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Inter-reserve distance

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Abstract

Since the mid-1970s, reserve planners have been advised to locate reserves in close proximity to facilitate biotic migration. The alternative, putting great distance between reserves as a safeguard against catastrophe or long-standing chronic degradation forces, has received little discussion. The demise of a population can be caused by both natural and anthropogenic agents and the latter, including poaching and global warming, could be the bigger threat. Reserves sharing biotic components, whether close together or far apart, have advantages as well as costs. We need to consider whether the result of adopting the proximate reserve design guideline to preserve maximum species number will contribute to the potential extinction or extirpation of some rare flagship species? Should such extinctions occur, will society be understanding of science-based advise? Current conservation dogma that claims reserves should be located in close proximity demands more scrutiny because that choice may be tested this century. Published by Elsevier Science Ltd.

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1. Introduction

Simberloff (1998) asked how the adoption of goals like "biological diversity management" supersedes management of their component species? The intent of the earliest reserve design guidelines (e.g. Diamond, 1975; Wilson and Willis 1975) were to preserve maximum species number. This review paper: (1) examines literature germane to inter-reserve distance; (2) looks at the issue of catastrophic biological impacts; and (3) explains why locating reserves close together may contribute to the extinction or extirpation of some rare flagship species.

2. Catastrophe and duplication

Catastrophe is one cause of extinction. A dictionary definition of catastrophe (Morris, 1969) is a "great and sudden calamity; disaster" or a "sudden violent change in the earth's surface; cataclysm." Thus, based on this definition, a catastrophe has three attributes: (1) large magnitude; (2) suddenness; and (3) often involves large, surficial phenomena (e.g. earthquakes, meteor strikes). In addition, scientists usually assume that such geological events are infrequent in historical time (Raup, 1984). When scientists use the term catastrophe for biological impacts, which may have natural or anthropogenic agents, inconsistency in application is the rule.

The concern about the impact of catastrophe on protected reserves dates back at least to 1920, when one scientist implied that a catastrophic event could wipe out fragile entities in US national parks (Sumner, 1920). To guard against loss from catastrophe, the Illinois Nature Preserves Commission (1972) argued for duplication of each type of reserve. Slatyer (1975) also stressed the need for reserve duplication as a catastrophe safeguard, as did Soulé and Simberloff (1986) and Shafer (1990, 1995). Mangel and Tier (1994) reminded us that the persistence of *any* population, even under the best of circumstances, cannot be ensured because of potential catastrophe.

Some early recommendations for reserve duplication, however, neglected to articulate the potential benefit. For example, Leopold (c. 1938) warned that "a species must be saved in many places if it is to be saved at all." In a similar fashion, an attachment to Wisconsin's 1952 nature reserve policy said "some duplication [of reserves], if in widely separated locations, is desirable"

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(Fosberg et al., 1963, appendix). Others recommended reserve "multiplicity" (Frankel, 1974), "replicates" (Specht et al., 1974), and "redundancy" (Ray, 1976).

Mostly since the 1960s, scientists had noted the survival benefits associated with a taxon's wide geographic distribution (e.g. see den Boer's, 1968, 1981, observations for some insects and Jackson's, 1974 finding regarding some marine invertebrates). Wide distributions would protect against loss of a species in the event of a major environmental perturbation. Species might also persist because individuals from one or more subpopulations disperse to the location of a declining or extinguished subpopulation, the "rescue effect" (Brown and Kodric-Brown, 1977), or move to establish a new subpopulation elsewhere. Some small mammal data lend support for the rescue effect (Henderson et al., 1985) though the empirical evidence on immigration in general remains meager (Simberloff et al., 1992).

Clinchy (1997) argues that too many scientists have presumed that the positive correlation between proximity and population persistence is a result of immigration. Clinchy asked, could spatial correlation between populations and environmental disturbance have some influence on observed persistence? An answer hinges on future progress in distinguishing between the contributions of environmental perturbation versus dispersal in spatially correlated population density observations (Koenig, 1999).

Recognition that one reserve or population is a poor survival safeguard probably stemmed from common folk wisdom: it is unwise to have all your eggs in one basket. This notion predated both the Single Large Or Several Small (SLOSS) debate (Diamond 1976; Simberloff and Abele 1976a, b; Terborgh 1976; Whitcomb et al. 1976) and metapopulation terminology (Levins, 1970), a theory which grows in popularity (e.g. Gilpin and Hanski, 1991; Hanski and Gilpin 1996; McCullough 1996; Hanski 1999). Some metapopulation modeling supports intuitive notions about the effects of catastrophe (Root, 1998).

Besides the obvious differences between SLOSS and metapopulations — considering multiple species in SLOSS and single species in metapopulations — the two approaches usually differ in scale. The distance between reserves sensu SLOSS is typically further than the distance individuals of a species must move from one subpopulation to another sensu metapopulations. For example, when Woolhouse (1987) concluded that "several small" woodlands would preserve more breeding bird species than a "single large" tract for the purpose of short-term conservation, distance between woodlands could exceed 175 km. In contrast, the Glanville fritillary (*Melitaea cinxia*), a butterfly, must move only 1.5 km from one (semi-independent patch network) (SIN) to another one, a feat accomplished by less than 1.0% of the SIN per generation and usually less than 0.1% (Hanski et al., 1996a).

3. Agents of catastrophe

Shaffer (1981, p. 131) distinguished between extinction caused by *environmental stochasticity* (defined as "temporal variation of habitat parameters, and the populations of competitors, predators, parasites, and diseases") and extinction caused by *natural catastrophes* (defined as "floods, fires, droughts"). His examples of environmental stochasticity were predation, parasitism, competition, and disease, but some of these agents can have catastrophic impacts.

There are many agents that can bring a species to the brink of extinction. Examples will be provided for four such agents. Most of them have also acted as the final *coup de grâce* (terminology Simberoff, 1986) for the last individuals.

3.3. Exotic species

Domestic cats kept by the lighthouse keeper on Stephen Island caused the extinction of the Stephen Island bush wren (*Xenicus lyalli*) in 1894 (Carlquist, 1965). The exotic brown tree snake (*Boiga irregularis*) presumably caused the extinction of six of 10 species of birds on the Island of Guam (Savidge, 1987) as well as some species of lizards and mammals (Rodda et al., 1997). The extinction of one-third of Hawaii's *Achatinella* land snails is attributed to the deliberate introduction of an exotic snail — Florida's predatory land snail (*Euglandina rosea* — to control another exotic snail already abundant in Hawaii — the giant African snail (*Achataina fulica*; Hafernik, 1992). The Nile perch (*Lates niloticus*), brought to East Africa in 1954, is the presumed cause of native fishes disappearing in Lake Victoria between 1975 and 1982 (Kaufman, 1992), and the loss may have consisted of as many as 200 species (Goldschmidt et al., 1993).

Exotic species can also include organisms that cause disease. The last wild population of black-footed ferret (*Mustela nigrepes*) was almost eliminated by canine distemper virus (Thorne and Williams, 1988), dropping from 128 individuals to nine in less than a year (May, 1986). The American chestnut tree (*Castanea dentata*), abundant throughout much of the eastern USA in the last century, is nearly extinct from chestnut blight (*Endothina parasitica*; Roane et al., 1986).

3.4. Weather

Drought apparently caused the 1985 proximate extinction of *Stephanomeria malheurensis* in the wild, a plant known from only a single locality (Parenti and Guerrant, 1990). A 1923 sandstorm caused the demise of the last three Laysan apaganes (*Himatione sanguinea freethii*), a honey creeper (Caughley and Gunn, 1996), and a 1963 hurricane nearly eliminated another bird, the

Laysan teal (*Anas laysanensis*; Greenway, 1967, in Simberloff, 1986).

3.5. Geological phenomena

Eruptions in 1933 and 1941 on Torishima Island, Japan, decimated the last breeding colony of short-tailed albatross (*Diomedea albatrus*; Greenway, 1967, in Simberloff, 1986), though the species is slowly recovering. Volcanic eruptions in 1830 almost extinguished the remaining population of great auk (*Alca impennis*) though its extinction was postponed until 1850 when overhunting and collecting completed the job (Caughley and Gunn, 1996). Little imagination is needed to predict that other weather-related events (floods, blizzards, tornados) or geological phenomena (earthquakes, tsunamis) have the capacity to cause an extirpation or extinction.

3.6. Habitat destruction/degradation

Habitat loss can be caused by either natural or anthropogenic agents. The loss precipitated by humans is the leading cause of species extinctions today (Norton, 1986) contributing to the decline of 1880 species of imperiled plants and animals in the United States (Wilcove et al., 1998). Some endangered butterflies in California survive on habitat fragments so small and few that one or two development projects could cause their extinction (Hafernik, 1992). To these butterflies, a new housing complex could be the shock leading to oblivion.

A catastrophic impact could cause an extinction, especially considering that some species are now confined to one reserve. In the US National Park System, examples include the Shenandoah salamander (*Plethodon shenandoah*) to Shenandoah National Park, Virginia, and the Devils Hole pupfish (*Cyprinodon diabolis*) to Death Valley National Park, California. Plants include the Presidio manzanita (*Arctostaphylos pungens* ssp. *ravenii*) to Golden Gate National Recreation Area, California and the Lee pincushion cactus (*Coryphantha sneedii* var. *leei*) to Carlsbad Caverns National Park, New Mexico (Shelton, 1994).

4. Natural versus anthropogenic agents

Authors have applied the term "catastrophe" to various natural agents: fire, insect infestation (Holling, 1973), drought (Slatyer, 1975), disease (Simberloff and Abele, 1976a), floods, mudslides, avalanches, and windstorms (Soulé and Simberloff, 1986), and mass emigrations or competitors (Mangel and Tier, 1993, 1994). Anthropogenic agents (i.e. human actions) such as land clearing, logging, poaching, and pollution can of course have catastrophic impacts. Humans should be recognized as potential agents of catastrophic impacts not only on islands (Olson, 1989) but most places people reside.

Hence, the definition of catastrophe provided by Ewens et al. (1987) — anything that harms a subdivided population genetically or demographically — warrants reexamination. The scientific literature has focused primarily on natural catastrophe, yet anthropogenic impacts could be the bigger threat.

Any notion that agents can be readily categorized as either natural or anthropogenic is not the case. For example, species extinctions have been attributed to predation, disease, and fire (Hester, 1967; Vermeij 1986), but all these agents may be traced to human actions. Predation disasters on islands typically involve exotic predators introduced by people (Ebenhard, 1988). Disease in wild animals is a natural process, though pathogens may be derived from livestock (Grenfell and Dobson, 1995). Similarly, fire is a natural phenomenon, though its intensity and frequency can be a function of human landscape modification (Pyne et al., 1997).

5. Catastrophe and catastrophic impacts

Some biologists have adopted the dictionary notion that an event's suddenness (i.e. the length of time required for an event to begin and end) determines whether it qualifies as a catastrophe (Soulé, 1984; Erb and Boyce, 1999). However, some anthropogenic events are not sudden. It took a century for hunters to obliterate the passenger pigeon (*Ectopistes migratius*; Schorger, 1955) and about 40 years to bring the American buffalo (*Bison bison*) to near extinction (Allen, 1974). If we choose not to categorize this or similar events as catastrophes, the end result was nevertheless catastrophic.

Others assume an event's frequency is a measure of natural catastrophe (Raup, 1984) and still others argue that catastrophe is just an infrequent expression of environmental stochasticity (Lande, 1993; Caughley, 1994), an unresolved issue (Turner and Dale, 1998). Were anthropogenic agents considered part of a catastrophe definition adopted in science, this debate might be moot. An event's severity (i.e. its impact on biota) would then be a better overall measure of catastrophe than its frequency.

Must the species go extinct? When Hurricane Hugo struck Puerto Rico in September 1989, the wild population of Puerto Rican parrots (*Amazona vittata*) dropped from 45–47 individuals to about 25 (Wilson et al., 1994). Though the wild population rebounded to 34–37 individuals by 1992, was the September 1989 hurricane a catastrophe for this species? It seriously jeopardized the species' viability. As a result of the 1993 floods on the Mississippi River drainage system, tree mortality was 50–90% in some areas (Sparks, 1996). Hypothetically, if the viability of no tree species was threatened, should we characterize it as a catastrophe?

Can catastrophe be defined based on the percentage of a population or species lost due to a stochastic event?

Most recorded large mammal local population die-offs leave survivors (Young, 1994). Specifying what percentage of a species or population must die is too arbitrary. During the bubonic plague of the 14th century, one third of Europe's human population was killed during an infamous 5-year period (Arnold, 1996). Is one third enough to qualify? In spite of such a great tragedy, it seems unlikely that Europe's human population was facing impending extinction.

Shaffer (1981) used the demise of the heath hen (*Tympanuchus cupido cupido*), described in Simon and Geroudet (1970), to illustrate that a *series* of events can cause extinction. Fire combined with three extrinsic forces — a harsh winter, predation by goshawks, and disease — delivered the coup de grâce (Simberloff, 1986, 1988); but before this sequence of bad luck, the population had been reduced by hunting, the "first strike" according to (Raup, 1991). Hunting, fire, a harsh winter, predation, and disease could all be considered agents of the resulting catastrophic impact.

Given the above considerations, catastrophic biological impacts might be described as those that reduce the population of a species enough to seriously jeopardize a species' viability. Regardless of how we define catastrophe, both natural or anthropogenic agents can have catastrophic results. Such impacts can be sudden or manifest over a long time period. They can be generated independently or be caused by other impacts, thus arriving alone or in series.

6. Proximate vs. ultimate causes

Scientists recognize *ultimate* and *proximate* causes of extinction. For example, if a disease event results in a species' extinction, disease is the ultimate cause, but the last individuals may die from a demographic accident or genetic erosion, which are proximate causes (Simberloff, 1986, 1988).

The extinction of some species or subspecies has been attributed directly to overhunting — the Falkland Island wolf (*Dusicyon australis*), Steller's sea cow (*Hydrodamalis gigas*), the Mexican silver grizzly bear (*Ursus arctos nelsoni*), and the Syrian wild ass (*Equus hemionus hemippus*) — and the last individuals were also killed by humans (Caughley and Gunn, 1996). In this case, hunting might be considered as both the proximate and ultimate cause of their demise and habitat loss could be the ultimate, ultimate cause.

Urban development of San Francisco caused the extinction of the satyr butterfly (*Cercyonis sthenele sthenele*) in 1880 followed by the xerces blue butterfly (*Glaucopsyche xerces*) in 1943 (Ehrlich and Ehrlich, 1981). We may never know whether the last individuals died from drought, vanished in a collector's net, or succumbed for other reasons.

7. Natural catastrophe and natural disturbance

Hurricanes, fires, and volcanic eruptions are natural *disturbances* essential to the maintenance of biological diversity (Pickett and White, 1985; Lugo, 1995). In fact, land managers sometimes simulate natural disturbances to maintain certain species (Hobbs and Huenneke, 1992). But when does the benefit of disturbance stop and long-lasting damage begin? This is the point at which a natural disturbance begins to take on characteristics of a catastrophe or a catastrophic impact. A look at two recent events in the United States is instructive.

The 1988 fire in Yellowstone National Park, Wyoming, Idaho, and Montana, was of a magnitude that occurs only every 100–300 years (Romme and Despain, 1989) yet no rare species suffered irreparable harm (Christensen et al. 1989). The *intermediate* disturbance frequency/intensity model predicts that the maximum number of species will survive at mid-levels of impact (Connell, 1978; Fox, 1979; Petraitis et al., 1989) and assumes that some extreme natural events could result in long-lasting damage. We have enough evidence for the Yellowstone fire to characterize it as an "intermediate disturbance."

Preliminary assessments of damage to Everglades National Park, Florida, from Hurricane Andrew in 1992 revealed that some endangered species, such as the Florida panther (*Felis concolor coryi*) and the snail kite (*Rostrhamus sociabilis*), were unaffected; others, such as the Schaus' swallowtail butterfly (*Heraclides aristodemus ponceanus*), suffered severe habitat damage (Loope et al., 1994). The hurricane was a disturbance in terms of its effects on the panther and snail kite, but it was moving towards catastrophe for the butterfly.

What influence does a consideration of natural catastrophe have on some core issues of conservation biology — reserve design and population viability analysis? What influence do anthropogenic catastrophic impacts have on these same issues? These questions will now be addressed.

8. The downside of proximate location

Based on the condition of homogenous habitat, Diamond (1975) recommended that when an area is broken into several disjunctive reserves, those reserves be located close together to permit migration. Wilson and Willis (1975) reommended reserve proximity as well. Simberloff (1978) criticized this guideline and Frankel and Soulé (1981) later elaborated on the benefits of locating reserves far apart. Soulé (1984) warned us that *proximity* may benefit only a few highly vagile taxa like birds, bats, some invertebrates and plants. Diamond (1975) and many subsequent scientists presume that

migration is critical for the short- and long-term genetic fitness of most species.

Why was so much attention paid in the 1970s and 1980s to the benefits of proximate location and so little attention given to reserve design features that lessen the risks associated with catastrophe? Perhaps because during this period there was growing awareness that periodic migration was essential to counter genetic erosion and demographic accidents? And this is where the quandary lies: if we choose proximate reserves to facilitate migration of a species, we cannot rely on those same reserves to guard against a catastrophic blow, or series of blows over time, to that species if the catastrophe(s) impacts a region larger than the distance between the reserves. Thus, the geographic spread of a catastrophic agent is significant (O'Neill et al., 1992). It seems odd that recent metapopulation theory has given this dilemma only brief acknowledgement (Hanski, 1989). Some subpopulations of a metapopulation could inhabit existing or future reserves provided such reserves coincided with the metapopulation's preferred patch of habitat and migration distance (Shafer, 1995; Wiens, 1997). Metapopulation theory aside, some facts remain: the average species has many subpopulations (Hughes et al., 1997), many species often use discontinuous habitat (Law and Dickman, 1998), and dispersal seems to influence population viability (Stacey and Taper, 1992).

9. Distance, size, number: how much insurance?

Back-up reserves are similar to taking out an insurance policy. The result of losing all of one's non-renewable assets is certain: there will be no replacements.

9.1. Distance

The manner populations are distributed within a landscape or region is a viability factor (Gilpin and Soulé, 1986). Slayter (1975) believed that two or more reserves would safeguard against catastrophe if they were geographically far enough apart, but he did not specify a safe distance. Any answer hinges on the geographic scale of the catastrophe.

Spatial correlation, a concept that arose in 1981 (Harrison and Quinn, 1989), may profoundly influence the persistence of a metapopulation, or biota in multiple reserves. Burgman et al. (1993, p. 170) explained that "spatial correlation, or autocorrelation, measures the amount of association between measurements of a variable made at points a given distance apart." Thus, if the extinction probabilities of two local populations are independent of each other, but each population faces a 10% risk of extinction over the course of 50 years, the probability of both becoming extinct in 50 years is only 1%. However, if the potential geographic reach of some natural phenomenon, for example a tsumani, encompasses both populations, the risk to both remains 10%.

Subdivided populations or reserves that are far apart may not provide enough distance to prevent harm from such large-scale phenomena as drought or severe winter (Quinn and Hastings, 1987). Lawton (1995) argued that hundreds of kilometers may be required to protect reserves from events that are spatially synchronous and environmentally stochastic. Examples might include blizzards or drought. Of course some sites, though appearing to be similar, may not sample winter severity the same way because the communities could have subtle distinctions which result in different effects (e.g. a herbivore starves at one spot but survives at another due to lack of a competitor). Other weather events are more spatially confined than blizzards. For example, tornadoes typically impact 50 ha, a distance greater than the 18.8 ha mean size of Wisconsin's scientific reserves (Guntenspergen, 1983).

If two reserves are too far apart, instead of duplicating (more-or-less) the other reserve's biota, sampling of different habitats and biota begins (Soulé, 1984). O'Connor (1996) argued that the spatial extent of a metapopulation is defined when autocorrelation ends. More information is needed about the spatial and temporal scale of major disturbances (Soulé and Kohm, 1989).

9.2. Size

Slatyer (1975) thought that extra reserves need to be "viable," and for good reason: if a catastrophe wipes out one or more species in all but one reserve, the remaining reserve should harbor populations that stand a chance of persisting. Regardless of the potential conservation benefit, land use politics in the United States can easily prevent the establishment of backup reserves of minimum viable area (MVA; Shaffer, 1987) for the widest-ranging large mammals. If a second reserve cannot provide a MVA, a suboptimal backup reserve is better than none — for example, two backup reserves each containing only 1/2 of the MVA or four connected reserves each containing 1/4 of the MVA. For species whose dynamics resemble the metapopulation model, preserving typically smaller patches of habitat, say in pursuit of the elusive "minimum viable metapopulation size" (Hanski et al., 1996b) for the Florida Scrub Jay (*Aphelocoma coerulescens*; Stith et al., 1996), is an endeavor that demands much less land.

9.3. Number

How many reserves are needed to safeguard against catastrophe? Without specific reference to catastrophe, a global conservation strategy (WRI/IUCN/UNEP, 1992) generalized that *two or more large* reserves of each type are needed. This guidance vaguely resembles

Soulé's (1984) recommendation that *two or more* minimum viable populations (MVPs) are needed, if not in one reserve, then in *two or more reserves*. The only general advise Soulé and Simberloff (1986, p. 32) could offer on reserve number was "…there should be many of them…" Reliable answers beyond this evade us.

9.4. Catastrophe and population viability analysis

Natural catastrophes are difficult to study empirically (Foley, 1997). Shaffer (1987) assumed that natural catastrophe sets the upper limit of population persistence for single, isolated, nonsubdivided populations of large mammals, as in African national parks, a prediction most pertinent to large mammals (Mangel and Tier, 1993). We must recognize that replicating most large landscape events is not possible (Carpenter, 1990; Hargrove and Pickering, 1992). Traditional population viability analysis (PVA; Boyce, 1992; Beissinger and Westphal, 1998) usually ignores catastrophe. Only a few researchers have tried to incorporate catastrophe into PVA (Mangel and Tier, 1993, 1994). Often data may be unavailable to judge non-anthropogenic catastrophe frequency or magnitude (Ludwig, 1999). Although the distance between reserves is a potential PVA factor (Harcourt, 1996), the general difficulty in any PVA analysis (Beissinger and Westphal, 1998) suggests reliable answers will not be forthcoming. PVA seems an unlikely source of illumination; so many variables are typically involved that simply exerting more effort is unlikely to reduce forecast uncertainty (Holsinger, 1995). The scale, diversity, and randomness of natural catastrophes precludes modeling and field experience from providing pat explanations for the impact of these events. Some anthropogenic catastrophic impacts may be easier to forecast.

Soulé and Kohm (1989) called for models that integrate genetic, demographic, and environmental stochastic events with catastrophe and geographic structure. Scientists have yet to rise to this challenge. Arguments are not data (Simberloff and Abele, 1984) but it would be foolish to postpone considering options until good data becomes available.

10. Poaching

The prospect of chronic anthropogenic degradation forces (e.g. habitat loss, exotic species, and pollution) causing a focal species' extinction might be reduced if two or more reserves harboring the species were further apart. One more of these factors, poaching, warrants examples.

10.1. The Indian rhinoceros

Poaching is believed to be the primary cause of Asian rhino population declines (Foose and van Strien, 1997).

As early as 1900, the Indian government began establishing multiple reserves to protect the almost extinct great one-horned Indian rhinoceros (*Rhinoceros unicornis*), as a safeguard against human catastrophic killing (Talbot, 1960). Today, with over 2000 in India and Nepal, the Indian rhinoceros is a success story when compared to the two other Asian rhino species. Successful translocation back to sites where they were extirpated enabled their persistence today at 13 locations in India, Nepal, and Pakistan. In 1993, these populations were estimated to vary from 2–1160 even though protected reserve area nowhere exceeded 1000 km². Planners must believe this multiple reserve/ translocation strategy contributed to the positive outcome because the recommended conservation strategy for all three Asian rhino species emulates this approach: 2000–3000 individuals distributed at a minimum of five separate sanctuaries, with each able to accommodate at least 100 rhinos; captive breeding; better safeguards against poaching; and others (Foose and van Strien, 1997). Poaching has had a catastrophic impact on many rhino species; six African countries lost their black rhino populations since 1981 (Hunter, 1996).

10.2. The mountain gorilla

In African savanna reserves, population declines below minimum viable levels have been attributed more to poaching than to reserve design (Western and Ssemakula, 1981). For African mountain reserves, two recent population viability analyses of the mountain gorilla (*Gorilla gorilla beringei*) population in the Virunga area of East Africa (Rwanda, Uganda, and Zaire) indicate that, providing current population structure is retained, the population is unlikely to go extinct solely from genetic or demographic reasons for several hundred years (ref. Harcourt, 1996). During the 1990–1994 Rwandan civil war, over 700,000 refugees in five camps occupied the three-country Virunga park (McNeely, 1998). Even though adjacent to the largest refugee camps in the world, apparently few gorillas in the Virunga park were poached. In contrast, many were killed for food in the nearby Kahuzi Biega National Park, Democratic Republic of Congo. The difference is attributed to conservation education in Rwanda and the Congolese custom of eating primate bush meat (Plumptre, 2000). Such an encouraging outcome may not be repeated.

10.3. Inter-reserve distance

Soulé (1984) may be correct that small reserves are more vulnerable to pillaging if civil authority breaks down. Common sense suggests that reserve size and number will influence how efficiently reserve staff can patrol for poachers (Ayres et al., 1991). It is difficult to know whether great distance between reserves will be a

poaching deterrent. The result could vary from place to place. Siegfried et al. (1998) bemoans that African national parks, on the average, are so widely spaced as to preclude biotic interchange. Could this African situation be an unappreciated blessing for some rare, flagship species? On the other hand, reserves might be too abundant and too distant. The endangered Sumatran rhinoceros (*Dicerorhinus sumatrensis*) persists at about 50 sites in Asia but such widespread distribution has been judged too difficult to protect against poaching (Foose and van Strien, 1997). Accessibility, not distance, is key to the defensibility of Amazonian reserves (Peres and Terborgh, 1995). If adequate patrolling is feasible, having multiple back-up reserves would seem prudent. The inter-reserve distance issue as it relates to poaching defies generalization.

11. Corridors

The important and contentious debate about the advantages of corridors between reserves (Noss, 1987) or disadvantages (Simberloff and Cox, 1987; Simberloff et al., 1992; Hobbs, 1992) generated essay coverage in *Science* (Mann and Plummer, 1995). Data on the actual use of corridors are meager (Simberloff et al., 1992). Beier and Noss (1998) reviewed the literature and concluded that observational evidence bolsters atypical well-designed studies suggesting that corridors are valuable in promoting migration. However, this debate sheds no light on whether migration between reserves is more important than safeguards to protect reserve populations against some catastrophes or catastrophic impacts.

Additional reserves may protect species from catastrophe (Simberloff and Abele, 1976a), and corridors may allow some animal species to retreat to safety (Noss, 1987). A 5-km corridor might enable some mammals to escape from fire or poaching. But that same corridor may allow some agents of extinction, such as disease or predators, to spread faster than they might otherwise (Simberloff and Cox, 1987; Hess, 1994). Because of hurricane scale, corridors may do little to reduce their impact on animals in reserves. South Carolina's Francis Marion National Forest lost 63% of its 1908 endangered red-cockaded woodpeckers (*Picoides borealis*) and 87% of their nesting trees to Hurricane Hugo in 1989 (Stolzenburg, 1999). Consequently, while corridors may provide added protection in some situations, they are not a panacea. Some modeling results indicate corridors provide no protective benefits from catastrophe (Wright and Hubbell, 1983; Ewens et al., 1987).

12. SLOSS

Another of Diamond's (1975) guidelines, later categorized as the SLOSS hypothesis, generated much more debate than did the guideline on proximate location. SLOSS asked the question: What will preserve more species, a single large reserve or several small ones of the same total area? The key debaters employed relatively few taxa (i.e. mostly birds, plants and invertebrates) to support their positions. Both sides recognized at the debate's outset that extra reserves were needed to safeguard against catastrophe (Diamond, 1976; Simberloff and Abele, 1976a).

The SLOSS argument was largely academic because the two SLOSS options are rarely available to planners in the real world (Shafer, 1990; Saunders et al., 1991). For two decades SLOSS focused on which of two options would capture more species or allow them to persist. But how far reserves are separated from each other may be the more important issue. SLOSS was subsequently described as a "red herring" (Murphy, 1989; Noss and Cooperrider, 1994). SLOSS "still raises its ugly head from time to time" (Noss and Cooperrider 1994, p. 140) perhaps because some questions peripheral to SLOSS still nag at us. Mangel and Tier (1994) argued we need to rethink SLOSS to include catastrophe.

13. Genetic problems beg a solution

13.1. Genetic analogs

The inter-reserve distance dilemma as it relates to catastrophe is reminiscent of the genetic dilemma. The genetic dilemma recognizes that smaller subdivided populations favor local adaptation and within-population genetic diversity (e.g. percentage of polymorphic loci) while larger populations preserve more heterozygosity. Periodic migration of a few individuals into subdivided populations is presumably the optimal strategy for preserving the maximum number of alleles (Chesser, 1983), which may be more important than optimizing heterozygosity. Computer simulations indicate that the best strategy for retaining valuable genetic diversity is to maintain several reserves that facilitate occasional inter-reserve migration (Boecklen, 1986; Boecklen and Bell, 1987). Researchers are now using metapopulation models to gain more insight into any potential optimal genetic strategy (Hedrick and Gilpin, 1997). Chesser et al. (1996) stressed that periodic high rates of inbreeding cannot be avoided if allelic spatial variation is to be maintained. A longer term consideration — translocation constraining evolution (Franklin, 1980; Shafer, 1990; Storfer 1999) — can be ignored if we accept Franklin's (1980) viewpoint: it is better to sacrifice evolutionary change at present if by doing so we conserve genetic variation for future generations.

13.2. Inbreeding effects

Inbreeding in zoo mammals is correlated with negative reproductive effects (Ralls and Ballou, 1983) and inbreeding is usually a component of population viability analysis (Boyce, 1992; Burgman et al., 1993). However, we cannot know the degree that inbreeding can effect viability without conducting detailed field studies on the species of concern (Ralls et al., 1988; Lacy, 1992). Therefore, our knowledge about the inbreeding sensitivity of particular taxa prohibits confident managed migration (Chesser et al., 1996). Some catastrophes could eliminate a population within a day, long before the negative effects of inbreeding could manifest generations later.

13.3. Translocation dangers

Scientists have long advocated multiple reserves provided there was occasional migration among them (Goodman, 1987). When natural migration is not feasible, translocation is the logical option (Simberloff and Cox, 1987). Translocation encompasses reintroduction, augmentation of depleted populations, and introduction to places where the species was not native. Managers understandably prefer natural migration to translocation because the former reduces the danger of disease transmission (Cunningham, 1996) and other potential problems (Griffith et al., 1989; Wolf et al., 1996). What if a field reconnaissance judges that the future persistence of a species would be more secure if reserves were far apart? Techniques for safe translocation are under debate (Hein, 1997) but both old (Stanley Price, 1989) and recent guidance (Miller et al., 1999) have been offered.

Some well-intended translocations that may have only hastened a species' extinction (Caughley and Gunn, 1996). Of 80 translocation projects for endangered bird and mammal species in Australia, Canada, New Zealand, and the United States, only 44% were successful (Griffith et al., 1989). "[W]hether populations should be kept isolated or linked, such as by corridors or translocations between reserves, are as yet unanswered questions" (Caughley and Gunn, 1996, p. 403) but the option of isolation carries heavy management responsibilities. Although translocation of plants is not risk free (Howard, 1996), this mitigation strategy can be used to create many populations. When widely distributed, many populations should be a safeguard against extinction.

13.4. Migrant number

Mills and Allendorf (1996) reassessed the genetic rule of "one-migrant-per-generation" and concluded that between 1 and 10 breeding individuals of a species need to migrate (or be translocated) per generation to minimize the loss of allelic diversity and heterozygosity *within* subpopulations and to permit the divergence of allele frequencies *among* subpopulations. Their model has five major built-in assumptions, but under "ideal" conditions where such assumptions presumably are satisfied, a lesson can be derived: only a few breeding individuals need migrate every generation to provide optimal genetic benefit. The results of some demographic modeling is encouraging too. Moving as few as one to six individuals of a species per year will dramatically increase the species' probability of persistence (Lubow, 1996). Potential translocations must address key questions: (1) how large must the donor population be before individuals are translocated; or (2) should the recipient population be subdivided (Maguire, 1986)?

Like corridors, translocation is not a panacea. Although translocation is a feasible management solution, it is a dangerous one that demands the utmost care.

14. Global warming

Average global surface temperature has risen 0.3–0.6°C since 1860. Such a continuing trend should cause an increase in glacial retreat, increased thinning of permafrost, a change in plant communities, a shift in the range of some diseases, and an increase in the intensity and frequency of hurricanes, fires, and floods. Based on regional short-term observations, such predictions have some empirical support. If sea-level continues to rise as it has over the last 100 years (i.e. 10–25 cm), coastal submergence is expected, a prediction documented for some US coastal marshes and forests. In addition, other global warming predictions include interior freshwater wetlands drying, more saltwater intruding into freshwater, increasing pest infestation, more coastal storm surges, and more drought and wildlife epizootics (Shafer, 1999) and these events could be common by 2050 (Intergovernmental Panel on Climate Change 1996a, b). These influences might benefit from reserve proximity because dispersal and migration would be facilitated. On the other hand, reserve distance might also be an asset. Without distant safeguard reserves, a species confined to its last, large protected sanctuary may be less likely to survive the predicted effects of global warming. Global warming could also create more refugees (Myers, 1993) who might poach more reserve biota to survive. Regardless of global warming, as the disparity between the rich and poor in developing countries widens, civil war is likely to increase (Homer-Dixon, 1999). McNeely (1998, 2000) documents the severe impacts of war on biota in protected areas.

15. Managing for catastrophe

Can we manage for some catastrophes or catastrophic impacts? Controlled burning may help reduce catastrophic fire. Segregating domestic stock from wild ungulates may lower the probability of transmitting disease to wild animals. Artificial sources of water may reduce the impact of drought and artificial feeding could reduce the number of individuals that die of starvation during severe winters. As flood waters approach, some species can be captured and moved to higher ground. More reserve guards can help combat poaching. Finally — the option discussed here — moving some individuals of a rare species to other suitable reserves or habitats, perhaps beyond their natural migration distance, might safeguard the species from extinction. Management for large disturbances is treated elsewhere (Dale et al., 1998).

16. Captive breeding analogs

Having a single captive back-up population is as risky as having a species confined to a single reserve. After being managed as captive stock since 1922, the entire population of the large copper butterfly (*Lycaena dispar* spp. *batavus* Obth.) in Woodwalton Fen (UK) was wiped out by a July 1968 flood (Duffey, 1977). An estate on the Island of Hawaii was home to the only captive flock of Hawaiian geese (*Nesochen sandvicensis*) when an April, 1946 tsunami drown 32 of the flock's 43 birds (Ripley, 1965). Disease is another reason why one captive population is not enough (Thorne and Oakleaf, 1991; Wilson et al., 1994). When rare or endangered species are captively reared in one US national park and then subsequently reintroduced to another park (e.g. the Hawaiian goose, peregrine falcon [*Falco leucocephalus*] and red wolf [*Canis rufus*]), the resultant subdivision yields two reserves with the species rather than one.

17. Where do we stand

Is any guidance feasible in the trade-off situation of migration versus distance in reserve design? At present, only reasoned speculation is feasible. *If* distant back-up reserves will decrease the risk of a species' extinction, the loss of natural migration may have to be accepted as a necessary evil. Natural migration, which proximate locations of reserves can facilitate, will provide no benefit if key populations that interchange individuals are eliminated by some calamitous human impact like poaching or a spatially synchronous natural catastrophe. In theory, managers can reduce inbreeding effects and the probability of random demographic accidents by periodically translocating some individuals.

Although the translocation of individuals from relictual populations has occasionally been recommended (Drury, 1974), such situations demand careful study beforehand and the utmost care must be exercised so translocation does not hasten rather than retard a species extinction. If reserves harbor commercially valuable birds and mammals with long generation times, past experiences with poaching and common sense suggests the need for back-up reserves.

Rare flagship species located in proximate reserves may in some cases reside there at great risk. Assuming the inter-reserve distance guideline now touted as optimal (i.e. reserves should be situated close to each other) could actually encourage the extirpation or extinction of some species highly valued by society, reserve managers and the conservation-minded public may wish to better acquaint themselves with the guideline's underlying assumptions. If preserving ecosystems is the reserve management goal, the identification of keystone species is one critical component (Simberloff, 1998). The argument presented here for flagship species is applicable to keystone species too.

The earliest reserve design guidelines were to maximize species number (Diamond, 1975; Wilson and Willis, 1975). Later, Thomas et al. (1990) listed five generlizations touted as sound advise (Wilcove and Murphy, 1991), and often repeated. To paraphrase one guideline: habitat close together is better than blocks far apart. Is there a difference between this Thomas guideline and the proximity guideline (Diamond, 1975; Wilson and Willis, 1975)? The Thomas guidelines assume a focal species. "Although these guidelines [Thomas] are oriented towards target species, they also apply to conservation planning at higher levels" (Noss and Cooperrider, 1994, p. 142). Some may indeed apply, but it is unlikely all are optimal for a target species and higher levels too. The need to preserve ecological processes introduces yet another goal (Shafer, 2000).

Long before the proximate reserve guideline was proposed in the 1970s, some successful conservation outcomes occurred because reserve planners intuitively created back-up reserves. These reserves, either by default or intention, were sometimes located too far apart to allow natural migration. The distance required between reserves is a function of the dispersal capability of a target species and the spatial independence of degradation forces. The dilemma we face is that some optimal, compromise distance needed to facilitate the inter-reserve dispersal for many diverse taxa, or even one focal species, could be very different from the distance needed by that same species to thwart the agents of natural and anthropogenic catastrophic impacts.

Scientists from the past (e.g. Leopold, c. 1938) advocated the old folk wisdom — it is dangerous to have all your eggs in one basket. If conserving rare flagship species is a societal reserve conservation priority, common

sense, at least for now, suggests that such folk wisdom be carefully considered. The protected reserve challenges that lie before us may increasingly become a one-shot opportunity.

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