Many birds that live in fields, on the other hand, use nearby hedgerows for singing perches or foraging.\textsuperscript{1333,808} Field animals often move to hedgerows as cover against predators\textsuperscript{1831}, or cover against weather, including sun, wind, and snow.\textsuperscript{862,1935,1936,1831,1300}

The concentration of animals in hedgerows also attracts predators from the surroundings\textsuperscript{431} (Fig. 6.10), just as hunters are attracted to wooded strips.\textsuperscript{239} Where large woods are scarce, certain owls and other predators require two or more smaller woods for their home range. So in a corridor connecting the woods, not much escapes the eyes and silent wing-beat of an owl. Nevertheless, compared with forest edges (chapter 3), predation rates in hedgerows are poorly documented.\textsuperscript{1588,1558,1589} Clearly, more study of these conspicuous lines of source-and-sink activity is warranted.

\textbf{WOODLAND CORRIDORS AS WILDLIFE CONDUITS}

Considerable evidence worldwide shows that many animals use wooded strips as conduits in crossing portions of a landscape (chapter
Species include kangaroos, cockatoos, many small birds, large game birds, nocturnal arboreal mammals, cottontail rabbits, and many other mammals. The concentration of road-killed mammals, where woodlands in open country adjoin or nearly adjoin both sides of a road, is often noted by highway police and wildlife biologists. The evidence is largely based on qualitative and quantitative field observations, and little experimental evidence exists.” Many of the observations are of vertebrate movement along narrow line corridors (chapter 5), rather than woodland corridors (Fig. 6.1).

Only scattered evidence exists that plants move along wooded strips. Some species slowly move short distances along a woody strip by vegetative spread or adjacent seedling establishment. However, most plant movement is ‘saltatory.’ Seeds are carried by wind or animals some distance to a spot in the corridor, where the species becomes established. Some individuals can reproduce in this environment, and seeds are then dispersed further.

Although some conduit evidence comes from roadside natural strips (chapter 5), these are rather poor examples of woodland corridors because concentrated disturbance lies alongside the entire corridor length. The road and open roadside on one side may bathe a woodland corridor with noise, dust, salt, lead, and heat from the paved tarmac, plus exotic species from the roadside. The road and roadside also significantly affect the source and sink functions of the woodland corridor.

Greenways, the linear conservation areas mainly near built suburban environments, usually have a primary focus on recreation and aesthetics. However, greenways (sometimes called ‘greenlining’ when networks are formed) are doubtless of considerable importance for species movement, due to the relatively hospitable and heterogeneous matrix nearby. Generalist and edge species presumably predominate in greenways.

Although we know animals use corridors as conduits, the more important question for conservation is whether corridors increase the rate of movement from point A to point B. For example, a species could move through the adjacent matrix at the same rate as in the corridor. In this case the corridor would be of no advantage to movement of the species. And of course, some species tend to avoid wooded strips in movement across a landscape. A small amount of evidence with marked animals indicates that some species use wooded corridors in preference to moving across open land.

To explore the ecological pros and cons of corridor conduits, and the factors controlling movement, we make certain simplifying assumptions. The two edges of the corridor differ (this is the norm, except where the matrix is the same on opposite sides, or the orientation angle is zero (chapter 4). No internal entity is present (chapter 5). A woodland corridor...
dor with interior environmental conditions is the focus, thus essentially ignoring windbreaks and hedgerows. Animals are assumed to be sensitive to the corridor at this scale, and may move inside or alongside the strip.

Enhancing and inhibiting movement

Several types of movement along corridors should be recognized. Home range movements, animal dispersal, migration, and wandering (nomadic movement) may take place in corridors. Individual animals move continuously or discontinuously along a corridor. Genes flow by sexual reproduction of resident individuals located progressively along a corridor. Whole communities or faunas may move along a corridor, as in seasonal migration or in response to climatic change.

Earlier it was suggested that movement along a corridor should increase with few narrows, few gaps, low curvilinearity, low patchiness, no environmental gradient, and a short length (chapter 5). Internal and external corridor attributes, and effects of the matrix, are now evaluated in terms of the conduit function of woodland corridors.

The corridor typically offers five parallel routes for an animal to move. A central interior environment is commonly sandwiched between two different corridor edges, which in turn are flanked by two different matrix edges. These five microenvironments provide options for a range of species to move. Although apparently no studies have been done, it is highly probable that woodland patch-interior species preferentially move in the central interior environment, patch edge species move mainly in the two corridor edges, and matrix species move mainly in the two matrix edges. Interweaving among the five lines is doubtless common, especially for patch edge species. A relatively continuous shrub layer somewhere in the corridor is probably important as cover for many mammals and some birds. Thus, a browsed or burned out understory can be expected to truncate movement of many species.

Corridor width is considered important for movement, though the evidence for this hypothesis is limited. Clearly many animals move along narrow hedgerows. It seems likely that wider woodland corridors would increase the rate of movement of interior species. Yet most movement in corridors is by edge species, and may not correlate with the width of woody strips.

Moving animals must pass and interact with corridor residents. Such residents are primarily disturbance-tolerant, generalist edge species. Resident vertebrates may have long home ranges. For instance, the white-footed mouse (Peromyscus) in southeastern Canada has a home range in hedgerows ten times longer than in nearby woods.
WOODLAND CORRIDORS AS WILDLIFE CONDUITS

<table>
<thead>
<tr>
<th>High rate</th>
<th>Medium rate</th>
<th>Low rate</th>
<th>Negligible</th>
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<td>(a)</td>
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High-quality habitat | Medium-quality habitat | Low-quality unsuitable habitat

Fig. 6.11. Expected movement rate of animals between large patches, related to habitat connectivity and quality. (a) Connected corridor; (b) cluster of small patches; (d) gradient; (g) patchy corridor; (g) row of stepping stones; (k) barrier intersection. String-of-lights pattern would be at left end.

One may only guess how this distinctive set of residents would affect moving animals.

External corridor attributes are also controls on movement. The effect of corridor length has not been evaluated. But based on general dispersal-distance models, we expect that movement drops exponentially with distance along a corridor. Such a pattern would be modified by an attractant at the end of the corridor, or a deterrent located along the corridor.

Habitat connectivity and quality may be the two primary variables controlling the Conduit function. A corridor connecting two patches, and surrounded by medium- or high-quality habitat, presumably supports the highest movement rate of patch species (Fig. 6.1 la). Decreasing connectivity of the corridor and decreasing habitat quality in and next to the corridor should reduce the movement rate.

For example, an environmental gradient along a corridor would be expected to decrease movement, since a species would be progressively encountering different environmental conditions and species (Fig. 6.1 ld). Patchiness along the corridor may decrease movement more, as the species moving encounters not only different environmental conditions and species, but also abrupt transitions and perhaps barriers (Fig. 6.1 lf, h, i, k and l). On the other hand, patchiness could provide rest stops for a few species, as in the saltatory spread of plants along corridors.

Overall, a string-of-lights combining a corridor and small patches is probably best.

If a high-quality corridor is not present or possible, a second choice is hypothesized to be a duster of small patches (Fig. 6.1 lb). This is a scatter of stepping stones through which objects such as animals may pass. Unlike a row of stepping stones (Fig. 6.1 lg), a cluster provides numerous optional routes; It should be effective in permitting moving
animals to avoid many predators and disturbances. Experimental studies to determine the optimal arrangement of small patches in a cluster would be welcome. Indeed, no studies exist comparing movement effectiveness in a corridor, a row, and a cluster.

Certainly, the presence of gaps and narrows in a corridor would decrease movement efficiency\(^{156}\) (Fig. 6.1c and g), a subject also much in need of study. For example, field observations support the hypothesis that some forest species avoid crossing open areas.\(^{1904,1939,1258,1059,1775}\) Indeed, arboreal mammals such as squirrels apparently require an essentially continuous line of trees to move between dispersed woods.\(^{93,1216,478,1650,1118,720,412}\)

If a gap is present in a corridor, ample opportunity exists for design to ameliorate its effect, and enhance faunal movement rate (Fig. 6.12). Corridor ends can be created with more points for crossing (Fig. 6.12e and g) (analogous to a nerve synapse), few points to minimize funneling animals to specific spots (Fig. 6.12b and f), wide tips (Fig. 6.12d and e), or associated small patches (Fig. 6.12h). Until empirical study of such gap designs is done, they must be evaluated using animal behavior and other theory. The size of gaps, the nature of the area in and around them, and gap aggregation presumably are also critical to movement. Indeed aggregated gaps produce a row of stepping stones (Fig. 6.1g). It would be interesting to know the shape of the curve simply relating movement to connectivity.

Unlike windbreaks and hedgerows that are almost always straight, woodland corridors are sometimes curvilinear and variable in width. Using a simulation model M. E. Soulé & M. E. Gilpin (1991) suggested that movement would be more effective along a straight than a curved corridor, because an animal would not have to search or alter direction. This could especially apply to juveniles that have not learned the route. In addition, coves in a curvilinear strip could harbor matrix species (chapter 3) that interfere with movement along a corridor.
Finally, the matrix also controls movement in a woodland corridor. Wind whistles through gaps and narrows, across which an animal must move. More significantly, wind may bathe an entire corridor with soil particles, snow, pesticides, fertilizers, or heat. Such a process can be inimical indeed to moving animals, just as it would be to a person. Gap formation and external disturbance are serious intrusions in a corridor compared with a patch of equal area. This difference in disturbance-proneness suggests that corridors themselves are changing more than are patches. Such changes provide windows of opportunity, as well as inaccessible times, for movement of species along a woodland corridor.

Ecological advantages and disadvantages

It is well to recall that woodland corridors are largely remnant or regenerated strips, where the matrix has been changed by human activity. Such corridors have been, are, and doubtless will be widespread in almost all landscapes with a heavy human imprint, except cities. Unlike many other products of human activity, they are inherently neither good nor bad. Faunal corridors are proposed-essentially only where an original habitat has been fragmented.

Some controversy lingers as to whether the disadvantages out-weigh the advantages of corridors, or vice versa. The key ecological issues are as follows.

Advantages of woodland corridors

(1) Enhance recolonization to a patch, following frequent local species extinctions therein (i.e., provide for metapopulation dynamics; chapter 11).

(2) Enhance gene flow to a patch, to minimize inbreeding depression in small populations (chapter 2).

(3) Enhance dispersal from a patch, to the matrix and neighboring patches.

(4) Enhance several types or 'needs' for movement in an animal's life history.

Disadvantages of woodland corridors

(1) Act as a mortality sink, by drawing animals to unfavorable conditions in a corridor.

(2) Increase the probability that pests, diseases, exotic species, and disturbances (e.g., fire) will spread to a patch.

The advantages are familiar from chapter 2, and are discussed further in chapter 11. We primarily examine disadvantages here.

A mortality sink is a location where considerably more animals enter than leave, and the difference is due to their deaths. If the collision rate between vehicles and small animals on a road is high, relative to the number of animals crossing (chapter 5), the road is a mortality sink. In studies of hedgerow quality, small mammals moving in low-quality
corridors are less successful in reaching the end than those moving in high-quality corridors.\textsuperscript{1118,720,112} The animals in the low-quality corridors are exposed to higher predation risk and less-favorable environmental conditions. The low-quality corridors appear to be mortality sinks. Thus, to overcome the disadvantage of corridors listed above, a corridor should be of high quality for the objects moving.

Yet, the effect of a potential mortality sink has to be balanced against the learning process in animal behavior and the adaptability of species. If an animal goes down a corridor alone and is eaten, the animal and the other individuals of its population may have learned nothing. If the animal is eaten, but another individual observes this and escapes, that individual has learned that the corridor may be dangerous. If other individuals learn similar information, either from this individual or their own experience, the population will begin to avoid the corridor. The corridor remains a sink for two types of individual. The young are susceptible because they have learned little. And dispersing animals from afar are susceptible because they also are unaware of local conditions.\textsuperscript{43} Therefore, in a low-quality corridor, it seems likely that some individuals will disappear, but the main direct effect on the population is to avoid the corridor.

Of course, if a low-quality corridor is avoided, it is no better or worse than no corridor for moving animals between patches. However, this pinpoints the importance of high-quality corridors, which are used for effective species movement between patches.

A proposed ecological disadvantage of wooded strips is the higher probability that pests and exotic species will spread. Most pests are specialists, and primarily attack one or a few species.\textsuperscript{1311,411,1282} Since most corridor species present are disturbance-resistant generalists, a corridor is a relatively improbable location for specialized pests. Damage to the widespread species of corridors normally is of little conservation importance.

However, some pests such as locusts, gypsy moths, blackbirds, and rats are generalists, and when numerous will damage many species. Large inhospitable distances may stop such species. However, the history of spread of such species suggests that they have spread quite effectively across a wide range of landscape patterns.\textsuperscript{451,1159,419} A continuous corridor habitat is of little consequence to species that move effectively along a series of stepping stones.\textsuperscript{1393} The same pattern can be expected for invasive exotic species. Indeed, the matrix surrounding wooded corridors itself is a major source of weeds, pests, and exotic species.\textsuperscript{1278}

The edge of a large patch contains most of the edge species in the landscape for that patch type (Fig. 6.13b and c) (chapter 3). Thus, few generalist species would be expected to reach a large patch in which they are not already present.
WOODLAND CORRIDORS AS WILDLIFE CONDUITS

(a) Original continuous forest
(b) Corridor and patches in open land
(c) No corridor

Species types; $S = \text{Specialists}$
$G = \text{Generalists}$
$f = \text{Of the forest}$
$e = \text{Of the edge}$
$o = \text{Of open land}$

Movement rate:

- = High
- e s - = Moderate
. . . . . . . . = Low

Fig. 6.13. Expected movement rates of patch and other species, related to specialists and generalists in the landscape. Patches in (b) and (c) have interior and edge environments.

A series of recent reviews provides a general picture of the few hundred best-known pest species in windbreaks and hedgerows, particularly in North America. Exotic species are included, as well as species moving from windbreak to adjacent fields, and control methods are described. The pests include tree diseases$^{1311}$, insects$^{411,1282}$, and vertebrates.$^{1721}$ The focus is on general life history of pests, not the conduit function of corridors. Nevertheless, no evidence was cited for any species indicating that pests move progressively along a windbreak, or that a continuous windbreak is required to move between two patches or areas. Similarly, the recommended techniques to prevent or control the spread of these pests leads to the same conclusion. Rather, the evidence indicates that the bulk, if not all, of these pest species moves across the field matrix (by wind, flying, or terrestrial locomotion).

In an area of southeastern Australia, Bennett (1990b) found that the six native small-mammal species present were more sensitive to habitat fragmentation than two exotic species. All eight of the small-mammal species were found in narrow roadside natural strips. However, in studying movements, only the native species were recorded moving along corridors between patches.

A few exotic species are reported to have moved along wooded corridors in Australia.$^{1057,111,962,1278}$ For example, the spotted grass frog ($\text{Limnodynastes}$) expanded 6.7 km along a roadside natural strip <20 m wide in the dry Northwest$^{1057,111}$, and a continuous corridor may have been critical to its movement. The ‘talkative’ common mynah

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(Acridotheres tristis tristis) represents the pattern for the other exotic species described. This bird is common along roadsides of main highways radiating from major population centers in Australia. These roadsides may have accelerated its spread, but in light of the woods and buildings scattered throughout the areas, it is likely the species would have spread without the corridors. In other words, corridors might increase the rate of spread, even though scattered patches are also suitable for spread.

It has been hypothesized that exotics and pests are favored more by corridors of natural vegetation than are native species. At present, the evidence for either exotics or pests is too sketchy to evaluate, but certainly native edge species appear to have no difficulty spreading along corridors, or from patch to patch (Fig. 6.13b). Weeds, for example, are reported to be abundant in some roadside natural strips in Australia. This is due to wind and especially animal dispersal, a high perimeter-to-area ratio, and abundant disturbance, including fire and nutrient contamination from surrounding agriculture. For each of three woody vegetation types, narrow corridors were found to have c. 25% more exotic species of herbaceous plants than wide corridors.

A corridor as a narrow channel also is an ideal location for human management to arrest the spread of an undesirable species. For example, the aggressive alien tree *Acacia saligna* in South Africa can be successfully controlled by inoculation with its native Australian fungus pathogen. A corridor would be a convenient location to accomplish this process and monitor the results. Similarly corridors may be convenient locations to control disturbances such as fire. Indeed, wildlife corridors could be monitored to keep a pulse on the health of the land, just as stream corridors are monitored for pollution, hydrology, and so on.

In summary, the proposed ecological disadvantages of corridors appear to be minor or non-existent. Most of the advantages appear to be of major importance (chapter 2). The evidence for all considerations is limited, though growing, so land-use decisions must continue to be made with incomplete evidence. Corridors are no panacea, but they are part of a careful plan for land use and management.

The discussion of trough corridors in chapter 5 shows that for most variables studied, the narrower the corridors are, the better they are ecologically. For wooded corridors, in contrast, most variables indicate the wider the better. Yet a closer look, e.g., at windbreak effects on wind, snow, and other microclimatic variables, shows that narrow, medium, and wide corridors are each optimum for different objectives. In short, conservation and planning decisions must be tailored to the type of corridor, and to the objective to be attained.

Society's decisions on the importance of corridors as conduits, of course, are based on a range of human and economic criteria, such as
land ownership patterns, management costs, and recreation, in addition to these ecological criteria. All planning and policy decisions have pros and cons. Just as we now see that the pros of large natural-vegetation patches far outweigh the cons (chapter 2), ecologists and land-use decision makers are moving beyond the pro-or-con controversy phase. We now appear to be well into the overlapping research and implementation phases.

The key questions now are: 'Where are the optimum locations? What are the optimum designs? And what can we learn from the corridors in place?'

APPENDIX: EQUATIONS FOR WIND AND EROSION

**Horizontal windspeed**

\[
\frac{U}{U_h} = f\left(\frac{x, z, h, \phi}{h, h, z_0, L}\right)
\]

where \( U = \text{average horizontal wind speed for a long thin windbreak on a large flat surface with wind direction perpendicular to windbreak axis; } h = \text{barrier height; } x = \text{perpendicular distance from windbreak; } z = \text{height above the surface; } U_h = \text{average horizontal wind speed at barrier-top height in the open; } z_0 = \text{roughness length taken from the uninterrupted wind profile; } L = \text{the Monin-Obukhov stability length (a measure of atmospheric stability); and } \phi = \text{porosity of the barrier. The Reynolds number } (hU_0/v, \text{where } v \text{ is the molecular viscosity of air}) \text{ also affects the average horizontal windspeed, but with air mixing over a field it is unimportant. After McNaughton (1988).}

**Wind erosion rate**

\[
E = f(I, K, C, L, V)
\]

where \( E = \text{potential average annual soil loss (in mass per unit area); } Z = \text{soil erodibility index; } K = \text{boil-ridge-roughness factor; } C = \text{climate factor; } L = \text{unsheltered travel distance of wind across field; and } V = \text{vegetation cover. After Woodruff \\& Siddoway (1965) and Lyles (1988).}