

Toward a Theory of Inter-Refuge Corridor Design

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Introduction

The accelerating fragmentation and isolation of wildlife populations as a consequence of habitat alteration has resulted in increased interest in the preservation of travel corridors between populations to minimize local extinction and genetic isolation (Harris 1984; Noss & Harris 1986). Landscape architects and other planners now frequently include such wildlife corridors in development designs. However, little work has been done on the theory underlying the parameters of effective corridors, and there are little data on the details of movements of animals through landscapes that would be useful to the development of corridor design. Except for riparian strips, natural corridors have rarely been mentioned in the literature (see Berger 1987). In this paper, I review natal dispersal patterns to begin to build a general theory of corridor design for mammals. I also make recommendations for future research and suggest minimum corridor widths for representative mammals.

Natal Dispersal Patterns of Mammals

It is very difficult to experimentally test any theory underlying corridor design by providing corridors for free-ranging mammals. The number of dispersing animals that find and use a specific corridor within a reasonable time period is likely to be very small. Precise replication is unlikely to be available. A more fruitful approach is to locate and describe natural corridors and to search for patterns in animal movement across unfamiliar landscapes. Mammals will be most likely to utilize an inter-refuge corridor during natal dispersal, because once dispersal is completed most adult mammals, with the exception of migrators, remain in the same general area

for the duration of their lives (Gaines & McClenaghan 1980). Hence, examination of movement patterns during natal dispersal can provide insights into the requirements for corridors.

Mammals that are potentially subject to predation, such as white-tailed deer (*Odocoileus virginianus*), wild horses (*Equus caballus*), and dwarf mongoose (*Helogale parvula*), reduce their vulnerability by making rapid transfers between groups and by joining neighboring groups (Berger 1987; Nelson & Mech 1987; Rood 1987). Mammals that are less subject to predation, such as black bears (*Ursus americanus*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), and wolves (*Canis lupus*), disperse until they locate unoccupied areas with suitable habitats (Storm et al. 1976; Griffith & Fendley 1982; Mech 1987; Rogers 1987). (Suitable habitat is defined here as habitat in which the species concerned may maintain permanent populations). Thus, level of predation risk strongly affects dispersal patterns and must be considered in corridor design.

In some species, such as black bears, white-tailed deer, dwarf mongoose, and tigers (*Panthera tigris*), the majority of females settle in a portion of their mother's home range, essentially not dispersing at all (Nelson & Mech 1987; Rogers 1987; Rood 1987; Kitchener 1991). Populations of such species expand into new areas slowly, through a series of overlapping home ranges established by the small number of females that do disperse (Mathews 1991).

There is evidence that topographic features such as lakes, mountain passes, and valleys may affect dispersal paths locally (Shirer and Downhower 1968; Seidensticker et al. 1973; Storm et al. 1976), but at present it is not possible to predict precisely the direction or distance of dispersal (see Robinette 1966). Few individuals disperse farther than necessary to find an accepting group or unoccupied habitat. Mammals typically disperse less than five home-range diameters (Chepko-Sade

and Halpin 1987), but while moving in search of these situations they may enter unsuitable habitat where they will experience high mortality. A strong tendency to remain within suitable habitat while dispersing has been observed in several species of rodents (Holekamp 1984; Garrett & Franklin 1988; Wiggett & Boag 1989). Dispersers will cross the territories of conspecifics, although they may prefer to remain on territory edges and thus in less suitable habitats (Fritts & Mech 1981).

Design Parameters of Corridors

Prey species that make rapid transfers between groups and that do not live alone and species in which females remain in or near their mother's home range require contiguous areas of suitable habitat for normal dispersal. Potential depredators, such as wolves, bears, and mountain lions, will also require suitable habitat and prey in order to remain within the bounds of the corridor and prevent mortality from owners of domestic livestock in areas adjacent to corridors. These dispersal patterns indicate that effective corridors must contain suitable habitat for the species of interest to reside permanently within the corridor. The habitats within the corridor will greatly influence the extent to which dispersers utilize it. Gaps between suitable habitat should be small relative to dispersal distances. Habitat thus emerges as a critical design parameter of corridors.

If a corridor must contain enough suitable habitat for a given species to permanently occupy the corridor, then the width of the corridor may be estimated from data on home-range sizes and shapes. Minimum corridor widths for seven representative mammals are presented in Table 1, assuming that corridors are one home range wide and contain rectangular home ranges that are twice as long as they are wide. In addition to this minimum width, the corridor must be wide enough to maintain the desired habitat against penetration of other vegetation types from edges.

The width required for a corridor to be effective may depend upon its length. Beier (1991) observed dispersing mountain lions effectively using a corridor of suitable habitat only .5 to 1.0 km wide, which is much less than the width suggested in Table 1. However, this corridor was only 6 km long, which is less than the length of one average mountain lion home range (approximately 12 km, based on home range sizes in Nowak & Paradiso 1983). Thus, effective corridors may be narrow if they are short enough that dispersers may pass through without foraging.

The effectiveness of corridors will be affected by the type and extent of human activities and land use practices both within and adjacent to the corridor. The impact of hunting and trapping, both legal and illegal, intrusion of domestic dogs, livestock grazing, and

Table 1. Examples of minimum corridor widths based on average female or pack home-range sizes.^a

<i>Species</i>	<i>Location</i>	<i>Minimum corridor width (km)</i>	<i>Home range size source</i>
Wolves	Minnesota	12	Nowak & Paradiso (1983)
Wolves	Alaska	22	Ballard & Spraker (1979)
Black Bears	Minnesota	2	Rogers (1987)
Mountain Lions	California	5	Hopkins et al. (1982)
Bobcats	South Carolina	2.5	Griffith & Fendley (1982)
White-Tailed Deer	Minnesota	0.6	Nelson & Mech (1987)
Dwarf Mongoose	Tanzania	0.6	Rood (1987)

^a Home ranges are designed to be rectangular and twice as long as wide.

disturbance due simply to human presence must be considered. The greatest human impact will occur near towns and along roads and edges where access to the corridor is easily available. Schoen et al. (1990) estimated that habitats on Admiralty Island, Alaska, lose one-half of their suitability for brown bears if they are within 8 km of communities of more than 500 people, within 1.6 km of any community of more than ten people, or within 1.6 km of arterial and collector roads. Also, the type of human development, such as agrarian or industrial, in the vicinity of corridors will affect the extent of illegal activities (Berger & Daneke 1988). Thus, corridors design may have to include buffer zones to reduce undesirable human impact.

Finally, the location of a corridor may be affected by the relationship between seasonal movement patterns and the specific purpose of the corridor. For example, white-tailed deer migrate between winter and summer ranges. Males disperse from June to November, but data are lacking on the timing of female dispersal (Nelson & Mech 1987). Corridors designed for gene flow via dispersing males may be located by summer or fall ranges. Corridors designed for reestablishment of populations must accommodate both sexes and may have to be designed for movement at other times.

Conclusion and Priorities for Future Research

Our knowledge of the basic principles determining the effectiveness of corridors is extremely limited. I have identified habitat, width, length, human activities, and location as critical variables, but we need much more data on dispersal patterns and the use of natural corridors before we can realistically attempt to direct the movement of free-ranging mammals across landscapes. The following list of critical research needs was easy to

generate because we have so little knowledge in any of these areas:

1. Monitor the movements of dispersing mammals *continuously* rather than intermittently in relation to habitat type, topographic features, and territories of conspecifics.
2. Investigate cues used to determine dispersal direction.
3. Investigate mortality and movement patterns in habitats that are not suitable to determine the effect of gaps between refuges.
4. Identify and monitor potential natural corridors for dispersal movements. It should not be assumed without observation that riparian zones, for example, are used as corridors.
5. Determine the minimum width of effective corridors, possibly by measuring the minimum widths of home ranges.
6. Quantify the impact of human activities on wildlife populations as a function of activity and distance from roads and other developed sites, in the manner of Schoen et al. (1990).

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