# **Movement Corridors: Conservation Bargains or Poor Investments?**

# DANIEL SIMBERLOFF JAMES A. FARR

Department of Biological Science Florida State University Tallahassee, FL 32306, U.S.A.

# JAMES COX

Florida Game and Fresh Water Fish Commission 620 S. Meridian Street Tallahassee, FL 32399, U.S.A.

## DAVID W. MEHLMAN

Department of Biological Science Florida State University Tallahassee, FL 32306, U.S.A. and Department of Biology University of New Mexico Albuquerque, NM 87131

Abstract: Corridors for movement of organisms between refuges are confounded with corridors designed for other functions, obscuring an assessment of cost-effectiveness. The rationales for movement corridors are (1) to lower extinction rate in the sense of the equilibrium theory, (2) to lessen demographic stochasticity, (3) to stem inbreeding depression, and (4) to fulfill an inberent need for movement. There is a paucity of data showing how corridors are used and whether this use lessens extinction by solving these problems. Small, isolated populations need not be doomed to quick extinction from endogenous forces such as inbreeding depression or demographic stochasticity, if their babitats are protected from humans. In specific instances, corridors could bave biological disadvantages. Corridor proposals cannot be adequately judged generically. In spite of weak theoretical and empirical bases, numerous movement corridor projects are planned. In the State of Florida, multi-million-dollar corridor proposals are unsupported by data on which species might use the corridors and to what effect. Similarly, plans for massive corridor networks to counter extinction caused Corredores para el movimiento: ¿Gangas de la conservación o malas inversiones?

Resumen: Los corredores para el movimiento de organismos entre refugios son confundidos con corredores designados para otras funciones obscureciendo una evaluación sobre costo-efectividad. Las funciones atribuidas a los corredores para movimiento son (1) disminuir la tasa de extinción definida en términos de la teoría de equilibrio, (2) disminuir la estocasticidad demográfica, (3) contrarrestar la depresión endogámica y (4) satisfacer una necesidad innata de movimiento. Existe una carencia de datos que demuestren como son usados estos corredores y si este uso minimiza las extinciones al resolver estos problemas. Poblaciones pequeñas y aisladas no están necesariamente condenadas a una rápida extinción causada por fuerzas endógenas, como depresión endogámica o estocasticidad demográfica, si sus ábitats están protejidos de los humanos. En instancias particulares, los corredores pueden tener desventajas biológicas. Las propuestas sobre corredores no pueden ser juzgadas apropladamente en forma genérica. Numerosos corredores para movimiento están proyectados a pesar de fundamentos teóricos y empiricos débiles. En el

Paper submitted August 13, 1991; revised manuscript accepted February 27, 1992.

by global warming are weakly supported. Alternative approaches not mutually exclusive of corridors might be more effective, but such a judgment cannot be made without a cost-benefit analysis.

## Introduction

A remarkable publicity campaign, much of it outside the bounds of mainstream science, has promoted corridors for conservation. Wilson and Willis (1975) originally proposed corridors based on the equilibrium theory of island biogeography (MacArthur & Wilson 1967); the suggestion was reprinted in World Conservation Strategy (International Union for the Conservation of Nature and Natural Resources [IUCN] 1980). With the imprimatur of the IUCN, the United Nations Environmental Program, and the World Wildlife Fund, the idea was widely accepted. The popular promotion of corridors entails lead articles in lay magazines (such as Arnold 1990), a videocasette (Suchy & Harris 1988), a pamphlet (Anonymous 1990a), the entire December 1986 issue of ENFO, and a special publication by Defenders of Wildlife (Mackintosh 1989). In Montana, a court has ruled that corridors are scientifically established as important (Breen 1991; Pace 1991). Keith Hay of the Conservation Fund argued that corridors "hold more promise for the conservation of the diversity of life than any other management factor except stabilization of the human population" (Chadwick 1990).

This hype is occurring in spite of a dearth of evidence of whether corridors will be useful in specific situations. "The workshops that discussed the values of corridors were certain that they were positive features despite the lack of supporting research" (Dendy 1987). That they facilitate movement "is now almost an article of faith" (Hobbs & Hopkins 1991). Saunders & Hobbs (1991*a*) believe that we do not have time to test the efficacy of corridors, while Noss (1992) argues that, in the face of uncertainty, it is prudent to maintain or restore "natural" kinds of corridors.

Discussion of corridors is confused (Anonymous 1986). We are concerned in this article with corridors for movement, but at least six senses of "corridor" appear in the conservation literature.

First, some habitats constitute corridors. A corridor may deserve protection as a distinct habitat, whether or not it aids movement (Simberloff & Cox 1987). For example, riparian communities are very threatened in estado de Florida, propuestas multimillionarias para corredores no están fundamentadas por datos que indiquen que especies usarian los corredores y con que propósito lo barían. En forma semejante, los proyectos de redes masivas de corredores para contrarrestar la extinción causada por el calentamiento global están pobremente fundamentados. Estrategias alternativas, que no son mutuamente excluyentes con los corredores, podrían ser mas efectivas, pero tales juicios no pueden ser becbos sin un análisis de costobeneficio.

some regions (Johnson 1989), but their value as habitats is independent of whether they allow movement between other habitats. To embed a discussion of riparian habitats in an argument about movement corridors (see Johnson 1989; Ames 1990) confounds assessment of strategies for land acquisition. Some linear artificial habitats, such as rights-of-way for highways (Adams & Dove 1989; Wilcox 1989), railroads (Noss 1992), and transmission lines (Anderson et al. 1977; Kroodsma 1982; Forman 1983), are also called "corridors," and can bolster animal populations and enhance urban and suburban green space (Adams & Dove 1989). Again, their utility as habitats is separate from their importance for movement.

Second, greenbelts and buffers are occasionally called "corridors," and their function of ameliorating the human environment is cited in discussions of movement corridors (see Gilbrook 1986; Budd et al. 1987; Adams & Dove 1989). Although such areas might aid dispersal, some envisioned uses (such as hiking and horse trails, boating, outfall for storm sewers) could impede their utility as either dispersal routes or habitats. In any event, the value of such constructs as aesthetic amenities is independent of their value for movement.

Third, Harris (1985) and Suchy and Harris (1988) call biogeographic landbridges such as the Isthmus of Panama "corridors." Such large regions have aided intercontinental movement of entire communities (Brown & Gibson 1983), but the relevance of this fact to maintaining viable populations in refuges is obscure (Simberloff & Cox 1987).

Fourth, a series of discrete refuges for migratory waterfowl is occasionally called a corridor (see Harris 1985; Anonymous 1991). Below we will suggest that such a system can be construed as an alternative to corridors or complementary to a corridor network.

Fifth, underpasses and tunnels are often now called "corridors." They are commonly used to allow animals to cross highways (reviewed by Bennett 1990*b*; Noss 1992), primarily to keep individuals from being killed on the road rather than to decrease demographic stochasticity, prevent inbreeding depression, or serve other population-level functions. Costs of such struc-

tures should be construed as part of road construction rather than as land acquisition.

Sixth, and our concern here, are strips of land intended to facilitate movement between larger habitats. Wilson and Willis (1975) and Harris and Scheck (1991), in the context of equilibrium theory, envision such movement as increasing immigration rates, thus raising the equilibrium number of species at each site. Harris (1984, 1985) suggested two other rationales for corridors. First, individuals of some species typically range widely; second, inbreeding depression will lead to extinction in small refuges. Recently, alleviation of demographic stochasticity has been a suggested benefit of corridors (see Merriam 1991; Thomas 1991; Noss 1992).

We are particularly concerned with the economic cost of corridors. Hobbs and Hopkins (1991) talk of corridors as adding an option to a sparse conservation repertoire, but options may be foreclosed if a particular corridor is reserved. Noss (1992 and personal communication) believes it is prudent to retain existing corridors, conceding that establishing new ones may be costineffective. But even an existing corridor is not necessarily free, and prudence when all options cannot be pursued requires some sort of cost-benefit analysis of each.

#### **Rationales for Movement Corridors**

#### The Equilibrium Theory of Island Biogeography

The equilibrium theory of island biogeography states that species number is constant, but that local turnover changes composition. Thus, corridors are useful by virtue of maintaining more species. An odd aspect of the rush to found a technology of refuge design based on island biogeographic theory is that, exactly when the IUCN and others were popularizing refuge design based on equilibrium theory, the theory was increasingly heavily criticized (Gilbert 1980; Williamson 1981, 1989; Williams 1984, 1986) as inapplicable to most of nature, largely because local population extinction was not demonstrated.

#### Demographic Stochasticity and the Metapopulation

Although not cited in the original recommendations for corridors, demographic stochasticity has been widely recognized as a potential threat to small populations (references in Simberloff 1988), and its diminution is now viewed as a rationale for corridors (see Merriam 1991; Thomas 1991; Noss 1992). No unified theory combines genetic, demographic, and other forces threatening small populations, nor is there accord on the relative importance of these threats. Lande (1988) believes that demography will usually be more important than genetics to very small populations, while Goodman (1987*a*) sees demographic stochasticity as important only when just a "handful" of individuals remain.

The metapopulation paradigm (Levins 1970) has replaced equilibrium theory for habitat islands (Merriam 1991), partly because of absence of evidence for turnover. The metapopulation is seen as lessening or redressing extinction by demographic stochasticity of the component populations. As with the equilibrium theory, however, there is now a tendency to take the metapopulation paradigm as broadly representative of nature, rather than as a new and untested hypothesis. Such statements as, "Many or most species are distributed as 'metapopulations'" (Noss 1992) are simply unwarranted. There are few empirical data, no specification of the range of dispersal rates that qualifies a group of populations as a metapopulation, and a variety of untested metapopulation models (references in Hanski & Gilpin 1991), none of which has been demonstrated to represent many situations in nature. Even if the metapopulation model should be shown to apply to a particular situation, the model requires movement, not corridors (Merriam 1991).

#### **Inbreeding Depression**

A genetic argument for corridors extends the concept of movement to genes as well as individuals. Harris (1984, 1985) argues that gene flow is required to prevent inbreeding depression from causing extinction and that corridors are needed for this gene flow.

Although a degree of inbreeding depression is usually found in captive animal populations, its threat must be established empirically. Some species with little genetic variation suffer no inbreeding depression (such as Pere David's deer and the European bison [Frankel & Soulé 1981]). It is often said that such species were luckytheir populations probably shrank gradually, and natural selection removed deleterious alleles that cause inbreeding depression. This line of reasoning implies that inbreeding depression is likely if normally outbred species suddenly inbreed (Frankel & Soulé 1981), as might be induced by rapid habitat fragmentation. However, in these cases most of the population decline occurred in a few generations. Therefore it remains mysterious why some species have little or no inbreeding depression. In nature, evidence from animal populations is extremely scarce (Charlesworth & Charlesworth 1987). The offcited evolution of behavior that reduces inbreeding need not have been selected by inbreeding depression (Charlesworth & Charlesworth 1987). In higher plants in nature, a measure of inbreeding depression has almost always been found when sought (Charlesworth & Charlesworth 1987). However, adequate data have been collected from far too few species.

Finally, finding that small populations are threatened by inbreeding depression is different from demonstrating its existence (Lande 1988). To evaluate the threat from inbreeding depression, it is important to bear in mind that a loss in genetic fitness need not endanger a population. "Inbreeding depression" means that more inbred individuals are less fit than less inbred ones. Most populations of most species, however, generation after generation produce some individuals less fit than others, yet are not endangered. So it is not axiomatic that inbreeding, even if it should lead to inbreeding depression, is a major threat to small populations, relative to other threats (Lande 1988). In any event, even if inbreeding depression is found to threaten a population, the key question is whether corridors are the best way to stem it; we return to this point below.

#### Need of Individual Animals for Movement

The Northern Spotted Owl (Strix occidentalis caurina) has a median pair home range in most areas of 1200 to 2000 ha (Thomas et al. 1990). Home ranges are larger in areas with less old-growth forest habitat (references in Thomas et al. [1990]), suggesting that the crucial requirement is enough small mammal prey inhabiting this habitat. There is an indication that owls that do not get enough favored prey experience lowered reproduction rates, but there is no suggestion that failure of space for movement per se is limiting. Mortality of dispersing juveniles is severe, but Thomas et al. (1990) argue against even wide corridors specifically for owl movement on the grounds that predators may thrive in them. Spotted Owls appear to disperse in random directions, which also argues against a corridor strategy (Noss 1992). Rather, Thomas et al. (1990) suggest management of the entire matrix surrounding owl habitat conservation areas to make it suitable for owl dispersal.

Harris (1985) and Noss and Harris (1986) have adduced the large home ranges of Florida panthers (Felis concolor coryi) and black bears (Ursus americanus) as a rationale for corridors. Most conservation areas in Florida are too small to provide the approximately 80 km<sup>2</sup> covered by a male black bear (Lindzey & Meslow 1977; Wooding & Hardisky 1990) or the approximately 400 km<sup>2</sup> covered by a male panther (Belden 1989) each year, and Maehr and Harris (1986) believe that areas as large as 800 km<sup>2</sup> may not support viable populations of either species. However, black bear populations have persisted despite confinement to small areas (Lindzey & Meslow 1977). Corridors might allow some species to avoid potentially fatal intraspecific encounters. Territorial battles between male panthers and between male black bears are sometimes lethal (Kemp 1976; Belden 1989). There are instances of black bear cannibalism (Tietje et al. 1986), and young black bears establish territories more readily at low densities (Kemp 1976; Rogers 1987). Therefore if corridors actually aided dispersal, they might be beneficial, but there is little evidence that dispersal is mediated by such social interactions (Rogers 1987) or that bears use corridors to disperse.

No Florida panther restricts its movements to one protected area, and panthers use a "hardwood strand" corridor linking the Big Cypress National Preserve to unprotected habitat (Machr 1990). Hardwood strands follow depressions and slow-moving watercourses in Florida (Maehr & Cox, unpublished data). This particular strand is less than 5 km long-much less than the daily ambit of a panther (Belden 1989)-and bounded by agricultural areas, which panthers avoid. How well panthers would use a much longer corridor is unknown. Long-distance dispersal by bears and panthers is not nearly as well documented. Maehr et al. (1988) describe one black bear dispersal of 120 km, but they also contend that well-defined corridors are not necessary for bears so long as habitat does not fully impede movement.

In sum, the need for movement per se is doubtful, though animals may be driven to move for specific purposes, such as finding food or avoiding conspecifics. The key questions are whether such movement is necessary in a specific refuge system and, if it is, whether corridors of specified characteristics are the best strategy to facilitate such movement.

#### How Inevitable is Quick Extinction of Small Populations?

Given the attention paid in recent conservation literature to threats to small populations, it might seem that any small, isolated population is doomed in the short term. Many go extinct (see Petterson 1985). But many small populations persist and cannot easily be dismissed as recently-reduced populations en route to extinction. Numerous endemic species of small islands are endangered primarily by either habitat destruction or introduced species (references in Simberloff 1986; see Craig 1991) but apparently thrived for millennia in the absence of humans, though many probably numbered at most in the low hundreds. Species in the highest trophic levels are particularly striking. For example, the Red-Tailed Hawk (Buteo jamaicensis socorroensis) of Socorro Island (southwest of Baja California) has had a stable population of about 20 pairs for at least the last few decades, and there is no reason to think the population was larger in antiquity (Walter 1990). Of course, we do not even know the fates of many isolated populations that disappeared in the absence of human interference, but rapid extinction is not automatic.

## **Evidence for Corridor Use**

Simberloff & Cox (1987) found few empirical data on corridor use and discovered that most reported obser-

vations were ambiguous. These problems persist (Hobbs & Hopkins 1991; Nicholls & Margules 1991; Saunders & Hobbs 1991*a*). There are still few data, and many widely cited reports are unconvincing.

Probably the first advocacy of corridors based on specific data was for birds of forest patches in the northeastern U.S. (MacClintock et al. 1977). This study is often cited (see Greenberg 1990) as showing that corridors increase diversity. The study was uncontrolled; there were no isolated sites not connected by a corridor to a larger forest, and no data on corridor use for sites that were connected to a larger forest. A frequently cited (see Noss 1992) recent paper (Saunders & Ingram 1987) contends that "Comparison of breeding results from all five populations studied and the amount of native vegetation remaining in each area showed that Carnaby's Cockatoo [Calyptorbynchus funereus latirostris] can breed successfully in areas which have been extensively cleared provided there are corridors of native vegetation connecting patches of remnant vegetation." In fact, data from this paper do not show that corridors are more important than amount of vegetation in the remnant (Saunders, personal communication 1987). However, additional uncited data (Saunders 1980) showed that, at the one site where the cockatoo disappeared, feeding areas near railway and road verges were used but did not connect to a nearby reserve.

Bennett (1987a), studying the long-nosed potoroo (Potorous tridactylus) in Australian forest patches, concluded that forest strips along roads and creeks aid dispersal and allow persistence in a fragmented landscape. No data in this paper addressed this question, but the paper cited a dissertation (Bennett 1987b). There the conclusion rested solely on two animals trapped in forested corridors, while there were no traps outside of corridors. Bennett (1990a) similarly felt that narrow forested corridors "facilitate continuity between populations" of eight mammals in Australia but did not study movement outside of corridors. Suckling (1984) argued that forested roadside strips connecting woodland patches prevent local extinction of the sugar glider (Petaurus breviceps) in Australia. However, he did not trap outside corridors and forest patches, and the only unconnected patch of the three studied was less than half the size of the others. Thus there are no data on increased dispersal with corridors or increased extinction without them. Bennett (1990b) argued that "all known dispersal movements" of the sugar glider involved corridors; in fact, none were sought otherwise.

Assessing these claims was difficult, entailing correspondence and examination of an unpublished document (Bennett 1987b) in Australia that could not be procured by interlibrary loan in Florida. One cannot expect management personnel to expend such effort, yet without this examination one would be left with a misleading impression. For example, Ogle (1989) noted that a 1986 corridor proposal in New Zealand was questioned on the grounds of lack of evidence on corridor use, "notwithstanding the plausibility of the concept and a growing body of supportive data from overseas." There were, at that time, virtually no supportive empirical data, only a plethora of statements advocating the concept (Simberloff & Cox 1987). Ogle (1989) went on to cite new supporting data:

Biological corridors have been the subject of considerable field research in Australia, and their importance for movements of fauna between otherwise discrete patches of habitat has been established on, for example, small marsupials (Bennett 1987) and Cockatoos (Saunders & Ingram 1987). Bennett showed that narrow strips of forest along road verges and water courses provide routes for the dispersal of adult long-nosed potoroo (Potorous) between remnants of native vegetation in agricultural lands of south-west Victoria. Saunders & Ingram have shown that Carnaby's Cockatoos (Calyptorbynchus funereus latirostris) in Western Australia nest in isolated forest remnants in agricultural land, and feed in remnants of native heathland. Native vegetation of road verges provides some feeding habitat and the routes (corridors) between nesting and feeding areas.

Ogle was at pains to show that corridors are critical for these species, but neither study cited demonstrated their importance.

Nicholls and Margules (1991) detail statistical difficulties of experiments to show that corridors enhance movement. Largely because of problems achieving sufficient experimental sample sizes, they acknowledge that observational studies could be useful. As the examples above show, however, many such studies are inconclusive, particularly because of failure to examine movement without corridors. That an animal uses corridors when these are present need not mean movement without them is impossible, or even less frequent. Of 36 papers in "The Role of Corridors" (Saunders & Hobbs 1991b), five present new data on animal movement (Arnold et al. 1991; Catterall et al. 1991; Date et al. 1991; Prevett 1991; Saunders & de Rebeira 1991). Of these, only Arnold et al. (1991) gathered data on movement between habitat patches without corridors. Only three (Arnold et al. 1991; Date et al. 1991; Prevett 1991) concluded that corridors have a very small role in conserving a particular taxon.

# **Regional Corridors to Alleviate the Effects of Global Warming**

The interaction of fragmentation with global warming has led to a different sort of corridor proposal. Global warming can cause a species' present sites to change more quickly than the species can evolve (Peters & Darling 1985). During earlier climatic changes many species could shift their geographic ranges to remain in their favored habitat. As habitats have become fragmented, routes are increasingly blocked (Peters 1988). Graham (1988), Hunter et al. (1988), and Harris and Gallagher (1989) suggest a vast network of corridors over North America. Hunter et al. (1988) feel that even a 300-meter-wide corridor stretching thousands of kilometers could be very useful. Few data are available to assess this plan. Whether a strip 300 meters wide would allow the range shifts that typified the Pleistocene has barely been discussed. Noss (1992) worries that the anticipated speed of temperature increase may render such corridors of little use for many species. Hobbs and Hopkins (1991) admit that the utility of corridors in counteracting effects of global warming is very uncertain, but they argue for going ahead anyway.

If a corridor is intended to preserve an entire community, as in the global warming recommendation, it is particularly important that it be wide enough to permit breeding as well as movement. One need only consider the limited mobility of many soil invertebrates and plants to realize that a range shift would be painfully slow and require many generations.

A corridor to permit survival and breeding is serving as more than a corridor for movement; it is a habitat in its own right. Such a requirement raises the stakes considerably. One must know if the interior of a corridor functions as the intended habitat rather than as edge. Both micrometeorological effects and biotic intrusions can propagate an edge effect far into the forest (see Levenson 1981; Janzen 1983, 1986; Wilcove et al. 1986; Kapos 1989). Nest predation studies (such as Wilcove 1985; Andren & Angelstam 1988) also point to a substantial edge effect. The modified habitat in thin corridors is the motivation for the Klamath Corridor Proposal (Pace 1991), which envisions a corridor 5.5 km wide, connecting two wilderness areas 26 km apart in the Klamath National Forest. This proposal specifically aims at a corridor that is a habitat, not just a travel route.

# Potential Biological Disadvantages of Corridors

#### Genetic and Demographic Costs and Benefits

Although the possibility of inbreeding depression would likely be lowered if corridors were used, the possibility of loss of alleles to drift in an ensemble of refuges would increase (references in Simberloff [1988]). This tradeoff is inevitable; which problem should be of more concern depends on the severity of inbreeding depression (an empirical matter) and how pronounced and dangerous the slowing of future evolution by drift will be. There is no unanimity on this matter (Simberloff 1988). Goodman (1987b) has argued that effects of demographic stochasticity can be greatly lessened by a modest amount of migration among refuges, though he gives no figure. Whether a corridor would be the only or even the best way to provide whatever movement is necessary would depend on information on how much movement would occur with and without corridors. Depending on metapopulation structure, as little as one breeding migrant per generation can render a population effectively panmictic (Lande & Barrowclough 1987), which raises the possibility that even if a corridor increased movement it might be unnecessary genetically.

## **Spread of Catastrophes**

Phenomena such as fires, diseases, or introduced species can spread through a corridor (Simberloff & Cox 1987). For example, in New Zealand, introduced feral pigs may eliminate *Paryphanta* snails from large forest fragments but do not invade small, isolated ones (Ogle 1987). Similarly, introduced vertebrate browsers in New Zealand have almost eliminated mistletoe from large forest fragments, but not from isolated small groups of trees (Ogle & Wilson 1985). In most instances, however, the added risk of spreading catastrophes via corridors may be low because introduced predators or diseases can reach fragments without corridors.

## Corridors as Reservoirs of Edge and Introduced Species

Several authors have suggested that corridors might be inimical as a habitat in their own right. For example, forest corridors have a high fraction of edge habitat and might attract edge-inhabiting predators (Ambuel & Temple 1983). The same concern is one reason for the disenchantment with corridors on the part of Thomas et al. (1990), and numerous other authors have pointed to this potential liability in particular systems (see Catterall et al. 1991). Others have warned that some corridors may favor movement by introduced species (see Forman 1991; Hobbs & Hopkins 1991; Panetta & Hopkins 1991).

## **Corridors as Traps or Sinks**

Henein and Merriam (1990) and Soulé and Gilpin (1991) propose on the basis of simulation modeling that low-quality corridors could act as sinks, decreasing the size of a metapopulation. Field data on this proposition are nonexistent.

## Discussion

The notion that corridors can't hurt, even if the possible biological costs could be discounted, is not necessarily always true. Much would depend on the relative costs and benefits of a proposed corridor and alternative uses of the funds (Simberloff & Cox 1987). Because there are so few data on the importance of movement through corridors, such an analysis will be very difficult. We believe no thorough analysis of this sort has ever been conducted. Possibly the most that can be done today is to say that some options are much less likely to be important than others, but even this attempt is rarely made. The enormous price of some corridor proposals surely implies that other options would not be pursued. For example, a 300-meter-wide corridor from south Florida to Canada, proposed by Hunter et al. (1988), would be approximately 720 km<sup>2</sup>, enough for a very large refuge. If it were possible to buy conservation lands of this magnitude, would this corridor be the best possible purchase?

Florida provides examples of the uncritical advocacy of extremely expensive corridors. Florida's Conservation and Recreation Lands (CARL) acquisition program has an annual budget of approximately \$50 million from the sale of real estate stamps and an additional \$135 million from the Landmark Preservation 2000 bond program. Preservation 2000 bonds have been authorized for the first two years only, although the program is envisioned to extend ten years. Proposed acquisitions still far exceed available funds. For example, of 93 CARL proposals passing a stringent double review by 1991, a priority list of 60 had a tax-assessed value of \$408,000,000 (fair market values are often twice taxassessed ones). Thus, every acquisition means other land will not be acquired. Citizens of several counties have voted to tax themselves to acquire land. Many such counties apply for joint acquisition projects to the CARL program. County governments also face lists of projects far exceeding available funds.

The Florida Natural Areas Inventory submitted the Blackwater-Eglin Connector project to the CARL program in 1988 (Anonymous 1988). This 2400-ha corridor was intended to connect Eglin Air Force Base (187,500 ha) with the Blackwater River State Forest and the adjacent Conecul National Forest (143,250 ha combined). Anticipated fair market value exceeded \$5 million. The corridor was "to join three large publicly owned areas ... into a single, uninterrupted ecological unit of nearly one million acres; to assure perpetual opportunities for gene flow among all populations in these areas; to allow for direct movements of individuals of more vagile species ...." (Anonymous 1988). The application spoke of the "urgency and desirability of developing systems of interconnected reserves for maintaining the full scope of biotic diversity" and stated that "connections between reserves create buffers against stochastic changes in populations, including local extinctions, and provide suitable pathways for 'natural' inoculations of new genetic material...."

No data showed that any species needed to move from one site to the other. Black bears are mentioned as potential users of the corridor, but they do not occur regularly in the Blackwater River State Forest or north of it (Brady & Maehr 1985). The corridor is complicated by Interstate 10, which separates Eglin from Blackwater. While small culverts run under the highway, there is no evidence that bears or other species use them or that they would substantially decrease highway mortality. Black bears are loath to cross interstate highways (Brady & Pelton 1989).

The Blackwater-Eglin Connector was also proposed to aid the movement of Red-cockaded Woodpeckers (*Picoides borealis*) (Anonymous 1988). The woodpeckers move up to 90 km (Walters et al. 1988*a*), but we doubt that this corridor would be effective. Of breeding females, 19% move per year, fewer than 5% of these move more than 5 km, and about 70% survive the year (Walters et al. 1988*b*). Therefore, the chance that a female will move that far and survive is about 0.7% per year. For all life-history categories together, the annual chance that a bird will disperse and survive is 4-8%. For breeding, this percentage is at least halved, because over 60% of dispersal is by first-year birds that produce only 20-67% as many fledglings as older ones.

Probabilities must be further reduced depending on the chance that a bird finds and uses the corridor. The distance traversed by the corridor is about 6 km, but midpoints of the two refuges are 45 km apart. Much less than 1% of the population monitored by Walters et al. (1988b) moved this far, so the great majority of dispersers will probably stay within their original refuge. The corridor itself is unsuitable for the woodpecker. Greatly altered by logging, it consists of streamside hardwoods and commercial pinelands. Several streams through the site have been impounded to create amenity lakes. It would surprise us if even 1% of dispersing individuals used this corridor, but if that many did, 0.04% of the population might reach the adjacent refuge and contribute to future generations. About 300 colonies inhabit both refuges (Wood & Wenner 1983), and each colony produces 1.2-1.7 fledglings per year (Walters et al. 1988b). So one successful dispersal might occur every 5–7 years. The corridor would thus be a very expensive way to move very few woodpeckers. It is unfair to ascribe the entire cost of a corridor to one or two target species when others would surely use it, but an expenditure of this size merits discussion of the full roster of species that would benefit.

This proposal was not approved by the CARL program. This fate contrasts with that of the Pal-Mar project, submitted to the CARL program in 1990 as a 8860 ha site in Martin and Palm Beach counties (Anonymous 1990b). Its fair market value was estimated at \$22 million. The site is a large, relatively intact system of mesic/ wet flatwoods and depression marsh/wet prairies containing many listed plant and animal species—perhaps the biggest relatively undisturbed functional wetland in south Florida east of the Everglades.

After the original application had been submitted, staff of the Florida Department of Natural Resources suggested expanding the project (Timmerman et al. 1991). They stated that the main thrust of a plan they had been

developing to protect biological diversity in southeast Florida was establishment of two large corridors, and they suggested adding a corridor connecting Pal-Mar to Jonathan Dickinson State Park, which contains approximately 4850 ha. This corridor, subsequently added to the proposed Pal-Mar project, is 1.6 km wide and 10 km long, with one other section of land. The corridor is thus 18 km<sup>2</sup>. It is bordered to the north by orange groves and to the south by residences. No estimate of cost was provided, but the proposed corridor contains substantial developable uplands, and its tax-assessed value is \$21,000,000. Not only did the proposal request addition of a corridor (without biological data on which species would use it or why it is necessary), but it added that the corridor was key to the whole project and should be purchased before the original proposed acquisitions. The letter failed to mention that this corridor is traversed by two major highways. The final project design with recommended acquisition phasing has not yet been completed.

The detailed assessment of the Pal-Mar project, prepared by staff of the CARL land acquisition selection body (Anonymous 1990b), stated: "Acquisition of the Pal-Mar proposal will secure a corridor connecting J. W. Corbett Wildlife Management Area to Jonathan Dickinson State Park, and prevent otherwise inevitable development that would isolate the state park and lead to faunal extirpations" (our italics). Indeed, despite the fact that acquisition of the site proposed initially would protect a vast wetland system containing many stateand federally-listed species, the project assessment said, "Acquisition of the Pal-Mar tract would serve several purposes of regional significance, the primary one being the protection of a large portion of a proposed wildlife corridor that would link Jonathan Dickinson State Park to J. W. Corbett ...." (our italics). The assessment even acknowledged that "Perhaps the most significant hurdle that this plan must overcome is the fact that wildlife routes between the state park and Pal-Mar are impeded by I-95 (six lanes) and the Florida Turnpike (four lanes), which run side by side less than a mile west of the park." Thus, even though large mammals have never been documented on the site and would need to cross ten heavily traveled lanes, the State of Florida is considering buying an 18 km<sup>2</sup> corridor on very expensive developable south Florida land.

We detail these examples because we feel that no abstract discussion of corridors can adequately guide acquisition and management decisions. There may well be specific cases in which a proposed corridor would be more effective than an alternative. For example, in parts of the American West, where many potential highquality corridors are already in public ownership, one might expect acquisition costs to be low (Noss, personal communication) and use high. Noss (personal communication) suggests that elimination of below-cost timber sales in such sites might even save public money. However, the same benefits might derive from other land that might be set aside in the same region; are these the acres we would most wish a public agency to sequester? Noss (1987) believes that even major corridor costs can be met by the right sort of publicity and/or by peace dividends. We hope he is correct, but if he is, could not other conservation expenditures similarly increase? Surely costs and benefits of alternative strategies should be considered.

It is important to realize that there are general alternative strategies to facilitate survival where refuges are insufficient. Franklin (1989) has recently propounded the "new forestry," a collection of methods by which even logged forests in the American Northwest might be more useful for conservation than they are now. The key is that the entire landscape be managed as a matrix supporting the entire biotic community. The specific costs entailed in such management have not been tallied. In the longleaf pine forests of the American Southeast, topography and aspects of the biology of key species suggest that such an approach would not be prohibitively expensive (Simberloff 1992). The tablelands of northern New South Wales can be managed so that the entire landscape, not just reserves, contributes heavily to the conservation of the community (McIntyre 1991).

Numerous authors have pointed to the importance of small *un*connected patches of forest or even single trees for the persistence of populations (see Date et al. 1991; Prevett 1991). McDowell et al. (1991) call for a network of such "stepping stones" connected by corridors to minimize extinctions in the South African fynbos community. If resources are insufficient for both, which would be more useful? How dense and how large must a network of stepping stones be to be useful in this system?

Of course these strategies are not incompatible; corridors and stepping stones could be part of an entire landscape managed for both extraction and conservation. However, limited funds will almost certainly prevent the simultaneous adoption of all possible approaches, and it is simply not useful in practice to advocate "strategically placed larger reserves complemented by local or regional networks of smaller reserves and short connecting links between them in as many directions as possible" (Blyth 1991). One must be willing to set priorities, and these should be based on relative costs and benefits. We do not agree with Saunders and Hobbs (1991a) that we should preserve all corridors now because we do not have the time to find out if they are useful. If, by preserving them, we fail to pursue other options, such an approach is not prudent.

Finally, to the extent that this trend is encouraged by the fact that the concept of corridors is easily understood by the public and legislators (Harris & Gallagher 1989) or that "people feel they are doing something for conservation" (Bennett, in Stolzenburg 1991), it is not a scientific phenomenon at all; but it still has costs and benefits, and these are not being addressed. Is it good conservation biology to sell legislators and the public on the easiest program for them to understand, in the absence of evidence that it is the most effective one? Is it beneficial for people to feel they are doing something important for conservation by preserving narrow roadside strips (Bennett's corridors) in the absence of evidence that they really are doing something? Even if they are, is preserving such corridors sufficient? Does it foster the belief that one has done enough and need not preserve larger tracts of valuable habitat? We cannot answer such questions, but we believe that it is important to raise them.

#### Acknowledgments

Bob Jenkins, Reed Noss, Jack Ward Thomas, and three anonymous referees provided numerous suggestions for improving this manuscript.

#### **Literature Cited**

Adams, L. W., and L. E. Dove. 1989. Wildlife Reserves and Corridors in the Urban Environment. National Institute for Urban Wildlife, Columbia, Maryland.

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology **64**:1057–1068.

Ames, L. 1990. The Otay River corridor. Coast and Ocean 6(2):13.

Anderson, S. H., K. Mann, and H. H. Shugart, Jr. 1977. The effect of transmission-line corridors on bird populations. American Midland Naturalist 97:216–221.

Andren, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69:544–547.

Anonymous. 1986. What happened to "corridors"? ENFO 86(6):5.

Anonymous. 1988. Blackwater-Eglin Connector. File No. 880131-57-1, CARL Program. Florida Department of Natural Resources, Tallahassee, Florida.

Anonymous. 1990a. America's Greenways: Linking the Nation's Open Space. Conservation Fund, Arlington, Virginia.

Anonymous. 1990b. Pal-Mar. File No. 901203-43-1, CARL Program. Florida Department of Natural Resources, Tallahassee, Florida.

Anonymous. 1991. Lee County Wildlife Corridor System Plan. Lee County Division of Environmental Sciences, Ft. Myers, Florida. Arnold, C. 1990. Wildlife corridors. Coast and Ocean 6(3):10-14,16,19-21.

Arnold, G. W., J. R. Weeldenberg, and D. E. Steven. 1991. Distribution and abundance of two species of kangaroo in remnants of native vegetation in the central wheatbelt of Western Australia and the role of vegetation along road verges and fence lines as linkages. Pages 273–280 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Belden, C. 1989. The Florida panther. Pages 515–532 in Audubon 1988/1989 Wildlife Report. National Audubon Society, New York, New York.

Bennett, A. F. 1987a Conservation of mammals within a fragmented forest environment: The contributions of insular biogeography and autecology. Pages 41–52 in D. A. Saunders, G. W. Arnold, A. A. Burbridge, and A. J. M. Hopkins, editors. Nature conservation: the role of remnants of native vegetation. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Bennett, A. F. 1987b. Biogeography and conservation of mammals in a fragmented forest environment in south-western Victoria. Ph.D. dissertation. Department of Zoology, University of Melbourne, Melbourne, Australia.

Bennett, A. F. 1990a. Habitat corridors and the conservation of small mammals in a fragmented forest environment. Landscape Ecology 4:109–122.

Bennett, A. F. 1990b. Habitat corridors: their role in wildlife management and conservation. Department of Conservation and Environment, Melbourne, Australia.

Blyth, J. D. 1991. The role of corridors in a changing climate. Pages 402–403 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Brady, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin 17:5–10.

Brady, J. R., and D. S. Maehr. 1985. Black bear distribution in Florida. Florida Field Naturalist 13:1-7.

Breen, B. 1991. Animals win the right-of-way. Garbage 3(2):18-20.

Brown, J. H., and A. C. Gibson. 1983. Biogeography. C. V. Mosby, St. Louis, Missouri.

Budd, W. W., P. L. Cohen, P. R. Saunders, and F. R. Steiner. 1987. Stream corridor management in the Pacific Northwest. I. Determination of stream-corridor widths. Environmental Management 11:587–597.

Catterall, C. P., R. J. Green, and D. N. Jones. 1991. Habitat use by birds across a forest-suburb interface in Brisbane: implications for corridors. Pages 247–258 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Chadwick, D. H. 1990. The biodiversity challenge. Defenders Magazine 65 (May/June):19-30.

Charlesworth, D., and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. Annual Review of Ecology and Systematics 18:237–268.

Craig, J. L. 1991. Are small populations viable? Pages 2546–2552 in Acta XX Congressus Internationalis Ornithologici, Vol. IV. New Zealand Ornithological Congress Trust Board, Wellington, New Zealand.

Date, E. M., H. A. Ford, and H. F. Recher. 1991. Frugivorous pigeons, stepping stones, and weeds in northern New South Wales. Pages 241–245 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Dendy, T. 1987. The value of corridors (and design features of same) and small patches of habitat. Pages 357–359 in D. A. Saunders, G. W. Arnold, A. A. Burbidge, and A. J. M. Hopkins, editors. Nature conservation: the role of remnants of native vegetation. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Forman, R. T. T. 1983. Corridors in a landscape: their ecological structure and function. Ekologiya (C.S.S.R.) 2:375–387.

Forman, R. T. T. 1991. Landscape corridors: from theoretical foundations to public policy. Pages 71–84 in D. A. Saunders and R. J. Hobbs editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Frankel, O. H., and M. E. Soulé. 1981. Conservation and Evolution. Cambridge University Press, Cambridge, England.

Franklin, J. 1989. Toward a new forestry. American Forests November/December 1989:1–8.

Gilbert, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? Journal of Biogeography 7:209–235.

Gilbrook, M. J. 1986. Choosing preserves and connecting links. ENFO **86(6):9–10**.

Goodman, D. 1987*a*. The demography of chance extinction. Pages 11–34 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England.

Goodman, D. 1987b. Consideration of stochastic demography in the design and management of biological reserves. Natural Resource Modeling 1:205–234.

Graham, R. W. 1988. The role of climatic change in the design of biological reserves: the paleoecological perspective for conservation biology. Conservation Biology 2:391–394.

Greenberg, K. 1990. Florida highways and landscape linkages: considering wildlife in transportation planning. Unpublished report. Florida Department of Transportation, Tallahassee, Florida.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Bulletin of the Linnaean Society **42:3–16**.

Harris, L. D. 1984. The Fragmented Forest: Island Biogeographic Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago, Illinois. Harris, L. D. 1985. Conservation corridors: a highway system for wildlife. ENFO Report 85-5. Environmental Information Center of the Florida Conservation Foundation, Inc., Winter Park, Florida.

Harris, L. D., and P. B. Gallagher. 1989. New initiatives for wildlife conservation: the need for movement corridors. Pages 11– 34 in G. Mackintosh, editor. Preserving communities and corridors. Defenders of Wildlife, Washington, D.C.

Harris, L. B., and J. Scheck. 1991. From implications to applications: the dispersal corridor principle applied to the conservation of biological diversity. Pages 189–220 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Henein, K. M., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology 4:157–170.

Hobbs, R. J., and A. J. M. Hopkins. 1991. The role of conservation corridors in a changing climate. Pages 281–290 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Chipping Norton, Surrey Beatty, New South Wales, Australia.

Hunter, M. L., G. L. Jacobson, Jr., and T. Webb III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. Conservation Biology 2:375–385.

International Union for the Conservation of Nature and Natural Resources. 1980. World Conservation Strategy, Gland, Switzerland.

Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. Oikos 41:402-410.

Janzen, D. H. 1986. The external threat. Pages 286–303 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Johnson, A. S. 1989. The thin green line: riparian corridors and endangered species in Arizona and New Mexico. Pages 35–46 in G. Mackintosh, editor. Preserving communities and corridors. Defenders of Wildlife, Washington, D.C.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5:173–185.

Kemp, G. A. 1976. The dynamics and regulation of black bear (*Ursus americanus*) populations in northern Alberta. Pages 191–197 in M. R. Pelton, J. W. Lentfer, and G. E. Polk, Jr., editors. Bears: their biology and management. International Union for the Conservation of Nature, Gland, Switzerland.

Kroodsma, R. L. 1982. Bird community ecology on power-line corridors in east Tennessee. Biological Conservation 23:79–94.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. Conservation Biology 1:143–158.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455–1460.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–123 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England.

Levenson, J. B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. Pages 13–39 in R.L. Burgess and D. M. Sharpe, editors. Forest island dynamics in mandominated landscapes. Springer-Verlag, New York, New York.

Levins, R. 1970. Extinction. Pages 77–107 in M. Gerstenhaber, editor. Some mathematical questions in biology. Lectures on mathematics in the life sciences, vol. 2. American Mathematical Society, Providence, Rhode Island.

Lindzey, F. G., and E. C. Meslow. 1977. Population characteristics of black bears on an island in Washington. Journal of Wildlife Management 41:408–412.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

MacClintock, L., R. F. Whitcomb, and B. L. Whitcomb. 1977. Island biogeography and the "habitat islands" of eastern forest. II. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. American Birds 31:6–12.

Mackintosh, G. 1989. Preserving Communities and Corridors. Defenders of Wildlife, Washington, D.C.

Maehr, D. S. 1990. The Florida panther and private lands. Conservation Biology 4:167–170.

Maehr, D. S., and L. D. Harris. 1986. Black bear distribution and conservation strategy in Florida, U.S.A. Abstract of paper presented at 7th International Conference on Bear Research and Management, Williamsburg, Virginia, February 21–26.

Maehr, D. S., J. N. Layne, E. D. Land, J. W. McCown, and J. Roof. 1988. Long distance movement of a Florida black bear. Florida Field Naturalist 16:1–6.

McDowell, C. R., A. B. Low, and B. McKenzie. 1991. Natural remnants and corridors in Greater Cape Town: their role in threatened plant conservation. Pages 27–39 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

McIntyre, S. 1991. Habitat variegation: an alternative model to vegetation fragmentation in a pastoral landscape. Abstract in the program Conservation Biology in Australia and Oceania. Centre for Conservation Biology, Brisbane, Australia.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. Pages 133–142 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Nicholls, A. O., and C. R. Margules. 1991. The design of studies to demonstrate the biological importance of corridors. Pages 49–61 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia. Noss, R. F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1:159–164.

Noss, R. F. 1992. Wildlife corridors. In D. Smith and P. Hellmund, editors. Ecology of greenways. University of Minnesota Press, Minneapolis, Minnesota. In Press.

Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. Environmental Management **10:**299–309.

Ogle, C. C. 1987. The incidence and conservation of animal and plant species in remnants of native vegetation within New Zealand. Pages 79–87 in D. A. Saunders, G. W. Arnold, A. A. Burbridge, and A. J. M. Hopkins, editors. Nature conservation: the role of remnants of native vegetation. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Ogle, C. C. 1989. An overview of reserve design and location in New Zealand. Pages 11–18 in D. A. Norton, editor. Management of New Zealand's natural estate (Occasional Publication No. 1). New Zealand Ecological Society, Christchurch, New Zealand.

Ogle, C. C., and P. R. Wilson. 1985. Where have all the mistletoes gone? Forest and Bird 13:8–15.

Pace, F. 1991. The Grider Creek story. Wild Earth 1(1):28-33.

Panetta, F. D., and A. J. M. Hopkins. 1991. Weeds in corridors: invasion and management. Pages 341--351 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Peters, R. L. 1988. The effect of global climatic change on natural communities. Pages 450-461 in E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C.

Peters, R. L., and J. D. S. Darling. 1985: The greenhouse effect and nature reserves. BioScience 35:707-717.

Petterson, B. 1985. Extinction of an isolated population of the middle spotted woodpecker *Dendrocopos medius* (L.) in Sweden and its relation to general theories on extinction. Biological Conservation **32**:335–353.

Prevett, P. T. 1991. Movement paths of koalas in the urbanrural fringes of Ballarat, Victoria: implications for management. Pages 259–272 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Rogers, L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northern Minnesota. Wildlife Monographs 97.

Saunders, D. A. 1980. Food and movements of the short-billed form of the White-Tailed Black Cockatoo. Australian Wildlife Research 7:257–269.

Saunders, D. A., and C. P. de Rebeira. 1991. Values of corridors to avian populations in a fragmented landscape. Pages 221– 240 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia. Saunders, D. A., and R. J. Hobbs. 1991*a* The role of corridors in conservation: what do we know and where do we go? Pages 421–427 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Saunders, D. A., and R. J. Hobbs, editors. 1991b. The Role of Corridors. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Saunders, D. A., and J. A. Ingram. 1987. Factors affecting survival of breeding populations of Carnaby's Cockatoo *Calyptorhynchus funereus latirostris* in remnants of native vegetation. Pages 249–258 in D. A. Saunders, G. W. Arnold, A. A. Burbridge, and A. J. M. Hopkins, editors. Nature conservation: the role of remnants of native vegetation. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Simberloff, D. 1986. The proximate causes of extinction. Pages 259–276 in D. M. Raup and D. Jablonski, editors. Patterns and processes in the history of life. Springer-Verlag, Berlin, Germany.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecological Systems 19:473–511.

Simberloff, D. 1992. Species-area and fragmentation effects on old-growth forests: prospects for longleaf pine communities. In S. Hermann, editor. Proceedings of the Conference on Longleaf Pine Forests. Tall Timbers, Inc., Tallahassee, Florida. In press.

Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1:63-71.

Soulé, M. E., and M. E. Gilpin. 1991. The theory of wildlife corridor capability. Pages 3–8 in D. A. Saunders and R. J. Hobbs, editors. The role of corridors in nature conservation. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Stolzenburg, W. 1991. The fragment connection. Nature Conservancy 41(4):19–25.

Suchy, W., and L. Harris. 1988. Landscape Linkages. Florida Films, Gainesville, Florida.

Suckling, G. C. 1984. Population ecology of the sugar glider, *Petaurus breviceps*, in a system of fragmented habitats. Australian Wildlife Research 11:49–75.

Thomas, C. D. 1991. Ecological corridors: an assessment. Department of Conservation, Wellington, New Zealand.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A Conservation Strategy for the Northern Spotted Owl. U.S.D.A. Forest Service, U.S.D.I. Bureau of Land Management, Fish and Wildlife Service, and National Park Service, Portland, Oregon.

Tietje, W. D., B. O. Pelchat, and R. L. Ruff. 1986. Cannibalism of denned black bears. Journal of Mammalogy. 67:762–766.

Timmerman, W. W., C. Tamborski, and J. B. Miller. 1991. Letter dated June 5 to O. G. Brock, Florida Department of Natural Resources. Included in Anonymous 1990.

Walter, H.S. 1990. Small viable population: the Red-tailed Hawk of Socorro Island. Conservation Biology 4:441-443.

Walters, J. R., S. K. Hansen, J. H. Carter III, P. D. Manor, and R. J. Blue. 1988a. Long-distance dispersal of an adult Redcockaded Woodpecker. Wilson Bulletin 100:494–496.

Walters, J. R., P. D. Doerr, and J. H. Carter, III. 1988b. The cooperative breeding system of the Red-cockaded Wood-pecker. Ethology 78:275–305.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Wilcox, D.A. 1989. Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. Environmental Management **13**:365–370.

Williams, G. R. 1984. Has island biogeography theory any relevance to the design of nature reserves in New Zealand? Journal of the Royal Society of New Zealand 14:7–10.

Williams, G. R. 1986. Some criticisms of generally accepted island biogeographic theory. Pages 229–237 in A. E. Wright and R. E. Beever, editors. The offshore islands of northern New Zealand. New Zealand Department of Lands and Survey, Wellington, New Zealand.

Williamson, M. 1981. Island Populations. Oxford University Press, Oxford, England.

Williamson, M. 1989. The MacArthur and Wilson theory today: true but trivial. Journal of Biogeography 16:3–4.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography, Pages 523–534 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts.

Wood, D. A., and A. S. Wenner. 1983. Status of the Redcockaded Woodpecker in Florida: 1983 update. Pages 89–91 in D. A. Wood, editor. Proceedings of the Red-cockaded Woodpecker symposium, vol. 2. Florida Game and Freshwater Fish Commission, Tallahassee, Florida.

Wooding, J., and T. S. Hardisky. 1990. Black bear habitat study. W-41-35. Final performance report. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida.