Terrestrial Nature Reserve Design at the Urban/Rural Interface

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Introduction

Wisconsin had 28 nature reserves five years after the Wisconsin State Board for the Preservation of Scientific Areas was created in 1951. Iltis (1956) remarked that "time is running out," indicating that 280 or even 500 reserves were needed. By 1993, Wisconsin had a remarkable 276 dedicated nature reserves. However, for much of the Midwest and other parts of the United States, time is running out in spite of some remarkable achievements (Figs. 1–2). Awareness is increasing that terrestrial conservation efforts in some parts of the United States must by necessity be on small pieces of habitat, supporting small populations of species (e.g., Mitchell et al. 1990). Small reserves are important in areas where landscape alteration is very high *and* very low (Shafer 1995).

The effects of people on any landscape can be either dramatic or subtle where human populations are dense (McDonnell and Pickett 1993). In California, documentation of the loss of biodiversity (e.g., Jensen et al. 1993) has resulted in endorsement of new planning approaches by the highest state government officials. Perhaps because urbanization is moving closer to our rural and wilderness areas, this interface is receiving more attention in research (e.g., McDonnell and Pickett 1990). Urbanization, with its accompanying loss of native habitat and creation of new habitat, has been correlated with a decreasing number of bird species, increasing avian biomass, and increasing dominance of a few species (Emlen 1974, Beissinger and Osborne 1982).

Urban areas, however, are not necessarily a death knell for all wildlife. In fact, many opportunities for wildlife habitat or corridors in urban/suburban areas, like golf courses, are overlooked. (Terman 1994). Red foxes in Great Britain use railroad corridors to travel in and out of towns and cities (Kolb 1985, cited in Adams 1994), and Adams indicates that white-tailed deer, coyotes, and raccoons are thriving in some U.S. urban areas. Their presence may cause concern when deer browse on home shrubbery and gardens, coyotes attack pets, and raccoons transmit disease or raid home garbage cans. Gill and Bonnett (1973) document how many species occur in London and Los Angeles. "The wolves, mountain lions, bears, salmon, and oysters that were part of Manhattan are gone, but the red fox, opossum (a new resident), flying squirrel, gray squirrel, muskrat, raccoon, several species of bats, and a host of birds remain" (Ehrenfeld 1972, 182–183).

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Fig. 1 A 48-acre virgin beech-maple forest in Indiana. The tree is a 68-inch DBH Shumard's red oak
Source: Photo taken 1973, courtesy U.S. National Park Service

Fig. 2 A 330-acre remnant tallgrass prairie near the eastern margin of Indiana's "Prairie Peninsula"
Source: Photo taken 1973, courtesy U.S. National Park Service

European Precursors

Westhoff (1970) categorized landscapes as natural (undisturbed—no longer present in western and central Europe), *subnatural* (human influenced but still related to the potential natural vegetation), *seminatural* (sites now very different from the potential natural vegetation such as heathlands and moors, undrained/mowed/leveled dry pastures and hayfields, hedges, coppices, or older coastal dunes), and *cultivated* (e.g., a bean field). Seminatural landscapes predominated in western and central Europe from the Middle Ages until the end of the 19th century. Westhoff maintains that human influence during this time was more positive than negative. His explanation for this claim is that land

management amplified and stabilized biotic variation. Land management methods stayed the same for centuries, people did not travel far from home, and their operations were gradual and of small scale. van der Maarel (1975) gives the distribution of plant species in the Netherlands by degree of naturalness: 20% near natural (e.g., woodlands, bogs, dunes), 60% seminatural (e.g., hay meadows, grazed salt marshes, coppices), and 20% agricultural and suburban. van der Maarel claims many plant species are tied to, or have an advantage in, seminatural environments. Similarly, Erhardt and Thomas (1991) claim a large percentage of British butterflies are confined to human-made niches, like secondary grassland created or maintained by agricultural practices.

Although Native Americans affected the North American landscape before Europeans arrived (Denevan 1992), their influence was much less profound compared with what Europe experienced. Much of the U.S. Midwest resembles the seminatural landscape that predominated in Europe for centuries. Europeans tried to devise conservation strategies for their countries accordingly. We have much to learn from this European example as parts of our country are modified to less wilderness characteristics (see Green 1981). Although we should focus much of our efforts on *remnant ecosystems/natural islands*, other classifications with more urban affinities also harbor some native biota, e.g., urban savanna, mowed/grassland, urban/forest plantation, rail-highway/grassland, and so forth (Brady et al. 1979).

Remnant Persistence

Statistics about how much is left of a particular biotic community are common and depressing. For ecosystems whose spatial extent has declined by more than 98% in the United States, the greatest losses are from grassland, savanna, and barrens (Noss et al. 1995). Only about 2% of California's interior wetlands remain. Some of these communities were not widespread to begin with; for example, vernal pools covered only 1% of the state and 80% are gone (Barbour and Whitworth 1994). Leopold (1949) long ago pointed out that some of the best examples of prairie communities are remnants found along railroad rights-of-way. Betz (1977) explains that many tiny tracts can still be found along fenced railroads, along farmers' creeks, in hay meadows, in cemeteries, and in some suburban areas. Some states, such as Minnesota, have gone to great lengths to inventory their highways for remnant prairies (see Harrington 1994). In southern Saskatchewan, less than 1% of the grasslands ecoregion is in highly protected reserves (Gautheir and Patino 1995). Less than 202 ha of intact oak savanna remain in Wisconsin, which is less than 0.01% of the original 5.5 million acres in the state (Department of Natural Resources 1995). A 1985 inventory of the entire Midwest revealed that only 0.02% of this plant community is left (Henderson and Epstein 1995). These intact remnants (prairie and savanna) are almost exclusively found on marginal soil types (with the exception of railroad rights-of-way).

The most important woodlands in England and Wales—the species-rich "ancient" tracts that have persisted since the Middle Ages—were recently better quantified by Spencer and Kirby (1992). They found that those woodlands still covered a remarkable 2.6% of the land surface, with 83% of the sites under 20 ha. They calculate that 7% of the ancient tracts were lost in the last 50 years. Such detailed baseline information is necessary in setting conservation priorities in human-dominated landscapes. Some British biotic communities are also very rare. For example, 0.1% of the peat fens in eastern England, such as Wicken Fen, remain undrained. The swallowtail butterfly *Papilio machaon* was lost from Wicken Fen in 1952, leaving only one other population in Great Britain. Studies have focused on why reintroductions have not yet worked, presumably because of food plant availability (Harvey and Meredith 1981).

The $140,000 \, \text{km}^2$ Western Australian wheatbelt once had $41,000 \, \text{km}^2$ of woodland, but only $1,000 \, \text{km}^2$ remain. The Australian government designated 639 forest patches as reserves, and thousands of other privately owned patches are scattered throughout the region. It represents an enormous

test case in potential cooperation with private landowners to preserve patches and decrease patch isolation. Many species have already been lost as a result of fragmentation, but positive action rather than resignation may permit others to persist (Saunders and Hobbs 1989).

At times native biotic communities can display surprising resiliency, and their persistence is known only after detailed inventory. For example, the Canterbury Plains in New Zealand was assumed to have lost many of its native biotic communities after 100 years of deforestation. In spite of its apparent continuous expanse of farmland and urban areas, a closer look revealed that many of these communities still survived (Molloy 1971). The Crown purchased 2 to 3 ha tracts of vegetation types that once covered approximately 100,000 to 200,000 ha. The best remaining examples of some vegetation types included 526, 16, and 3 ha tracts.

Remnants As Refugia

Species and Area

The theory of island biogeography (MacArthur and Wilson 1963, 1967) has been equated with the beginning of conservation biology (Simberloff 1988). The theory served as a foundation for thinking about nature reserve design in the 1970s and later. The empirical basis supporting such use is slim, and respect for the theory's conservation usefulness has declined (Shafer 1990, Formann 1995). "The inability of ecological theory to predict precisely future population sizes, the rate at which a fauna will collapse following insularization of its habitat, or the response of an ecosystem to a complex series of insults does not necessarily represent failure of the theory . . .. The problem of balancing precision against generality is much more difficult for ecological theoreticians than it is for theoretical physicists" (Ehrlich 1989, 315). Complete agreement in the scientific community about the theory's empirical foundation does not exist even today (Rosenzweig 1995). However, most would agree that much more autecological information is needed for specific reserve design prescriptions. McCoy (1983) pointed out that the minimum area needed by a suite of butterfly species can only be determined by detailed autecological study, and area alone may not be the most important factor.

The species-area relationship (see Williamson 1988), one component of the theory of island biogeography, may have relevance to conservation practice in some situations (see Shafer 1990 for detractors). That species increase with area is well known, with very rare exceptions (e.g., Dunn and Loehle [1988] for plants). Birds are one of the best studied groups in this regard. The number of rural studies that found that bird species increased with woodlot size is substantial: Freemark and Merriam (1986) outside Ottawa, Canada; Opdam et al. (1985) in the Netherlands; Lynch and Whigham (1984) on Maryland's coastal plain; Woolhouse (1985) in Great Britain; Ambuel and Temple (1983) for southern Wisconsin; and Kitchener et al. (1982) for western Australia. For more urban areas, habitat size has been shown to determine species number for birds (Gavareski 1976, Tilghman 1987, Vizyova 1986), for reptiles and amphibians (Dickman 1987, Vizyova 1986), and for small mammals (Matthiae and Stearns 1981).

Small but Not Vacant

That small, urban parks could play a role as nature reserves has often been ignored in our focus on recreational/psychological values (e.g., Seymour 1969), but this is changing (e.g., Spirn 1984, Gilbert 1991, Adams 1994, Platt et al. 1994). Dickman (1987), based on species-area relationships in the city of Oxford, thought mammal species (excluding deer) could be maintained in a system of small 0.65+ ha habitat patches and amphibians and reptiles in 0.55+ ha patches with permanent water. Because there was no temporal dimension to the study, presence may not necessarily mean persistence.

Based on a survey of 72 remnant grasslands in the Chicago area between 1982 and 1994 and other information, Panzer et al. (1995) concluded that around 25% of the insect species are remnant dependent. One small English garden contained 21 of the 70 known butterfly species in Britain (Owen 1978, cited in Adams 1994). However, more than one patch may be needed to ensure their survival (Hanski and Thomas 1994). One square foot of Pacific Northwest old-growth forest soil and litter can yield 200 to 250 species of invertebrates (Moldenke and Lattin 1990).

Some authors have concluded that suburban and urban parks are unsuccessful as avifaunal reserves due to small size, isolation, and vulnerability to human impacts (e.g., Lynch and Whitcomb 1978). An ongoing study of 225 forest fragments in Prince Georges County, Maryland, including some urban tracts, has a minimum size cutoff of 0.5 ha (Robbins, personal communication). Some birds will nest in the smallest tracts, often "suburban" species (Robbins et al. 1989a). In their literature review, Adams and Dove (1989) made predictions for expected species number as a function of habitat size—they thought some woodland and chaparral birds would be present in 1 ha remnants. Such remnants can provide habitat to produce some birds, which is different from providing viable habitat by themselves. Sometimes a small remnant can be the last refuge for a plant or invertebrate species (Shafer 1995). Ehnström and Waldén (1986, cited in Hansson 1992) describe a 5 ha old oak forest in Sweden that is the last refuge for some species of rare beetles.

Population Viability

The persistence of *minimum viable populations* (MVP) has been defined as hinging on genetic, demographic, and environmental stochasticities, and natural catastrophe (Shaffer 1981), although the term MVP was in use earlier (e.g., Frankel 1970). Early on, very rough generalizations emerged about how large a population needed to be to persist for a certain length of time. For example, it was proposed that a mean of 2,000 vertebrates (give or take one order of magnitude) was needed for a 95% expectation of population persistence for 200 years (Soulè 1987b). Soulè and Simberloff (1986, 32) state: "Thus, not only is there no magic number, there is no magic protocol. Intuition, common sense and judicious use of available data are still the state of the art." Thomas (1990) proposed to move Soulè's (1987b) well-known generalization of "low thousands" to a mean of 2,000 to 10,000 (Note: Soulè [1987b] also used the terms "few thousand" or "several thousand.") Lande (1995, 789) argues for an effective population size of 5,000 "to maintain normal levels of potentially adaptive genetic variance in quantitative characters under a balance between mutation and random genetic drift" (*see also* Culotta 1995). A *population viability analysis* or PVA (Gilpin and Soulè 1995), reviewed in detail by Boyce (1992) and Ballou et al. (1995), is far better than relying on any generalizations. As Holsinger (1995) pointed out, only a few endangered species are likely to receive a complete population viability analysis because of the enormous data-gathering work required. Such best-data scenarios will still not allow fine predictions about needed population size. Why is this?

Genetics is presumed the least important component of MVP, and catastrophe the most important (Shaffer 1987). Since catastrophe is so difficult to account for, long-term predictions by PVA are still in the realm of guesswork (Barrow-clough 1992). Additionally, the deterministic human dimension (e.g., human population density, development and pollution, or exotic species and climate change) could overshadow any so-called stochastic events in traditional PVA. Demographic stochasticity was claimed to be more important than genetics (Lande 1988). Similarly, Brakefield (1991) maintains that an insect population size that minimizes ecological extinction (providing effective population size does not go below several hundred individuals and longer-term evolutionary potential is not taken into account) should automatically take care of genetic variation. Nunney and Campbell (1993), in contrast, maintain that genetic and demographic concerns dictate a similar population size threshold. Regardless, we can still be fairly confident that the upper threshold will be dictated by catastrophe.

The Nature Conservancy concluded that 1,678 United States plant taxa (8.4%) are known from five or fewer locations or less than 1,000 individuals (Falk 1991). In spite of the pressing need, addressing MVP for plants is more recent (Menges 1990). Menges suggested that minimum island size may not be important for plants but metapopulation considerations will be. Weaver and Kellman (1981) concluded that area and isolation did not explain tree species persistence or loss in ten Ontario woodlots. Ouborg's (1993) data from the Dutch Rhine caused him to conclude that metapopulation structure, the negative effect of isolation, and population size was important for some plant species. Widén and Svensson (1992) assume that self-fertilizing annual plants that are selected for inbreeding may not be harmed genetically by habitat fragmentation but outbreeding perennials could be. However, they conclude that present empirical knowledge about genetic diversity and population size in plants is still insufficient to confidently devise strategies to thwart habitat fragmentation. Inbreeding depression in plants has been invoked as a cause of poor survival (Menges 1991, Waller 1993). Schemske et al. (1994) found that the primary cause of endangerment for all but 1 of 98 U.S. plant species listed as threatened or endangered by the U.S. Fish and Wildlife Service was human activity. Most ultimate causes of animal extinction today are probably anthropogenic, although the proximate cause (i.e., reason the last individuals die) could be genetic, demographic, by catastrophe, or through direct human action like collecting or hunting (Simberloff 1986b).

Caughley (1994) contrasted the small population versus declining population paradigms, arguing that the latter has received much less attention but is more germane to conservation. Unless these two things are combined in PVA, the factors probably most significant to a population's survival will be ignored. The National Research Council (1995) concluded that all PVAs are limited by data and methods; that most PVAs vary only some important influences, resulting in casual estimates; and that single factor PVAs will underestimate extinction threats. Because "formal population viability analyses are complex and are impossible to conduct on a routine basis" (Ruggiero et al. 1994, 371), these authors recommended a shortcut to allow managers to do some impact assessment. PVA should be made more available and digestible to managers, with or without shortcuts. Better yet, we need to focus on the real driving factors in any PVA, which requires transdisciplinary approaches. The traditional approach at PVA may be more comfortable to biologists (e.g., Remmert 1994) but is not a depiction of the real world. (Note: There is further debate on these points in the August 1995 issue of *Conservation Biology*.)

Metapopulations

The term *metapopulation* is usually attributed to Levins (1968, vi): "any real population [that] is a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear," although Simberloff (1988) pointed out a form of the idea that arose earlier. The rough metapopulation idea involves a set of geographically distinct populations together comprising a larger population. These subpopulations occasionally receive immigrants amongst one another; there can be a "winking" on and off (local extinction) of subpopulations; but the overall metapopulation persists (see Gilpin and Hanski 1991, Wilson 1992). Conservationists have used the metapopulation model as rationale for preserving multiple-habitat patches or reserves, presuming some species are adapted to this population structure. Some others have used it as a reason why it is acceptable to give up some local populations! The degree to which this model has been supported by field data hinges on the rigidity of model definition (see Shafer 1995). However, the idea that some species now exist in small patches is not arguable. For example, Hanski (1994) indicates that the Finland butterfly *Melitaea cinxia* lives in a series of 50 small patches, most under 1 ha.

The important underlying conservation assumption is that one habitat or reserve is not enough if we want to simulate a population's natural metapopulation structure. Bank voles showed a pattern of recolonization following local patch extinction. Extinctions were most likely in woodlots under

0.5 ha, and their abundance decreased as distance increased from woods of more than 25 ha (van Apeldoorn et al. 1992). Even an enormous population of small organisms is not necessarily safe on a small habitat patch. Tscharntke (1992) concluded that populations of 180,000 adult moths *Archanara geminipuncta* cannot persist on 2 ha *Phragmites* nature reserves without nearby reservoir populations. However, most questions about reserve size, numbers, and distance between habitat patches for invertebrates remains a mystery due to lack of dispersal data (Thomas and Morris 1995).

After three decades of research on the bay checkerspot butterfly *(Euphydryas editha bayensis)*, the modeling of Murphy et al. (1990) permitted a reserve design conclusion: small, low-quality, serpentine grassland patches within seven miles of the largest reservoir patch could be as important, or more important, to the survival of the metapopulation than larger, higher-quality patches at greater distances. Computer simulation modeling conducted by Fahrig et al. (1983) led to the following conclusions: links between habitat patches are important and there is a minimum number of patches needing connection.

The metapopulation concept involves *replicates* of habitat. However, the early recognition that more than one reserve is desirable was not tied to metapopulation theory (e.g., Specht et al. 1974) but to intuitive common sense. The replication message became intertwined and perhaps obscured with the academic Single Large Or Several Small controversy (abbreviated SLOSS) that began in 1976 (Simberloff and Abele 1976). The early SLOSS debate centered around whether it is more desirable to have *(but not necessarily retain over a long period)* species in one large reserve or in a number of smaller reserves whose total area equals that of the single large one. Whether one large reserve is better than several small reserves was raised earlier (e.g., Bourliere 1962, 66) but not as a scientific hypothesis. The advantages of replication, irrespective of SLOSS, was occasionally pointed out (e.g., Soulè and Simberloff 1986; Shafer 1990, 1994, 1995). The mean size of scientific areas in Wisconsin (18.8 ha) is smaller than the 50 ha typically affected by individual tornados (Guntenspergen 1983).

Lessons from the Temperate Zone

Moore (1962, 390) implied that a biotic community has a minimum size—"The smallest viable size of a habitat is the smallest which supports a viable population of its weakest species." There have been efforts for some time to gauge it from species-area relationships (e.g., Vestal 1949). However, Usher's (1986) review led him to claim that minimum biotic community size is yet to be determined for any community. This claim has not stopped scientists from providing their best judgements for biotic communities however defined or demarcated. For example, plant diversity declined with heathland fragment size in Dorset, England (Webb and Vermaat 1990), and the authors recommended 55 ha for maximum heathland plant representation. Levenson (1981) estimated a 4 to 5 ha undisturbed tract was needed to secure the future of all plants characteristic of a southern Wisconsin mesic beech-maple forest and 7 to 8 ha was needed for a dry mesic oak forest. The reason was that below this size the invasion rate by edge-adapted, shade-intolerant tree species was too high. Another biotic edge effect is nest predation. Species like cowbirds are severely decreasing the survival of neotropical migrant birds, no longer protected in deep interior forests because of habitat fragmentation (Wilcove 1985). Woodlot edges are also created by human impacts (Matlack 1993). Some think edge effects encompass a plethora of human encroachments on national parks (e.g., National Park Service 1980), but many might best be called matrix effects. Schonewald-Cox and Bayless (1986) proposed an all-encompassing boundary effects model. The intuitive assumption that human impacts would be greater in small tracts arose earlier (Wright et al. 1933, 43).

Mader (1984) indicates that very small tracts (less than 0.5 ha) in West Germany should be disregarded because they are all edge and no core. This does not mean, however, that they have no biological value to conservation. Although very small reserves might not allow long-term persistence for certain species, particularly large mammals, many other species use them and some small

HOW SMALL A RESERVE?

Arctic National Wildlife Refuge, Alaska	7,804,819 ha
Everglades National Park + Big Cypress National Preserve, Florida	796,809 ha
Shenandoah National Park, Virginia	79,055 ha
Congaree Swamp National Monument, South Carolina	6,126 ha
Muir Woods National Monument, California	224 ha
Davis-Purdue Experimental Forest, Indiana	21 ha
Weston Cemetery Prairie, Illinois	2 ha

Fig. 3 Each U.S. protected area is approximately one-tenth the size the one listed above it

species may be able to persist in them (Fig. 3). Small tracts have other values too (Shafer 1995), like education, science, habitat to facilitate dispersal, and providing propogules for restoration.

Really small tracts (e.g., 0.1 ha of vegetation) "do not reveal any fundamental diversity properties of the places or the taxa being sampled" (Rosenzweig 1995, 279). In other words, there is some data to suggest the typical species-area plot is *not* found below some area threshold—not surprising as biotic communities on such small tracts will not be unaltered representative examples of pristine species assemblages.

Lessons from the Tropics

The decline of neotropical migrant songbirds in North America is well known. What is influencing this trend the most—forest tract size for spring breeding in North America versus deforestation in the tropics where they spend the winter—is not yet known (Robbins et al. 1989b). Some neotropical migrant bird species need forest tracts of at least 3,000 ha to breed in North America (Robbins et al. 1989a). However, we should not overlook that some forest-dependent neotropical migrant songbirds do survive the winter on the Yucatan Peninsula in small patches of trees in an agricultural landscape (Greenberg 1989). Patches with eight small trees (ungrazed) and ten small trees (grazed) gave three times more sightings than patches with fewer trees. Schelhaus and Greenberg (1993) provide a good compendium and analysis of tropical literature, some of which I will use here.

Lovejoy et al. (1984) found that Amazon butterflies with uniform distributions needed 10 ha tracts of tropical forest for representative communities but that butterflies with patchy distributions needed 100 ha tracts. Klein (1989) found that dung and carrion beetle communities in the Brazilian Amazon had fewer species as forest patch size decreased—100 ha, 10 ha, and 1 ha. Lovejoy (1987) indicates that the howler monkey *Alouatta seniculus* was able to persist and reproduce in all of their 10 ha isolated Brazilian rainforest patches, though many other monkey species were quickly lost. Lovejoy et al. (1986) reported that tree mortality (over 10 cm DBH) in isolated 1 and 10 ha tropical forest fragments was almost twice as high as in continuous forest. Laurence (1991) believed a tropical forest reserve that is too small may end up preserving species that could have survived outside of the reserves anyway.

A species can be found in a fragment long after its population is presumably too low to persist (Janzen 1988). Some scientists have recorded low extinctions in some tropical forests (e.g., Brown and Brown 1992), though massive extinctions are predicted by species-area relationships (e.g., Simberloff 1986a). There can be a long lag effect. The remaining species could be doomed because the species loss period following deforestation is not immediate. Science journalists (e.g., Mann 1991) might stress that continued species presence over the short term may not invalidate some species-area extinction predictions. On the other hand, these doomed species could form the nucleus of a species salvage effort.

One Danger of Guidelines—Biotic Community Size

The provision of guidelines to planners on how small a tract is too small for a population is useful, if based on thorough research. Guidelines are much more difficult for *communities*. In most cases, we simply do not know how many species and what species a small remnant will preserve. We presume that some plants and insects will fare better than medium-sized mammals and area-sensitive birds. The umbrella-species approach at gauging needed reserve size assumes that the area required to protect viable populations of large vertebrates like bears will automatically be large enough to protect other species with small home ranges (Wilcox 1984, Shafer 1995). Unfortunately, it tells us nothing about the space requirements of smaller species in the biotic community. The umbrella species may have been lost from the region long ago or the isolated remnant has become so small as to make such an approach pointless.

Misuse of size guidelines is a danger. Size guidelines do not mean sites below this size should be abandoned, serving no purpose for a "flagship" species, other species, or for science or education (Shafer 1995). Size is only one consideration. Habitat management, connectivity, replication, and buffering will also greatly influence the perpetuity of species in a habitat patch or reserve.

Value of Dispersal Corridors

Corridors have captured the attention of scientists (e.g., Saunders and Hobbs 1991), elicited guidance to planners (e.g., Smith and Hellmund 1993), and generated grassroots action to create greenways (e.g., Little 1989, Flink and Searns 1993). The pros and cons of corridors are discussed in Noss (1987) and elsewhere. I will highlight here some research that is particularly germane to very human-dominated landscapes.

Studies in the actual use of any corridor by a species is still meager (Simberloff et al. 1992). Based on painstaking research, fencerows in farmland near Ottawa, Canada, appear to allow the dispersal of chipmunks and white-footed mice, allowing populations in isolated woodlots to persist (Wegner and Merrian 1979, Fahrig and Merriam 1985, Henderson et al. 1985). However, looking at fifteen 1 to 25 ha Ottawa farmland woodlots varying from 300 to 500 meters apart, Middleton and Merriam (1983) concluded that only 7 of 86 taxa (trees, herbs, squirrels, or invertebrates) reflected any isolation influence. Most of these species may be adapted to medium-distance movement. Hence, one has to be cautious about making "island" assumptions based only on casual landscape observation. Some species may need corridors but others may not. Soulè et al. (1988) observed some California chaparral bird species occupying 1 to 10 ha ribbons of habitat and then presumed that the ribbons were needed for dispersal between larger tracts.

There are certainly documented barriers to dispersal. Mader (1984) found that some species of beetles rarely cross highways in West Germany, but mice, far more able to navigate this distance, rarely cross either. Eversham and Tefler (1994), however, argue roadside verges in the Netherlands are used by carabid beetles not as corridors but as refugia. Klein (1989) found a 100 m gap in Brazilian rainforest would affect the movement of dung and carrion-feeding beetles. Volant species presumably will be less affected by isolation, but some are poor dispersers. For example, one butterfly species *(Mellicta athalia)* rarely moves between boreal forest gaps of 1 km (Warren 1987). Knaapen et al. (1992) estimated that butterflies would have much more difficulty traversing a built-up landscape (residential, commercial, or industrial, especially with less than 5% forest cover) in the Netherlands than would deer, squirrels, or forest birds. Dispersal is important for the survival of arthropods (der Boer 1990) and barriers do exist (Mader et al. 1990).

Moon (1990) described koalas moving from one park sanctuary to another through open paddocks. These paddocks contained sparsely distributed trees as much as 300 m apart. The koalas

commonly used individuals of the tree *Eucalyptus tereticornis* 14 to 18 m in height for movement, suggesting tree plantings might be feasible to enhance corridor appeal for koalas in degraded areas.

Elton (1958, 156–158), discussing the virtues of hedgerows, remarked "I cannot think of any ecological system in Britain that so clearly has all the virtues inherent in the conservation of variety. . ... They form, as it were, a connective tissue binding together the separate organs of the landscape." We need to know the habitat needs of a species to complete its life cycle before we conclude a particular habitat linkage means the difference between extinction and perpetuity. Preferably, research should come first to ascertain whether corridors would be useful for a particular species, and if so, what its dimensions should be (Simberloff et al. 1992, Hobbs 1993). However, that is a luxury often not available in places like San Diego County, California (Mann and Plummer 1995). In lieu of good data, perhaps the best advice is to maintain habitat connectivity until we know more. Elton may have agreed with this logic. Once connectivity is gone, it is very difficult to re-create. England lost roughly a quarter of its hedgerows—96,000 miles—from 1945 to 1985. A further study gave a decline of 53,000 miles between 1984 and 1990 (Bryson 1993).

Whyte (1968, 389–399) said. "The most pressing need now is to weave together a host of seemingly disparate elements—an experimental farm, a private golf course, a local park, the spaces of a cluster subdivision, the edge of a new freeway right-of-way." His reasons were not based on conservation biology but because this linearity created more "visual space" for humans to see. His idea is nevertheless valid for animal movement. Isolation may have some pluses—for example, restricting exotic species, limiting transfer of disease, and denying entry of domestic predators like cats and dogs (Simberloff and Cox 1987)—but the greater danger lies in not being able to re-create natural landscape connections (Noss 1987).

Reserve Design

More Science

Reserve design guidelines for terrestrial ecosystems, reportedly derived from island biogeography theory, were soon advocated for incorporation in the planning process of nature reserves (Balser et al. 1981). Based on a study of chaparral fragments in San Diego, California, Soulè (1991) concluded that at least three of Diamond's (1975) general reserve design guidelines would be applicable to this urbanized setting as well: large is better than small, single large is better than several small (SLOSS), and corridors are better than no connection.

Wildlife conservation efforts in urban areas must proceed based on available scientific guidance, often inadequate in providing explicit directions to planners (Adams and Leedy 1987, 1991). Although they are not a substitute for detailed information on a particular species of concern, Shafer (1994) nevertheless proposed some updated graphic nature reserve design guidance (Fig. 4). These guidelines are a mix of very broad ideas, but are real-world oriented. Most are also germane to densely populated regions.

There may be no single answer about what a minimum viable population is for a species, and hence there is no consensus on the best reserve design (Nunney and Campbell 1993). McCoy (1983) concluded that minimum area and best-choice options for remaining habitat patches can only be determined from detailed information about species natural history and the patches themselves, not from simple species-area equation calculations. Since local extinction of fragmented populations is common, an understanding of a particular species' dispersal characteristics is essential if the most optimal patches for future reserves are to be sought from the pool of remaining patches (Fahrig and Merriam 1994). I think Wright (1990) correctly indicated that general reserve design guidelines
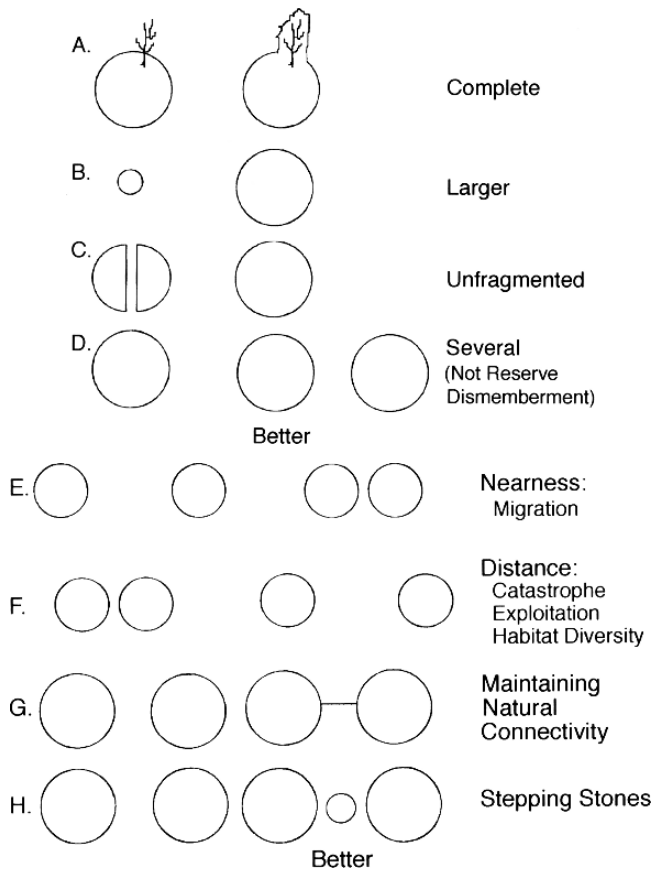
Fig. 4 The option on the right is proposed as better than the one on the left. See text for discussion.
Source: From Shafer 1994, reprinted with permission of Elsevier Science, Amsterdam

- **A.** Complete watersheds, migratory routes, feeding grounds are preferable inside reserves.
- **B.** Larger is better than smaller, especially for wide-ranging large mammals.
- **C.** Unfragmented is better than fragmented.
- **D.** Several reserves (e.g., two reserves, each $1,000\,\text{km}^2$, instead of one $1,000\,\text{km}^2$ reserve) are better because replication guards against catastrophe and human exploitation, and may capture more endemic or patchily distributed species. This is not a recommendation for reserve dismemberment.
- **E.** Nearness is better than being father apart because it facilitates migration to a sister reserve, providing the landscape is traversable by the species.
- **F.** A greater distance may be better, however, to reduce the effects of catastrophe, disease, and human exploitation; increase the likelihood of more habitat heterogeneity and thus more species; and enhance the possibility of more intraspecific genetic variation.
- **G.** Maintaining existing natural connectivity/usable corridors is a far better alternative than no connection.
- **H.** Small stepping-stone reserves, if used, are better than none at all.
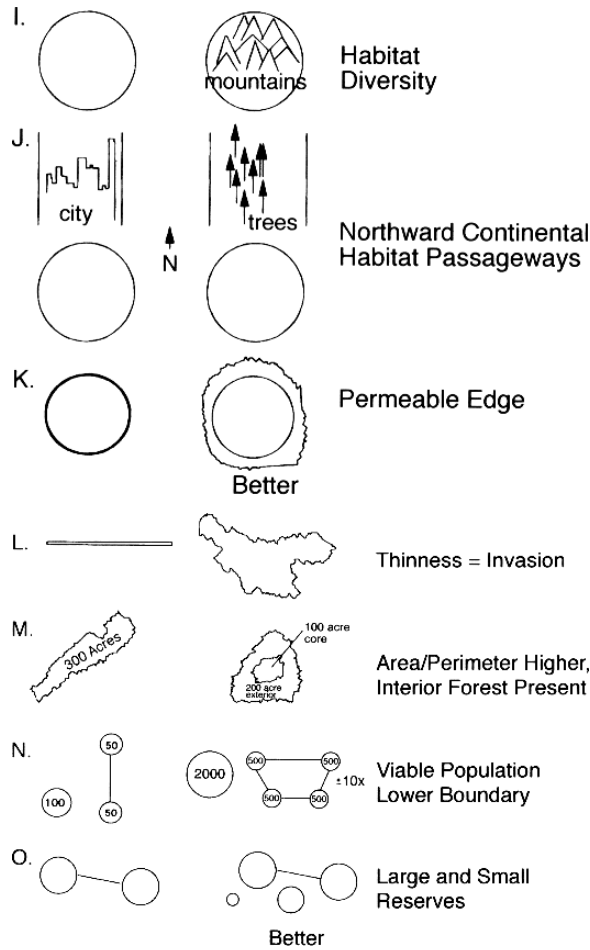
Fig. 4 (continued)

   I. Higher within-habitat heterogeneity (e.g., mountains, lakes) should allow for more species due to more habitat. The elevational diversity that mountains provide is also helpful in thwarting climate change.

  J. Continental habitat passageways may be vital for overcoming climate change, especially toward higher latitude.

  K. A permeable edge encourages animal movement across a park boundary. Edge abruptness, width, vertical structure, and natural discontinuities influence permeability (Forman and Moore 1992).

  L. Very thin reserves (e.g., roughly 200–500 m) can encourage invasion by avian predators or weedy species.

  M. Similarly, reserves with no or too little core interior forest may lack area required for some U.S. neotropical migrant birds. Theory and some modeling also suggest higher area-perimeter ratios may be better for buffering some external influences and facilitating animal movement across boundaries.

  N. A thoughtful guess at the lower limit for minimum viable population size (Soulè 1987b) is better than assumed nonviable ones. However, be forewarned that "there is no single 'magic number' that has universal validity" (Soulè 1987a). This is not a recommendation for reserve dismemberment but for reserve connection as needed. Note: some (e.g., Lande 1995) would argue this lower limit should be upped tenfold.

  O. Small reserves can provide a useful purpose for some species in any reserve system.
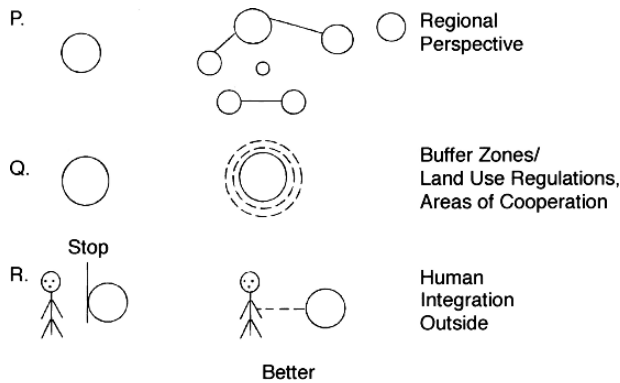
Fig. 4 (continued)

P. A regional perspective rather than a local perspective is crucial in preserving reserve biota.

Q. Buffer zones/land use regulations or areas of cooperative planning outside reserve boundaries are crucial to minimizing human impacts.

R. Human population outside the reserve must be socially and economically integrated into a reserve management plan so the park boundaries are not viewed as an abrupt wall or the park considered an island. Application of social sciences, e.g., Q and R, not just application of ecological theory, is among the foremost nature reserve planning challenges.

derived from model populations are potentially useful only when detailed information on a species' requirements are unavailable.

Bennett (1990) concludes that forest fragmentation in southwestern Victoria, Australia, leads to four recommendations for mammalian conservation: a regional perspective, maintenance of substantial total area of forest, maintenance and enhancement of forest continuity, and protection and promotion of faunal habitat. The broad generalities of needing large tracts of habitat, avoiding fragmentation, and maintaining connectivity were later made by Shafer (1990) and Wilcove and Murphy (1991). These ideas are indeed simple (see Soberon 1992) but their adoption could have a profound positive effect.

Other Realities

Kelly and Rotenberry (1993, 85) said, "In regions that are undergoing rapid urbanization, such as much of Southern California, the question of preplanning the establishment of reserves of sufficient size and configuration to maintain population or community viability is often moot because of high land values and the extent of pre-existing habitat fragmentation." They nevertheless argue for a scientific framework for buffer zone establishment; otherwise the reserves will be "gradually eroded away by external forces." Vast reserves in some parts of California may now be precluded, but networks of smaller ones are not.

San Diego County has initiated one of the most detailed nature reserve design planning efforts in the country, which could serve as a template elsewhere (City of San Diego 1995, Boucher 1995). Gap analysis has been applied to a 235,387 ha area in the southwest portion of the county, identifying core reserves, linkages, and available buffer zones. The analysis involved 15 layers of GIS design information (including land ownership and projected land use) and four proposed reserve design options (Stallcup, personal communication). Observers await its potential adoption in an extremely urbanized and fast-growing region of the country. Reid and Murphy (1995) and Manson (1994) discuss similar efforts in other California counties.

An ongoing effort in Wisconsin, led by The Nature Conservancy, is a good example of reserve planning for multiple small nature reserves within a specific regional landscape. The landscape design for Baraboo Hills, Wisconsin, consists of a plethora of small fragments and buffer zones, connected by other habitat or corridors. The results of this planning effort, and others like it, is not yet known.

Falk (1992, 398) said "The daily practice of conservation is as different from the world of theory and scholarly research as is the blackboard at a military academy from the battlefield. As every conservationist knows, decisions in the field are as likely to be influenced by real-estate transactions, land use, the economics of resource extraction, state and federal taxation, political expediency and the vagaries of public opinion as they are by careful planning grounded in sound conservation biology." The economic, political, and legal considerations gain importance when one is looking at regional landscapes (Shafer 1994).

The issue is therefore not just one of science. The social, economic, and political circumstances must be dealt with (Frankel 1974) or scientific guidance may become irrelevant (Shafer 1990, 1994, in press). Many other factors come into play, such as funding, accessibility, land cost, level of protection, owner attitude, adjacent landowner sympathy toward regional planning, and proximity to large urban areas. Goldsmith (1991) indicated reserve selection criteria for London includes public access, aesthetic appeal, proximity to urban communities, and degree of open-space deficiency.

Role of Nonreserves

Seminatural areas, as we have seen, can contribute to the conservation of biological diversity. In the San Diego County plan, more than just strict nature reserves are being sought. Nearly three-quarters of the remaining coastal sage scrub is on private land. Planners are treating the entire existing landscape as a de facto reserve system. Besides the buffer zones and corridors essential for the strict reserves, homes on large lots can also be a asset (Reid and Murphy 1995). Elsewhere in the United States, some urban parks, county fishing reservoirs, certain resorts, and even golf courses might be assets. We need to think of habitat wherever it occurs, not just in terms of reserves. The agricultural landscape has often been proposed as an alternative approach for biological diversity conservation (e.g., Green 1989), adopted in much of Europe, in part by default. Far more species exist in agricultural/forestry and other human-dominated ecosystems, covering 95% of the terrestrial environment, than in protected reserves (Pimental et al. 1992). In British urban areas, railway embankments, ancient forts, old quarries, gardens, and "wasteland" can provide habitat for some species (Gilbert 1991). In eastern Denmark, a primary function of small *biotopes* is to mark the boundaries of fields and estates. These boundary markers also provide habitat, and permission is required from authorities to disturb some of them. A gross categorization of biotopes include hedges, roadside verges, drainage ditches, small brooks, bogs, marl pits, natural ponds, thickets, and prehistoric barrows (Agger and Brandt 1988).

Insects Are Important

Insect ecology was once studied with the sole aim of potential control (e.g., Price 1984), but a new subdiscipline (i.e., conservation biology of insects) has emerged (Samways 1994). Insect conservation does matter (e.g., Kim 1993), in large part because they constitute 55% of the world's 1.4 million named organisms (Wilson 1992). Insects have been called the "little things that run the world" (Wilson 1987, 344) because of the vital role they play in ecosystem function.

Thomas and Morris (1995) think terrestrial invertebrate extinction rates in Britain have matched or exceeded those of vertebrates or vascular plants during the present century. There are success stories: Thomas (1991) provides accounts of endangered British butterfly populations recovering on small, isolated reserves with proper management. However, the rate of butterfly extinction in Europe is depressing in spite of valiant efforts (Warren 1992).

Looking again at California, the El Segundo blue butterfly *(Euphilotes battoides allyni)* resides on less than 1% of its original geographic range, which once extended about 36 miles along the shore of Santa Monica Bay, from Marine Del Ray to San Pedro. Its survival is closely tied with the Seacliff buckwheat plant. As of 1986, it survived on only two dune remnants—122 ha and 0.6 ha. Chevron, the owner of the 0.6 ha remnant, fenced off this area in 1975 and made it a butterfly sanctuary. Weed removal and outplanting of buckwheat on Chevron's remnant dune habitat occurred in 1983, 1984, and 1986. From 1977 to 1984, the estimated population declined by 70%, but 1985 and 1986 censuses indicated a slowing of this trend. Assuming this was a cause-effect relationship, a recommendation was made to continue outplanting buckwheat and clearing weeds. This was all for the perpetuation of a very small (0.6 ha) but critical piece of habitat for an endangered butterfly species (Arnold and Goins 1987). For their examples in California and elsewhere, see Beatley (1994).

Insect conservation can benefit other species. Launer and Murphy (1994) showed that if all central California serpentine grassland fragments containing the bay checkerspot butterfly *(Euphydryas editha bayensis)* were set aside, about 98% of the native spring flowering plants would receive some protection. The largest number of invertebrate extinctions and candidates for federal listing in the United States is in Hawaii and California (Hafernik 1992). California and Hawaii have the highest number of imperiled species (i.e., 600 or more) in the United States (Stein 1996). Hawaii is, however, our country's extinction capital—two-thirds of all extinct plants and animals come from this one state (Vitousek et al. 1987).

Remnant Restoration

Habitat restoration around habitat fragments can sometimes be accomplished by just allowing natural revegetation to proceed. For example, New York's Onondaga County had only 8% of its area in forest islands in 1930. However, forest cover increased by 40% by 1980, surrounding many older forest islands with younger 50-year-old trees (Nyland et al. 1986). Mladenoff et al. (1994, 752) proposed a design model for harvested Wisconsin forest that incorporates an "old-growth restoration zone surrounding old-growth patches to buffer and enhance forest-interior habitat and link nearby old-growth remnants. A larger secondary zone is delineated for uneven-aged forest management." The important point is that there may be opportunities to enhance remnant viability by allowing succession to proceed outside its boundaries and thereby expand its effective size or connect it to another fragment.

At a much larger scale, Alverson et al. (1994) proposed the creation of *diversity maintenance areas* (DMAs). The center of these idealized DMAs would consist of old-growth remnants. These centers would provide the building blocks for regeneration of large unfragmented tracts of late successional forests adjacent to them. The overall goal is to create mature, wild, old-growth forests and their natural ecological processes and disturbance regimes. The focus of Alverson and colleagues is primarily U.S. Forest Service lands, especially in Wisconsin, but they indicate the idea is applicable elsewhere.

True restoration can take a long time (e.g., hundreds to thousands of years). Tropical lowland dry forest can take 150 years to recover from timber harvest, and tropical lowland wet forest can take 1,000 years (Opler et al. 1977, cited in Reid and Miller 1989). Young successional forest inside or outside a fragment may increase the viability of a fragment in a much shorter time.

Private Initiative

Establishing vast reserves often requires the help of governments, but perhaps less so for smaller parcels. Prime (1992, 11) relates a situation in India, one of the world's most densely populated countries. Historically, between Indian villages three types of reserves were common: forest sanctuaries (raksha), dense forest (ghana), and planted single-species sacred groves (e.g., mango). The forest sanctuaries were off limits to the Hindu people, but the dense forest could be used to collect dry wood, forest produce, and a small amount of green timber. These one- to ten-acre tracts were cared for by the village communities, because they depended on it for their livelihood and they had a tradition of respect for nature. The standard of protection reportedly often exceeded that of current huge government-operated reserves. In the United States, Henry David Thoreau in 1859 thought each town should have "a primitive forest of five hundred or a thousand acres where a stick should never be cut for fuel, a common possession forever" (cited in Udall 1963, 173). Many small reserves are protected by a plethora of private organizations in the United States without the help of government (catalogued in The Nature Conservancy 1982). Throughout the world, private initiative in setting aside reserves is impressive (Alderman 1994).

In 1966, the U.S. Congress held hearings on senate bill S. 2282, a sweeping proposal for a nationwide effort at ecological survey and research. It was an early partial vision of what transpired in 1993—the creation of the U.S. National Biological Survey (later National Biological Service, and still later the Biological arm of the U.S. Geological survey). The role of this organization encompasses some of the need identified in 1966. The potential role it can potentially play is large (National Research Council 1993). The first Natural Heritage Program was created in 1974 under the leadership of The Nature Conservancy (TNC), now expanded to all 50 states, Latin America, and Canada, another example of private initiative at its best. Small tracts were often the focus of early TNC inventories, and some current gap analysis efforts also now consider them (Scott et al. 1993).

U.S. Midwest

It can be argued the U.S. Midwest is a success story in setting aside small remnant tracts. One can always bemoan biotic losses, but it is important to look back at the status of the small protected area enterprise here only 50 years ago. Progress was the result of commitment by thousands of individuals. Reserve location here was the result of an early but still very useful form of gap analysis. Reserve design was based primarily on academic and amateur field notes, common sense, and intuition.

Science-based management can accomplish much, but some problems stem from initial reserve size and layout. In highly urbanized regions, options to create new preserves or improve existing ones may be limited. It can be done, however, using sympathetic landowners, easements, or land purchases. Many states and private conservation organizations already have done this and can continue to do so. Monitoring is needed to gauge preservation success (Drayton and Primack 1996).

Ultimately, reserve design hinges on the value society places on preserving small natural areas. In other words, do we prefer a potentially higher quality of life amidst some native species, or a higher standard of living amidst landscape blight? One recent and able attempt to better educate Wisconsin natural resources personnel (Department of Natural Resources 1995) should be extended to other states. Other such attempts have surfaced (e.g., Nigh et al. 1992). State and federal natural resources personnel, from the maintenance staff to the politically appointed senior executives, need some basic information about what biological diversity means if they are to be effective land stewards in the next century.

An oversimplification of Leopold's (1949) famous land ethic is that humans should treat the outdoors as they would their home. If only this simple but profound idea were adopted as a personal

and national principle by the general public, top officials, and politicians. Until then, only proactive foresight will help retain more species and biotic communities in highly impacted landscapes, sometimes their only remaining potential sanctuary.

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