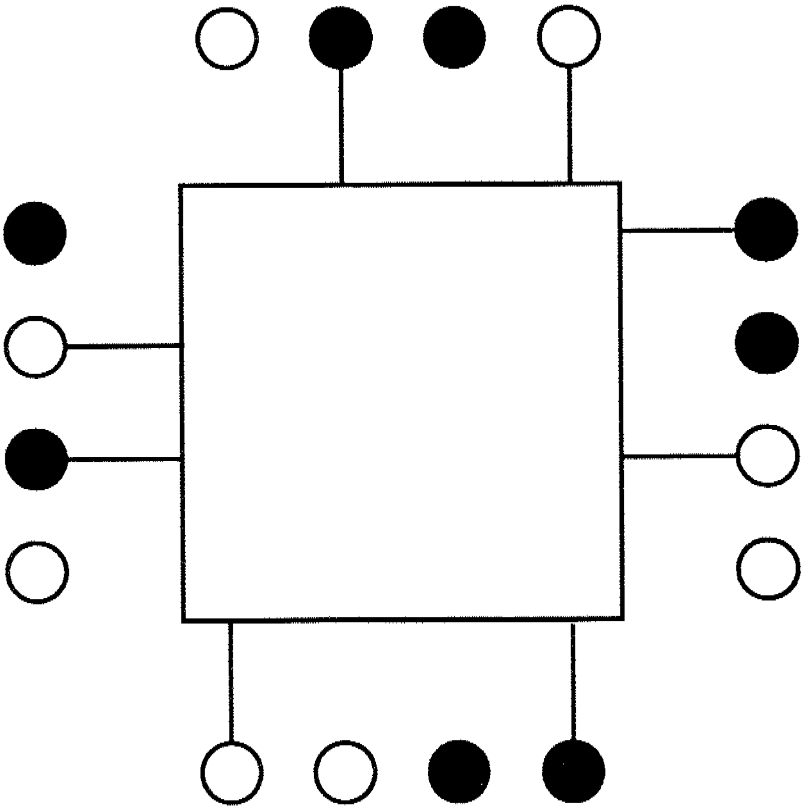
CONDUIT FUNCTION

Model studies

Before discussing direct evidence for a conduit function, the kind of studies that might prove corridors to be effective in recolonisation are outlined. In this context, studying the movement of individual species is not advocated (in disagreement with Saunders *et al.* 1991), since the amount of work necessary to prove that an estimated rate of movement along corridors significantly accelerates the arrival of successful colonists generally would be prohibitive. Studies of movement may be useful in selecting species and situations for further study, however. Nor are landscape measures, like Opdam's (1991) landscape resistance recommended, as these do not distinguish the conduit function of corridors from other functions.

Nicholls and Margules (1991) examined the requirements of an experimental approach to the question of whether movement between patches connected by corridors is more frequent than that between unconnected patches, and specifically whether recolonisation is more frequent on the former than the latter. Their recommended study would compare matched pairs of patches, one connected and one not; half the pairs would be cleared of the subject species, the others left as controls. If the characteristics of the patches and corridors can be standardised, the minimum recommended replication is 16 patches arranged in 4 blocks (Figure 21). Allowing more realistic variation in these characteristics would require greater replication.

Figure 21 An experimental design to test whether corridors assist recolonisation. The central block of habitat is connected by corridors to half of the satellite patches (circles) and the other half are identical, but unconnected. On half of the connected, and half of the unconnected, patches (the black ones) the species is driven to extinction. (After Nicholls & Margules 1991).



Some such study is needed to confirm experimentally the patterns established in previous work (Taylor 1990), but it is very difficult to carry out experiments on landscapes (Hansson 1977; Johnson *et al.* 1992). For this reason such experiments would be most inadvisable as a first step. Also many species would not be expected to require corridors, so that the dimensions of the experiment would have to be matched to the behaviour of particular habitat specialist species. However Nicholls and Margules' design can be used as a guide for the details that would also be required for surveys of the distribution, or studies of movement, of species to test the conduit proposition. Such studies would have to cover the issues of replication, control sites, the matching of the studied system to the subject species and the history and current state of the corridors and patches (Johnson *et al.* 1992). The results have to be subject to statistical analysis to reject the "null hypothesis". These are the requirements used in the following section to evaluate existing studies claiming a conduit function.

Studies of corridors as conduits

So far the review has been of studies, not directly of corridors, but of other factors that should obtain if corridors are to be effective as conduits between habitat patches; that is of the effects of isolation, area, turnover and habitat diversity, and studies suggesting which species may be sensitive to these effects and thus in need of corridors. None of the studies provided direct evidence of a conduit function, although many of their authors recommended corridors (eg Robbins *et al.* 1987). In other cases the authors of the original studies did not claim good evidence for corridors function, but others have cited their work as demonstrating this (eg Turner 1989; Bunce 1993). In fact many such studies provide better evidence for the effectiveness of stepping stones than of corridors (Thomas *et al.* 1993).

Corridor theories

While there has been much controversy over the other aspects of the 'island biogeographic principles' few have criticised their application to corridors. However, Simberloff and Abele (1984) considered the application of peninsular theory to reserve design uncritical, as there is no evidence to exclude alternative explanations, such as habitat differences.

The theoretical considerations that corridors may also act as conduits for disease, fire or pollution (Diamond & May 1976; Soule & Simberloff 1986) have seen very little study.

The direct evidence

Many recent works have cited the work of Soule *et al.* (1988) on birds in chaparral fragments in San Diego as justifying corridors (eg Lyle & Quinn 1991). Their evidence that isolation of the fragments might be overcome by corridors was that some of the species concerned had been observed in strips of vegetation of width 1-10 m, but none of the strips connected habitat patches to other one another. As there were no corridor connections, they could not demonstrate movement along them.

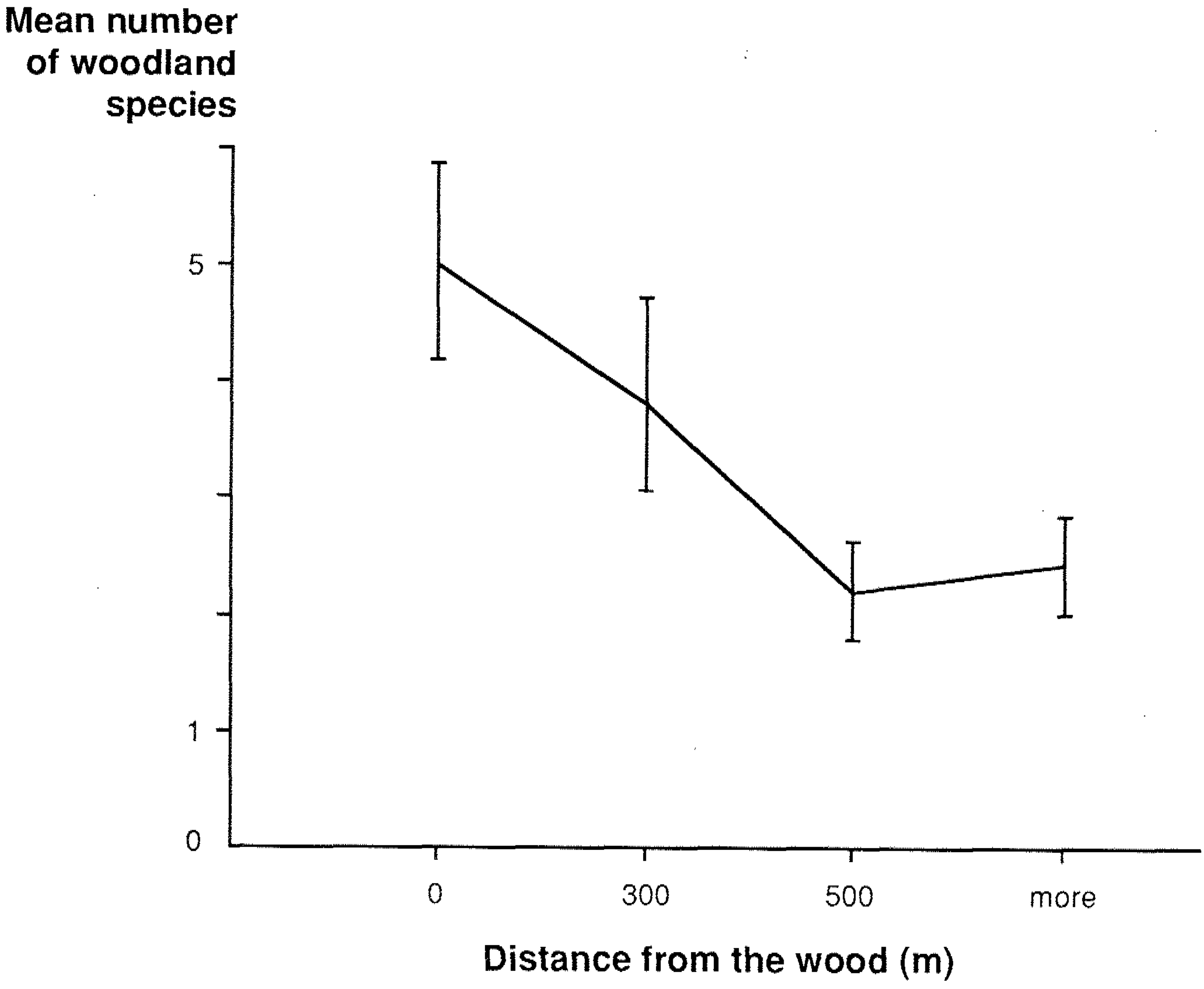
Some studies suggest corridor functions, but do not amount to a test of these functions (Simberloff & Cox 1987). An example is the corridor used by MacClintock *et al.* (1977) to account for the presence of forest interior bird species in a small wood, which is still cited by, for example Turner (1989) as evidence for a corridor function. This study was neither replicated, nor did it distinguish distance *per se* from the corridor connection, because there were no equidistant control sites without corridor connections. Similarly Eldridge's (1971) work on small mammals in hedgerows has often been cited as showing that corridors promote movement, but in fact all it showed was that small mammals may use the hedgerow habitat. Harris and Scheck (1991) cited several further works that fall within this category.

Another oft-cited work is Merriam (1984) on small mammals in woodland patches. Here corridor connections enhanced population growth, rather than survival. This, Merriam argued, was due to the rescue effect of Brown and Kodric-Brown (1977). The empirical findings, however, do not meet the statistical requirements; such work should be adequately replicated and the conclusions tested against a null hypothesis.

A declining incidence with distance from source

Another line of evidence comes from studies of distance effects in linear habitats. Baudry (1988) and Burel and Baudry (1990) studied plants (Figure 22) and animals in hedgerows and Verkaar (1990) studied animals and plants of road verges. Here a decline in species occurrence with distance from the source area has been taken as proof of the utility of the corridor connections. In neither case, however, was comparison made with comparable habitat lacking corridor connections; the species may occur naturally in some places this small or remote, regardless of corridor connections. Other studies failed to establish distance effects (Helliwell 1975).

Figure 22 The number of woodland plant species in hedgerows was found by Baudry (1988) to decrease with the distance from patches of woodland. The error bars are 95% confidence intervals. This is not evidence for a corridor function as there were no unconnected control areas for comparison.



Burel (1984) published preliminary findings (but presented no data) from a study of plants in hedgerows and claimed that forest tree species and many shrubs were more frequent in hedgerows connected to another hedgerow, or to a wood, than in unconnected hedgerows. These findings cannot be accepted without the data. Burel and Baudry's (1990) study of hedgerow plants in New Jersey unfortunately is statistically faulty (in some cases the data are not given, in others no statistical test is made, and the data of their Table 12.1 are mutually inconsistent), casting doubt on their conclusion that such plants are more frequent where the hedgerow is connected to a source than where it is isolated. Further, they were unable to demonstrate such an effect in Normandy.

Studies of animal movements

Another line of evidence used in support of corridor functions is studies of animals' (I found none of plants', but see Bennett 1991b) movements in relation to potential habitat barriers and corridors. Such studies (Turner 1989) typically track the animals visually, with radio telemetry, or follow their movements through capture, marking and recapture. Wegner and Merriam (1979) found that few Canadian woodland birds and mammals crossed open country compared with the number moving along rows of trees. Suckling (1984) found that sugar gliders *Petaurus breviceps* dispersed along a roadside strip of vegetation. Merriam and Lanoue (1990) found that the white-footed mouse preferred to move along wide fencerows, that had continuous shrubs and many trees. Bennett (1990) found that some native Australian mammals move between patches of forest along roadside forest strips. Saunders and de Rebeira (1991) found most birds dependent on remnant native vegetation in the Western Australian wheatbelt were recaptured in places they could have reached along corridors. Dover (1991) found that the hedge brown butterfly (*Pyronia tithonus*) kept to hedgerows. Hobbs (1992) listed further recent studies, some of them unpublished, that showed movement to be more frequent in corridors than in the surrounding matrix. Such results are convincing evidence that corridors are be important to some species in the context of central place foraging, and possibly home range. However none of these studies had sufficient unconnected "control" areas, so they do not show that recolonisation would be impeded significantly without corridors (Forman & Godron 1984; Opdam 1990; Dennis & Shreeve 1991). These studies were all of movements between small, closely spaced patches of habitat in agricultural landscapes and do not therefore demonstrate corridor effectiveness at any larger scale.

While these animals should recolonise linked patches faster than those without a corridor link, this would be of little practical import if the time difference were small. Similarly the supplementation of the population on a remote patch should be greater if it is linked, but not necessarily enough to materially improve its chance of survival. There is a need for studies that address this issue of how much better the recolonisation would be, and hence whether corridors significantly ameliorate any deleterious effects of isolation.

Burel and Baudry (1990) divided the ground beetle (carabid) species in their study of hedgerows in Normandy into three approximately equal groups: those confined to the forest core; those that penetrate up to 500 m of connected hedgerow and those that are found at any distance from the forest. These categories nicely match those predicted by Gilpin's (1981) peninsular theory, but unfortunately the authors did not produce data to support their division.

Most applications of corridor theory are at the larger scale, where whole populations of animals are supposed to be enabled to persist in habitat patches because their corridor connections enable recolonisation. Here the evidence of lack of movement can provide the necessary proof only if the studies were continued over time periods comparable with those involved in the extinction events on isolated patches and the study was sufficient to give an accurate estimate of rare colonisation events. Even if a species crosses a barrier only very rarely, this can be often enough to ensure its survival in a patch of habitat where it would die out without such rare replenishment. The periods over which the failure to cross putative barriers need to be established are in the order of months or years; not surprisingly the review found no such studies.

Dog's mercury

Some of the most convincing evidence for corridors functioning as conduits comes from special studies. The first is of linear habitats that extend out from a source of species and which show that slow-moving species are found in all of the linear habitat that is nearest to the source, but not at all in the further extremity. Pollard *et al.* (1974) found six planted hedgerows extending from Short Wood, Northamptonshire, in each of which the herbaceous plant, dog's mercury (*Mercurialis perennis*) was found in a continuous length of hedge only near the woodland source (Figure 23). A simple statistical null hypothesis would be that such continuous lengths with the species would be as likely to be separated from the source as to be continuous with it; the probability of finding a situation where all six hedges were the same is 1/32, so the null hypothesis can be rejected. Three of the hedges were dated from historical records, to enable an estimate that the plant progressed at only about 20 cm a year. This study is interesting also because the rate of movement is so slow that it would not serve the human desire to see results within a lifetime.

That this species may be unusual in so using corridors is suggested by Baudry and Forman's results, summarised in Forman (1991); the distribution of forest interior species in New Jersey hedgerows could only have come about by dispersion across the matrix of other habitats, rather than along the hedgerows. Helliwell's (1975) failure to show an effect of distance from a woodland on the number of woodland species found in hedgerows supports the same conclusion.

Freshwater streams

Another observation, however, is the much faster recovery of animals and plants in freshwater streams following pollution incidents. Return of species from the unaffected headwaters is suggested as the mechanism, the stream acting as an effective corridor (Hynes 1960; Boreham & Birch 1990). It may be because a corridor function is such an obvious explanation in this situation that the studies have not been fully critical in eliminating alternative explanations; the review found no study where the alternatives of survival in situ, invasion from unaffected side streams, or invasion by other means over land, or in the air, were properly eliminated from consideration.

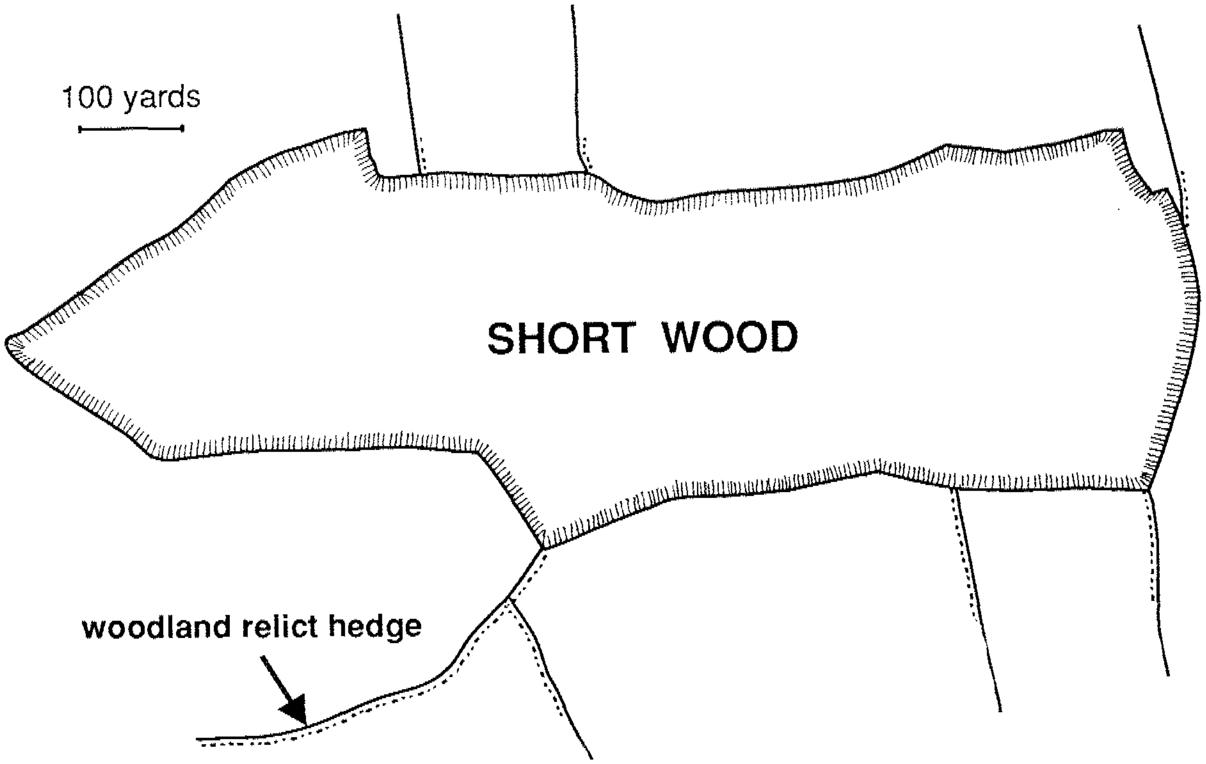
Experiments

Removal experiments have been undertaken. Henderson, Merriam and Wegner (1985) removed chipmunks (*Tamius striatus*) from woods and found that most recolonisation took place along hedgerows, but that some required animals to move up to a kilometre and that some recolonisations involved crossing a pasture barrier. The study was deficient both in replication and statistical analysis. Merriam (1991a) considered the results of Henderson *et al.* (1985) to prove that corridors were vital to recolonisation but, while these authors showed both recolonisation and use of corridors, and the results were consistent with an enhancement of recolonisation by the corridors, they were also consistent with no effect whatsoever.

An experimental approach has been taken also by Lovejoy *et al.* (1986), see also Bierregaard (1990), as Brazilian rainforest is cleared. In one case ant-following birds persisted in a patch of habitat only whilst it was connected by a wide corridor to larger areas of rainforest two kilometres away. They argued that the habitat patch was too small to assure continuous supply of the birds' food and presented evidence that birds readily crossed cleared land to other forest in search of places with food.

Presumably the larger areas of rainforest had continuous supplies of food and so the reverse movement was less often undertaken once the corridor was severed. It remains to be seen whether antbirds will return, despite the severed corridor, as happened on a smaller and earlier isolated patch in the same study. This long-term study continues, and it may ultimately provide the replication which is currently lacking.

Figure 23 Six planted hedgerows radiate out from Short Wood, Northamptonshire (or from a woodland relict hedge in one case). All have dog's mercury growing in a continuous length from the edge of the wood, but not at all beyond. The lengths correlate with the time since the hedgerows were planted (after Pollard *et al.* 1974).



Animal habitat requirements

Studies of the habitat requirements of individual animals can suggest a conduit function. Saunders and Ingram (1987), see also Saunders and Hobbs (1989) and Saunders (1990), found that roadside remnants of natural vegetation acted as corridors for Carnaby's cockatoos (*Calyptorhynchus funereus*) breeding in the Western Australian wheatbelt, allowing them to use remote patches of suitable habitat. Remnant populations died out in the absence of such corridors. Such results suggest that corridors are effective in fulfilling a size threshold for a species constrained by central place foraging, but are not relevant to recolonisation.

The only study found of the effects of the width of corridors (Burel & Baudry 1990) was statistically faulty (see above).

What have the studies shown?

The direct tests of a conduit function reviewed in this section have revealed few convincing examples and mostly in relation to size threshold rather than recolonisation or climatic change. There seems to have been even less work on the possible adverse ecological effects of corridors, as described by Simberloff and Cox (1987). However, these effects seem less likely where corridors are kept, or created, to link patches which were linked naturally, than where naturally isolated patches are to be connected; the latter provision is not being advocated (Noss 1987).

One may argue that, while individual studies fail to meet the scientific test for validity, the bulk of studies consistent with corridor effects itself amounts to proof. This is not so. Studies of scientific reporting show that fashions exist, and that uninteresting results may not get published. Both of these have been suggested earlier in this review. These processes are likely to lead to the publication of corridor speculations rather than to the conclusion that corridor effects are not evident. Popper (1963) stresses that it is easy to find evidence in favour of many hypotheses, but that science should instead pose testable hypotheses and then try to falsify them.

For those who want practical advice on where, when and for what species corridors may act as conduits, very little help is available, despite the abundance of speculation in the literature. A similar conclusion was reached by Forman and Godron (1981), Noss (1987), Simberloff and Cox (1987), Soule *et al.* (1988), Adams and Dove (1989), Forman (1991) and Saunders *et al.* (1991). Certainly corridors are no panacea.

Recommended studies

The two previous sections lead to the need for recommendations for work testing the conduit function. Paucity of data is not a case against corridors, but a case for collecting more (and better) data (Hobbs 1992).

The first suggestion is to compare a large number of patches of habitat suitable for the species, in a matrix that is unsuitable. These patches should be as uniform as possible in all measurable habitat components, or these components should be studied as covariates. Some of them should be connected via putative corridors of suitable habitat to other patches of the same habitat and others should be totally unconnected. The corridors, too, should be as uniform as possible in habitat and dimensions. All the patches should be surveyed in precisely the same way for established populations of the subject species, and an appropriate statistical test should show that the species is established more often in the connected than in the unconnected patches.

The second would parallel Pollard *et al.*'s (1974) study of the planted hedgerows around Short Wood, but document species which might be able to move within a period better matching human desires. In putative corridors of recent origin, the distribution of the species should be documented in several such corridors and the test would be that the species were found significantly more often in the parts near to the source area and not in the far parts.

These two recommendations test the recolonisation function, which is where we do not at present have enough good empirical work.

While there is good work to show that corridors can allow enough migrants to complete their journeys or animals to move between enough habitat patches to find their minimal requirement for survival, we need much more work of this kind so as to identify just which species are sensitive to barriers and just which kind of corridor may help them. It is in this context that detailed studies of movement may be useful (Forman & Godron 1981; Bennett 1991a).

Surveys of corridors can establish which species occur along their length and thus presumably find their habitat there (Bennett 1991b). Without surveys also to show that the matrix is a barrier to movement, however, such surveys do not show what role, if any, corridors play in the dispersal or migration of these species.

Johnson *et al.* (1992) suggest that studying microcosms is one way to overcome the problems of expense and scale which preclude experimental work at a landscape scale. Whilst such studies may provide valuable insights, they do need confirmation in the real world.

Some of these research suggestions may be onerous (Turner 1989; Taylor 1990; Saunders & Rebeira 1991; Hobbs 1992; Johnson *et al.* 1992) but excellent work, such as that of Pollard *et al.* (1974) on corridors and of Game and Peterken (1984) and Thomas and Harrison (1992) in the related study of habitat patches, show that the suggestions are far from impossible.

CONCLUSIONS

The review has shown that the preconditions for corridors to act as useful conduits can occur. While corridors are unnecessary for some species, others may cross barriers with difficulty, or not at all, within a time period to match people's desires. The latter two categories of species may be assisted by corridors. These categories match well with Gilpin's (1980) conclusions from his model of stepping stone islands.

It is clear, however, that all-purpose corridors do not exist; each species has its own requirements for habitat, its own ability to move, and its own behaviour. Nevertheless, corridors of a given habitat and dimensions should serve a group of species with similar requirements. Even beyond these group requirements it is also likely that general principles can be found (Gilpin 1991; Merriam 1991b).

Of the various theoretical models that have been put forward, it seems that the recent fashionable bout of metapopulation work has suffered from the same problems of oversimplification and irrelevance that affected the use of island biogeography. One hardly dares suggest that source and sink models may often prove more useful, for fear that they too will be abused. The island biogeography model does describe a limited number of circumstances quite well and should not be abandoned simply because of pervasive misuse. Those who advocate autecological work (Abele & Connor 1979; McCoy 1982; Simberloff & Abele 1982; Boecklen & Simberloff 1986; Simberloff & Cox 1987) should be more forthcoming with general principles if they are to assist in more than a few high-profile situations.

The mathematical intractability of realistic models of the real world probably means that simulation models will be of increasing use, but there are not yet any general models of corridors as conduits which take us beyond the present theoretical problems.

In relation to the size threshold function of corridors, the evidence is good. It does seem that some animals may be able to use well connected habitat fragments to find sufficient habitat, where a single fragment would not suffice. This occurs in situations where corridors enable animals to move readily and often between patches of habitat to find their daily requirements but they are not able or willing to move so readily through the inhospitable matrix in which the corridors lie. Where animals have to return to one place often (for example, to a nest, "central-place foraging") it is clear that these fragments need to be close, and so the corridors are short. Whether longer corridors can permit survival of individual animals that are not tied down to a central place is less clear (Simberloff & Cox 1987).

Suitable corridors are also obviously necessary where animals must move (migrate) between different resources to meet their seasonal requirements, and their habitats are isolated one from another in a matrix which they cannot cross readily. Not all migrant species fit this description, but it may apply to some amphibia, reptiles and large mammals in both the seasonal tropics and the arctic. While there is a considerable body of literature on the flyways used by birds on migration, it is quite clear that generally bird migration can take place over habitats of all kinds. Some individual birds use stepping stones, but it may be that most of the places where they feed on migration are optional, rather than essential. The situation must be different for many migratory freshwater animals (eg fish). Continuity of the corridor for these species is obviously vital.

Intermediate between the requirement of individual species for a minimum area (size threshold) and the possible function of corridors in recolonisation is the concept that local processes integrate in the landscape to regional ones (Saunders *et al.* 1991). It is possible that a network of corridors and stepping stones serves the need for long-distance movement, but no good studies could be found to demonstrate this. Indeed reviews of metapopulation studies (Taylor 1991, Harrison 1991) suggest that usually it is survival on the large habitat fragments that ensures species survival, not an equilibrium turnover on many smaller patches.

These confirmed functions of corridors apply to animals, but apparently not to higher plants. We turn now to the recolonisation function, which should apply to both animals and plants. The studies reviewed have been insufficient to provide a proof of the utility of corridors for recolonisation, or details of where recolonisation may be expected. The studies certainly do not rule out the function either.

Conclusions are made on whether or not this utility will prove to be there once the proof is available. It must be stressed that this is an opinion, subject to test as better studies become available. Such a view is necessary because land use and management decisions are being made every day and these decisions need to be based upon the best scientific advice, so as to avoid unnecessary wastage of resources or effort. It is also important to stress again here that this review is addressing corridors as conduits, and only as conduits; there may be perfectly good reasons for retaining corridors for public amenity, pollution control, or access, and they may qualify as good habitat for animals and plants of their own right. This latter consideration could be very significant in landscape ecology, given the conclusion that more species are found where the total area of their habitat is large, regardless of how it is subdivided.

The extensive work on dispersal abilities of animals and plants in relation to isolation suggests that many species do not need corridors for recolonisation of habitat patches after local extinction, or to prevent the extinction in the first place, and that some species would pass along the corridors too slowly for them to be effective. It is logical to presume, however, that there must be species that have middling powers of dispersal and that are habitat specialists, such that corridors permit recolonisation where otherwise it would not occur. While there must be such species, one can only speculate on their identity and number.

Many rare and threatened species are be unlikely to benefit from corridors. This is because the corridor would have to contain their rare habitat if it is to be any better than the matrix within which it lies. Rare species may require odd corridors.

Wilcove *et al.* (1986) considered the utility of corridors for recolonisation, and considered distance rather than taxa. They concluded that corridors are unlikely to reduce the isolation of two distant reserves, and that dispersal might occur anyhow if the reserves are close. They did not conclude, as one might, that there could be an intermediate class of distances at which useful effects may be felt, nor that corridors may assist the crossing of small gaps. Simberloff & Cox (1987) find that studies of the movement of animals and plants suggest that corridors may sometimes be effective, but that autecological considerations need to be taken into account.

It is almost impossible to provide specific conclusions on just which species are sensitive to the absence of corridors, except to observe that these may often be the same as those which are sensitive to the fragmentation of their habitat, as reviewed under the selective loss of sensitive species and the edge effect above. They may be specialists for habitats that have been stable for many years and thus have poor powers of dispersal and a low rate of reproduction. Their populations may be small or particularly variable. Fragmentation of their habitat has reduced their populations to numbers that bring the risk of local extinction. Clearly, too, corridors can help only species that have a significant barrier to cross and which are physically and behaviourally able to use the habitat of the corridor. Empirical autecological findings are likely to be most useful in this context. Friend (1991) suggested that priority should be placed on the needs of animal species high in the food chain and on "keystone" (Terborgh 1971; Wilcox & Murphy 1985) species.

The theories are found to be incomplete and there are few good studies showing the various functions of corridors. Suggestions are made, above, for research to remove these doubts, but there is a pressing need for guidance now. This is to apply the same precautionary principle that is being increasingly used to justify action on issues like "greenhouse" gases in the absence of precise or conclusive proof of their effects (O'Riordan 1992). The practical conclusion, then, is that habitat corridors should be kept, improved or created to connect other identified nature conservation sites and to lead into the inhospitable surrounds, where this can be cost-effective. This is partly because the corridors would serve as conduits for some animals and probably plants, and also because we cannot await proof for which species these are (Saunders *et al.* 1991; Harris & Scheck 1991). Hobbs (1992) drew attention to the ease of retaining existing corridors, in comparison with the prospect of replacing them in the future, if lost.

But it must be clear that our knowledge is not sufficient to predict in any detail which species would use such corridors as essential conduits, nor precisely what the composition or width of the corridors should be (Noss 1987; Friend 1991). We know little of how gaps in corridors may impair their function. It is obvious, however, that a wide, rich and continuous corridor must perform better than a narrow, poor or discontinuous one; one would expect it to suit more species and to provide a link along which movement could be more sure, if not more speedy. Just how wide and what habitats are best will depend upon the target species.

The findings of this review support those who stress that the retention, enhancement or provision of corridors should be balanced against alternative measures to conserve biodiversity and that there are situations where scarce resources dictate that the effort goes to these alternatives as a priority (Forman 1991).