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# Corridors in Real Landscapes: A Reply to Simberloff and Cox

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**Abstract:** *Habitat corridors have become popular in land-use plans and conservation strategies, yet few data are available to either support or refute their value. Simberloff and Cox (1987) have criticized what they consider an uncritical acceptance of corridors in conservation planning.*

*Any reasonable conservation strategy must address the overwhelming problem of habitat fragmentation. Although Simberloff and Cox use island analogies to illustrate advantages of isolation, these analogies do not apply directly to problems in landscape planning. Genetics also does not offer unequivocal advice, but the life histories of wide-ranging animals (e.g., the Florida panther) suggest that the maintenance or restoration of connectivity in the landscape is a prudent strategy. Translocation of individuals among reserves—considered by Simberloff and Cox a viable alternative to natural dispersal—is impractical for whole communities of species that are likely to suffer from problems related to fragmentation.*

*Many of the potential disadvantages of corridors could be avoided or mitigated by enlarging corridor width or by applying ecologically sound zoning regulations. Corridors are not the solution to all of our conservation problems, nor should they be used as a justification for small reserves. But corridors can be a cost-effective complement to the strategy of large and multiple reserves in real-life landscapes.*

**Resumen:** *Los corredores naturales se han hecho muy comunes en proyectos de uso de terreno y estrategias de conservación, pero hay muy pocos datos disponibles que puedan apoyar o rechazar su valor. Simberloff and Cox (1987) critican lo que ellos consideran es una aceptación poco crítica de los corredores naturales en la planificación de estrategias de conservación.*

*Cualquier estrategia razonable tiene que dirigirse al problema preponderante de fragmentación de hábitat. Aunque Simberloff y Cox usan el ejemplo de las islas como analogía para ilustrar las ventajas del aislamiento, estas analogías no aplican directamente a problemas en la planificación del uso de la tierra. La genética tampoco ofrece consejo inequívoco, pero la historia natural de animales con ámbitos extensos (ejem. Florida panther) sugiere que el mantenimiento o restauración de una conexión entre áreas naturales es una estrategia prudente. El movimiento de individuos de una u otra especie entre las reservas, considerado por Simberloff y Cox como una alternativa viable a la dispersión natural, es impráctico para comunidades enteras de especies que son vulnerables a la fragmentación.*

*Muchas de las desventajas potenciales de corredores naturales se pueden evitar o mitigar ensanchando el corredor, o estableciendo reglamentos de zonificación que sean congruentes con principios ecológicos establecidos. Los corredores naturales no son la solución a todos los problemas de la conservación natural, ni tampoco deberían ser usados como una justificación para reservas pequeñas. Pero los corredores naturales pueden ser un complemento de bajo costo y rendimiento efectivo a la estrategia de establecer muchas reservas de gran extensión.*

Corridors are a hot topic, perhaps even a fad, in conservation planning these days. Planners and environ-

mentalists from county to federal levels are busy drawing “greenbelts” and other habitat corridors into their designs, sometimes with only a vague awareness of the biological issues underlying the corridor strategy. Re-

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*Paper submitted 12/9/86; revised manuscript accepted 3/31/87.*

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Conservation Biology  
Volume 1, No. 2, August 1987

cently, some biologists have expressed concern that the corridor idea has been thrown into the political arena prematurely, without adequate field research or discussion among conservation biologists.

Soulé and Simberloff (1986), briefly, and Simberloff and Cox (1987), in more depth, have discussed some possible advantages and disadvantages of the corridor strategy. Simberloff and Cox (1987) place particular emphasis on disadvantages, because they believe that “much of the current literature concerning corridors fails to consider potential disadvantages and often assumes potential benefits without the support of sufficient biological data, or even explicit recognition that such data are needed.” No doubt more research is needed to develop optimal connectivity strategies, but the continuing severance of natural linkages in many landscapes suggests that active strategies to combat the process and the consequences of fragmentation must proceed quickly, with or without “sufficient” data.

Many conservation biologists agree with Wilcox and Murphy (1985) that “habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis.” Conservation strategies, therefore, might be evaluated on the basis of how well they counter the effects of fragmentation in real landscapes. The fragmentation problem has essentially two components: 1) a decrease in total habitat area, and 2) an apportionment of the remaining area into ever more isolated pieces (Wilcove et al. 1986). The two ways to counter fragmentation, then, are 1) increase effective habitat area, and 2) increase connectivity. My purpose in this note is to offer an alternative viewpoint to Simberloff and Cox (1987) and to evaluate potential advantages and disadvantages of corridors in the context of an integrated landscape conservation strategy.

## Potential Advantages and Disadvantages of Corridors in Human-Dominated Landscapes

Some potential advantages and disadvantages of corridors in human-dominated landscapes, with particular reference to conservation of terrestrial species and habitats, are listed in Figure 1. These lists are not comprehensive, as many important functional attributes of corridors will not be discussed here. For example, vegetated riparian corridors are important in maintaining water quality in streams (Karr & Schlosser 1978, Schlosser & Karr 1981), and hedgerows and shelterbelts have well-known advantages in inhibiting soil erosion (Forman & Baudry 1984).

Simberloff and Cox (1987) propose that corridors be evaluated individually on their own merits, and that theoretical considerations cannot be applied universally. Few ecologists would quarrel with that statement. But although Simberloff and Cox (1987) criticize the use of biogeographic analogies in pro-corridor arguments, much of their argument against corridors (or in favor of habitat subdivision) is based on island analogies. The common goal in this debate—conservation of biodiversity—might be served best if all parties, whenever possible, refrain from arguments based on theory and analogy, and devote their efforts to solving concrete problems in real-world landscapes.

The extent to which a habitat corridor might facilitate dispersal and thus increase immigration rates to reserves is strictly an empirical matter, and would depend upon habitat structure within the corridor, corridor width and length, and the autecologies of the particular organisms in question (Forman 1983, Harris 1984, Forman & Godron 1986, Noss & Harris 1986). If we determine that immigration rate is enhanced, we still do not know

Potential Advantages of Corridors	Potential Disadvantages of Corridors
<ol style="list-style-type: none"> <li>1. Increase immigration rate to a reserve, which could               <ol style="list-style-type: none"> <li>A increase or maintain species richness and diversity (as predicted by island biogeography theory);</li> <li>B increase population sizes of particular species and decrease probability of extinction (provide a “rescue effect”) or permit re-establishment of extinct local populations;</li> <li>C prevent inbreeding depression and maintain genetic variation within populations.</li> </ol> </li> <li>2. Provide increased foraging area for wide-ranging species.</li> <li>3. Provide predator-escape cover for movements between patches.</li> <li>4. Provide a mix of habitats and successional stages accessible to species that require a variety of habitats for different activities or stages of their life-cycles.</li> <li>5. Provide alternative refugia from large disturbances (a “fire escape”).</li> <li>6. Provide “greenbelts” to limit urban sprawl, abate pollution, provide recreational opportunities, and enhance scenery and land values.</li> </ol>	<ol style="list-style-type: none"> <li>1. Increase immigration rate to a reserve, which could               <ol style="list-style-type: none"> <li>A facilitate the spread of epidemic diseases, insect pests, exotic species, weeds, and other undesirable species into reserves and across the landscape;</li> <li>B decrease the level of genetic variation among population or subpopulations, or disrupt local adaptations and coadapted gene complexes (“outbreeding depression”).</li> </ol> </li> <li>2. Facilitate spread of fire and other abiotic disturbances (“contagious catastrophes”).</li> <li>3. Increase exposure of wildlife to hunters, poachers, and other predators.</li> <li>4. Riparian strips, often recommended as corridor sites, might not enhance dispersal or survival of upland species.</li> <li>5. Cost, and conflicts with conventional land preservation strategy to preserve endangered species habitat (when inherent quality of corridor habitat is low).</li> </ol>

Figure 1. Potential advantages and disadvantages of conservation corridors.

whether the net effect of this increased immigration is good or bad for conservation. (Fig. 1; item number 1). According to island biogeography theory (MacArthur & Wilson 1967), increased immigration should result in a higher equilibrium species number. But higher species richness at the local scale may not be a goal in conservation, particularly if the species that invade are alien to the landscape or not in need of reserves for survival (Diamond 1976, Noss 1983). Augmentation of local population size with immigrants from the same species ("rescue effect"; Brown & Kodric-Brown 1977) and re-establishment of extinct local populations (Fahrig & Merriam 1985) might be considered an advantage of increased connectivity, but not if the organism so benefitted is a competitor, predator, parasite, or pathogen of a species of greater conservation concern.

The genetic consequences of increased immigration rate are also controversial, as discussed by Simberloff and Cox (1987). On the one hand, inbreeding depression and genetic drift might be minimized with the influx of genetically different individuals, resulting in increased fitness for the average individual and increased genetic variation in the population. Evidence for immigrants contributing much to heterozygosity or fitness in a small population is meager, however (Frankel & Soulé 1981). Furthermore, increased gene flow between demes might lead to genetic swamping and homogenization of the gene pool. Corridors have never been implicated in this problem, although the possibility worries Simberloff and Cox (1987).

Gene flow might also disrupt local adaptation and coadapted gene complexes, resulting in outbreeding depression. Although outbreeding depression is likely to be a temporary phenomenon, rapidly eliminated by selection and sometimes replaced by a superior coadapted gene complex, it could greatly increase the chances of extinction in small populations (Templeton 1986). Outbreeding depression is a potential problem in captive breeding programs, when animals from distinct populations are mated (e.g., de Boer 1983, Templeton et al. 1986). On the other hand, maintaining or restoring natural landscape connectivity never has been shown to cause outbreeding depression in populations.

On the genetics issue, Simberloff and Cox (1987) suggest that "the subdivision of a larger population allows the effects of genetic drift to assist in the maintenance of genetic variability in the species" (see Chesser 1983). When inbreeding becomes a problem, manual translocation of individuals between isolated populations is considered preferable ("genetically advantageous and much less expensive"; Simberloff & Cox 1987) to protecting corridors for natural dispersal. The esthetic and perhaps ethical question of whether shipping animals around in crates is a satisfactory substitute for natural movements warrants philosophical discussion.

Although translocation might fulfill genetic manage-

ment objectives for a few focal species, moving all the species of a community among reserves is clearly impractical. Fragmentation thus far has been documented to have deleterious effects in a relatively few sensitive species, but many secondary extinctions may be forthcoming (Wilcove et al. 1986). Small populations of organisms that today seem relatively secure, such as long-lived forest herbs with limited dispersal capabilities and slow responses to potentially significant forest changes, may prove vulnerable in the long term (Middleton & Merriam 1983). The same may be true for many forest songbirds (D. Wilcove, personal communication). Furthermore, because of mutualistic dependencies among certain species and the natural shifting of habitat patches over time and space, levels of biological organization above the population may depend on habitat connectivity for long-term persistence (Noss & Harris 1986). In the face of scientific ignorance about these phenomena, maintenance of habitat connectivity would seem to be the prudent course.

Simberloff and Cox (1987) choose the Florida panther (*Felis concolor coryi*) as an example of a species where proposed corridor strategies (Cristoffer & Eisenberg 1985, Noss 1985a, Noss & Harris 1986) are inappropriate. Unfortunately, they fail to consider the most critical component of that strategy: the re-creation of wilderness landscapes by closing roads and limiting access in large core areas of public lands in the present range of the panther in south Florida, and in proposed reintroduction sites in north Florida, as detailed in Noss (1985a, 1985b) and summarized in Noss and Harris (1986). In this admittedly idealistic strategy, large roadless areas would be surrounded by multiple-use buffer zones and connected by broad habitat corridors (revised map in Noss 1987a). Thus, corridors are envisioned as one critical component of an integrated landscape conservation strategy, not as panaceas. Wilderness restoration may be the only hope for the Florida panther, an animal demonstrably intolerant of habitat fragmentation. Like other pumas, it does not prosper in human-dominated landscapes (Noss 1985a, USFWS 1986, Van Dyke et al. 1986).

Simberloff and Cox (1987) propose that "a better method of preserving extant levels of genetic variability might be to isolate new translocated populations" of panthers, but their reasoning is unconvincing in light of *Felis concolor's* natural history. *F. c. coryi* was originally distributed continuously from Florida northeast to South Carolina, and west to Arkansas and east Texas or west Louisiana (Goldman 1946, Hall 1981). Habitat fragmentation and direct persecution subsequently eliminated this subspecies from all of its range except south Florida, which until recently was remote wilderness (Belden, in press; USFWS 1986). Although the current level of genetic variation in the 20 to 50 remaining panthers and how this relates to fitness is unknown, this may be a classic

case of inbreeding depression. All five males examined to date have had greater than 93 percent abnormal sperm (Roelke 1986, USFWS 1986). The Florida panther as we know it today is an "inbred subset" of the *F. c. coryi* recognized by Goldman (1946), and strategies to enhance genetic variation are being discussed (Eisenberg 1986).

Given what is known about the former continuity of panther distribution and the long-distance movements of individual *Felis concolor* (often over 100 km; Young 1946, Hornocker 1970, Dewar 1976, Hemker et al. 1984, Logan et al. 1986), it is possible that a single deme may have occupied all of peninsular Florida. Documented dispersal of juveniles and immigration of transients suggest that *F. concolor* cannot adequately be managed site-by-site, but instead requires management on a regional basis (Logan et al. 1986). Because several individuals often travel common corridors that are influenced by topography (e.g., Young 1946), the safest strategy may be to provide numerous, carefully selected, and well-protected swaths of habitat (including highway underpasses) for this movement. The alternative of isolated reserves would virtually assure that individuals will continue to be shot and run over in the mortality sink of the developed landscape.

Evidence that corridors on a finer scale can help animals avoid predation is accumulating, contrary to the suggestion of Simberloff and Cox (1987) that thin corridors may increase the exposure of animals to predators. Studies of fall movements of blue jays in Wisconsin have demonstrated that jays usually follow wooded fence-rows in crossing open farmland. Apparently this is a response to predation from numerous migrating hawks, for jays frequently dive into fencerow cover when hawks approach (Johnson & Adkisson 1985). Experimental and radio-telemetry studies of *Peromyscus* movements along fencerows in Ontario farmland are providing data on what type of cover is preferred by these mice (Merriam 1986). Simberloff and Cox (1987) correctly note that the question of whether a corridor represents safety or a threat to an animal can be answered only by considering ecological factors specific to the organism and the site.

Most of the other potential advantages and disadvantages of corridors listed in Figure 1 are self-explanatory. Two, however, warrant further comment. Although biologists seldom consider the anthropocentric functions of "greenbelts" or "open space" in developed landscapes, these quality-of-life factors are of utmost importance to landscape architects and planners. Scenery, recreation, pollution abatement, and land value enhancement are what usually motivate planners to draw corridors into their designs (various human uses of corridors are mentioned in Forman & Godron 1986). And many of these corridors are being drawn. It would be auspicious for biologists and planners to work together

to develop corridor designs that can optimize the quality of both the human and the nonhuman environment.

Finally, a major concern of Simberloff and Cox (1987) is that the cost of corridors will conflict with conventional conservation objectives to preserve endangered species habitat. I prefer to think of the corridor strategy as a complement to efforts to save "the last of the least and the best of the rest," as in The Nature Conservancy's heritage approach (Jenkins 1985). Whereas the heritage approach generally focuses on relatively small, discrete sites chosen for their occurrences of endangered elements (often plant species), corridors are an element of a landscape-level approach designed to restore and protect intact ecosystems and wide-ranging animals, many of which are critically endangered (Noss 1983, 1987a, b). I share Soulé's concern (personal communication) that corridors might be prescribed as an answer to every problem, or as a justification for preserves that are too small. But the fact remains that almost all existing reserves are far too small to maintain natural ecological processes and viable populations of the species with the largest home ranges (Pickett & Thompson 1978, White & Bratton 1980, Lovejoy & Oren 1981, Schonewald-Cox et al. 1983, Harris 1984, Noss & Harris 1986).

The corridor strategy can be an important complement to the strategy of large and multiple reserves (cf. Soulé & Simberloff 1986). Although money for conservation is never easy to come by, conservationists probably have not made strong enough demands for funds. For example, assuming that 26,000 ha of Florida wildland can be purchased for \$20 million (i.e., a recent state acquisition of a critical coastal corridor), then over 4.5 million ha could be purchased for the cost of one \$3.5 billion space shuttle. Furthermore, many corridors can be protected by conservation easements, tax incentives, management agreements, registry programs, and other less-than-fee negotiations (e.g., Noss & Harris 1986), although these options all involve their own complications (J. Cox, personal communication).

## Conclusions

Perhaps the best argument for corridors is that the original landscape was interconnected. This is not to deny that dispersal barriers such as rivers and mountain ranges have been important in biogeography and evolution, or that naturally isolated habitats such as lakes, caves, mountain tops, and edaphic patches are important features of natural landscapes. But as can be observed readily in aerial photographs of undeveloped land, presettlement landscapes in general are interdigitating mosaics with high connectivity of similar habitats. Connectivity declines with human modification of the landscape (Godron & Forman 1983). Hence, wide-ranging animals such as large predators that once were dis-

tributed almost continuously over entire continents are now confined to the few remaining pockets of unfragmented land. Corridors are simply an attempt to maintain or restore some of the natural landscape connectivity. No one, to my knowledge, is suggesting that we build corridors or other connections between naturally isolated habitats.

Certainly, humans and associated disturbances will impinge on corridors, just as they impinge on small nature reserves. For this reason, corridors should generally be as wide as possible. Planners and conservationists often ask how wide corridors need to be, and corridor widths (especially for riparian corridors) are often specified in land-use plans. In reality, the necessary width will vary depending on habitat structure and quality within the corridor, the nature of the surrounding habitat, human use patterns, and the particular species that we expect to use the corridor. Narrow fencerows might suffice for many farmland species, but wilderness species such as large carnivores may require corridors many miles wide to travel safely among reserves. A wide enough swath, of course, effectively creates one large reserve out of two or more smaller reserves.

Corridors are not *the* answer to our conservation problems. Undoubtedly, in many situations acquiring marginal habitat for corridors should be of lower priority than preserving isolated sites for endemic or endangered species. The major area of common ground among the various conservation biologists involved in this debate is that we are all interested in maintaining biodiversity, and most of us are wary of facile generalizations and analogies as guides to conservation. We furthermore agree that conservation actions must be based on the autecologies of the species concerned, and on other site-specific attributes. But a holistic, "top-down" framework can be useful in providing context to autecology. When money is limited, as it always will be, alternative actions should be weighed carefully. Weighing alternatives is made easier by evaluating their potential contributions to a landscape conservation strategy that addresses the overwhelming problem of habitat fragmentation.

## Acknowledgments

My thinking on corridors has benefitted from discussions and correspondence with Jim Cox, Richard Forman, Larry Harris, Michael Soulé, Jack Stout, David Wilcove, and many others. I particularly thank Jim Cox, David Ehrenfeld, Robert May, and an anonymous referee for their helpful comments on an earlier draft of this paper.

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