On Experimentation and the Study of Corridors: Response to Beier and Noss

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The use of corridors for the conservation of biological diversity in fragmented landscapes has been debated for over two decades. This debate has been shaped by a number of reviews that typically are either strongly skeptical (Simberloff & Cox 1987; Simberloff et al. 1992) or strongly supportive (Noss 1987; Beier & Noss 1998) of the value of corridors in conservation. Empirical studies, particularly the results of recent experiments, support an intermediate position (e.g., Andreassen et al. 1996; Machtans et al. 1996; Burkey 1997; Schmiegelow et al. 1997; Gonzalez et al. 1998; Rosenberg et al. 1998; Bowne et al. 1999; Danielson & Hubbard 2000; Haddad 1999*a*, 1999*b*, 2000; Haddad & Baum 1999). Together, these studies suggest that corridors are valuable as conservation tools for some species and landscapes and that trade-offs exist between connectivity and other means of landscape management (Hobbs 1992; Rosenberg et al. 1997). In their recent review, Beier and Noss (1998: 1250) reach a different conclusion, one that "supports the utility of corridors as a conservation tool." In doing so, they eschew a critical aspect of the scientific method, experimentation, in corridor studies, asserting that "Controlled and replicated experiments on animal movement in artificial corridors have scant utility because they have little relevance to the kinds of landscapes and species for which decisions on conservation corridors will be made." Based on the studies in their review, on additional studies, and on our own experience, we have reached a different conclusion about the value of experiments in the study of corridors: experiments, combined with observational studies, offer the best test of theory and the most likely source of general principles about the value of corridors in conservation.

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Beier and Noss make two primary arguments to justify their pessimism about the value of experiments that test corridor effects on animal movement. First, they argue that corridor experiments do not have merit because they do not study threatened, endangered, or large-bodied species. For example, Beier and Noss (p. 1242) seem to restrict meaningful discussion of corridors and landscape connectivity to large-bodied species when they state that ". . . we suggest that species studied must be those that require connectivity on a landscape scale—fragmentation sensitive species such as mammals with large home ranges." Thus, they dismiss out of hand the value of landscape studies conducted on small-bodied organisms with low vagility. Smaller species are also threatened by habitat loss and fragmentation, however, and such species are the most amenable to experimental manipulation.

Beier and Noss imply that the responses of smaller species to corridors are somehow different from those of larger-bodied organisms. To the contrary, the mechanisms that lead to corridor use by small-bodied, common species, such as aversion to cross or tendency to follow habitat boundaries (Haddad 1999*b*), are likely to be those that will lead to corridor use by threatened, endangered, or large-bodied species. In addition, corridors are likely to affect hundreds of species in any landscape, not only the handful of threatened or endangered species for which they are initially conceived. Clearly, species will vary in their responses to corridors (Rosenberg et al. 1997; Beier & Noss 1998; Haddad 1999*b*; Haddad & Baum 1999). The challenge for conservation biology is to uncover general principles that predict behavioral and population responses to corridors across species and landscapes.

A second argument put forward by Beier and Noss is that corridor experiments are conducted at the wrong spatial scale, but there is no inherent scale of measurement that defines a landscape. Connectivity arises from the interaction between the scale at which an organism operates and the scale of landscape pattern. In this sense, beetles are just as amenable to landscape studies as bison. Beier and Noss do make a good point that landscape studies should be justified in terms of the movement abilities of the organisms under study. It is our perspective, however, that the study of ecological processes should not be restricted to broad spatial and temporal scales. One of the advantages of small-scale experiments is that links can be made between the mechanisms of individual behaviors and their consequences for population redistribution and dynamics (Ims et al. 1993; Wiens et al. 1993). Gilliam and Fraser (2000) demonstrated this approach, showing that the effects of predators on fish movement between tributaries through river corridors were consistent with predictions generated within smaller experimental streams (Fraser et al. 1995).

Neither of Beier and Noss's arguments invalidates conclusions from experimental corridor studies. Concerns of species and scale are known quantities in experiments that can be incorporated into the design of a study or included as parameters in statistical models (Inglis & Underwood 1992), whereas confounding factors in observational studies are often not known or are ignored.

Beier and Noss do support the use of certain types of experiments in the study of corridors. They state that "experiments using demographic parameters as dependent variables—even if unreplicated—can demonstrate the demographic effects of particular corridors in particular landscapes" (p. 1249). Presumably, the mechanisms that lead to any observed demographic responses to corridors are related to differential movement rates between connected and unconnected patches. Thus, Beier and Noss's support of studies that measure demographic parameters in corridor experiments is difficult to reconcile with their pessimism about corridor experiments on animal movement. In addition, they specifically condemn "artificial experiments," a phrase that is unclear in that some aspect of every experiment is controlled and therefore artificial.

We do not wish to disparage observational studies of corridors. Nonexperimental studies have contributed important tests of effects of corridors and have led to the formation of new hypotheses (e.g., MacClintock et al. 1977; Fahrig & Merriam 1985; Dunning et al. 1995; Haas 1995; Sutcliffe & Thomas 1996). As Beier and Noss (1998) note, however, observational studies have been plagued by confounding variables, such as covariation in patch area and corridor quality, that raise serious doubts about the observed effects of corridors (Nicholls & Margules 1991; Rosenberg et al. 1997; Haddad & Baum 1999). It is the ability to control these confounding variables that makes experimentation desirable (e.g., Manly 1994). In an experiment, a scientist can control the assignment of treatments to experimental units. The power of an experiment is in its ability to disclose mechanisms and to demonstrate causality. An additional advantage of an experiment is its reproducibility, which derives from control over how treatments are assigned. In an observational study, in contrast, a scientist does not control the assignment of treatments. Instead, nature assigns the treatments, and any assertion that observed conditions are attributable to the treatment is a statement of belief (Smith & Sugden 1998). Consistent with the scientific method (e.g., Platt 1964; Manly 1994; Hilborn & Mangel 1997), an experimental approach within a framework of multiple working hypotheses will allow strong inference about the conditions for which corridors are most useful in conservation.

A growing number of researchers have adopted experimental approaches to studying corridors. Many insights have emerged primarily because of the experimental nature of the research, including the following: (1) corridors may increase the movement and population sizes of habitat-restricted species (Haddad 1999*a*, 1999*b*; Haddad & Baum 1999); (2) movement rates within corridors may increase as habitat quality of the matrix decreases (Rosenberg, et al. 1998); (3) animals may have higher settling rates in high-quality corridors, thereby decreasing actual movement rates (Andreassen et al. 1996; Rosenberg et al. 1998; Haddad 2000); (4) conversely, animals may compensate for low-quality corridors by increasing their movement rates (Fraser et al. 1995; Rosenberg et al. 1998; Gilliam & Fraser 2000); and (5) demographic responses to corridors may be sensitive to whether or not the corridor was created or retained prior to fragmentation (Coffman 1997).

Well-designed experiments, in conjunction with observational studies, will provide the greatest insights into corridor use by plants and animals and will be crucial in the assessment of corridors relative to other land-management strategies. Experimentation and observation should be viewed as complementary approaches, balancing the trade-off between control and realism (Hairston 1989; Peet 1991). Werner (1999:12) said ". . . studies must be integrated in such a way that the artifacts introduced by experimental control are eventually canceled out by the guiding hand of reality, and the intractableness of reality must be whittled away by the surgical knife of control." In their review, Beier and Noss appear ready to dismiss science's most powerful approach to understanding—the experiment—with poorly supported assertions regarding its intractability and irrelevance to one of conservation biology's most pressing issues, the need to reverse the isolation of habitats and populations caused by fragmentation. The science of conservation biology should be guided by methods that will lead to strong inference. A combination of approaches—observation, experimentation, and theory—offers the best hope for identifying general principles that can guide the application of ecology to conservation.

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