approach is focused squarely on an understanding of the mechanisms that underlie the function and structure of an ecosystem, it appears that it might suggest entirely new ways of managing a problem, rather than the successive-approximation approach that dominates adaptive management. For

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# A framework for the improved management of threatened species based on Population Viability Analysis (PVA)

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Considerable funding and effort is dedicated to the conservation and recovery of threatened species in Australia. We describe a series of five iterative steps that will improve the effectiveness of programmes for threatened species management. These steps are best integrated using Population Viability Analysis (PVA) in an approach to management where the key stages are completed concurrently. In this way management actions for the conservation of threatened species can be regularly assessed and upgraded as more information and improved computer simulation models become available.

## INTRODUCTION

A LOT of the conservation effort in Australia is dedicated to preventing the extinction of threatened species (Australian National Parks and Wildlife Service 1989, 1992). Over the past 12 months the Endangered Species Programme coordinated by the Australian National Parks and Wildlife Service allocated five million dollars for the conservation and recovery of threatened species (Common and Norton 1992). At a State level, Victoria committed a total of \$653 000 in the 1991–1992 financial year to the implementation of management plans for the Helmeted Honeyeater *Lichenostomus melanops cassidix*, Leadbeater's Possum *Gymnobelideus leadbeateri* and the Eastern-barred Bandicoot *Paramelops gunii* (Department of Conservation and Environment 1991).

Recent efforts to conserve and manage threatened species have concentrated on the development of species recovery plans and biological research. However, much of this work proceeds by the educated guesses of scientists and managers familiar with the target species and not through the objective assessment of alternative management options. In this paper we outline a more objective and efficient approach for managing threatened species based on a sequence of steps that are integrated using Population Viability Analysis (PVA).

Once a species has been identified as threatened, we argue that there are five tasks that need to be completed simultaneously within a programme for its recovery; (1) collating existing information on the species; (2) listing and costing management options; (3) ranking management options using PVA; (4) using sensitivity analysis

to test the ranking and guide future research; and (5) implementing the best option with repeated monitoring and re-evaluation of the programme. The use of PVA is fundamental to most of these steps, and we discuss some of the more valuable features of the technique for threatened species management. In this paper we define threatened species as those categorized by the I.U.C.N. as rare, vulnerable and endangered (Mace and Lande 1991).

## WHAT IS POPULATION VIABILITY ANALYSIS (PVA)

Population Viability Analysis (PVA) is a process in which the likelihood that a population will become extinct is assessed, within a specified time and under particular circumstances (Shaffer 1981; Possingham 1991; Boyce 1992). This process often involves the use of mathematical models that are explored using computer simulation.

Although PVAs have probably been carried out on over 50 populations (Boyce 1992), the details of many studies are published in literature that is generally not accessible, while many others remain unpublished. Some overseas examples of the use of PVA are: work by Shaffer (1983) on the grizzly bear *Ursus arctos horribilis*, several papers and reports on the northern spotted owl *Strix occidentalis caurina* (e.g., Marcot and Holt-Hausen 1987; Lande 1988; Thomas *et al.* 1990; Lamberson *et al.* 1992) and several reports and papers that use a PVA package called VORTEX to assess the viability of small populations (Lacy 1992).

Within Australia the application of PVA is advocated by a range of Australian Federal Government agencies responsible for sustainable natural resource management and the conservation

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of biodiversity (e.g., Ecologically Sustainable Development Working Group 1991; Resource Assessment Commission 1992). Possingham and Noble (1991) use PVA to examine the probability of persistence of the Powerful Owl *Ninox strenua* under different forest management scenarios in south-east New South Wales. Based on a range of biological data on the eastern barred bandicoot *Perameles gunnii* input to the PVA programme VORTEX, Lacy and Clark (1990) predict that the population of the species in western Victoria will be extinct within 25 years. Lindenmayer *et al.* (1991) explore the viability of Leadbeater's possum *Gymnobelideus leadbeateri* under several scenarios including climate change.

Measures other than the probability of extinction within a certain time can be used to assess population viability. The median time to extinction is the time at which there is a 50 per cent chance the population is extinct. Quasi-extinction (*sensu* Ferson and Burgman 1990) is the probability that a population will decline to a small number like twenty. Quasi-extinction is an important measure because little is known about the dynamics of very small populations and the associated decline of genetic diversity. As the conservation of small remnant populations can be very expensive (Menkhorst and Middleton 1991) measures of quasi-extinction can be used to help manage populations before they reach a minimum critical size.

The probability of extinction and/or quasi-extinction is usually derived from a Monte Carlo simulation of an array of interacting processes that may influence populations of animals. Most programmes for PVA typically emphasize those processes considered to have the greatest impact on the probability of extinction, including estimates of the life-history and demographic parameters of a species, the frequency and relative impact of catastrophes on populations and a range of potentially significant environmental and genetic factors.

Despite all these studies, only a few have explicitly and adequately used PVA to choose between different management options. The most celebrated example is that of the northern spotted owl, where Thomas *et al.* (1990) use PVA, to choose critical areas that would support about 20 pairs each and ensure landscape management that reduces dispersal mortality (a significant threatening process for this population).

#### PVA AND THREATENED SPECIES MANAGEMENT

There are two broad objectives in threatened species management. A short-term objective is to minimize the probability that the target species will become extinct. A longer term objective is to ensure that the species retains its potential for

evolutionary change without intensive management. Notably, few species recovery programmes have such a long-term focus. PVA can assist in realizing both these objectives. Within this context, the approach can be used to address three aspects central to threatened species management: design of programmes for further research; compilation of lists of threatened species; and identification and assessment of management options.

#### Planning research and data collection

The most important data for applied species conservation are those necessary to assess the relative viability of the species and to list and rank management options. PVA may reveal that population viability is insensitive to particular parameters. Consequently, it may be unnecessary to expend additional effort and resources to obtain better estimates of those parameters. Research should be targeted at those factors identified by PVA as having a potentially significant impact on extinction probability or the ranking of management options.

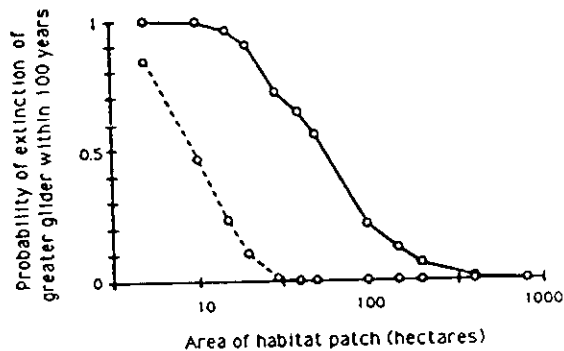


Fig. 1. Output from the programme for PVA, ALEX, showing the predicted probability of persistence of the greater glider *Petauroides volans* in patches of different sized high quality habitat with (—) or without (---) owl predation.

Figure 1 shows that the viability of a population of greater gliders *Petauroides volans* in optimal habitat is very sensitive to whether or not there is owl predation (Noble and Possingham 1991). Figure 2 shows that the viability of a southern brown bandicoot population in a forest block in the south-east of SA is relatively insensitive to the probability of adult dispersal (Possingham *et al.* 1993).

#### Listing of threatened species

Lists of threatened species are becoming increasingly important in the development of policies and legislation for the conservation of threatened species. PVA can provide an objective mechanism to assess the vulnerability of a species

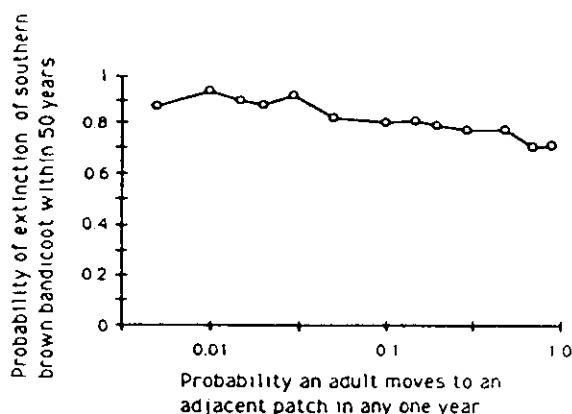


Fig. 2. Viability over 100 years of the southern brown bandicoot *Isoodon obseleus* in Honan's scrub in the SE of SA as a function of the probability that adult females move between adjacent forest compartments in any year.

to extinction (Mace and Lande 1991) and, in turn, to compare it to other taxa believed to be threatened. This ranking can be used with other criteria such as cultural significance (Davis *et al.* 1992) and taxonomic uniqueness (Faith 1992) to set priorities for species conservation programmes.

Although the task of assessing the viability of large lists of species using computer models is currently too great, Belovsky (1987) has used empirical observations and mathematical models to estimate minimum viable population sizes for many North American mammals.

#### Ranking management options

The most important use of PVA is to guide threatened species management by estimating the extinction probability associated with different management options. The approach can be used to predict the likely response of a species to management actions such as re-introduction, captive breeding (Lacy *et al.* 1990), prescribed burning (Possingham *et al.* 1993), timber harvesting (Possingham and Noble 1991), the

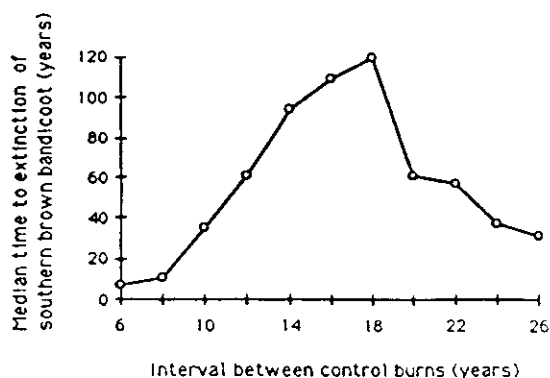


Fig. 3. Viability over 100 years of the southern brown bandicoot *Isoodon obseleus* in Honan's scrub in the SE of SA as a function of interval between control burns for those compartments scheduled for control burning.

acquisition of a network of reserves (Thomas *et al.* 1990) and the implementation of wildlife corridors.

Thomas *et al.* (1990) use a spatially explicit PVA model to determine the optimal size of Habitat Conservation Areas for the northern spotted owl. For single species reserve design it is useful to know the relationship between the size of a patch of habitat and the viability of a population within that patch (Fig. 1).

A PVA of a population of southern brown bandicoots in Honan's scrub (a forest reserve in south east South Australia) suggests that the optimal interval between control burns for this species is about eighteen years (Fig. 3, Possingham *et al.* 1993).

#### STEPS FOR THREATENED SPECIES MANAGEMENT

A sequence of five main steps for threatened species management is outlined in Figure 4. These are treated in more detail below. Where urgent action is required, management strategies may need to be implemented before several of the steps are initiated. However, the success of each step will largely depend on the success of the others in the sequence. The most effective threatened species management programmes are most likely to be those where the processes of data collection, computer simulation modelling, on-ground management and monitoring are integrated.

##### Step 1. Collate existing information on a species

Before gathering new information on a species it is essential to assemble existing data. Even though there will be uncertainty about the value of many parameters, it is worthwhile attempting a PVA because the process of assembling input data for analysis will focus future research by highlighting gaps in existing knowledge.

If adequate information exists for the target species, then a first step is to determine if it is threatened. PVA can be used to quantify the probability of extinction for a range of time frames (e.g., 100–200 years). Different species can be ranked according to their extinction probability (and other PVA outputs). We believe that there should be an attempt to quantify the probability of extinction as one means of setting priorities.

##### Step 2. Generate, list and cost management options

The process of generating, listing and then costing management options is often forgotten in the conservation of threatened species. For some species there may be no practical management options that can be funded in the foreseeable

future, regardless of the conservation status of that species. An option like maintaining a species in long-term captive breeding programmes may be unacceptable. In these cases, further research may be pointless unless it might lead to alternative management options. It appears inevitable that some species will be lost irrespective of the management action that is taken. A risk analysis framework can be useful at this step (Maguire 1991).

### Step 3. Assess each management option using PVA

PVA generates predictions of trends in population behaviour and dynamics in response to various influences and the interactions between

such factors. The relative effects of key parameters on the viability of a species to extinction can be quantified for any time frame and spatial scale. Thus, management options can be ranked according to their impact on the viability of populations of organisms.

### Step 4. Sensitivity analyses

Estimates of population viability will be sensitive to the parameters input to the programme used for PVA at all stages in the sequence of steps for threatened species management. As the values for given attributes are varied, there will be changes in the predicted probability of extinction. Large changes in some parameters may have a

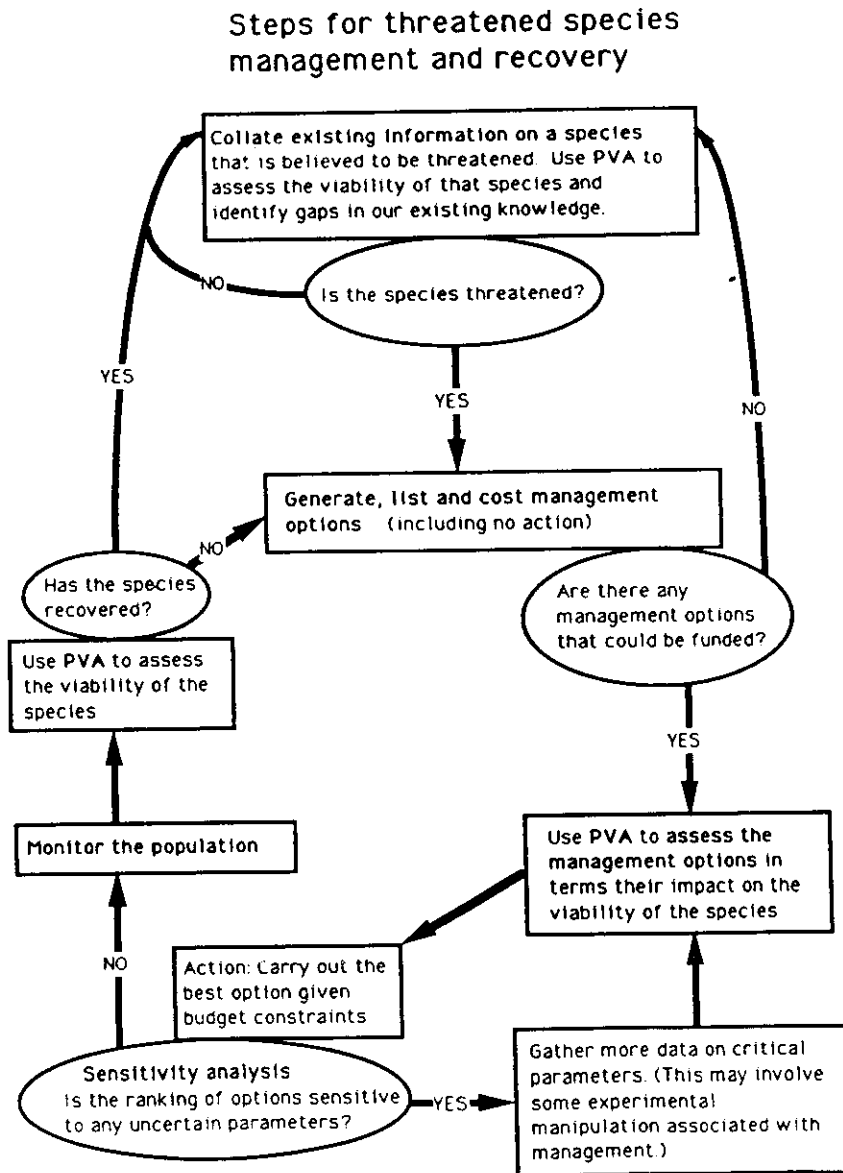


Fig. 4. Key steps and iterative framework for threatened species management and species recovery programmes.



minimal effect on the probability of extinction (Fig. 2). Conversely small variations in other factors may have considerable impact on extinction probability (Figs 1 and 3) and PVA should be used to carefully assess the response of the population to these critical attributes. This process is termed sensitivity analysis and it is an important procedure for assessing and ranking management options for a threatened species programme. This is because for wildlife management, the most important consideration may not be the absolute extinction probability but the extinction probability *relative* to those derived for other management options. Furthermore, most options for conservation will be relatively insensitive to realistic variations in many parameters input to PVA.

#### Step 5. Monitor the population

Monitoring is a critical component of any programme for the management of threatened species. It is essential for any recovery programme and must not be viewed as second-rate science or management practice (Common and Norton, in press). Field-based monitoring should be coupled with on-going sensitivity analyses using PVA. Thus, as further information on key life-history attributes or other population parameters become available, programmes for PVA can be refined and the more comprehensive dataset subjected to re-analysis. The procedure for coupling data collection, ongoing analyses and the regular re-assessment of management options is termed "adaptive management" (Holling 1978). Such an approach is valuable as it allows management actions to be relaxed if the target species recovers and is no longer threatened. Resources can then be re-allocated to the conservation of other taxa of higher priority.

#### DISCUSSION

The use of PVA offers a wide range of benefits for programmes designed to ensure the conservation of threatened species. Some of the most important of these are allied to the quantitative and objective nature of the technique (Lindenmayer and Possingham 1991; Lindenmayer *et al.*, in press). Its application can help place a quantitative value on the impact of proposed resource development and exploitation activities. PVA can also help overcome the problems associated with the subjective judgements made by wildlife biologists and managers who may have pre-determined opinions about the conservation status of, and management strategies for populations they know well. Although we have emphasized the role of PVA in the management of threatened species, the approach can also provide information that is valuable for the conservation of other organisms that are not threatened, but which may be important for ecosystem function (Norton and Possingham 1991).

PVA is a single species approach to conservation biology. However, suitable management strategies for many species may also conserve a wide range of other organisms. For example, appropriate forest management practices for Leadbeater's possum will assist the survival of the greater glider and other fauna dependent on trees with hollows (Lindenmayer 1992). However, a management regime for the conservation of a particular organism is unlikely to be appropriate for every species. Given this, together with the impossibility of completing PVA for all taxa, the identification of those species best targeted for PVA is crucial. Some important target organisms for analysis include:

- i. *Well studied species*. These are valuable to assess because the accuracy of predictions from PVA are dependent on the accuracy of the data used to run the model. Analyses of these species can be used to develop, test and validate various components of programmes used for PVA.
- ii. *Keystone species*. These are organisms that are important to a number of other species or critical for ecosystem function.
- iii. *Indicator species*. These are easily censused species that are sensitive to changes in the environment such as some invertebrates.
- iv. *Threatened species*.
- v. *Species of special cultural value*.

#### Programmes for use in PVA

There is a range of models for use in PVA (Lindenmayer *et al.* 1991). Three that are currently available include VORTEX (Lacy 1992), ALEX (Possingham *et al.* 1991) and RAMAS/Space (Akçakaya and Ferson 1992). These are presently being compared in a detailed assessment of key models for use in the assessment of population vulnerability. This will assist users to decide which programme is best suited to the analyses and management of the target species. For example, for a very small, isolated population, the impacts of inbreeding depression and genetic drift may be important and the use of the programme VORTEX may be most appropriate. Conversely, the analysis of metapopulation dynamics involving the examination of numerous sub-populations of varying size may be better completed using ALEX or RAMAS/Space. In other cases, the development of new programmes for PVA may be required to meet the needs of a particular species management problem. This approach was adopted for PVA of the Helmeted Honeyeater (Menkhorst and Middleton 1991).

Finally, although PVA is useful for enhanced threatened species management, its application *must* be accompanied by serious attempts from Government agencies to stem the loss of biodiversity

and address major conservation issues and threatening process such as vegetation clearance, over-grazing and inappropriate forestry practices (Norton and Lindenmayer 1991; Common and Norton 1992).

#### ACKNOWLEDGMENTS

We thank Mr. Russell James from the Endangered Species Unit of the Australian National Parks and Wildlife Service for access to unpublished reports on species recovery programmes. We are grateful to Dr. M. Burgman for discussions about the computer model presently being designed for PVA of the Helmeted Honeyeater. Two referees made many useful comments.

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## CHAPTER 22

# Gap Analysis for Biodiversity Survey and Maintenance

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Ehrlich (1988) postulated that reversing the loss of biodiversity will require a "quasi-religious transformation" of the way contemporary cultures view the value of human life and the intrinsic values of organic diversity. Even if that transformation were to occur today, we would be faced with a cruel reality: maintaining viable examples of every natural community, including the myriad of species they support, is the fundamental mechanism for conserving biodiversity (Noss and Cooperrider, 1994), but you cannot conserve biodiversity if you do not know where it is located. The elements of biodiversity, from genes and species to ecosystems, have distributions, but they have not been mapped at scales useful for developing a national biodiversity conservation and management strategy.

Centuries of scientific collectors have deposited tens of millions of specimens in the world's museums and herbaria. These form the foundation of our knowledge of species distributions, yet many areas and taxa remain poorly sampled. The Gap Analysis Program, a program of the National Biological Service, uses two relatively new technologies, satellite remote sensing and geographic information systems (GIS), to assist in the assessment of the status and distribution of several elements of biodiversity (Scott et al., 1993). While not a substitute for traditional biological surveys, we feel that gap analysis can provide a preliminary, landscape-scale assessment of the distribution of both species and ecosystem diversity in the United States that can be used to guide future field research and to provide a spatial framework for a preliminary national biodiversity conservation strategy. The gap analysis approach to biodiversity surveys holds promise for the rapid development of information on the distribu-

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1997. Biodiversity II: Understanding and Protecting  
our Biological Resources. Joseph Henry Press.

tion of several indicators of biodiversity in areas of the world that have been less well sampled.

Burley (1988) identified four steps in gap analysis: (1) identify and classify biodiversity, (2) locate areas managed primarily for biodiversity, (3) identify biodiversity that is un- or underrepresented in those managed areas, and (4) set priorities for conservation action. While these steps remain essential to gap analysis, the distribution of vegetation cover and species, gathered as a precursor to analysis, has considerable application to natural resource inventory and monitoring in and of itself.

#### HISTORY OF GAP ANALYSIS

Kepler and Scott (1985) used the distribution of endangered Hawaiian forest birds, gathered through field surveys (Scott et al., 1986), to perform a simple "gap analysis" on the island of Hawaii (Figure 22-1). They found little overlap between the distribution of endangered forest birds and the location of nature reserves. The Nature Conservancy of Hawaii and the U.S. Fish and Wildlife Service responded by establishing the Hakalau Forest National Wildlife Refuge in one of the areas where distribution of three endangered species overlapped.

Extensive field inventory, at the level of detail undertaken in Hawaii (Scott et al., 1986), is prohibitively expensive for large continental regions. To avoid these expenses, the Gap Analysis Program has developed methods to take advantage of currently available information to produce land cover and terrestrial vertebrate distribution maps (Scott et al., 1993). Other taxa, such as butterflies, can be added to data layers where sufficient information is available.

Pilot programs of gap analysis were initiated in Idaho in 1987 and in Oregon in 1988. By 1995, there were active programs in 36 states, and programs in 4 states—Utah, Idaho, Oregon, and Arizona—had been completed. Cooperation with state and federal agencies and private conservation groups has been an essential component of successful programs. Over 200 different public cooperators and private businesses now are involved in various state programs. Common needs, such as access to satellite imagery and databases on species, have encouraged cooperators to pool resources. While programs are state-based for administrative reasons, biodiversity analyses are best carried out for entire biological regions or at the national level. State-level information eventually will be merged to facilitate regional and national analyses.

#### CLASSIFYING AND MAPPING ECOSYSTEMS

Gap analysis requires three primary GIS data layers: vegetation cover, species range maps, and the location of land managed primarily for native species and natural ecosystem processes. Where available, information on other environmental factors, such as elevation, slope, aspect, soils, aquatic features, and

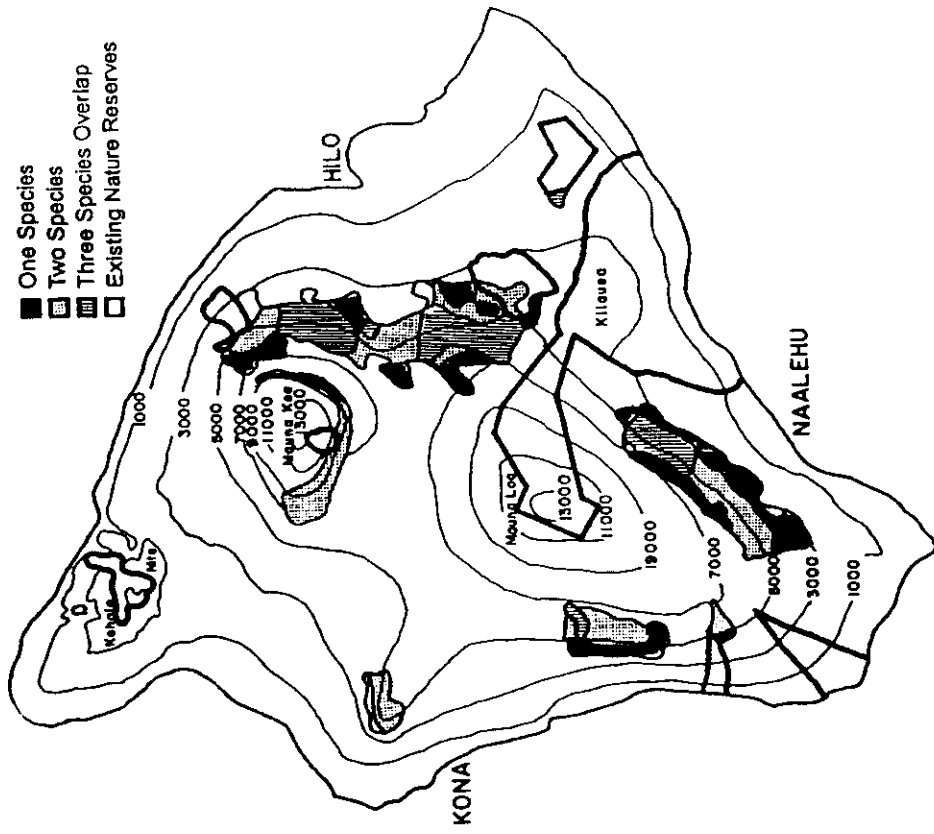


FIGURE 22-1 Ranges of four endangered forest birds on the island of Hawaii in comparison to the distribution of areas managed for biodiversity in 1982.

climate, can be used to improve the accuracy of maps of vegetation and species distributions. Additional information on socioeconomic attributes of landscapes (e.g., projected population trends, projected housing starts, ownership of land by state and federal agencies, zoning, etc.) can be examined to refine planning efforts for land use (Machlis et al., 1994).

Orians (1993:206) correctly pointed out that there is "no previously established, generally accepted taxonomy of habitats, communities, or ecosystems." Plant communities are the most visible component of ecosystems and have been

widely considered to be acceptable surrogates for ecosystems (Austin, 1991; Austin and Margules, 1986). Gap analysis assumes that plant communities serve as integrators of many physical factors (type of soil, moisture regime, aspect, elevation, temperature) that interact at a site (Thomas, 1979). Floristic composition (described by the dominant or codominant species in the uppermost vegetation layer) provides a common denominator for description of plant communities. These communities then can be aggregated into any of a number of taxonomic schemes, such as that proposed by the United Nations Educational, Scientific, and Cultural Organization (1973).

In 1993, cooperating with the U.S. Geological Survey (USGS), the Environmental Protection Agency (EPA), and the National Oceanic and Atmospheric Administration (NOAA), the National Biological Service's Gap Analysis Program purchased complete LANDSAT Thematic Mapper satellite imagery for the conterminous United States. Imagery from one or two dates with favorable weather conditions in the years 1991-1993 will be made available to state programs and cooperators. The imagery will be preprocessed and archived by the U.S. Geological Survey's EROS Data Center in Sioux Falls, South Dakota. With cooperation from the EPA, USGS, and other groups, interpretation of this imagery will serve as the framework for a seamless national vegetation map.

LANDSAT Thematic Mapper imagery measures reflectance of  $30 \times 30$  m pixels (picture elements) on the Earth's surface at seven wavelengths (see Scott et al., 1993, for details). Upland vegetation cover is mapped by aggregating pixels of similar reflectance into polygons using a minimum mapping unit of 100 hectares. Smaller minimum mapping standards have been used by most states to meet local needs.

Gap analysis programs use GIS software with vector data structure as a standard for vegetation mapping (ARC/INFO, Environmental Systems Research Institute, Inc., Redlands, California). Stands are delineated either by on-screen digitizing or by computer algorithms (Figure 22-2). Many plant communities are mapped as stands larger than 100 hectares. These usually contain considerable internal heterogeneity. An attribute file is created for each vegetation polygon containing information about primary, secondary, and tertiary plant communities within the polygon as well as other special features, such as the presence of small wetlands and other microhabitats. Wetlands larger than 40 hectares are mapped when identifiable from satellite imagery. Ultimately, 1:24,000 scale maps produced by the USGS National Wetlands Inventory will be available in digital form to represent this critical habitat element.

Although LANDSAT Thematic Mapper imagery provides a geographically consistent and repeatable spatial framework for vegetation mapping, identification of floristic dominant or codominant species often requires ancillary information, such as aerial photographs, low altitude airborne videophotography (Graham, 1993), existing large-scale vegetation maps, or field reconnaissance.

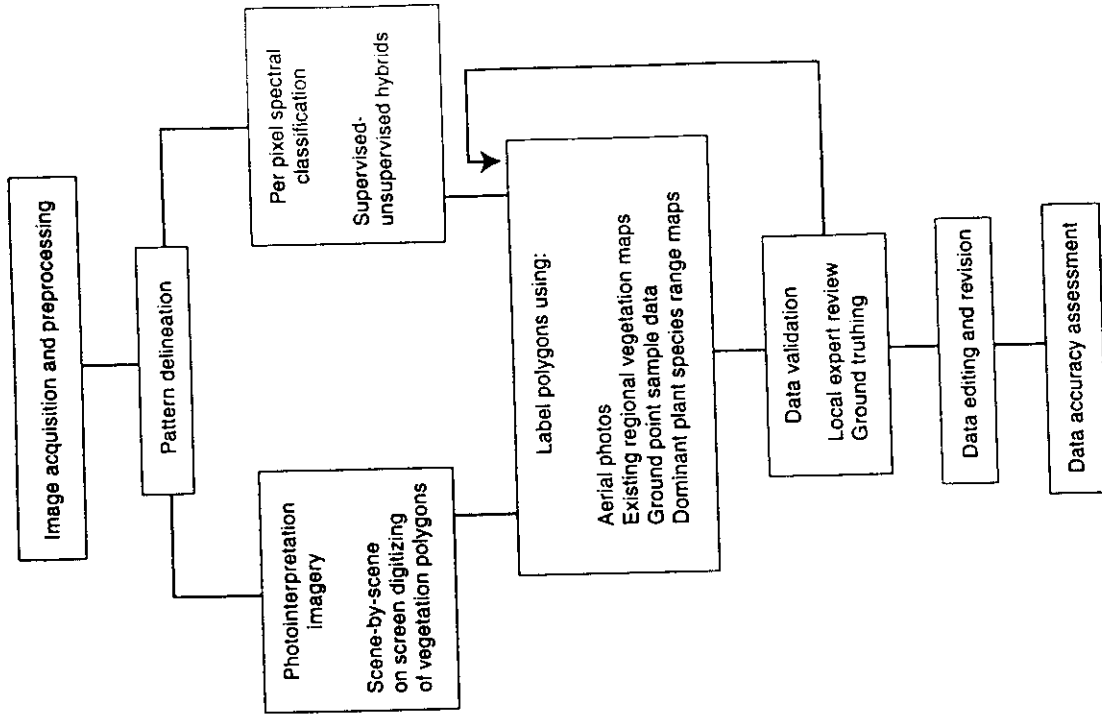


FIGURE 22-2 Flow chart showing steps in development of vegetation cover map from LANDSAT Thematic Mapper imagery and ancillary information. Two widespread approaches to pattern delineation are used by various states. Photointerpretation offers advantages for pattern recognition in complicated landscapes, while machine classification is more consistent and repeatable. National minimum mapping unit and labeling protocols must be followed regardless of the pattern delineation technique.

State gap analysis programs use a variety of available sources to label vegetation maps, keeping a record of the sources used for each polygon.

### DISTRIBUTION MAPS OF SPECIES

Museum and herbarium specimens are the ultimate source of knowledge about the classification and distribution of species. Specimen locality records can be supplemented by reliable observations that are published in the literature or maintained in quality-controlled databases, such as the U.S. Fish and Wildlife Service's Breeding Bird Survey (see also Farr and Rossman, Chapter 31, and Umminger and Young, Chapter 32, in this volume). Continued scientific specimen collection is vital to more fully understand the distribution and variation among living organisms, but the rapid decline of many natural communities places urgency on development of a comprehensive biodiversity conservation strategy in the absence of a truly complete biological survey.

All distribution maps are statements of the probability of encountering a species in time and space. The distributional limits of many species fluctuate from year to year and may display long-term expansion or contraction. Within those distributional limits, populations appear and disappear from patches of suitable habitat (e.g., *Dipodomys deserti* in Joshua Tree National Monument, California; Miller and Stebbins, 1964) and may occur sporadically in unsuitable habitat. Specimen records are sparse even for many common species, and most collecting has taken place along transportation corridors, leaving vast areas unsurveyed. With some qualifications, these shortcomings can be overcome by interpolating and extrapolating the probable presence of a species in suitable environments between verified collection localities within the outer bounds of a species' range. Gap analysis uses this approach to develop distribution maps of species for which distributional and ecological data are readily available. To date, distribution mapping has focused on terrestrial breeding vertebrates, although distributional data for other well-studied groups, such as butterflies, are being gathered by some programs.

The distributional limits of each species are defined by specimen locality records or confirmed observations. They are represented as attributes of a geographic unit, in effect creating a rasterized distribution map. Raster data structure divides an area into units and assigns each a unique attribute (presence or absence of a species in this case). A 635 km<sup>2</sup> hexagonal grid array (White et al., 1992), developed to create a sampling framework for the EPA, is being used as the geographic unit of reference by several state programs, while the traditional county of occurrence is used by others.

The ancients recognized the relationship between species and natural communities (Morrison et al., 1992), and early concepts of the ecological niche had their foundation in natural history observations of the links between species and environmental features (Grinnell, 1914, 1917; Hutchinson, 1978). With cer-

tain qualifications, it is possible to relate the distribution of most species to that of plant communities in which they normally occur (Scott et al., 1993). Final maps of species' distributions are created by overlaying distributional limits with a vegetation map (Figure 22-3). A database indicating which plant communities provide suitable habitat for each species then identifies those vegetation

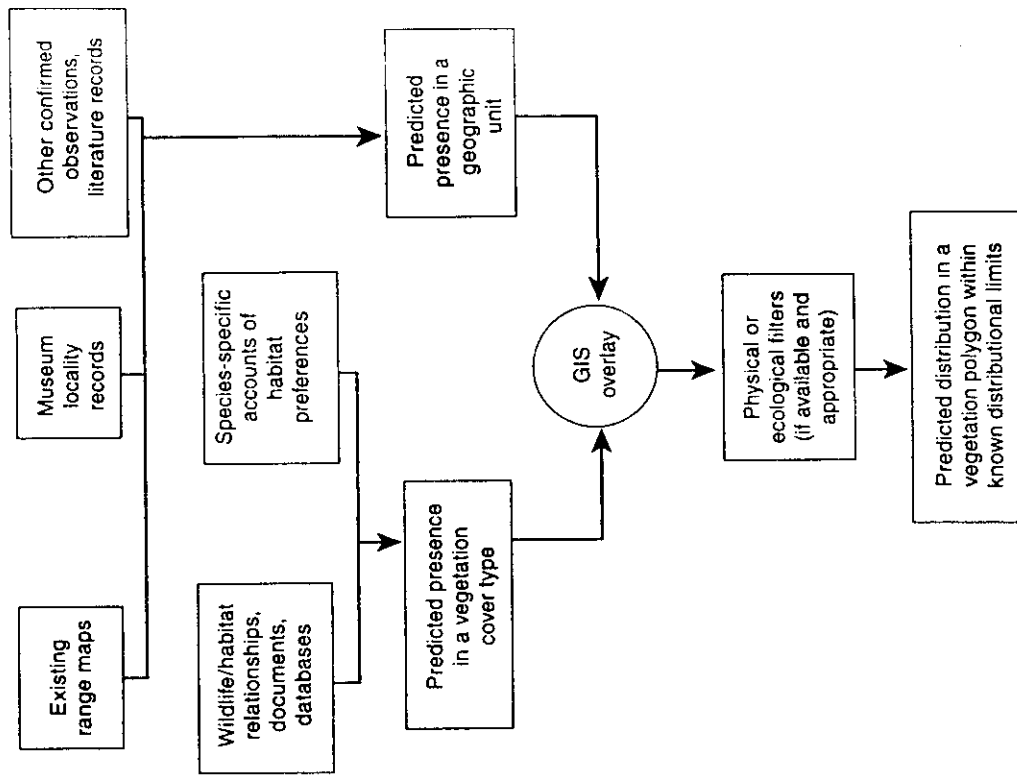


FIGURE 22-3 Flow chart showing steps in development of predicted distribution maps for breeding terrestrial vertebrates.

polygons within a species' range that probably are occupied (Figure 22-4). In this way, areas of unsuitable habitat are excluded from the predicted distribution. For example, species typical of coniferous forests are not predicted to occur in desert scrub or alpine fell fields.

The two most important limitations in this approach concern scale: (1) Many species will be present in a plant community only if certain microhabitat requirements also are present, and (2) many important habitat components are physical features (streams, cliff-faces, snags) that are too small to map. For this reason, species maps based on wildlife-habitat relationships can best be used "to predict the occurrence of species in general vegetation types and in environmental conditions across broad regions rather than at the scale of an individual stand" (Morrison et al., 1992:246). Put another way, it is virtually certain that California Thrashers (*Toxostoma redivivum*) occur in the Berkeley Hills, as they did in Grinnell's day (Grinnell, 1917), but there is less chance of encountering one in a particular 1-hectare stand of coyote bush (*Baccharis pilularis*) on any particular spring morning.

Maps of species distribution generated for gap analysis are intended to be used and validated at landscape scales ("kilometers in diameter," Forman and Godron, 1986:11), not at individual field sites (Edwards et al., 1996). The total number of species expected to occur in each vegetation stand can be displayed, creating a state map of species richness (Figure 22-5). Because of different biogeographic histories, areas of similar species richness in different ecoregions are likely to differ in species content. The richness maps used in any conservation evaluation will vary with the questions being asked (e.g., what is the distribution of endemic species, or what is the distribution of declining species of neotropical migrant birds?).

A further caveat concerns endangered, rare, or locally distributed species. Gap analysis does not predict that these species will occur other than at documented locations. Occurrences of virtually all the rarest and most endangered elements of biodiversity are tracked in databases of the Conservation Data Center which are established in all 50 states by The Nature Conservancy (Jenkins, 1988). The location of habitat for rare species can direct searches for additional populations, but only known occurrences, obtained from cooperating Conservation Data Centers, are used for developing a conservation strategy.

#### LOCATIONS OF AREAS MANAGED PRIMARILY FOR NATIVE SPECIES AND NATURAL ECOSYSTEM PROCESSES

As in the example from Hawaii (Figure 22-1), and others from Idaho (Figures 22-6 and 22-7), gap analysis compares the distribution of elements of biodiversity with that of areas in which the maintenance of biodiversity is a primary management goal. The boundaries of state and federal management units that meet this criterion are placed in a GIS format. State Conservation Data

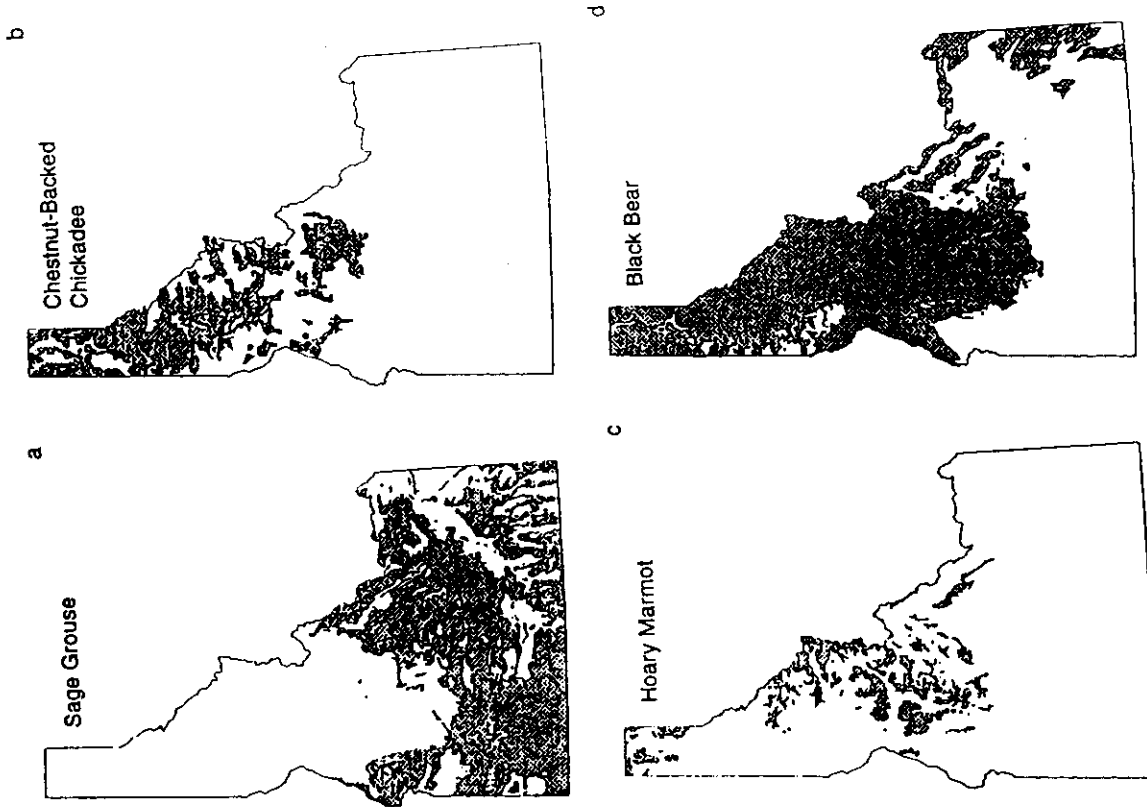


FIGURE 22-4 Predicted distribution of four species produced by intersection of occurrence in a geographic unit (counties, in this example) and polygons of suitable vegetation cover during the breeding season: (a) sage grouse (*Centrocercus urophasianus*), (b) chestnut-backed chickadee (*Parus rufescens*), (c) hoary marmot (*Marmota caligata*), (d) black bear (*Ursus americanus*).



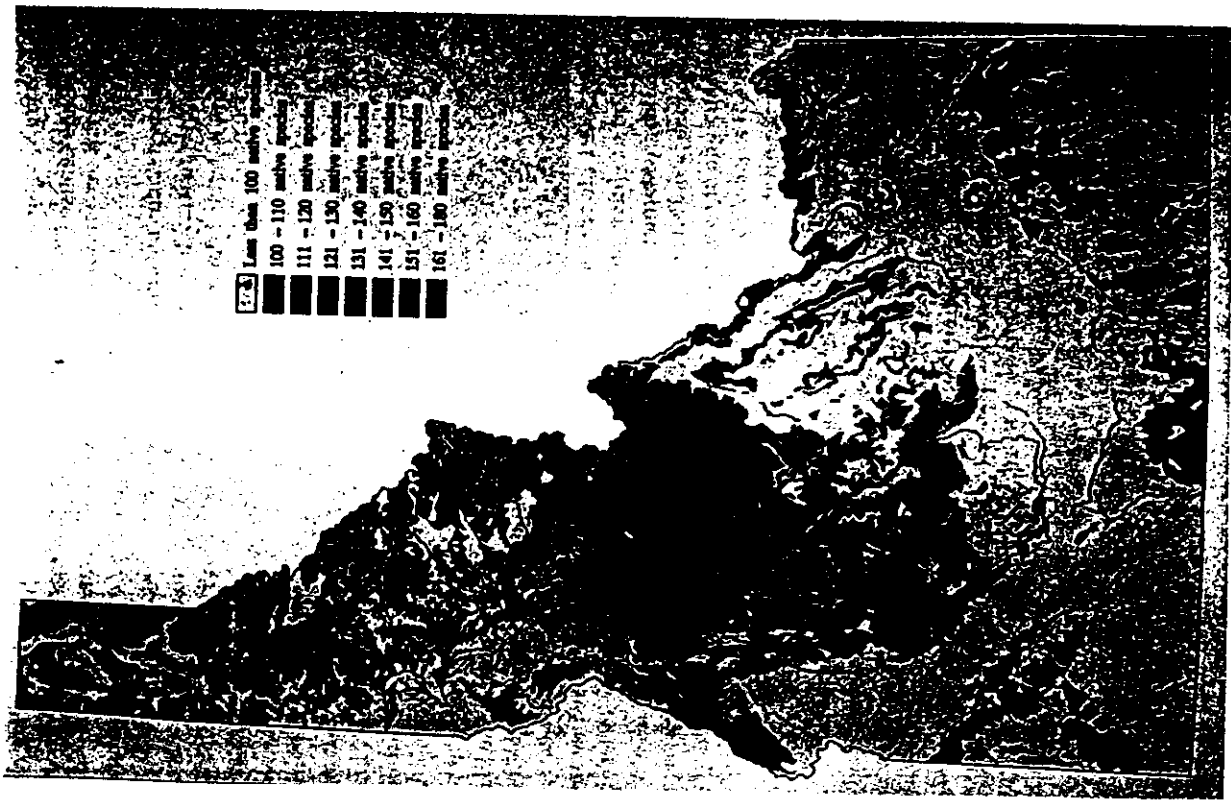
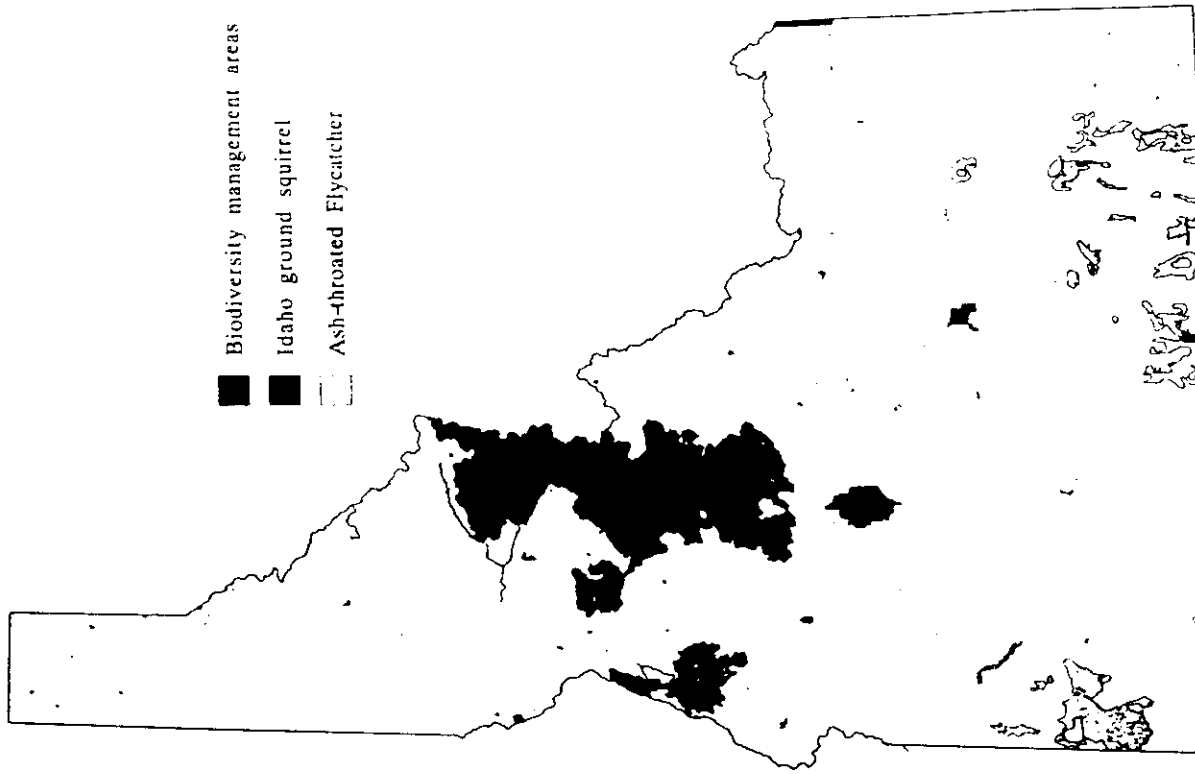


FIGURE 22-5 Species richness for native terrestrial vertebrates in Idaho.



- Biodiversity management areas
- Idaho ground squirrel
- Ash-throated Flycatcher

FIGURE 22-6 Distribution of Idaho ground squirrel (*Spermophilus brunneus*) and Ash-throated Flycatcher (*Myiarchus cinerascens*) in Idaho versus areas managed for long-term maintenance of natural communities.

Centers and Natural Heritage Programs maintain files on each of these public management units, and their managed area files are the usual source for managed area boundaries for state programs. Examples of such areas include national parks, wilderness areas, research natural areas, and some national wildlife refuges (see Scott et al., 1993, for further details).

**GAP ANALYSIS AS A CONSERVATION STRATEGY**

It is impossible to manage for the long-term maintenance of biodiversity unless all the elements of biodiversity are represented in the areas to be managed in the first place (Margules et al., 1988). Gap analysis is a conservation evaluation technique (Margules, 1989; Usher, 1986) that identifies areas in which selected elements of biodiversity are represented. Once those areas are identified, other principles of conservation biology, such as population viability analysis, ecosystem patch dynamics, and habitat quality can be used to select specific sites and determine appropriate management area boundaries.

Noss (1987) and Noss and Cooperider (1994) describe "coarse filter" and "fine filter" conservation strategies. Coarse filter strategies assume that most common species, including those of groups difficult to inventory, such as most invertebrates, will be represented in a reserve network that contains viable examples of all natural communities. Some species, especially those with restricted distributions, will be missed by the coarse filter. These species are captured by a fine filter that tracks the location of populations of individual species or rare natural communities.

The United States currently has no strategy to conserve biodiversity (Noss and Cooperider, 1994). The most visible program to conserve biodiversity is the Endangered Species Act of 1973, a fine filter approach that protects one species at a time. The Endangered Species Act is a powerful tool with which to rescue species from the brink of extinction, but it is a reactive strategy that is in danger of being overwhelmed by growing numbers of species in peril and inadequate funding. Furthermore, many species that are not currently endangered will become so as their habitats are lost to human activities (Margules, 1989). The Endangered Species Act needs to be supplemented with a strategy to identify places that must be managed for their natural values if all communities and species are to persist (Scott et al., 1987; Tear et al., 1993). Like the Endangered Species Act, the ranking system of The Nature Conservancy's Conservation Data Centers provides a standard methodology for evaluating potential natural areas on the basis of threatened or endangered species or rare natural communities (Pearsall et al., 1986), but directs conservation action to elements of biodiversity already in peril.

Gap analysis provides a hierarchical approach to address conservation needs of both species and communities. Scott et al. (1987) called for an ecosystem approach to protecting biodiversity, supplemented by protecting species-rich

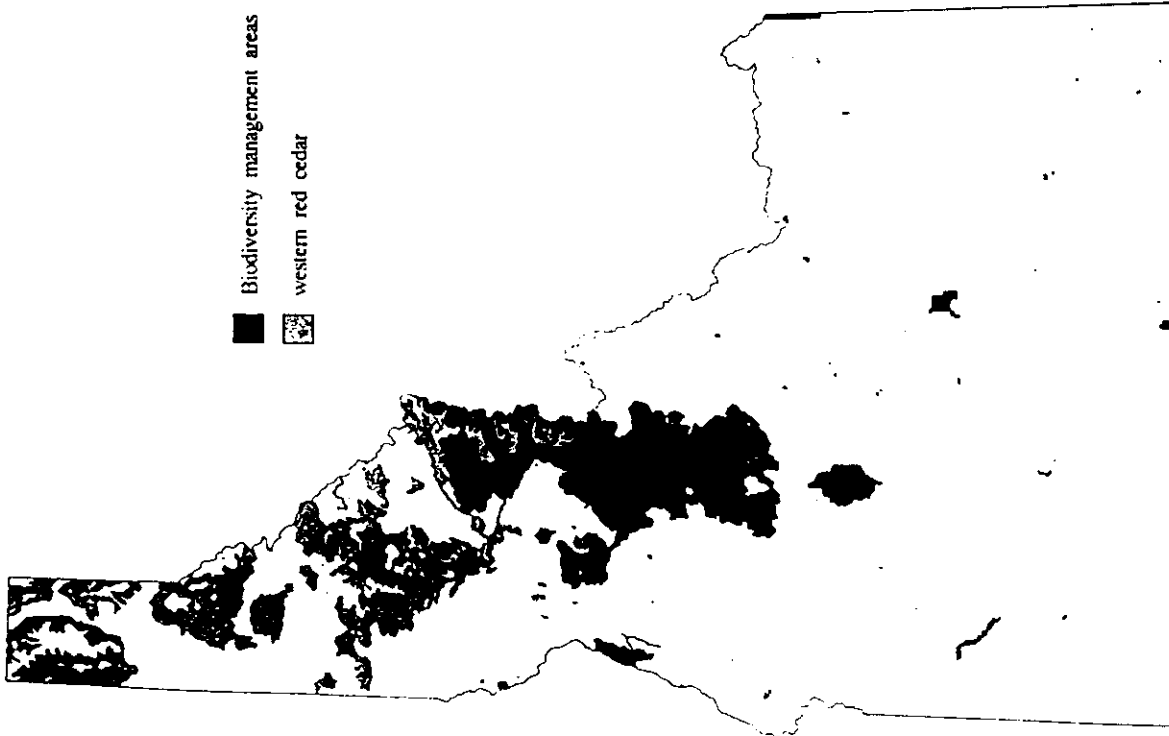


FIGURE 22-7 Distribution of western red cedar as a dominant type of cover in Idaho versus areas managed for long-term maintenance of biodiversity.

areas for a variety of taxa. These areas should be selected to maximize their complementarity (see below). Finally, species not already captured in the network would be added on an individual basis.

Despite the contribution of biodiversity management areas to a conservation strategy, many mobile species and landscape processes require far more area than will ever be managed strictly for biodiversity (Brussard, 1991). The fate of these species will rest on the management of multiple-use lands surrounding nature reserves (Scott et al., 1990). Gap analysis data layers provide information about the context of areas being managed for different values, as well as opportunities to maintain connectivity between natural areas through landscape linkages (Csuti, 1991).

#### METHODS OF ANALYSIS: SELECTING COMPLETELY REPRESENTATIVE BIODIVERSITY MANAGEMENT NETWORKS

The simplest way to ensure that all ecosystems and species are represented in areas managed for biodiversity is to designate several areas for each species or ecosystem. Given sufficient time, local populations or ecosystems will experience catastrophic stochastic events. Species persist because populations elsewhere escape these events (Goodman, 1987). This strongly argues for multiple representation of species or ecosystems throughout their geographic range. Tear et al. (1993) suggest protecting at least three viable examples of each element of biodiversity (e.g., vegetation type, species) within each ecoregion.

Evidence from the study of island biogeography further suggests that only large areas will maintain anything like their original complement of species over evolutionary time. Barro Colorado Island, with an area of 16 km<sup>2</sup>, has lost one-fourth of its species since its isolation in 1914 (Wilcox, 1980). Brown (1986) suggests that areas smaller than 500 km<sup>2</sup> are likely to lose more than half their species in a few thousand years.

There is a practical limit to the amount of land that any nation can manage primarily to maintain biodiversity (Pressey, 1990). The need for relatively large areas for management of biodiversity (e.g., >500 km<sup>2</sup>) demands that those areas be maximally efficient in capturing all species and ecosystems. It simply is not possible to designate an appropriately large area (let alone several areas) for management of each and every species and ecosystem. By taking advantage of the fact that examples of many ecosystems occur in close proximity to one another and that species ranges overlap, it is possible to identify a subset of areas in which most elements of biodiversity are represented.

Pressey et al. (1993) articulate three principles for selecting reserve networks: (1) complementarity: the greatest efficiency in adding species or communities to a set of areas will be achieved if the areas are maximally different (or complementary); (2) flexibility: there are usually alternative areas that can add particular species or communities to a reserve network, therefore the selection

process is somewhat flexible; and (3) irreplaceability: some elements of biodiversity will occur only in one area, therefore these areas must be a part of any completely representative biodiversity management network—they are irreplaceable.

Considerable progress on quantitative approaches to efficient selection of reserve networks using iterative algorithms has been made in Australia (Bedward et al., 1992; Margules, 1989; Nicholls and Margules, 1993). A simple reserve selection algorithm identifies the area with the most species or types of vegetation, then the area with the most species or types of vegetation not represented in the first choice, and so on. In some cases, it is more efficient to use an algorithm that selects the area with the rarest element first, then the area with the next rarest element that also contains the largest number of other elements, and so on (Pressey and Nicholls, 1989). Iterative algorithms can be extended to ensure that each element (species or ecosystem) is represented a number of times (once, twice, three times, etc.).

Similar results can be obtained if all possible combinations of two, three, four (and so on) areas are examined to identify those combinations that capture the most diversity at each step (Figure 22-8). This analysis (an example of an exact set coverage problem; Pennisi, 1993) identifies a family of areas, one of which is selected at each step. It also presents a more difficult computational problem and can be calculated for only a small number of steps for state or regional data sets. For example, for the state of Idaho, there are  $25.3 \times 10^{13}$  possible combinations of 389 hexagons taken 7 at a time.

While maximizing species richness (or diversity of types of vegetation) at each step in a selection process can lead to an efficient reserve network (Scott et al., 1987; Terborgh and Winter, 1983), some species may not occur in centers of richness. An area may contain relatively few species but still be a necessary part of a completely representative biodiversity management network due to the presence of species not found in other areas. Kareiva (1993), Prendergast et al. (1993), and Saetersdal et al. (1993) have pointed out that centers of species richness for different groups, such as birds and butterflies, may not coincide (see also Robbins and Opler, Chapter 6 in this volume). The analysis of data layers is therefore a complex process, proceeding hierarchically from the community level of organization to complementary areas of high species richness and finally to species still not represented. Separate analyses for major taxonomic groups or ecoregions may identify priority areas with higher internal diversity than an analysis of all species throughout a political unit, where earlier choices are dominated by the taxon with the most species (i.e., birds) and later choices add only a few species but are otherwise redundant with earlier choices.

Because most species or plant communities occur in more than one area, the analysis itself becomes iterative. As an element of biodiversity occurs in more management areas, the priority of other areas which contain that element is reduced. Other factors can be used to assign priority among management areas.

Including threat, proximity to other areas (Nicholls and Margules, 1993), and taxonomic distinctness (Faith, 1994; Vane-Wright et al., 1991). Pressey and Bedward (1991) and Stoms (1994) have pointed out the influence of scale on biodiversity analysis. Determining the optimally sized subunits of a region for biodiversity remains an important research issue in conservation evaluation.

Predicting the biological value of priority areas for managing biodiversity is an efficient first step toward developing a conservation strategy. It must be followed by field reconnaissance to verify the value and condition of each area and to apply the principles of conservation biology to boundary delineation. Patterns of land ownership and economic activities affect the potential of managing any particular area solely for biodiversity and can be factored into the iterative process of building a reserve network.

### AN EXAMPLE FROM IDAHO

The distribution of 119 types of vegetation and 357 species were mapped for the Idaho gap analysis. The representation of types of vegetation in managed areas is discussed elsewhere (Caicco et al., 1995). An analysis performed by A. R. Kiestler and his colleagues (Kiestler et al., 1996) determined that 49 terrestrial vertebrates were inadequately represented on existing managed areas in Idaho. Species were defined as inadequately represented on existing managed areas if they occurred less than three times on at least 10,000 contiguous hectares of land managed primarily for native species and natural ecosystems. The state was divided into 635 km<sup>2</sup> hexagonal sampling units following White et al. (1992). An exact set coverage algorithm identified 119 combinations of 4 hexagons in which 47 of 49 unprotected species were represented (Figure 22-8). Predicted distributions of unprotected species need to overlap hexagon boundaries only slightly to be assigned to a hexagon; therefore, actual areas that would support viable populations of these species will differ considerably from hexagonal sampling units. Analyses of the same data set using different definitions for unprotected species or different sample unit sizes are expected to identify somewhat different priority areas. The analysis presented here is one of many that can be integrated into a flexible conservation strategy for a completely representative network of areas that can be managed for the long-term maintenance of biodiversity.

### ACKNOWLEDGMENTS

We thank Christopher R. Margules and Robert L. Pressey for their comments on Australian approaches to conservation evaluation. Bart R. Butterfield developed distribution maps for species in Idaho (Figures 22-5 and 22-6), and A. Ross Kiestler carried out the exact set coverage analysis for Idaho that is illustrated (Figure 22-8).

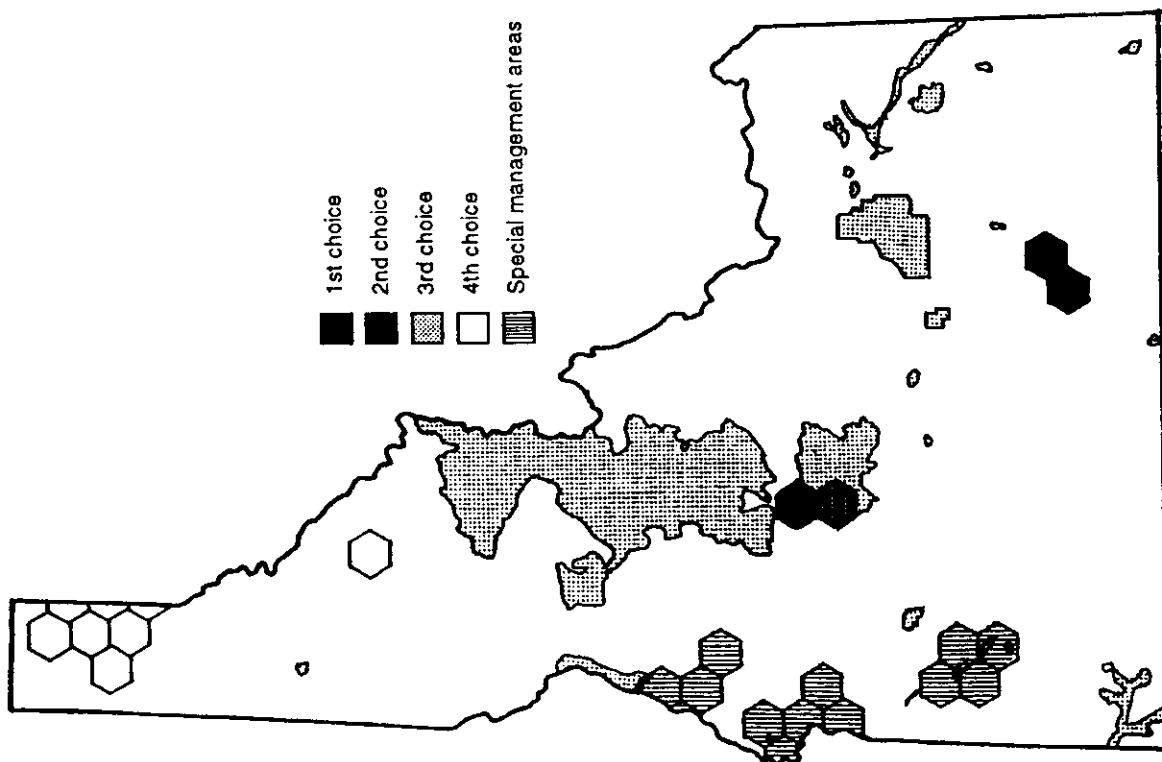


FIGURE 22-8 An exact set coverage algorithm identified four 635 km<sup>2</sup> areas in Idaho in which underrepresented species in existing reserves are predicted to occur. One choice from each of the four families will yield a set of four hexagons in which 97% of unprotected species are predicted to occur. Hexagon boundaries are arbitrary and are disregarded when designing boundaries for biodiversity management (Kiestler et al., in press).

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## A COMPARISON OF RESERVE SELECTION ALGORITHMS USING DATA ON TERRESTRIAL VERTEBRATES IN OREGON

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### Abstract

We compare the number of species represented and the spatial pattern of reserve networks derived using five types of reserve selection algorithms on a set of vertebrate distribution data for the State of Oregon (USA). The algorithms compared are: richness-based heuristic algorithms (four variations), weighted rarity-based heuristic algorithms (two variations), progressive rarity-based heuristic algorithms (11 variations), simulated annealing, and a linear programming-based branch-and-bound algorithm. The linear programming algorithm provided optimal solutions to the reserve selection problem, finding either the maximum number of species for a given number of sites or the minimum number of sites needed to represent all species. Where practical, we recommend the use of linear programming algorithms for reserve network selection. However, several simple heuristic algorithms provided near-optimal solutions for these data. The near-optimality, speed and simplicity of heuristic algorithms suggests that they are acceptable alternatives for many reserve selection problems, especially when dealing with large data sets or complicated analyses. © 1997 Published by Elsevier Science Ltd. All rights reserved

### INTRODUCTION

The resources that can be devoted to the conservation of biodiversity are limited. Existing nature reserves constitute a small fraction of total area, and there are limited funds available to expand the current system of reserves. In addition, many existing natural areas

managed for conservation were selected not for their biological value but because of their scenic beauty or because they had no obvious economic value (Pressey, 1994). Given these facts, it is critical that conservation resources be utilized efficiently so that most, if not all, species and ecosystems are represented in a limited reserve network. As Margules *et al.* (1988) observed, you cannot manage nature reserves to preserve elements of biodiversity if they are not included in the reserve network in the first place.

A number of approaches to the problem of selecting which sites to include in a reserve network have been suggested. A common approach for the site selection problem is to use a stepwise (iterative) algorithm (e.g. Kirkpatrick, 1983; Ackery & Vane-Wright, 1984; Margules *et al.*, 1988; Pressey & Nicholls, 1989; Rebelo & Seigfried, 1990; Vane-Wright *et al.*, 1991; Bedward *et al.*, 1992; Nicholls & Margules, 1993; Kershaw *et al.*, 1994; Margules *et al.*, 1994; Lombard *et al.*, 1995; Williams *et al.*, 1996). The "greedy" (richness-based) algorithm starts with the site containing the most species and sequentially includes sites that add the most additional species. The greedy algorithm has the advantage of speed and simplicity. In addition, by design, it incorporates the principle of complementarity (Pressey *et al.*, 1993). Other stepwise algorithms, "rarity-based" algorithms, choose sites in order of the rarity of species they contain or weight heavily species with small distribution. Rarity-based algorithms tend to be more effective than the richness-based greedy algorithm in finding the minimum number of sites necessary to represent all species at least once (Kershaw *et al.*, 1994). A somewhat different approach to the site selection problem is to make use of spatial patterns in the data. Starting from a given solution, such as the greedy algorithm, an

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improved solution may be found by searching for substitute sites in the neighborhood of the original solution. This operation forms the basis of the "simulated annealing" algorithm.

As has been noted by a number of authors, heuristic algorithms may not find an optimal solution to selecting a reserve network (May, 1990; Vane-Wright *et al.*, 1991; Underhill, 1994; Camm *et al.*, 1996; Pressey *et al.*, 1996a; Williams *et al.*, 1996). Optimal solutions to the reserve network problem can, at least in theory, be found by application of integer programming algorithms developed in operations research, such as linear programming-based branch and bound algorithms. These algorithms have been applied to the design of a reserve network in several studies (Cocks & Baird, 1989; Sætersdal *et al.*, 1993; Church *et al.*, 1996; Willis *et al.*, 1996). When the number of potential reserve sites is large or the stated objective is more complex than representing a species once, a branch and bound algorithm may not find a solution in a reasonable amount of time (Pressey *et al.*, 1996a).

The purpose of this paper is to compare the performance of different types of reserve selection algorithms: (a) greedy richness-based algorithms; (b) rarity-based algorithms; (c) a simulated annealing algorithm; and (d) a branch-and-bound algorithm. A linear programming-based branch and bound solution is, by definition, an optimal (efficient) solution to the reserve network selection problem, which provides a benchmark to measure the performance of other algorithms. However, because it may not be possible to find a solution for large or complex problems using a branch-and-bound algorithm, it is important to understand how well or poorly alternative methods work. In general, we would like to know both the speed with which a solution is found and how close the solution is to optimal. We compare the performance of 19 algorithms on terrestrial vertebrate species distribution data for the State of Oregon (USA) on the basis of both rates of richness accumulation and the total number of sites required to represent all species at least once.

#### DEVELOPMENT OF THE SPECIES DISTRIBUTION DATA BASE FOR OREGON

Distribution maps for 426 species of terrestrial vertebrates that breed in the State of Oregon were developed as a part of a pilot program of a cooperative national biodiversity mapping effort in the United States, known as the Biodiversity Research Consortium. We selected this subset of all species for analysis because their distributions are the best known. Observations of animals in the field, often accompanied by voucher specimens, form the basis of our knowledge of species distributions (Udvardy, 1969). Distribution maps can be developed from locality records in a number of different formats. A simple approach to data modelling inter-

polates distribution patterns by placing a boundary around marginal records for a taxon. Grid-based maps record the occurrence of a species in cells of a regular grid (e.g. Sharrock, 1976; Udvardy, 1981). This format makes it possible to record specific information about the species in each grid cell. We created grid-based distribution maps, using a coverage of 635 km<sup>2</sup> hexagons, that were developed for the US Environmental Protection Agency (White *et al.*, 1992). There are 441 sampling units that completely or partly overlap the political borders of Oregon. The reserve selection algorithms discussed here are not limited by either the taxa, number of species in the data set, or any particular spatial unit of analysis. Many geometric, political or economic spatial units, as well as many different taxa, have been used with site selection algorithms (e.g. Margules *et al.*, 1988; Bedward *et al.*, 1992; Kershaw *et al.*, 1994; Williams, 1994). Distributional information for species (or other elements of biodiversity, such as land systems) is the only data requirement for this type of spatial analysis.

Relatively few regions in Oregon have been intensively surveyed, so many sites (hexagons) lack occurrence records. In constructing the distribution maps, a method of interpolating the probable presence of a species between confirmed records of occurrence was used. The probability of a species occurring in a site (hexagon) was given one of three ratings: (1) confident—a verified sighting of the species in the site has occurred in the two past decades; (2) probable—the site contains suitable habitat for the species, there have been verified sightings in nearby sites, and in the opinion of a local expert, it is highly probable that the species occurs in the site; and (3) possible—no verified sightings have occurred in the site, the habitat is of questionable suitability for the species, and in the opinion of a local expert, the species might occur in the site. The ranking of possible is highly speculative. Only the classifications of confident and probable were used to assign the presence of a species in a site. All distribution maps were circulated to local experts for review prior to use of the species data base in this analysis.

#### DESCRIPTION OF ALGORITHMS

The reserve site selection problem can be represented formally as follows:

$$\text{Max } \sum_{i \in I} y_i \quad (1)$$

subject to

$$\sum_{j \in N_i} x_j \geq y_i \quad \text{for all } i \in I \quad (2)$$

$$\sum_{j \in J} x_j \leq k \quad (3)$$

$$y_i = (0, 1) \quad \text{for all } i \in I \quad (4)$$

$$x_j = (0, 1) \quad \text{for all } j \in J. \quad (5)$$



where  $J = \{j \mid j = 1, \dots, n\}$  denotes the index set of candidate reserves from which to select, and  $I = \{i \mid i = 1, \dots, m\}$  denotes the set of the species to be covered. The set  $N_i$ , a subset of  $J$ , is the set of candidate reserves that contain species  $i$ . The variable  $x_j = 1$  if site  $j$  is selected, 0 if site  $j$  is not selected. Constraint (3) limits the total number of sites selected to no more than  $k$ . The variable  $y_i$  will be one except when  $x_j = 0$  for all  $j$  in  $N_i$  (since constraint (2) will force  $y_i = 0$  in that case). In words, constraint (2) enforces that the species not be counted as preserved if none of its sites is selected. The following algorithms represent different ways of finding solutions to this problem.

#### Greedy (richness-based) algorithms (algorithms 1–4)

In the richness-based greedy algorithm, the first site chosen is the one that has maximal species richness. Inclusion of more sites is done so that at each step, the inclusion of the next site adds the most additional species to those already represented. When two or more sites add the same number of additional species, several procedures can be used to break ties. In algorithm 1, when there is more than one site that yields that maximum number of additional species at a step, we choose the first site encountered (i.e. the site with the lowest site number). In algorithm 2, for each site that yields that maximum number of additional species at a step, we choose the site with the highest range-size rarity score (see below) for the complementary species (Williams, 1994). The algorithm can be modified to check for within-set redundant choices, i.e. sites selected that are found at subsequent steps to contribute no unique species (Williams *et al.*, 1996). In these data, no redundant site selections were found.

Where computationally feasible, the optimal solution is guaranteed by enumerating all possible combinations of sites. In this data set, complete enumeration is practical with four sites or fewer. Algorithm 3 begins with the complete enumeration solution through four sites. Beyond this point, a greedy algorithm (algorithm 1) is used.

Algorithm 4 begins with a greedy algorithm (algorithm 1) as an initial solution. After completing the greedy solution, the algorithm attempts to solve a Lagrangian dual formulation of the reserve site selection problem. Initial dual multipliers are chosen, based on the greedy solution, and the numerical technique known as sub-gradient optimization (Fisher, 1981) is used iteratively to update the dual multipliers. At each iteration, a feasible solution to the problem is generated. If it is better than the current solution (the greedy solution at first), then the current solution is replaced by this improved solution. This technique has the added feature that it generates a bound on the optimal solution, allowing us to know the maximum deviation that the current solution can be from the optimal solution. This heuristic algorithm is phase one of a two-phase exact branch and bound algorithm described in Downs and Camm (1996).

#### Rarity-based algorithms

##### *Rarity weight algorithms (algorithms 5 and 6)*

These algorithms weight site selection by the relative rarity of the fauna in each site (e.g. Rebelo & Seigfried, 1990; Williams *et al.*, 1993; Kershaw *et al.*, 1994). A score is calculated for each site based on: (1) the number of species; and (2) how infrequent the species are among all the sites. In the algorithm weighting richness by inverse range-size rarity (algorithm 5), each species is scored as the inverse of the number of sites in which it occurs. In the algorithm weighting richness by the inverse square of range size (algorithm 6), each species is scored as the inverse of the square of the number of sites in which it occurs. The site score is the sum of the component species scores. The selection algorithm proceeds by selecting the site with the highest score. The scores are then recalculated with the represented species removed, and the site with the highest new score is then selected. This process is continued until all species have been represented.

##### *Progressive rarity algorithms (algorithms 7–17)*

We used 11 algorithms that are based on the algorithm described by Margules *et al.* (1988). The first sites selected are those that contain species unique to that site (i.e. occur in no other sites). Next, a site containing the least frequent unrepresented species (i.e. those species occurring in just two sites if there are any, if not, in three sites, etc.) is chosen. If there are ties, the different algorithms use a number of different rules for which sites to select next. The rules used and the order in which these rules are used are described in Table 1. Algorithms 9–17 contain a random selection rule. Each of these algorithms was run 100 times. Results reported are for the best of the 100 runs. Algorithms 8–17 check for and eliminate redundant sites. In addition, algorithm 8 reorders the sites in the chosen set to maximize the number of species covered at each step.

##### **Simulated annealing (algorithm 18)**

This algorithm begins with the complete enumeration solution through four sites. Beyond this point, an algorithm consisting of a spatially explicit variation of simulated annealing methods is used (Kirkpatrick *et al.*, 1983; Press *et al.*, 1992). For each  $n$  greater than 4, an initial or "seed" set of  $n$  sites was determined by choosing the first four sites to be those found by complete enumeration and then using a greedy algorithm (algorithm 1) to determine an additional  $n - 4$  sites. Additional seed sets were then chosen by fixing all possible combinations of 2 of the initial seed set sites and then determining the remaining  $n - 2$  sites using algorithm 1. This process yields a number of distinct seed sets up to the number of possible combinations of two sites taken from a set of  $n$  sites. Annealing was then performed on each of these seed sets by setting a radius about each site in the seed set and randomly searching the space within this radius.

Table 1. Rarity-based algorithms

A.	Description of the rules used in the algorithms
1.	<i>Unique</i> : choose sites with a species that is unique to that site.
2.	<i>Next Rarest</i> : choose a site containing the next least frequent unrepresented species (i.e. those species occurring in just two sites if there are any, if not in three sites, etc.).
3.	<i>Greatest Number of Next Rarest</i> : choose the site containing the greatest number of the next least frequent unrepresented species.
4.	<i>Next Next Rarest</i> : choose a site containing the next next least frequent unrepresented species.
5.	<i>Greatest Number of Next Next Rarest</i> : choose the site containing the greatest number of the next next least frequent unrepresented species.
6.	<i>Richest</i> : choose the site with the highest number of unrepresented species.
7.	<i>Percent Richest</i> : choose the site with the highest percentage of unrepresented species out of the total number of species in the site.
8.	<i>Total Rarity</i> : choose the site with the highest sum of rarity values for all unrepresented species, where the rarity value for a species is the inverse of the number of sites containing the species.
9.	<i>Average Rarity</i> : choose the site with the highest average rarity value for all unrepresented species.
10.	<i>Random Selection</i> : site is randomly chosen from eligible sites.
11.	<i>First Encountered</i> : choose the first site encountered (lowest number site).
B.	Algorithm Description (order of application of rules).
Algorithm 7:	
(a)	<i>Unique</i> .
(b)	<i>Greatest Number of Next Rarest</i> : ties broken with <i>Richness</i> and further ties broken with <i>First Encountered</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 8:	
(a)	<i>Unique</i> .
(b)	<i>Greatest Number of Next Rarest</i> : ties broken with <i>Greatest Number of Next Next Rarest</i> , further ties broken with <i>First Encountered</i> .
(c)	Repeat (b) until all species have been represented.
(d)	Selected sites are re-ordered to maximize complementary richness at each step.
Algorithm 9:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 10:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Richest</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 11:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Average Rarity</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 12:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Total Rarity</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 13:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Next Next Rarest</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 14:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Percent Richest</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 15:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Richest</i> , further ties broken with <i>Next Next Rarest</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 16:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Richest</i> , further ties broken with <i>Total Rarity</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.
Algorithm 17:	
(a)	<i>Unique</i> .
(b)	<i>Next Rarest</i> : ties broken with <i>Richest</i> , further ties broken with <i>Next Next Rarest</i> , further ties broken with <i>Total Rarity</i> , further ties broken with <i>Random Selection</i> .
(c)	Repeat (b) until all species have been represented.

As the algorithm progressed the search radius was decreased analogously to the decrease in temperature in classical annealing. Because the simulated annealing algorithm takes advantage of spatial correlations between the seed sets and optimal solution sets, the effectiveness of the algorithm is inversely proportional to the distance between the members of the seed sets and the desired solution set members.

#### Branch and bound algorithm (algorithm 19)

Optimal solutions for the mathematical model of the reserve selection problem may be solved using a linear programming-based branch-and-bound algorithm. Initially, the linear programming (LP) relaxation of the integer programming model (that is, the binary restrictions replaced by lower and upper bounds of 0 and 1) is solved. If the LP relaxation is an integer, the optimal solution has been found. If one (or more) of the variables is fractional, branching takes place. A branch is the creation of two new problems (nodes), one with the fractional variable set to 0 and the other with the fractional variable set to 1. The LP relaxation for each of the new problems is solved and the process repeated until all nodes under consideration have been fathomed. A node is fathomed if its solution is infeasible, is an integer, or has a value worse than the current incumbent integer solution.

The basic branch-and-bound process described above can be computationally intense. However, intelligent preprocessing of problem data and algorithmic improvements make the solution of relatively large problems feasible. As an example of preprocessing for the reserve selection problem, if two or more species are located in the exact same set of locations, only one of them needs to be explicitly represented in the model (with an objective function coefficient equal to the number of such species). This simple scheme reduces the number of coverage constraints from 426 to 368 in the Oregon data, a reduction of roughly 14% in the row size of the model. Algorithmic enhancements, such as logical and cost-based variable pegging (fixing a variable permanently to 0 or 1 in the branch-and-bound), are helpful. The software package LINDO used in this work uses a cost-based pegging scheme.

Often, it is useful to find multiple combinations of sites that yield optimal or near-optimal solutions. Finding multiple solutions can be done by resolving the model with a constraint that prevents the original solution from being chosen. Using this method repeatedly allows us to find as many solutions, ranked in order of declining number of species represented, as desired (Camm *et al.*, 1966).

## RESULTS AND ANALYSIS

The main results of the algorithm comparison using data on all 426 breeding terrestrial vertebrate species in

Oregon are reported in Table 2. The rows of Table 2 represent the different number of reserve sites included in the reserve system, starting with one site and continuing up to the total number of sites necessary to represent all 426 species in the reserve system at least once. The results of different algorithms are reported in different columns. Each entry in the table corresponds to the number of species covered in the reserve system selected by an algorithm for a given number of reserve sites. Figure 1 graphs the accumulation curve for a subset of the algorithms.

The results of the branch and bound algorithm (algorithm 19) are reported in the last column of Table 2. The branch and bound algorithm solution gives the maximum number of species that can be covered with a given number of sites for these data and the minimum number of sites needed for complete representation of all species. This solution represents a useful benchmark with which to compare the performance of other algorithms. Not only can we judge relative performance of various algorithms but we can also judge how close an algorithm comes to the optimal solution.

Most of the species in Oregon can be represented in a reserve system with relatively few sites. In the branch-and-bound solution (algorithm 19), over 90% of the species can be represented with five sites (384/426), and over 95% of the species can be represented with 10 sites (406/426). Beyond 10 sites, adding an additional site yields an increase of only one or two species in all of the richness based algorithms. To represent all of the species in the state at least once in the reserve system requires selecting only 23 of the total of 441 sites. Like many temperate regions, the majority of species in Oregon have fairly wide spatial distribution after interpolation. Over 63% of species are located in more than 100 sites and less than 10% of the species are located in 10 sites or fewer. There are seven species that are located in a single site.

The rapid accumulation of species in relatively few sites, in contrast to the larger number of sites needed for complete representation, has implications for conservation planning. Noss (1987) has suggested that most species may be represented in relatively few areas representing major habitat types (the "coarse filter"), while the conservation needs of the small number of species not represented in those areas are best addressed on an individual basis (the "fine filter"). The results presented here offer another way of identifying a few areas in which most species are thought to be represented. These areas could form the nucleus of a network of ecosystem reserves. The identity and conservation needs of species not represented in the network could be examined to determine if they could be conserved in less ambitious ways.

One pattern that emerges from Table 2 is the different relative performance of greedy richness-based and rarity-based algorithms. Greedy richness-based algorithms do relatively well at finding large numbers of species when

Table 2. Species accumulation table

Alg. no. Site no.	1 Simple Greedy	2 Greedy w Rarity Tie-Break	3 Enumeration and Greedy	4 Greedy w Subgradient Optimiz.	5 Inverse Rarity Weight	6 Sq. Inverse Rarity Weight	7 Progressive Rarity
1	254	254	254	254	221	224	224
2	306	306	318	306	290	290	290
3	347	347	356	356	330	305	330
4	365	365	374	374	354	345	345
5	379	379	384	384	363	357	357
6	388	388	390	388	372	361	361
7	394	394	394	394	376	365	365
8	398	398	398	400	380	373	373
9	401	401	402	403	388	381	379
10	404	404	404	404	396	396	381
11	406	406	406	406	399	401	386
12	408	408	408	408	401	403	390
13	410	410	410	410	403	405	391
14	412	412	412	412	405	407	392
15	414	414	414	414	407	409	394
16	415	416	415	416	410	411	397
17	416	417	416	417	414	413	407
18	417	418	417	418	416	414	415
19	418	419	418	419	418	416	416
20	419	420	419	420	420	418	417
21	420	421	420	421	421	421	420
22	421	422	421	422	422	423	422
23	422	423	422	423	424	425	424
24	423	424	423	424	425	426	426
25	424	425	424	425	426		
26	425	426	425	426			
27	426		426				

Alg. no. Site no.	8 Progressive Rarity	9 Progressive Rarity	10 Progressive Rarity	11 Progressive Rarity	12 Progressive Rarity	13 Progressive Rarity	14 Progressive Rarity
1	254	224	224	224	224	224	224
2	303	290	290	290	290	290	290
3	343	330	330	330	330	330	330
4	360	345	345	345	345	345	345
5	377	357	357	357	357	357	357
6	387	361	361	361	361	361	361
7	392	365	365	365	365	365	365
8	396	367	373	367	367	373	373
9	400	375	381	368	375	381	381
10	403	379	384	371	379	383	384
11	405	380	387	374	382	385	387
12	407	382	389	378	384	387	389
13	409	385	391	379	386	390	391
14	411	400	402	380	398	404	405
15	413	405	404	384	401	409	409
16	415	407	406	387	402	411	411
17	417	408	407	396	406	413	413
18	419	411	410	403	414	414	414
19	421	414	418	405	416	416	417
20	422	417	419	407	418	418	418
21	423	419	420	410	419	421	419
22	424	420	423	412	422	423	420
23	425	423	425	415	424	425	423
24	426	424	426	417	426	426	425
25		426		419			426
26				421			
27				422			
28				423			
29				426			

contd.

Table 2—continued

Alg. no. Site no.	15 Progressive Rarity	16 Progressive Rarity	17 Progressive Rarity	18 Enumeration and Simulated Annealing	19 Branch and Bound
1	224	224	224	254	254
2	290	290	290	318	318
3	330	330	330	356	356
4	345	345	345	374	374
5	357	357	357	384	384
6	361	361	361	390	390
7	365	365	365	395	395
8	373	373	373	398	400
9	381	381	381	403	403
10	384	384	384	405	406
11	387	387	387	407	408
12	389	389	389	409	410
13	391	391	391	411	412
14	405	405	405	413	414
15	410	408	410	415	416
16	412	410	412	417	418
17	414	412	414	418	419
18	415	413	415	419	420
19	418	416	418	420	422
20	419	418	419	421	423
21	422	419	422	422	424
22	424	420	424	423	425
23	425	423	425	424	426
24	426	425	426	425	
25		426		426	
26					
27					

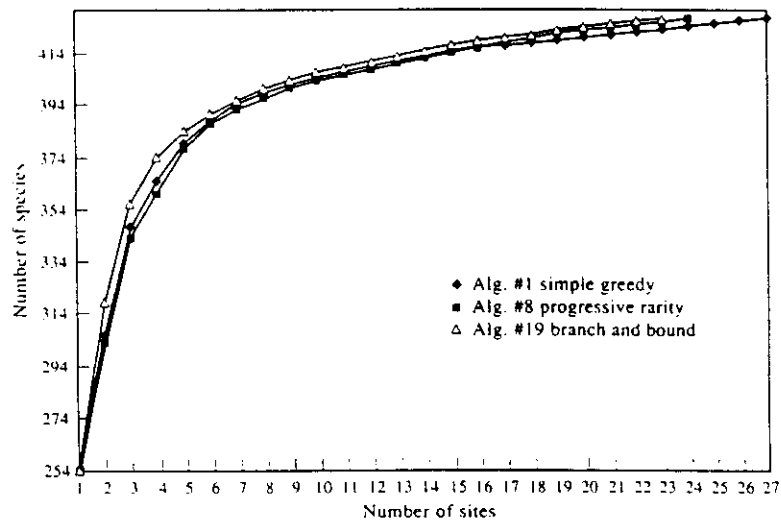


Fig. 1. Species accumulation curve.

the number of sites is restricted so that not all of the species can be covered. Rarity-based algorithms do well at finding a near-minimum number of sites needed to cover all species.

Greedy richness-based algorithms (algorithms 1-4) are near optimal, in the sense of covering a near-maximal

number of species, when the number of sites selected is between six and 15. All of these richness-based algorithms are within two species of the maximum number of species throughout this range. Between two and five sites, algorithms 1 and 2 fall well short of achieving the maximum number of species represented. The gap

between the solutions for algorithms 1 and 2 and the optimal solution is 12 species at two sites, 11 species at three sites, nine species at four sites, and five species at five sites. Algorithms 3 and 4 are optimal or near-optimal for a small number of sites, with the exception of algorithm 4 for two sites. In fact, algorithm 4 is optimal for one, three, four, five, eight and nine sites. However, none of the four algorithms does well at finding the minimum number of sites necessary to represent all species. All four algorithms need 26 or 27 sites to represent all species, which is more sites than needed by other algorithms included in the study, with one exception.

In contrast, many of the rarity-based algorithms (algorithms 5–17) represent the entire set of species in 24 sites. These algorithms place a high priority on sites that contain species with narrow distributions even though they may not contain a large number of species. Since many of these sites must be included in order to cover all species, rarity-based algorithms are relatively efficient in finding the minimum number of sites to represent all species (Kershaw *et al.*, 1994). Rarity-based algorithms, however, do not represent as many species as do simple richness-based algorithms when the number of sites is not close to the number needed to represent all species (Williams & Humphries, 1994). In general, rarity-based algorithms will not fare well in choosing reserve networks with many species when the number of sites allowed is small and where sites with rare species do not coincide with sites with numerous species.

Algorithms 9–17 were also used in a recent study by Pressey *et al.* (1996) using data from New South Wales Western Division. Table 3 shows a comparison of the relative efficiency of algorithms on the Oregon and Western Division Data in finding the minimum number of sites necessary to represent all species. Both the minimum values and the average values are reported. In general, the algorithms performed relatively better on the Oregon data than they did on the Western Division data. Using the Oregon data, the average over the nine algorithms for the minimum number of sites to represent

all species was 24.8 sites, only 7.7% above the minimum number of sites (23). Over all 100 runs for each of the algorithms, the average number of sites needed to represent all species was 25.9 sites, 12.7% above the minimum. Using the Western Division data, the average over the nine algorithms for the minimum number of sites to represent all species was 63.7 sites, 17.9% above the minimum number of sites (54). Using all runs, the average number of sites needed to represent all species was 67.2 sites, 24.4% above the minimum. With the exception of algorithm 12, those algorithms that performed well (poorly) in the Oregon data did well (poorly) in the Western Division data. Algorithm 12 needed only 24 sites to represent all the species in Oregon but needed 66 sites to do so in the Western Division. Algorithms 10, 13, 15, 16 and 17 also needed only 24 sites in Oregon but all of these algorithms needed less than 60 sites in the Western Division. Algorithms 9 and 14 needed 25 sites in Oregon and the high 60s in the Western Division. Algorithm 11 did relatively poorly in both data sets, indicating that the average rarity rule is not an effective selection rule.

The advantages of both richness and rarity algorithms may be obtained to a large extent by combining them sequentially (Williams, 1994). Algorithm 8 is equal to the best of the rarity algorithms for obtaining representation of all species with relatively few sites, and yet by re-sequencing for complementary richness, it achieves a higher species accumulation rate.

The simulated annealing algorithm (algorithm 18) is either optimal or near-optimal for cumulative richness through the entire range of sites. Up to four sites, algorithm 18 uses complete enumeration of all combinations and by definition finds the maximum number of species covered. For these data, the simulated annealing algorithm is able to find optimal solutions beyond four sites as well (at five, six, seven and nine sites). The simulated annealing algorithm is usually midway between the optimal solution and the solution for a greedy algorithm beyond nine sites. In order to represent all species, the simulated annealing algorithm needs 25 sites.

Table 3. Comparative results of nine algorithms for complete representation of all species in Oregon and New South Wales Western Division data

Algorithm	Oregon Data		Western Division Data	
	Minimum Number of Sites	Average Number of Sites	Minimum Number of Sites	Average Number of Sites
Optimal Solution	23	—	54	—
Algorithm 9	25	28.12	69	75.47
Algorithm 10	24	24.65	57	59.75
Algorithm 11	29	33.09	79	86.94
Algorithm 12	24	25.69	66	68.37
Algorithm 13	24	24.00	59	62.33
Algorithm 14	25	25.00	67	71.68
Algorithm 15	24	24.00	59	60.25
Algorithm 16	24	24.71	58	59.65
Algorithm 17	24	24.00	59	59.98

A key concern in conservation planning is flexibility (Pressey *et al.*, 1993). Having flexibility in choosing sites for the reserve network may be important because constraints may preclude certain combinations of sites from being selected. In the Oregon data, there are usually many different combinations of the same number of sites that represent the maximum number of species. In Table 4, using the branch-and-bound algorithm, we report the number of combinations of sites that yield the optimal solution for reserve networks from one site to 23 sites (full representation). Other algorithms, e.g. simulated annealing, are also capable of finding multiple solutions in cases where they find an optimal solution. There is a unique optimal reserve network when the number of sites is four or less. Also, there are few combinations that are even close to optimal. For example, for two sites, there is only one combination of sites that represents 317 species, one less than optimal, and only one combination of sites that represents 316 species. Somewhat surprisingly, there is also a unique optimal combination with eight sites, though here there are numerous combinations that yield near-optimal results. On the other hand, when the number of sites is more than 10, with the exception of 19 sites, there are more than 100 combinations of sites that yield the optimal solution. In the case of 12 sites, there are more than 1000 combinations that yield the optimal solution.

In Fig. 2, we show the irreplaceability values for the various sites in Oregon. Irreplaceability is the percentage of all fully representative sites in which each individual site occurs (Pressey *et al.*, 1994). There are 144 solutions (combinations of sites) that completely represent all species in the minimum number of sites. Note that 19 out of 23 sites show up in all solutions and have irreplaceability values of 100%. If we allow a larger number of sites to be reserves (e.g. 24 or 25 sites), the irreplaceability values for the sites that do not contain a species located in a single site will fall below 100%. Any combination of sites that involves selecting all 19 sites labeled with 100% in Fig. 2 and one site from each of the following sets of hexagons (each identified with its 5 digit label) constitutes an optimal path: (a) 24 651 or 24 652 (50%); (b) 24 520, 26 425 or 26 860 (33.3%); (c) 26 647, 26 967, 27 073 or 27 177 (25%); (d) 25 029, 25 030, 25 152, 25 153, 25 274 or 25 275 (16.7%).

In Fig. 3a, we show the spatial pattern of the reserve network solution for two algorithms, the branch and bound algorithm (algorithm 19) and the squared inverse rarity weight algorithm (algorithm 6) for 10 sites and for full representation. The squared inverse rarity weight algorithm solution is fairly representative of the spatial pattern of the solution of most of the rarity-based algorithms. For 10 sites (Fig. 3(a)) there is not much overlap between the solution of the branch-and-bound algorithm and the squared inverse rarity weight algorithm. Only three of the 10 site choices coincide and several choices lie in different parts of the state. The squared inverse rarity weight algorithm tends to pick

Table 4. Number of optimal solutions

Number of Reserve Sites	Number of Solutions
1	1
2	1
3	1
4	1
5	5
6	7
7	12
8	1
9	12
10	11
11	200+
12	200+
13	200+
14	200+
15	200+
16	200+
17	200+
18	200+
19	12
20	108
21	200+
22	200+
23	144

sites with species with restricted ranges, while the branch-and-bound algorithm tends to pick areas that have many complementary species. In contrast, at complete representation of all species in the reserve network, Fig. 3(b), 19 site choices can be the same for both algorithms. (Since there are multiple solutions for the branch-and-bound algorithm, there is some flexibility on which sites are included.) Two more site choices are adjacent and one more site choice is two sites apart. With complete representation, all sites containing species with restricted ranges tend to be chosen by all algorithms, leading to a convergence of spatial patterns.

In Fig. 3(c), we show the 10 sites that individually have the greatest number of species. Notice that all of these sites are clustered together in one part of the state. It is interesting to note that only one of these sites is chosen by the algorithms both at 10 sites and at full representation. These maps clearly show the importance of complementarity vs. species richness in designing a reserve system (Williams *et al.*, 1996).

One concern with using relatively complex algorithms like the branch and bound or the simulated annealing algorithm is that it may take so long to find a solution with these algorithms that using them on real conservation problems is not practical. This concern did not turn out to be a problem in our analysis conducted with the Oregon data. Using a 486 PC and a commercial software package (LINDO), it took 23.4 min to find the complete branch-and-bound algorithm solution for the maximum number of species that could be covered from

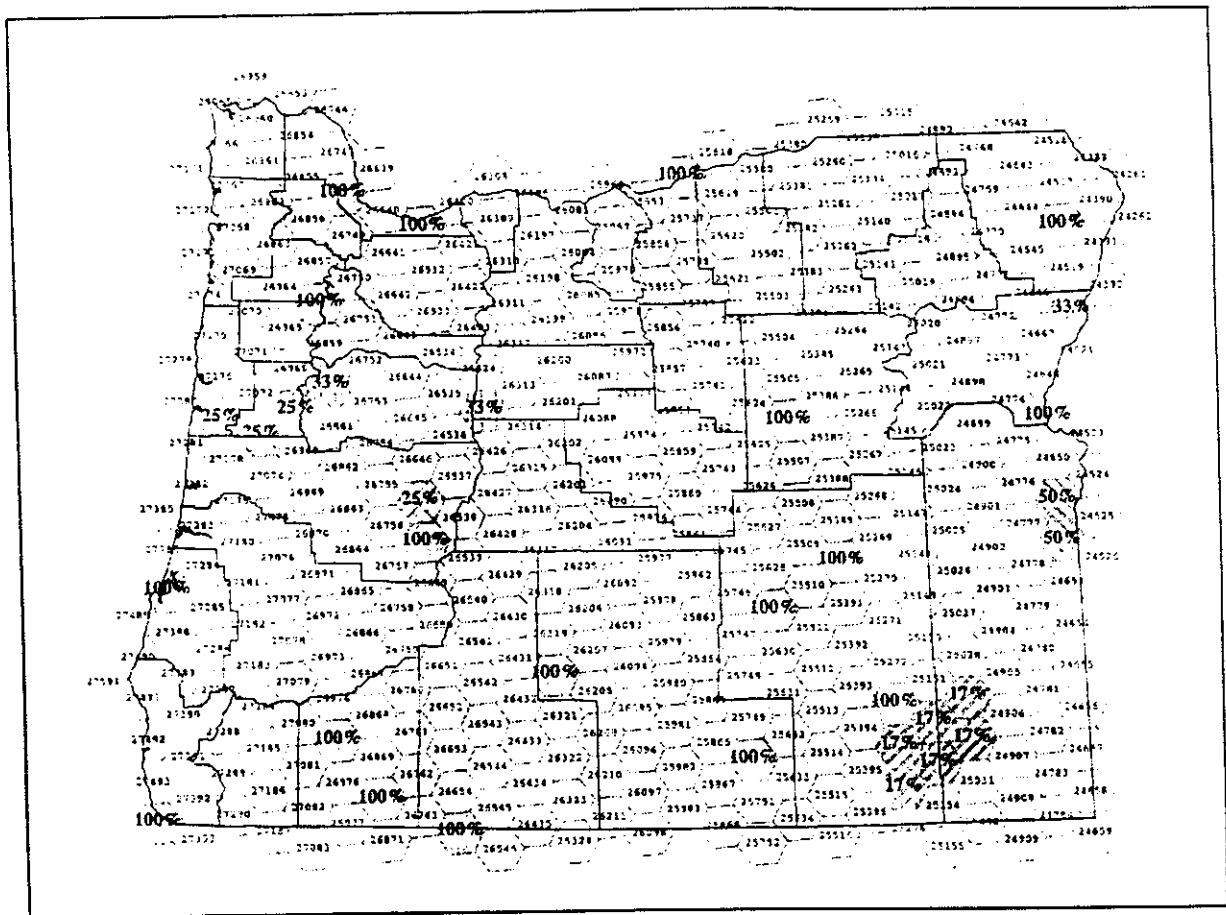


Fig. 2. Irreplaceability values for sites in Oregon.

one site up to full coverage (23 sites). The maximum time to find a solution for any given number of sites was 4.7 min for six sites. In 16 out of 23 cases, an optimal solution for a given number of sites was found in less than 1 min. Using more specialized software or a more powerful computer would shorten these times further. How much larger the data set can be in terms of sites or number of species or how much more complex the objective can become before the branch and bound approach becomes impractical is still an open question. In a problem with 1885 sites and 248 attributes (land systems), finding an optimal solution took 10 days on a SUN IPX workstation (Possingham *et al.*, 1993), though the solution time was reported to be cut to 10 h more recently (Possingham, pers. comm.). The simulated annealing algorithm also found a solution within a reasonable period of time. Complete enumeration is the time consuming part of the approach. Up to four sites, the solution takes  $\approx$  2.5 min. At four sites, it takes almost 2 h (119 min) to find the solution. However, beyond four sites, the time taken to find a path using simulated annealing is  $<$  1 min for any given number of sites.

At the other extreme, the simple richness and rarity algorithms take just 4–5 s (or 8 s with within-set redundancy checks at each step) on a 486 PC. Computing time is not an issue when using these algorithms, even with very large data sets.

## DISCUSSION

Reserve selection algorithms can be used to find efficient combinations of sites capable of representing a group of species in a region. The analysis yields results that are indicative of combinations of areas that may be high priority for conservation. This analysis, however, does not address issues of the size, shape, or quality of a natural area necessary to maintain viable species populations or functional ecosystems. No information is available in this data set about habitat condition in different sites. Field surveys are needed to confirm the conservation value of potential reserve sites. Further, landscape context should be considered during natural area design (Noss, 1987). Additional factors, such as acquisition and management costs, political constraints



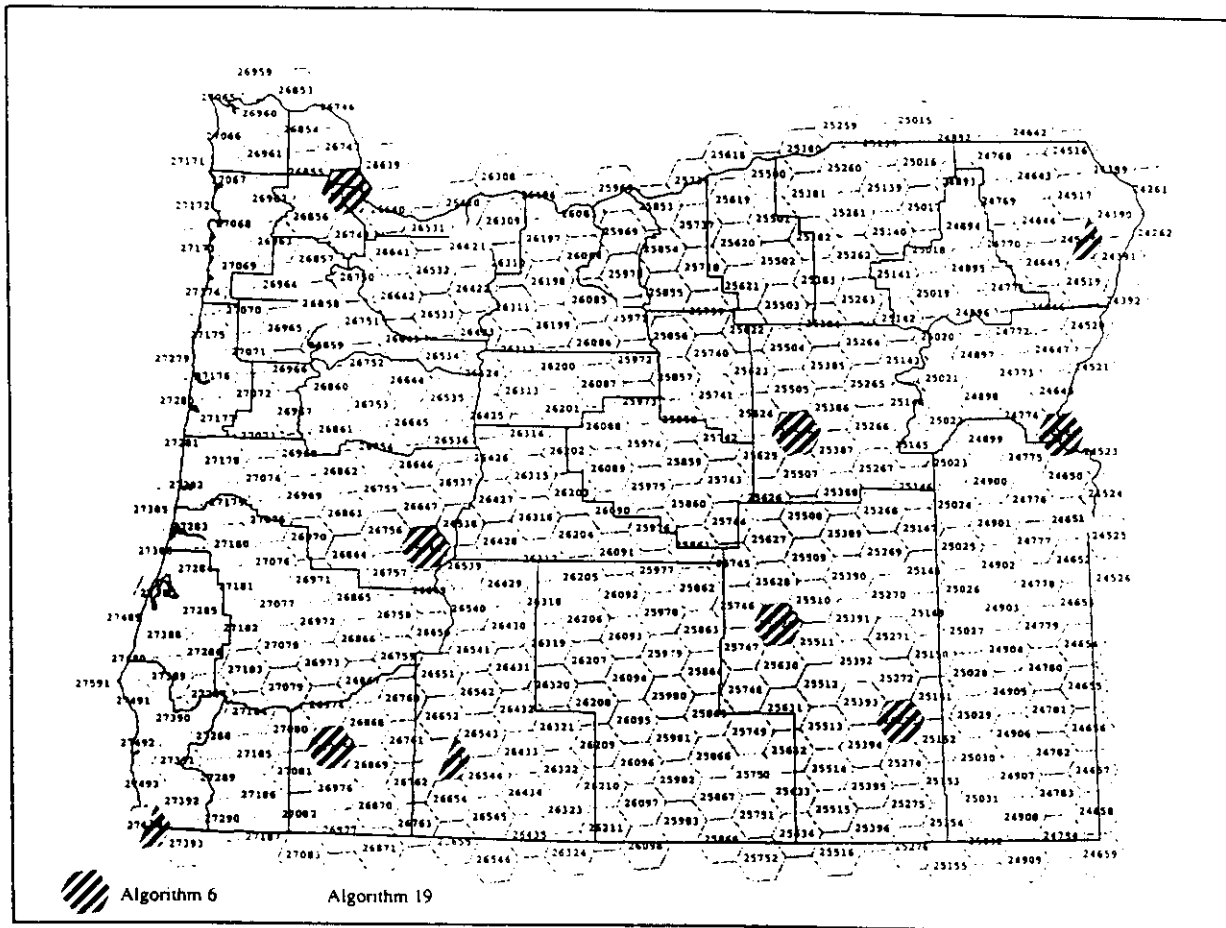


Fig. 3a. Branch-and-bound (algorithm 19) and square inverse rarity weight (Algorithm 6): 10 sites.

and proximity to other reserves may also need to be addressed when recommending a natural area network in a real-world context (Pressey *et al.*, 1996).

For simplicity, we have assumed that a species is represented in the reserve network if it is contained in at least one selected site. A more conservative approach would be to modify the algorithms to require multiple representations of each species (Williams *et al.*, 1996), or to require that a certain percentage of the species geographic range be represented. Algorithms can also be modified to give preference to sites in proximity to one another, increasing the opportunity for landscape linkages (Nicholls & Margules, 1993).

Many regions have existing natural reserves, which can be factored into the analysis. The effectiveness of the current reserve network can be evaluated by looking at coverage of the existing network and by comparing reserve networks both with and without a constraint to include the current reserve sites. Further, if the biological potential of a currently degraded site can be modelled, one can assess the contribution that restoring a particular site would have. In the Oregon data, the hexagonal grid cells used to develop species distribution maps are larger

than most natural areas. Quantifying the representation of species in existing natural areas will require higher resolution maps. Such maps are being developed for the Gap Analysis Program (Scott *et al.*, 1993; Scott & Csuti, 1997) by linking species to a higher resolution (100 ha minimum mapping unit) vegetation cover type map. While various algorithms are useful in identifying a minimum set of areas in which all species are predicted or known to be represented, we do not mean to imply that natural and semi-natural lands outside of nature reserves do not play an important role in maintaining regional species and ecosystem diversity (Scott *et al.*, 1990).

The combined terrestrial vertebrate data set used here represents only a small subset of all species, albeit ones about which we have the best distributional information. Several recent studies (Prendergast *et al.*, 1993; Saetersdal *et al.*, 1993; Lawton *et al.*, 1994; Williams & Gaston, 1994) have pointed out that areas of species richness ("hotspots") for different major taxa may not coincide, raising questions about the appropriateness of selecting a reserve network based on only a few major taxa. There is a difference, however, between selecting

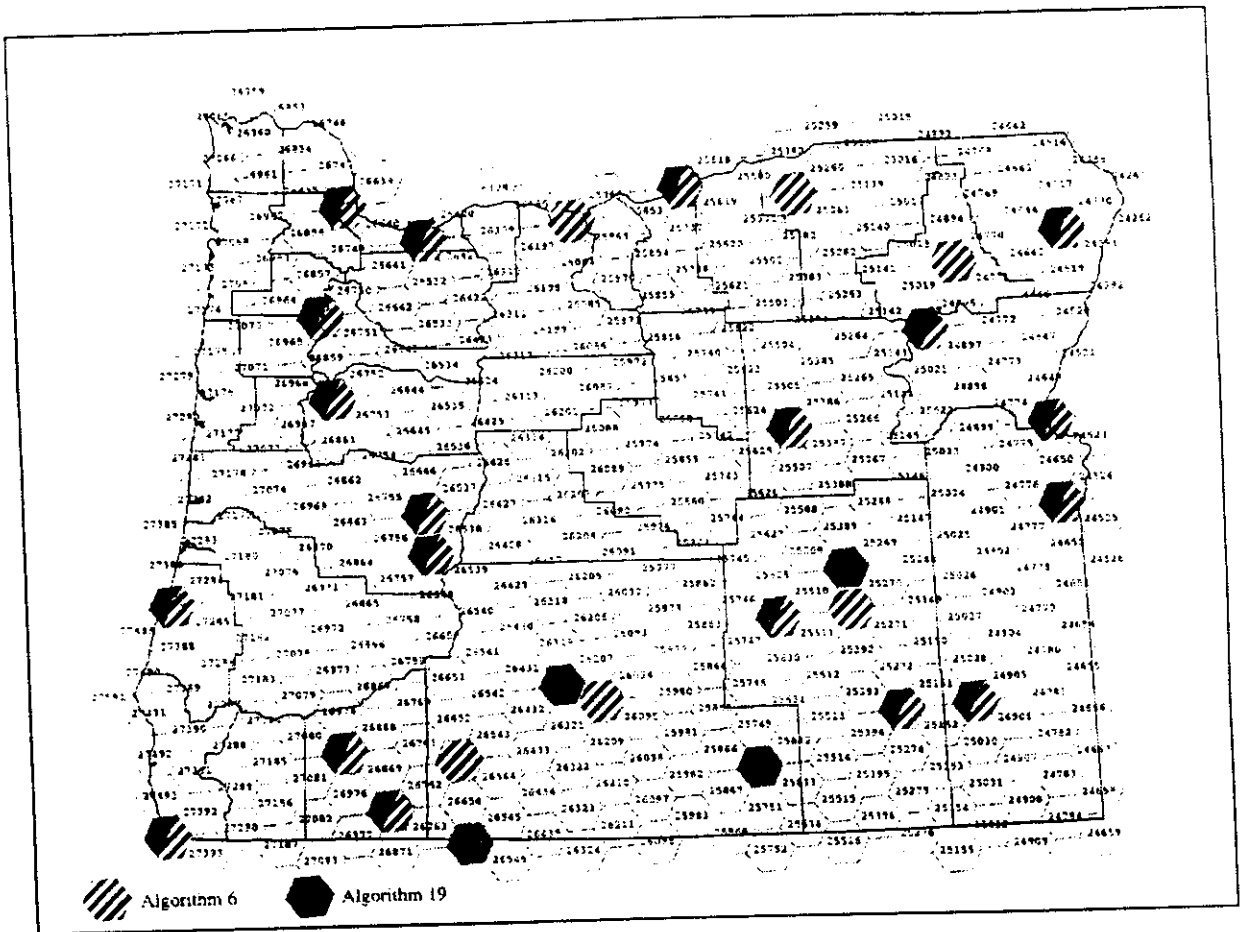


Fig. 3b. Branch-and-bound (algorithm 19) and square inverse rarity weight (Algorithm 6): full coverage.

hotspots for a taxon, whose species lists are often spatially correlated (Fig. 3(c)), and selecting a set of areas in which most or all species of the taxon are represented. These areas reflect dissimilar species lists, often the result of dissimilar environments. Complementary areas may be relatively depauperate, but are included because of maximally different species content. As a result, we hypothesize that a set of areas in which one major taxon is completely represented may also do a good job representing the diversity of unrelated taxa. Further analysis of the Oregon data set by some of us (Kiester, Huso and Sahr) supports this hypothesis among terrestrial taxa (vertebrates, trees and butterflies).

The number of sites needed to represent all species in a taxon varies greatly. Large-bodied, mobile species that are habitat generalists and have a wide geographic distribution need the fewest sites to be fully represented. Taxa that exhibit high beta and gamma diversity require a greater proportion of sites to represent all species in the region. In Natal, South Africa, all 570 bird species can be represented in 27 out of 166 quarter degree grid squares by an iterative richness algorithm, while all 65 carnivore and ungulate species can be represented in

nine sites. In contrast, plant species, that show much higher inter-site turnover due to their lower mobility and greater habitat specificity, require 140 of the 166 sites to represent all 6111 species. The 400 species of grasses require 51 sites to be fully represented (M. Kershaw, pers. comm.). When woodlands were selected iteratively in Norway, only 20% of the total area was needed to incorporate all bird species, compared to 75% to include all plant species (Saetersdal *et al.*, 1993).

Ideally, an evaluation should be made at a distinct biogeographic level to minimize the problem of giving equal weight to endemic species vs. those widely distributed outside of the region. Both Hunter and Hutchinson (1994) and Lesica and Allendorf (1995) argue the merits of protecting peripheral populations of widespread species. Regional conservation requirements may make it valid, in some cases, to target conservation of species that are rare in the region but common elsewhere—for example to represent ecotypic variation (Rebello, 1994). In general, however, we feel that conserving species that are locally rare but common elsewhere should not take precedence over conserving species that are globally rare. A practical solution to this

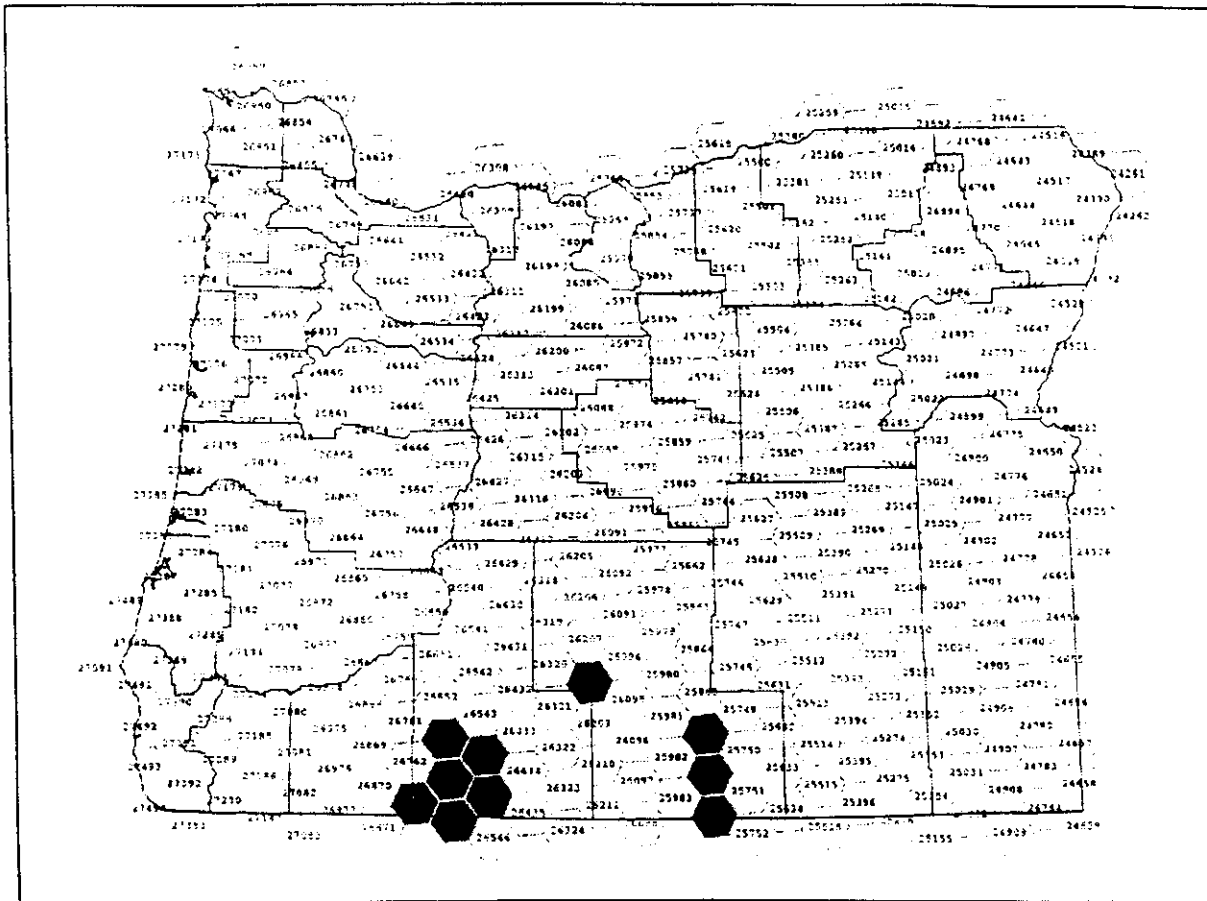


Fig. 3c. Sites of maximum species richness.

problem would be to apply a consistent criterion to eliminate species peripheral to the region of analysis or to base measures on data for rarity at the global scale (Williams *et al.*, 1996). In reality, most practical conservation decisions are made at national or other political levels. Sensible processing of the data, and choice of scale to be used can help to avoid some of these potential problems. We recognize the limitations inherent in carrying out a reserve selection exercise for a political unit, rather than for a biologically defined region, and intend to pursue bioregional analyses when data for surrounding states become available.

It should be noted that the data we used are still being edited and refined. Also, the data have not yet been subjected to field validation. Species lists for units of analysis (i.e. hexagons) are largely predicted rather than confirmed lists. A similar data set, developed for 419 terrestrial vertebrates in the State of Idaho (USA), was used to predict species lists for natural areas for which there were existing species lists based on field observation. Comparison of predicted and observed lists indicated a 11% omission error and a 21% commission error (Scott *et al.*, 1993), although some commission

errors may reflect species difficult to detect. We expect similar levels of accuracy in Oregon. When an actual reserve is created, it may contain a different set of species than did the (hexagon) site. Given complementarity, the potential contribution of other sites will change and a new analysis should be performed to select additional sites.

## CONCLUSIONS

A wide range of approaches to selecting reserve networks has been explored and methods for finding optimal solutions are now available. However, as Pressey *et al.* (1996a) point out, there are a number of practical constraints that are likely to be encountered in developing a reserve network for any jurisdiction (e.g. land tenure, habitat quality, costs, social attitudes, political opposition). Incorporating these constraints makes the job of finding a solution more difficult. Work remains to be done in devising methods to solve for optimal solutions in more complex problems and in assessing the relative performance of various algorithms (Pressey *et*

al., 1996a). The existence of alternative paths to satisfactory reserve systems gives land use planners and decision makers the flexibility (Pressey *et al.*, 1993) needed to balance conservation goals with competing land uses.

The work of Kirkpatrick (1983) and others has demonstrated the practicality of iterative methods of reserve selection for achieving the conservation goal of representing the maximum number of species or land classes in a constrained reserve network. Here, we have compared a number of approaches to reserve network selection and described the strengths and limitations of each. We agree with Underhill (1994) that linear integer programming algorithms, such as branch-and-bound algorithms, are most likely to find optimal solutions to the reserve selection problem. Simpler heuristic algorithms can, however, come very close to the optimal solution in the right circumstances. Their speed and convenience for interactive analysis, when used in software programs such as WORLDMAP (Williams, 1994), will continue to make them a valuable conservation tool.

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