A CRITICAL EXAMINATION OF THE CORRIDOR CRITERIA

So far the review has described the historical development of theories used by those who have advocated corridors. Recent authors disagree on whether the function of corridors in species conservation is soundly based in theory. The island biogeographic (or biotic collapse) criteria, including corridors, were quickly and widely adopted, for example in the World Conservation Strategy (IUCN 1980) and are still current among many practitioners (Bridgewater 1987, Burkey 1989, Verkaar 1990 and Harris & Scheck 1991). However the criteria resulted in a long and bitter controversy in the scientific community and Simberloff and Cox (1987) find little convincing evidence for corridors in the studies. The next section of this review examines the theories and empirical evidence in an attempt to resolve this disagreement.

The section begins with situations that may require corridors to promote movement. The theories assume that the populations of organisms are isolated in habitat fragments and cross the matrix between them with difficulty; the extent to which this is so is examined. Evidence on this may come also from the "turnover" of species on habitat fragments, and from the "relaxation" of the species richness to a new equilibrium after fragmentation of their habitat, considered next. Then the characteristics of the habitat patches that may influence the success of corridors are considered - their dimensions, or size, their habitat composition and adverse habitats on their edges. Next the adequacy of landscape ecological theories as a basis for corridor recommendations is examined, followed by a similar examination of metapopulation theories. The ideas on just which species may be sensitive to fragmentation and thus require corridors are considered. Finally methodological aspects of the studies are reviewed.

Following this, the review turns to the requirements of studies to demonstrate corridor effects, and this leads to a consideration of studies that bear directly upon the conduit function, and finally to recommendations for further work.

Do corridors help to overcome Isolation?

One argument for corridors is that they facilitate movement through a matrix of otherwise unfavourable habitat and so overcome the adverse effects of isolation on habitat fragments.

Crowell (1963), Hamilton *et al.* (1963), Williams (1964) and Lack (1973, 1976) suggested that impoverishment of island avifaunas had much more to do with the bird species failing to find suitable habitat there, than to their failure to cross the gaps. Temperate birds seemed more able to cross oceanic gaps than tropical species (Diamond 1974, Terborgh 1975, Wilcove *et al.* 1986). Studies of "Beta diversity" (large-scale diversity) of British plants and animals suggest that species turnover at this scale is more a product of range and habitat restriction than of dispersal limitation (Harrison, Ross & Lawton 1992). Forman and Godron (1981) and McCoy (1982) also emphasised that terrestrial habitat patches differ from true islands in that they are not surrounded by totally inhospitable habitats and so may not be so isolated.

It has also proved difficult to confirm one of the two empirical patterns that island biogeographic theory first sought to explain: that the number of species on patches of habitat is less than that which is found on an equivalent area of the nearest "mainland" source and therefore the patch species-area curve is steeper than the mainland one (Diamond 1969; Helliwell 1976b; Schoener 1976; Simberloff 1978a; Nilsson & Nilsson 1978; Connor & McCoy 1979; Williamson 1981; Haila *et al.* 1982; Coleman *et al.* 1982; Connor *et al.* 1983; Kelly *et al.* 1989; Hart & Horwitz 1991). This again raises questions about the isolation of populations of these species.

Middleton and Merriam (1983) examined the spatial distribution of higher plants, squirrels and invertebrates in large blocks of Canadian forest compared with remnant patches in farmland, and concluded that these species did not find the farmland any barrier. Such findings indicate that isolation, for these species, may be no more important between distant patches than it is between samples within larger patches.

Where isolation is unimportant, in the terms of Figure 4, there is effectively but one immigration curve - that for "mainland samples" - so that the number of species decreases with decreasing patch area, but not with isolation. For temperate birds Haila et al. (1982), Haila (1983), Tilghman (1987) and Hart and Horwitz (1991) conclude this is commonly the situation in patchy environments on continents: situations for which there is an "archipelago" of habitat patches with little barrier between them. This is clearly a situation where corridors are not required, as movement between habitat patches can occur readily without them.

In multiple regression studies of habitat patches, a lower species richness with isolation may be evidence that corridors or stepping stones are required to overcome the isolation (Opdam et al. 1985; van Dorp & Opdam 1987; Soule et al. 1988). However, few of these studies are sufficiently detailed to eliminate other reasonable explanations of the distribution. Often the isolated patches studied are too few to distinguish isolation from other factors, such as the history of the patches, their habitat composition or their size (Opdam et al. 1985).

Is isolation important for particular sensitive species?

It remains possible that real effects on sensitive species are masked in the aggregate statistics of whole communities (Howe 1984). In the extreme isolation clearly does matter: the scarcity of mammal species, apart from bats, on remote islands (Wilcox 1980); the record of successful introductions to islands by human agency (Brockie et al. 1988); successful re-establishment of butterflies (Oates & Warren 1990; Thomas 1991) in parts of Britain; and the large numbers of species endemic to islands, all demonstrate that many species of animals and plants very rarely cross large gaps unaided (Williamson 1981) or may take a very long time to do so. Fishes in lakes and rivers may be as isolated as are terrestrial organisms on islands (Barbour & Brown 1974; Sheldon 1988).

Brown's (1971) study of mammals isolated on mountaintops is a much-cited example where immigration is assumed to be impossible. Morris and Webb (1987) consider many rare insects of semi-natural habitats to be in the same situation. For these species and distances (or inhospitality of the barrier), in the terms of Figure 4, the patches are so very "far" that the equilibrium species number is very near zero and the species present are being very gradually lost after some historic change had left the the habitat patch isolated.

Taylor (1990) distinguished three categories of isolation in metapopulation models:

1.	local extinctions and recolonisation occur frequently;

2.	isolated local populations frequently would go extinct but migration ("dispersal" in the terminology of this review) prevents this; and

3.	isolated local populations usually would persist but fluctuate and migration reduces the magnitude of the fluctuation.

The first of these is the most often studied, and for good practical reasons. For some species, one can be confident that failure to detect them in a habitat patch is because they are really absent, rather than difficult to find. This is because, given suitable habitat, a successful colonisation will soon lead to population of the patch to a level that is readily detected. Such clear evidence is much more difficult to obtain for Taylor's other two categories.

Taylor believed, however, that his second two categories might be more frequent, and that these have received little empirical attention. That Taylor's three categories lie on a continuum, and the first is the most extreme, means that evidence for the first implies that the other two must also occur. Thus the easy empirical work should have wider applicability than appears so at first sight.

The rate at which plant species invade new polders is influenced by their dispersal mechanisms (Nip-Van Der Voort, Hengeveld & Haeck 1979) and terrestrial animals colonising Britain differ greatly in their rates of spread into new territory, which is evidence for greatly varying abilities to cross inhospitable barriers (Macdonald & Smith 1990) even if this should be qualified by another factor that may influence this variation: the species' intrinsic rates of increase (Williams, Dransfield & Brightwell 1992).

Some authors (Wilcove et al. 1986) have used atypically consistent relationships with distance (such as that in Figure 14) to reach more confident conclusion on the general response of species to isolation than is justified. Studies that fail to establish a clear-cut effect of isolation (eg Middleton and Merriam 1981, 1983; Munguira & Thomas 1992) may be less interesting and so less often published.

Lynch and Wigham (1984) confirmed earlier findings that few long-distant migrant birds are found in isolated forest fragments in the eastern USA. They agree that it cannot be inability that prevents colonisation of these patches and they posit a "psychological" avoidance of adjacent open habitats. An alternative explanation for this finding advanced by Askins et al. (1987) is that the absence from some patches merely reflects a low regional population.

Studies of animals in relation to roads as barriers have established that, for some species, movement may be much more frequent within the habitat patch than across the road (Oxley et al. 1974; Adams & Geis 1983; Mader 1984; Merriam et al. 1989; Mader et al. 1990; Lyle & Quinn 1991; Bennett 1991a; Munguira & Thomas 1992). Other studies show lesser effects on abundance and movement of animals around roads as a source of disturbance (McLellan & Shackleton 1988; van der Zande, Keurs & van der Weijden 1980). Some of these effects are so pronounced (Figure 15) as to obviate various methodological and statistical deficiencies in the studies (many of them had inadequate control areas and very few applied statistical tests, or calculated confidence intervals). Nevertheless it is nearly impossible for a direct study of movement to establish that rare colonisation events do not occur (the binomial confidence limits for an observation of zero movements are 0 to 3.7). Thus this evidence on roads as barriers does not show them to be effective in preventing eventual recolonisation nor gene flow, but they might be effective in preventing the attainment of a minimum size threshold. It is also true that the movements of many species are little affected by such features as roads (Duelli 1990).

Merriam et al. (1989) reviewed many of these studies to reach more detailed conclusions, but these are not supported by the examination of the studies' statistical adequacy.

The existence of such barriers to movement also suggests that, for some species, a single patch of poor habitat within what might otherwise be an excellent corridor could prevent movement along it.

Figure 14 The incidence of dog's mercury *Mercurialis perennis* in woods 100 to 150 years old in relation to the distance of the woods from the nearest older wood having the species (the error bars are 95% binomial confidence limits, after Game & Peterken 1981, corrected M.Game *pers. comm.*).

Percentage with Dog's mercury
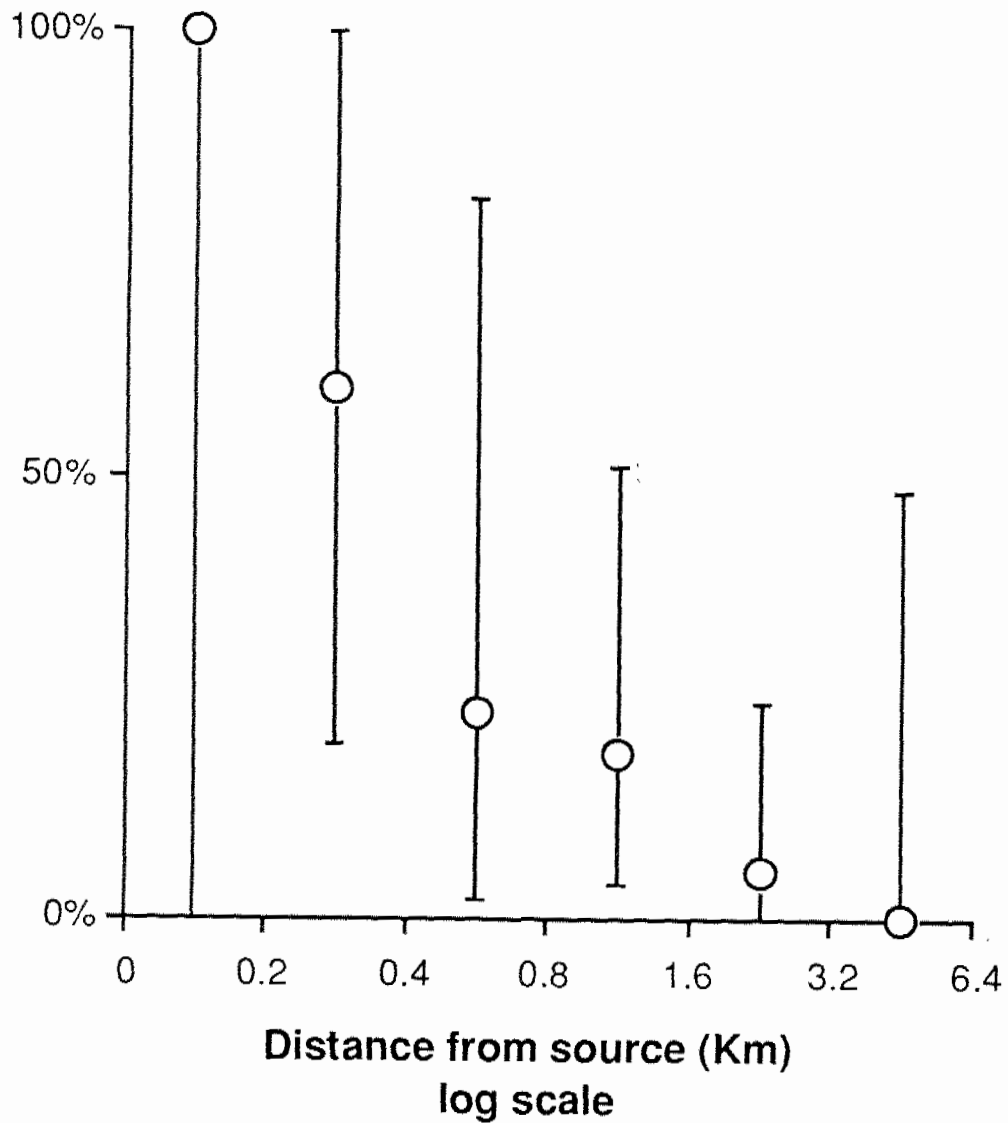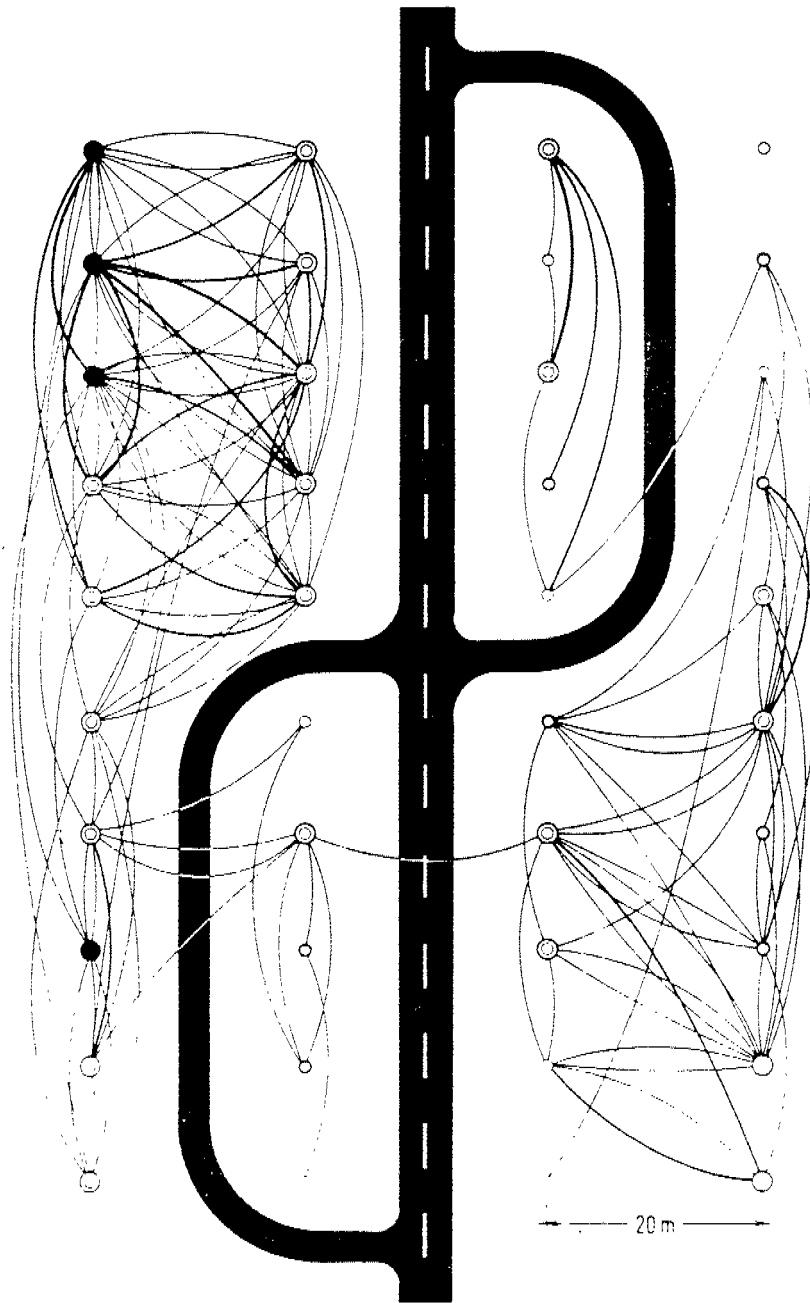
Distance from source (Km)
log scale

Figure 15 The movements shown by the ground beetle *Abax ater* Vill. between patches of woodland isolated by a road and two parking loops (after Mader 1984). Movements were much more frequent within the woodland than across the roads.

The plant dog's mercury (Mercurialis perennis) was absent in most Lincolnshire woods less than 300 years old in a study by Peterken and Game (1981). They suggested that it spreads almost entirely vegetatively, rarely by seed, and that new populations have established in the last 300 years mainly by vegetative spread to near sites, and rarely by seed over greater distances (Figure 14). Using similar evidence, Harrison, Murphy and Ehrlich (1988), Thomas and Harrison (1992) and Thomas *et al.* (1993) demonstrated, for several butterfly species, that long-distance dispersal is extremely rare (Figure 16). In this regard Dempster (1991) and Thomas (1991) suggested that isolation of populations can result in an evolved loss of mobility.

Figure 16   Occupancy of patches of suitable habitat by the silver-studded blue butterfly *Plebejus argus* in North Wales in 1990. Most patches larger than about 0.1 ha were occupied (o), provided that they were within about 600 m of another occupied patch. Beyond this distance no patches were occupied (o), regardless of size (after Thomas & Harrison 1992).
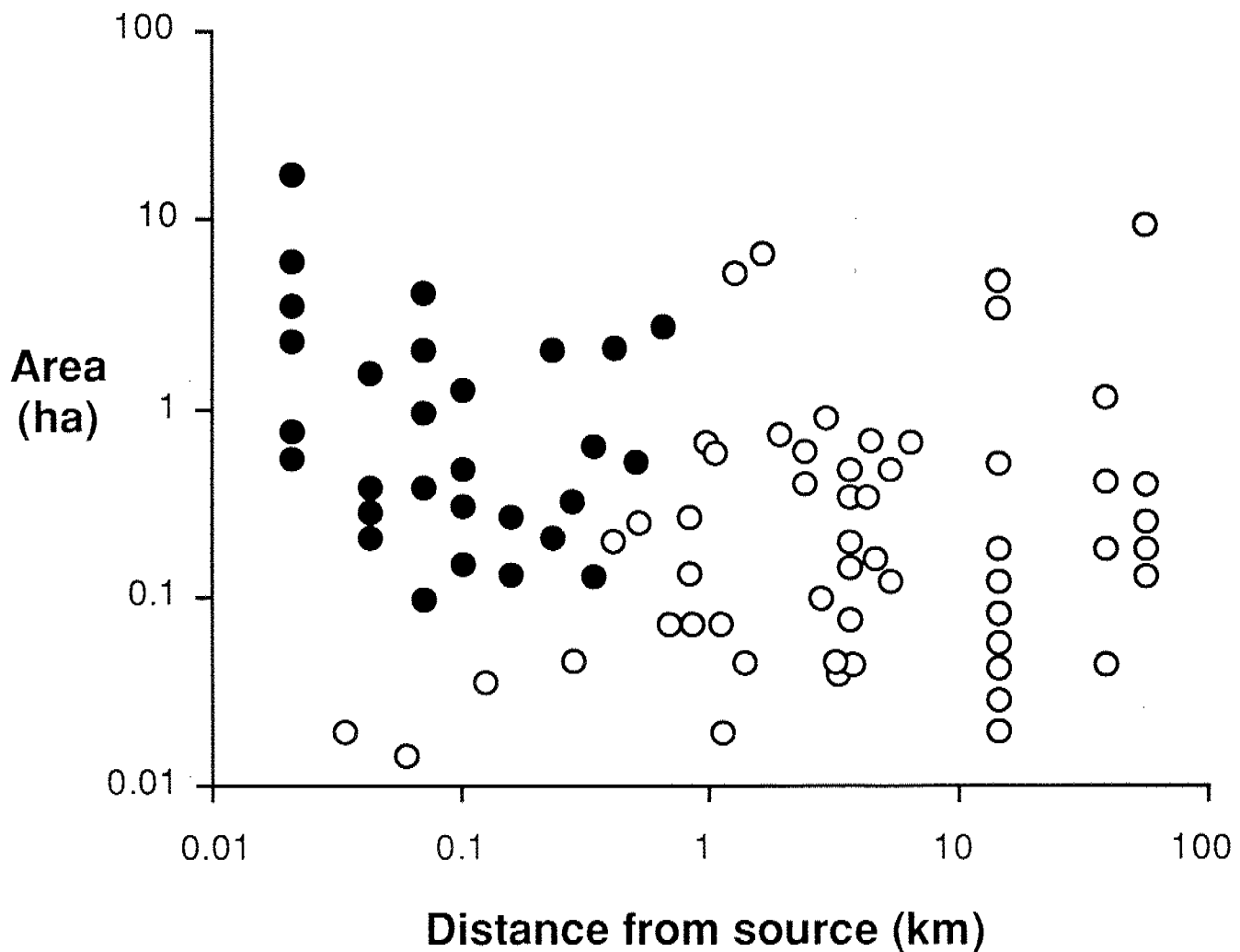
Opdam *et al.* (1985) and van Dorp and Opdam (1987) found an effect of isolation on the number of woodland bird species in the Netherlands but could not demonstrate an effect for any individual species.

Does mortality in the matrix cause effective isolation?

The review did not find studies that related mortality in the barrier, or matrix, to the overall population survival of the species concerned, though statistics like the 45% of all known Florida Panther (*Felis concolor coryi*) deaths that occur on highways (Harris & Scheck 1991) suggest that this may be a significant factor for some species. Bennett (1991b) reviewed studies of mortality of animals on roads to conclude that, for most species, while the gross numbers dying may be very large there would be little effect on the population. Even for the species where the mortality may be significant, there were not any studies showing that movement was prevented.

Are the genetic effects of isolation significant?

Despite studies like that of Reh and Seitz (1990) which suggest that isolation might increase homozygosity, there seem not to be studies showing the extent to which such genetic effects impair population survival, if at all (Harrison 1991; Saunders *et al.* 1991).

Are the effects of isolation always deleterious?

Most authors have assumed that the effects of isolation are entirely deleterious, but Simberloff and Cox (1987) and Panetta (1991) warn that the immigrants may be predominantly catholic species, common competitors, pests, weeds, or top predators which could displace interesting, rare or endemic ones. Blyth (1991) makes a similar point in relation to corridors to escape changing climate. Crowley's (1981) model of predator-prey interactions reviewed under "metapopulation" above gives some theoretical backing to these suggestions and the history of species introduced by human agency shows that this does occur, particularly on remote islands. Such effects are not so likely in remnant natural habitat patches, but are still possible.

Isolation and corridors

The practical question about isolation resolves down to which of three circumstances apply; the species under consideration may:

1.   colonise so readily that isolation matters very little;

2.   have so much difficulty crossing gaps, with or without corridors to aid the crossing, that colonisation is impossible in any realistic time; or

3.   have sufficient difficulty with colonisation that the distance from the source has an important effect.

Many species are known to behave in such a way that corridor connections are unnecessary to account for their presence in a given patch of habitat (Helliwell 1975; Pollard *et al.* 1974; nip-van der Voort *et al.* 1979; Cameron *et al.* 1980; Forman & Godron 1981; Frankel & Soule 1981; Margules *et al.* 1982; Ambuel & Temple 1983; Hopkins & Webb 1984; McDonnell 1984; Fahrig & Paloheimo 1988; Dale 1988; den Boer 1990; Date *et al.* 1991; Murdoch & Lyle 1993). This includes species of birds, butterflies, spiders and higher plants that may fly or drift long distances in the air, or otherwise have good powers of dispersal that do not appear to be affected markedly by the underlying habitat (Bennett

1991a). Many of the species behave as if they were adapted to disperse under favourable conditions as part of their life cycle (den Boer 1990).

Other species disperse poorly (Helliwell 1975; Cameron et al. 1980). Some of these would not be expected to move along corridors sufficiently fast to satisfy peoples' desire to see the species in a reasonable time. Such species could include plants that reproduce through vegetative clones and otherwise have very poor powers of dispersal, such as most ancient woodland indicator plant species (Peterken 1993). Hobbs (1992) considered that these relatively sedentary species may be at greater risk of extinction.

Between these two groups of species there should be a group with dispersal powers in the middle range. These might use corridors and thus be found where they otherwise would not.

In the context of recolonisation most species fall under 1 or 2 above, and therefore would be little influenced by corridors. This view is based on studies of the movement abilities of individual species and also on the difficulty of demonstrating a convincing isolation effect on total species number in most studies. The view is shared by Gilpin (1980) in his development of stepping stone theory; Gilbert (1980) in his examination of early island biogeographic studies; Levinson (1981) for tree species in Wisconsin woodlots; Middleton and Merriam (1983) for Canadian forest plants and animals; Morris and Webb (1987) for insects in British field boundaries and Macdonald and Smith (1990) for mammals in British farmland. Thomas and Harrison (1992) considered the silver-studded blue butterfly (*Plebejus argus* L) in north Wales to fit in the first category within distances of about 500m, the third for distances up to a few kilometres and the second beyond these distances. This effect of isolation on the probability of recolonisation is also reflected in the time taken to recolonise: remote patches take longer (Thomas et al. 1992).

There is however a second aspect to corridor functions. The fact that some animals rarely cross barriers, or suffer very significant mortality in them, shows that their daily needs for habitat have to be found in well-connected areas (Lyle & Quinn 1991; Wegner & Merriam 1979). This is especially so of earthbound migrants, such as many amphibia (Andrews 1993; Sinsch 1989) and the migratory mammals of the seasonal tropics (Harris & Scheck 1991). For these, movement must be so easy that whole populations can undertake it without significant mortality. The effects of isolation on habitat size thresholds will therefore be important to some animals' population biology.

We do not know what kind of corridor would serve bird species which appear to show psychological avoidance of the edges of their habitat patches or of the inhospitable matrix between them. Opdam (1991) sought explanations for these isolation effects, but could find no good work on how birds actually disperse through the landscape.

In conclusion corridors seem to have a value in reducing isolation for only a limited group of plant or animal species as far as recolonisation is concerned, and to have a potentially greater value in meeting the daily and migratory needs of animal species.

Turnover

Evidence for the effects of isolation, immigration and extinction, in the context of either island biogeographic or metapopulation theory, can be taken from studies of individual species' populations in a system of habitat patches, where on any one patch the species is seen to go extinct, only to re-establish. Opdam (1990) and Merriam and Wegner (1992) reviewed studies of a variety of taxa which showed turnover on habitat patches, as evidence that metapopulation "spatial dynamics" was operative. However these are not evidence that the patches are any more isolated than are contiguous

areas of habitat. If the patches are small enough to be around the threshold size to hold a viable population of a species, it would be expected to be present in them by chance just as it would be in similar-sized samples from larger areas of continuous habitat (Opdam 1991).

In this context Lynch and Johnson (1974), Simberloff (1976) and McCoy (1982) showed that a good deal of the turnover measured in studies of island biogeography was "pseudoturnover" of vagrant or transient species which would never establish populations (see also McCoy 1982; Williamson 1983). Such places are of little conservation importance unless the metapopulation that inhabits them has nowhere more secure to exist. Smith's (1975) robins in apple trees illustrate this point well:

> Fluctuations may bring a species to extinction in a system. I can accept a moderate amount of this but not very much. Obviously, extinction is more frequent in smaller systems. At a ridiculous extreme every death or movement creates an extinction at that exact point. Robins become extinct in an apple tree many times each day whenever they fly elsewhere. To me, frequent extinction is a signal that the system under study is not large enough to include the processes being studied. Move the system boundaries out until extinction becomes rare. This ensures that the organising forces of the system lie within the system.

Merriam and Wegner (1992) and Middleton and Merriam (1981) discussed small mammal populations that may go extinct on small isolated Canadian woodlots over winter, but which are recolonised rapidly after the thaw. Bellamy *et al.* (1993) reported a similar turnover of breeding birds on small isolated British woods. These are not as trivial as robins in apple trees, but are small scale processes and almost as predictable as returning migrants and hardly deserve the term "extinction"; these populations persist in the long-term. The key point in this context is whether the isolation of the patches has an important influence on the turnover and, crucially, whether corridors can affect this.

Abbot (1983) listed further problems with studies of turnover: bias, thoroughness, treatment of missing species, scale, collecting effort, and lack of breeding confirmation; he concluded for Australian islands that most "turnover" of birds and mammals, but not of plants, was in fact due to human effects; this is included in "non-equilibrium turnover" by Abele and Connor (1979). Other methodological problems with studies of turnover are that it is difficult to detect or to quantify rare events affecting rare species (Taylor 1991), and that it is difficult to be sure that habitat changes have not occurred. Thomas and Harrison (1992) attributed most turnover of a British butterfly to habitat changes. Abele and Connor (1979) reviewed the evidence for high rates of turnover to conclude that rates of equilibrium turnover were generally overestimated. McCoy (1982) examined Whitcomb *et al.*'s (1977) study of turnover, and concluded that analytical problems meant it was grossly overestimated.

Lynch and Johnson (1974) also introduced the term "cryptoturnover" for species which go extinct locally, but re-invade between study visits and so are not detected as having gone extinct. This is related to the rescue effect of Brown and Kodric-Brown (1977), discussed above, and was discussed also by Simberloff (1976) and Diamond and May (1977), who termed it "silent turnover". Bellamy *et al.* (1993) found the rescue effect to operate with breeding birds in small British woods, as the actual turnover of marked populations was considerably greater than the apparent turnover shown by the incidence of the species in successive years. It likely that most species exhibiting silent turnover will have a high colonisation rate and thus be unlikely to benefit from corridors.

Therefore the existence of turnover cannot by itself be taken as evidence that island biogeographic (or metapopulation) processes are the predominant explanation for the presence or absence of species on habitat patches, most especially of sensitive species (Boecklen & Simberloff 1986). In this context

it is the evidence turnover provides of barriers to dispersal that is important. The evidence falls far short of proof.

## Can corridors help species otherwise doomed to "relax" to extinction?

Boecklen and Gotelli (1984) examined Terborgh's (1974) classical study of "faunal collapse" on Barro-Colorado Island and that by Soule *et al.* (1979) for Nairobi National Park, to conclude that there was such imprecision in estimates of extinction rates as to invalidate specific conservation recommendations (Figure 17). This criticism applies also to Wilcox's (1980) analysis of the mammals of the Sunda Islands and of birds and lizards (Faeth & Connor 1979). Boecklen and Simberloff (1986) examined Diamond's (1972) relaxation times for land bridge islands near New Guinea to find similarly wide confidence intervals.

Figure 17   Calculation of confidence intervals shows that Terborgh's (1974) estimated extinction coefficient for birds on Barro-Colorado Island is so imprecise as to be uninformative. The open symbol is Terborgh's estimate from the line fitted to K values for other places, and the curved lines are 95% simultaneous confidence limits (after Boecklen & Gotelli 1984).
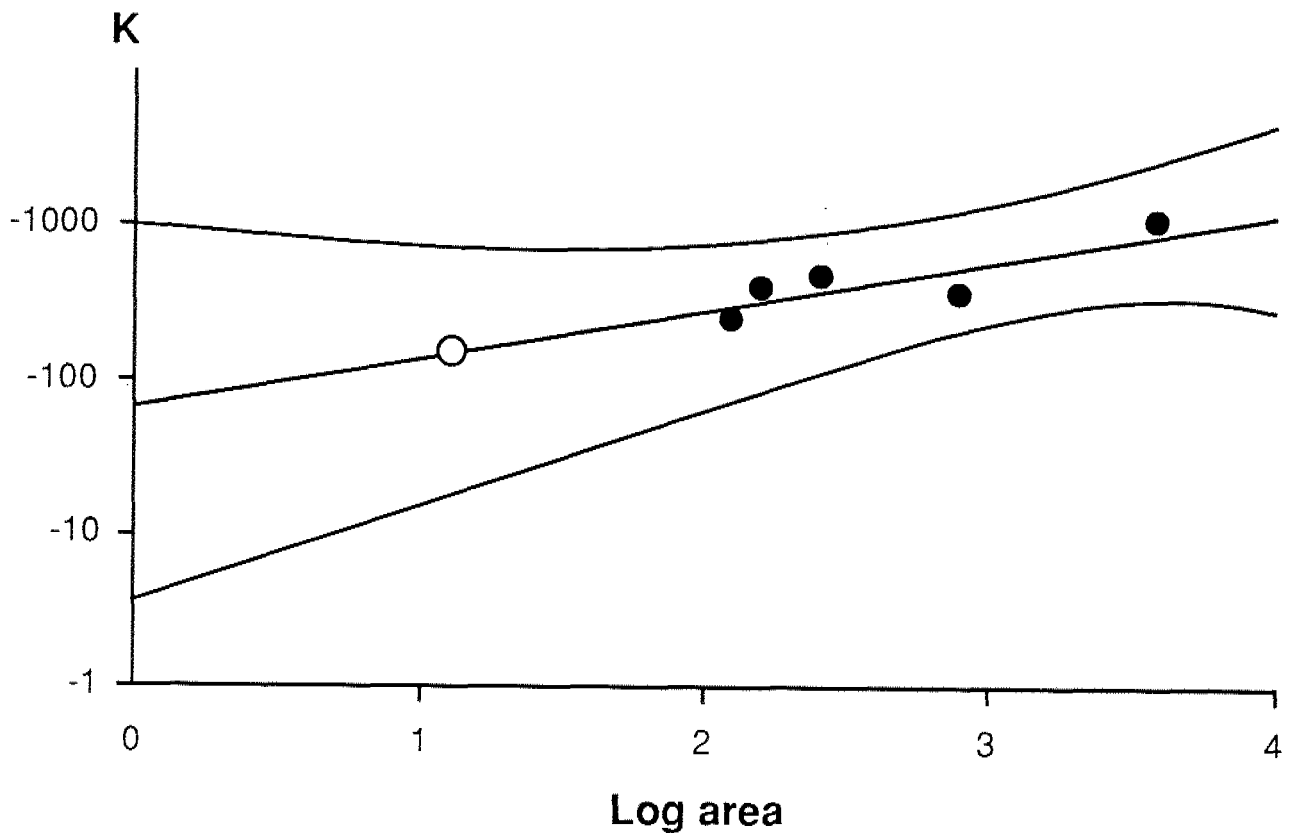
No studies were found of terrestrial habitat patches to suggest that relaxation back to equilibrium of short-lived species there will be the very slow process described by Diamond (1972) and Terborgh (1976), although Saunders (1989) considered that bird species were still being lost from Australian wheatbelt habitat patches through relaxation. Kitchener *et al.* (1980) found no evidence for such relaxation of the number of lizard species in Western Australian wheatbelt reserves, nor did Simberloff and Gotelli (1984) find any for plant species in a prairie-forest ecotone, nor Peterken and Game (1981) for ancient woodland species in Lincolnshire (Figure 18).

Figure 18 Peterken & Game (1981) found no evidence that the woods in Lincolnshire that had been greatly reduced in area in the previous 160 years (X) had any more species than woods which had not been so reduced (O). In contrast to the results of Figure 7, therefore, there is no evidence that relaxation is still in progress.

Number
of
species

100

50

1   10   100

Area (ha) - log scale

47
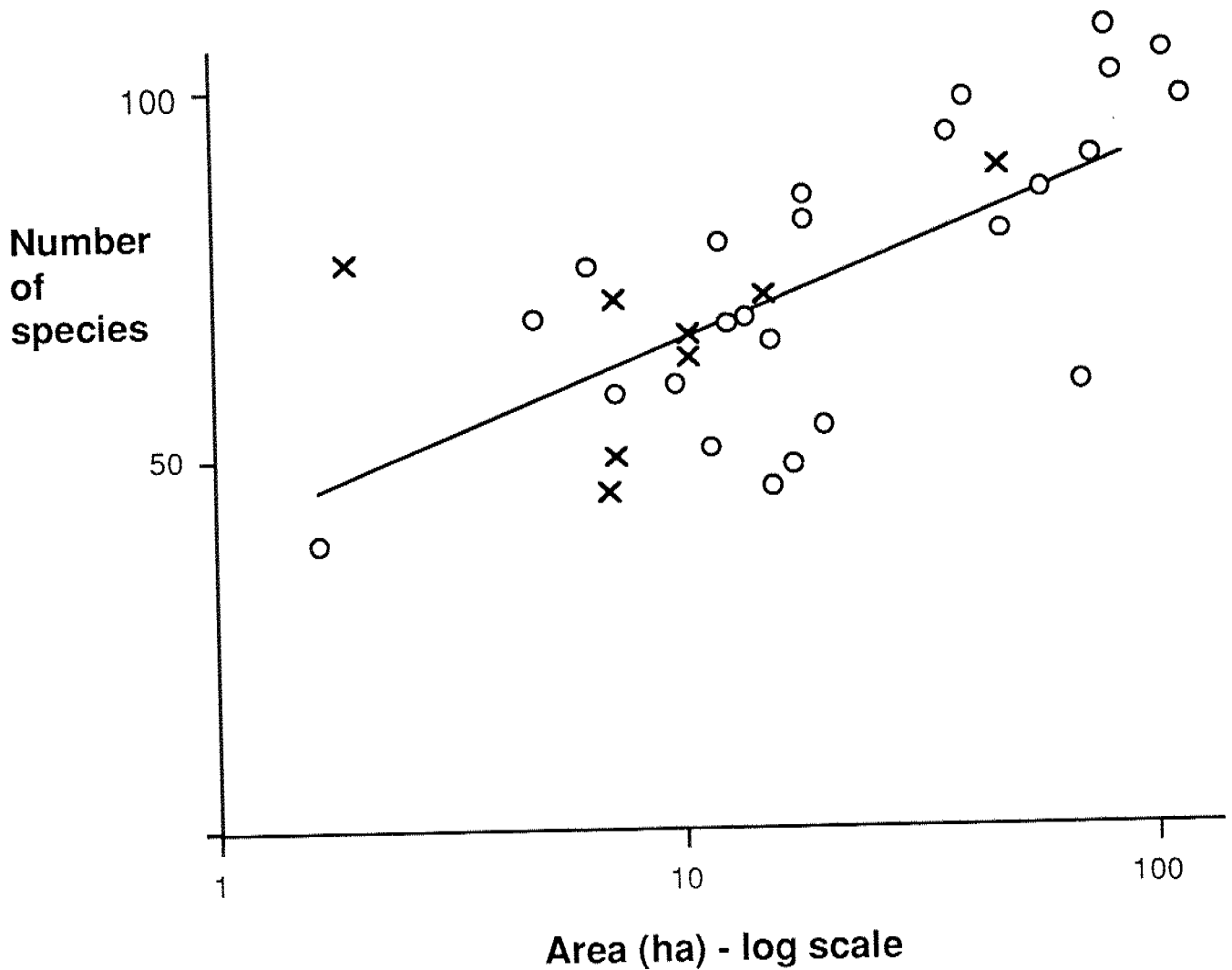
Soule et al. (1988) described the slow loss of birds from chaparral fragments in San Diego as "relaxation", a conclusion that depends upon a multiple regression study that showed that the number of species in a patch was related to the time since isolation as well as with the area of chaparral habitat. However the area of chaparral was being reduced and degraded greatly over this time period, so that the "relaxation" could simply reflect the species richness responding quickly to the habitat changes.

"Relaxation" of short-lived species may in fact generally be much quicker than is suggested by the few publications on the subject. However species may persist for many years simply through being long-lived (Saunders et al. 1991). Game and Peterken (1984), studying ancient woodland plant species in Lincolnshire could not detect relaxation even over hundreds of years. Cameron et al. (1980) showed that hedgerows in Britain that are relicts of woodland have almost all of the snail species found in intact woodland, again suggesting little relaxation over hundreds of years. It is possible that some such species have such a low extinction rate that relaxation takes a very long time indeed. For such species, however, extinction can be taken as zero within the usual time period for planning. It is the species of intermediate life span that may go extinct at times significant in the context of reserve design.

Thus those who extrapolate from the findings on birds of tropical oceanic islands (Forman et al. 1976; Brown 1978) may reach erroneous conclusions, but it is necessary nevertheless to beware of species which may be doomed to go extinct as a consequence of past changes. To the extent that corridors may link areas together, some such losses consequent on a reduction of area may be averted.

Corridor width, area and habitat diversity

The "island biogeographic" criterion which favours large reserves over small ones, suggests that wide corridors will serve their function better than narrow ones and also that corridors may enhance the patches they join by adding to their area.

The MacArthur-Wilson island biogeography model assumes that extinction rate depends upon the mean size of a species' population, and that in turn depends upon the size of the patch and the number of species belonging to the taxon on it. Extinction rates on islands do seem to relate to population size, as is assumed in both the island biogeographic and metapopulation models (Rey 1981; Schoener & Schoener 1983; Wright & Hubbell 1983; Diamond 1984; Schoener & Spiller 1987; Quinn & Hastings 1987; Pimm et al. 1988). This is still a commonly-held explanation of the area effect (Abele & Patton 1976; Usher 1991), but there are, in fact, a large number of other models that can account for the species-area effect (Simberloff 1978b; Abele & Connor 1979; Connor & McCoy 1979 and for a recent review see Hart & Horwitz 1991).

An early alternative suggestion was that the "area effect" (more species in large habitat patches) is due to large patches having a greater diversity of habitat and not to area per se (Hamilton et al. 1963; Williams 1964; Ouellet 1967; Lack 1973, 1976). This would also invalidate the assumption of homogeneity common to the MacArthur-Wilson and most metapopulation models (Martin 1981; Haila 1983; Wilcove & Robinson 1990; Usher 1991). The variety of habitats (or niches) available, is summarised here by the phrase "habitat diversity" and contrasted with the theoretical homogeneity.

Diamond (1973) and Diamond and May (1976) do allow that the effect of area may be because of a variety of habitat factors in addition to the straightforward effect of area on population size:

> "Area also affects immigration and extinction in several other ways: through its relation to the magnitude of spatial and temporal variability in resources; by being correlated with the variety of available habitats, as stressed by Lack (1973); and by being correlated with the number of 'hot spots', or sites of locally high utilisable resource production for a particular species (Diamond 1975)."

Area and habitat diversity often correlate closely, so that their effects are difficult to separate (Connor & Simberloff 1978; Abele & Connor 1979; Connor & McCoy 1979; Juvick & Austring 1979; Kitchener et al. 1980; Forman & Godron 1981; Kitchener 1982; Van Dorp & Opdam 1987; Hart & Horwitz 1991). Simberloff's (1974) experiments on Florida mangrove islands and Abele and Connor's (1979) studies of coral heads are among the very few studies where an effect of area per se is likely, although even Simberloff's work is not considered sufficient proof by Williamson (1981).

In the majority of studies, habitat diversity has proved to correlate with species number at least as well as does area. The few that could separate the two effects show that habitat diversity often is more important than area per se (Western & Ssemakula 1981; Lynch & Wigham 1984; Hart & Horwitz 1991; but see Opdam et al. 1985; Rafe, Usher & Jefferson 1985; Freemark & Merriam 1986; Van Dorp & Opdam 1987; and Nilsson, Bengtsson & As 1988 for exceptions). An added complication is that a patch may be seen as one habitat by, for example a predatory bird, but as several habitats by smaller insect-eating species.

Thus, it is not sufficient to assume, as was commonly done (Goeden 1979; Usher 1979), that a correlation between the size of a patch and the number of species it holds is confirmation that area per se has been the main determinant of the number of species, or that an equilibrium between immigration and extinction is the major organising process in its community. Area may act through larger patches having a greater or better range of habitats present, or through other factors reviewed by Boecklen and Simberloff (1986) and Hart and Horwitz (1991).

Although there is doubt about the mechanism, there is little dispute that large patches will conserve more species than small ones (Usher 1991). A review by Connor & McCoy (1979) shows that, while the actual shape of the relationship may differ, there is almost invariably a correlation between the size of a habitat patch and the number of species of a given taxon that it holds. Even in exceptional cases, like the species-poor British lowland heaths, large patches hold more of the subset of species which specialise in the habitat (Webb & Hopkins 1984; Hopkins & Webb 1984; Webb 1989).

Are predictions from the "area effect" sufficiently precise?

Western and Ssemakula (1981) pointed out, however, that the species-area curve may be statistically insignificant over the practical range of areas used for reserves. Boecklen and Gotelli (1984), further, found that the confidence limits around many of the published species-area relationships were so wide that they lacked utility for precise predictions, such as the minimum area necessary to conserve a given number of species; the determinants of species richness are, as noted above, often too complex to be modelled by area alone. They recommended the incorporation of other variables like habitat heterogeneity or resource availability. They also stressed that use of the species area curve ignores species identity and population size (Haila & Jarvinen 1981).

It is certainly true that more precise predictions of the number of species are possible if there is information available not only on the area, but also on the habitat, or species composition, of the candidate patches (Western & Ssemakula 1981; Simberloff & Abele 1984). For shade-tolerant higher plants Game and Peterken (1984) were able to show that information on the habitat types, rare species and location of individual woods allowed the selection of a better set of woods for species conservation than consideration of area alone. However, theories on minimum viable populations have yet to be validated in the field (Saunders *et al.* 1991) and, frequently, decisions have to be made on limited information, or a system of reserves selected for biological diversity *per se* rather than for particular taxa. In these instances, including area and habitat diversity among the design criteria will improve the system.

While it is not at all clear that the superiority of large patches is a consequence of the equilibrium of the MacArthur-Wilson theory, for practical purposes it does not matter how the superiority comes about, provided that it is likely to persist (Miller & Harris 1977; Verner 1986). An additional criterion is called for by the pervasive importance of habitat diversity (Western & Ssemakula 1981). Simberloff and Abele (1982) and Simberloff (1986) stressed that an unwarranted focus on theory had detracted from the main task of refuge planners, determining which habitats are important.

These studies have been on the size and habitat diversity of the patches, rather than on corridors *per se*, but applying their findings to corridors suggests that, the width (area) and habitat composition of corridors is important. If they are to act either as conduits, or to add to the area of a habitat patch, the wider the better. The desirable habitat composition and its management will depend upon the requirements of the taxa for which they are supposed to act as a conduit; the nearer the habitat to the optimum for those taxa the better the corridor. The imprecision of the size and habitat diversity effects does not invalidate this conclusion, but it certainly suggests that other factors will often be important when evaluating the quality of corridors as conduits, or managing them.

Edge effect

The edge effect is supposed to be particularly important to thin corridors, which may be largely or wholly edge. Here too there are difficulties. Wilcove *et al.* (1986), for example, reviewed several studies that demonstrate that nest parasitism and predation on song birds are greatest near to the edges of woodlots in the Eastern USA. They made the logical jump to conclude that this has been responsible for the decline in songbird populations in small woods there since the late 1940s, without any discussion of the overall regulation of numbers in these species. The effects they illustrated were not major and other explanations for this long-term decline are surely possible (Opdam 1991). Further, Wilcove & Robinson (1990) found that many of the species that are confined to large patches nevertheless do not avoid edges.

Studies of the edge effect, like those of Webb *et al.* (1984), Lovejoy *et al.* (1986), Wilcove *et al.* (1986), Burel and Baudry (1990), Lynch and Saunders (1991) and Usher (1991), have, however, established that some species do prefer the "core" of habitat patches and so such species may be sensitive to fragmentation of their habitat. Saunders *et al.* (1991) and Hansson and Anglestam (1991) reviewed the many physical and biotic edge effects that can change small habitat patches. These mean that often small patches are of a quite a different habitat than is found in the core of large ones and this habitat may be less suitable for sensitive species. A source and sink model may therefore be the most appropriate theory in many cases (Figure 9).

The question that remains unanswered in the context of corridors is whether a preference for core habitat precludes their use as corridors by sensitive species which see them as entirely edge. In the absence of good empirical studies this proposition remains theoretical, but seems likely at least for plants, which must establish a population within a corridor to use it. Meanwhile it would be prudent, where possible, to conserve corridors of sufficient width to contain some core habitat.

Do corridors function at a landscape scale?

It is difficult to conduct experimental manipulations at the large spatial scales that are the traditional focus of landscape ecology (Johnson 1992). The studies we have are correlative. Corridors have been related to the distribution of species on a landscape scale. Askins *et al.* (1987) found that forest interior birds in Connecticut were less often found in patches where there was little surrounding forest. Van Dorp and Opdam (1987) found that up to 30% of the variation in the number of forest interior bird species in the Netherlands could be accounted for by the density of nearby linear wooded features. They could not, however, distinguish between these features as a corridor or as additional feeding areas for birds found in the woods. Similarly Laan and Verboom (1990) found an effect of nearby woodland on the number of amphibian species found in pools in the Netherlands, but could not distinguish these woodlands as corridors, from their function as habitat. The same confounding of habitat and conduit functions affects Bright *et al.*'s (1992) work on dormouse distribution in Herefordshire woodlands, while Bellamy *et al.*'s (1993) study of birds in English woods was even further confused by not being confined to woodland specialist species.

Clearly more careful studies are needed to confirm the corridor function at the landscape spatial scale.

Metapopulation

The original metapopulation model (and most subsequent models) assumes an effect of isolation that does not change with distance from source (Hastings 1990). In this regard the models are less realistic than the island biogeographic model. Distance effects have been modelled subsequently in simulations (see references in Merriam 1991a), but have not yet been generalised.

Taylor (1990, 1991) and Harrison (1991) reviewed studies where metapopulation processes might be important to local extinction. Some of these studies lacked convincing data (Taylor 1991) and, of the remainder, few seemed to fit the classical metapopulation model, where habitat patches are all much the same size and character and all may act as a source for any of their number. They found three different cases to be common:

1.   mainland-island and source-sink situations (Figure 9) in which persistence depends on one or more extinction-resistant populations (see also Opdam 1991, Thomas & Harrison 1992 and Thomas & Jones 1993);

2.   systems of patches where dispersal is so high that the system is effectively a single extinction-resistant population; and

3.   non-eqilibrium situations in which extinction occurs in the course of a species' overall regional decline.

In the first two cases regional extinction does not occur and in the third it is not a consequence of a metapopulation process. It is this third case that has been described by the biotic collapse, or island biogeographic, theorists, however.

Henderson et al. (1985) and Merriam (1991a) described a metapopulation of the eastern chipmunk (*Tamius striatus*) in Canadian woods, and concluded that corridors would assist survival, but this study did not feature in Taylor's (1991) or Harrison's (1991) reviews. The information on this study in Henderson et al. (1985) is unfortunately insufficient to place it into Harrison's categories.

Harrison (1991) included in the second category den Boer's (1981) study which has often been cited in the context of connectivity and in the third category one of the classical faunal collapse studies (Brown 1971). Harrison (1991) and Taylor (1991) found no bird studies to discuss, in agreement with Opdam (1991) who reported a serious shortage of good bird studies on habitat patches.

Corridors could aid species conservation on the "islands" or "sinks", but are clearly unnecessary for the "mainland" or "source". They would help little where dispersal is high. They may help where a species is in regional decline because of habitat fragmentation, and especially where no large fragments remain, but not where the decline has some other cause.

Can corridors link areas together to provide for sensitive species?

An argument for corridors is that, by linking up small areas to create larger ones, species that require large areas will be able to survive. Corridors may achieve this linkage without requiring much additional habitat and thus the single large or several small (SLOSS) question becomes relevant.

The examination of the concept of sensitive species has largely been through a protracted debate over the SLOSS problem, that continues to generate many scientific papers (Burkey 1989). Most of the debate has concerned recolonisation.

Hooper (1971) foreshadowed a criticism of the SLOSS criterion when he advocated the preservation of a series of small reserves, each of a different habitat type. MacArthur & Wilson's theory does not provide a prediction to resolve the SLOSS problem (Simberloff & Abele 1976; Abele & Connor 1979; Burgman et al. 1988) and the evidence from faunal collapse is badly flawed (Boecklen & Simberloff 1986); the criterion depends rather on the proposition that there are sensitive species that require large areas and, as a consequence of this, that there is a considerable similarity in the species complement of small habitat patches (Higgs & Usher 1980). The SLOSS deductions from metapopulation theory have yet to be subject to critical scrutiny, but one may observe that these theories too may not describe many real situations at all well and assume habitat homogeneity (see the previous section).
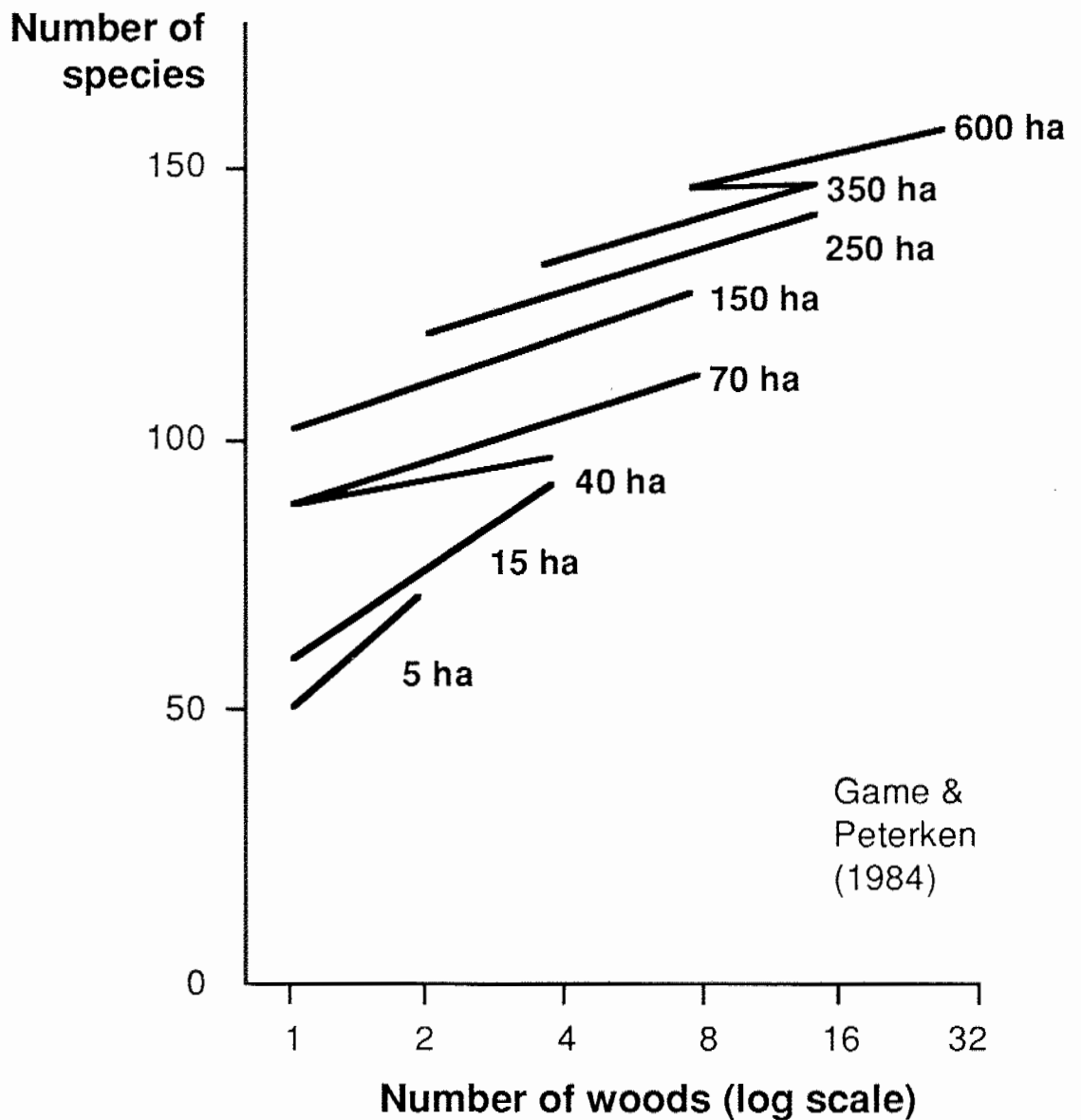
The empirical evidence has been reviewed by Simberloff and Abele (1982) (see also Kitchener et al. 1980 and Hart & Horwitz 1991), who found that species number in one large patch rarely exceeded that in several small ones of the same total area (Figure 19).

Turning to studies of individual sensitive species we find that the proposition that they are found solely in large patches of habitat often disguises a departure from the SLOSS comparison; the authors do not have data from sufficient small patches to sum to the same area as the large one (Simberloff & Gotelli 1984). Much of the evidence for large area specialist species comes from correlative studies, for which it is notoriously difficult to be sure that it is area, rather than some other factor that may vary with area, which is the causative factor (see area and habitat diversity above).

Figure 19 Comparing differing numbers of woodland patches adding up to the same total area shows that there is some small advantage in taking several small patches rather than a few large ones and that more species are found where the total area conserved is high, regardless of how that total is subdivided (after Game & Peterken 1984).

Woodland herbs in central Lincolnshire

Number of species

150

100

50

0

600 ha

350 ha

250 ha

150 ha

70 ha

40 ha

15 ha

5 ha

Game & Peterken (1984)

1   2   4   8   16   32

Number of woods (log scale)

Another problem is that some authors use data from species which clearly do not match the model. For example Wilcove *et al.* (1986) illustrated the incidence of great spotted woodpeckers in British woodlands of differing size, apparently because it is one of the few species in Moore and Hooper (1975) to give a convincingly steep and smooth incidence curve (see Figure 20). However this species does not find the gaps between British woods an effective barrier to dispersal. Whitcomb *et al.* (1981) studied neotropical migrant birds in eastern USA deciduous forest fragments and Hart & Horwitz (1991) analysed bird species on Swedish peat bogs, but all these are migratory species which recolonise each year and surely therefore do not fit either the metapopulation or island biogeography model. Corridors do not help such species to move (Lynch & Wigham 1984).

Figure 20 Imposition of 95% confidence bars onto the incidence of great spotted woodpeckers in British woods of different sizes shows that the curve may be less smooth than implied by the data points alone (data recalculated from Moore & Hooper 1975).
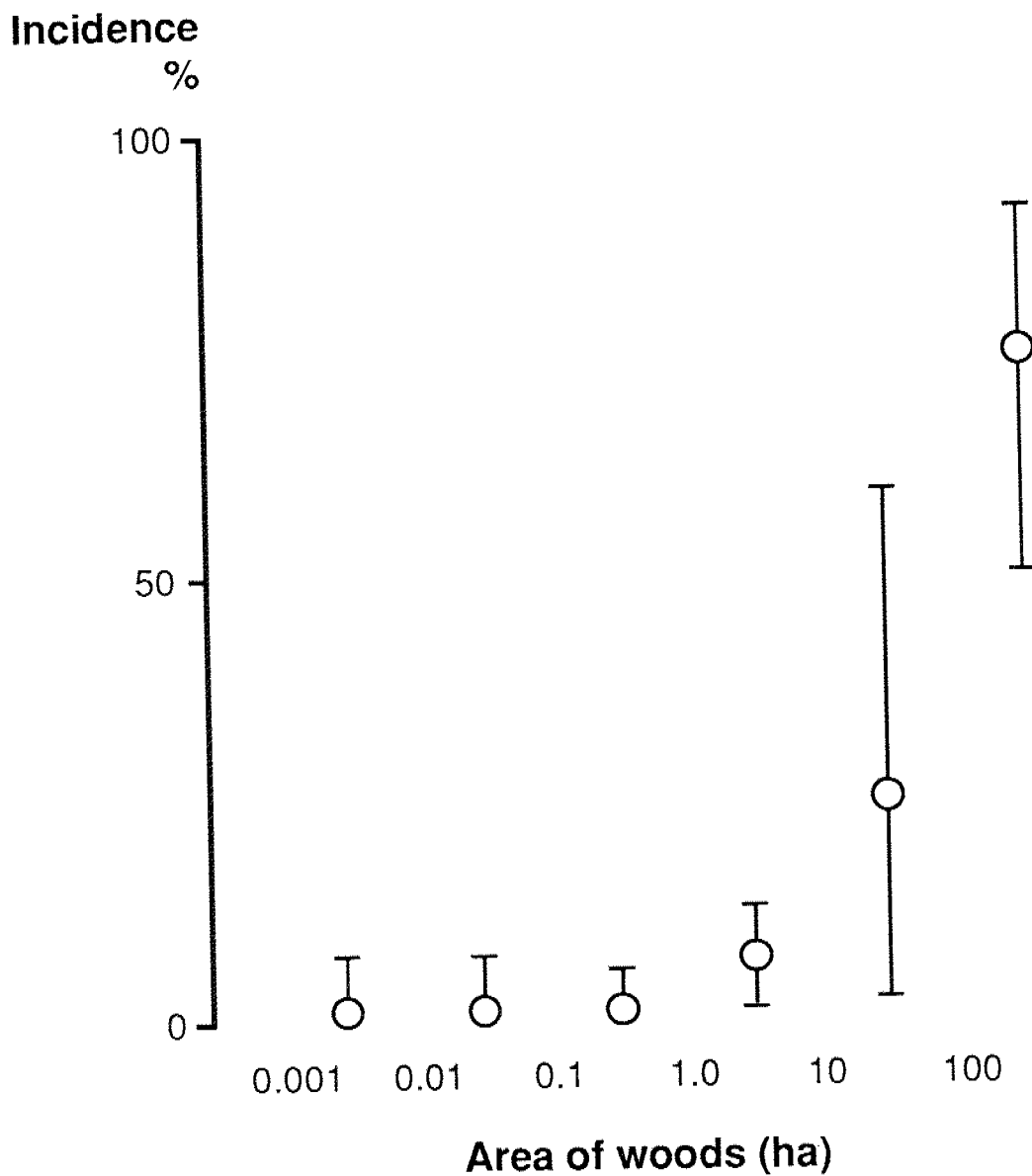
In practice, too, the habitat homogeneity assumption may not hold (Diamond & May 1976); small patches are spread over a greater geographic area and so may represent a greater variety of habitats (Kitchener et al. 1980; Simberloff & Abele 1982; Game & Peterken 1984; Boecklen & Simberloff 1986; Soule & Simberloff 1986). Such regional variation in habitat type is suggested by Pimm's (1986) observation that, though the area of forest in the eastern USA has been reduced to 5% of its former extent, only 2% (not the 50% predicted from the species-area relation) of its bird species have been lost from all causes. Thus recent theoretical examination of the SLOSS question (Burkey 1989), in still assuming habitat homogeneity, may be describing an extreme situation, rarely approximated in the real world.

Habitat diversity may be the reason for Simberloff and Abele's findings, but it is also an adequate reason to question uncritical adherence to the advice of the early 70's (Diamond 1974, 1975; IUCN 1980); each case should be examined on its merits, and often several small patches are to be preferred to a single large patch of the same total area (Soule & Simberloff 1986; Boecklen & Simberloff 1986; Burgman et al. 1988). Recent authors (eg Shafer 1990) continue to rely on indirect and equivocal evidence to support the single large recommendation. Few autecological studies have established that sensitive species in fact require large patches of habitat, beyond the obvious minimum requirement to sustain a breeding population.

Thus corridors may be needed to link small habitat fragments together, where otherwise the subject species could not achieve a viable population on the habitat patches available. Also a network of corridors and patches might provide a single large area which has the diversity of habitat normally associated with several small areas. In this context the corridor question therefore remains open. This is especially so since linking patches with corridors is a special case that may provide linking habitat while resulting in little increase in total habitat area.

The detailed examination and controversy over the SLOSS question has diverted attention away from a more secure finding not always appreciated by those examining the question; more species are found where the total area of habitat is large, regardless of how it is subdivided (Figure 19, Forman et al. 1976; McLellan 1979; Simberloff & Gotelli 1984; Simberloff & Abele 1984; Game & Peterken 1984; Dawson 1984; Shaffer & Samson 1985; Haila 1986). This too has an implication for the provision of corridors; wide corridors add appreciably to the area of patches they adjoin, so that a network with wide corridors conserves significantly more habitat than one without.

Which species should be sensitive?

The various ideas on which species may be candidates for local extinction or be poor colonists, and thus potential users of corridors, were covered in the first half of this review. A recent review and study of risks of extinction (Pimm et al. 1988) confirmed that low population is the major correlate of extinction and that variable population also has an influence. However their work on bird data from British offshore islands was flawed, so that their detailed conclusions on the effects of body size on the risk of extinction are in some doubt. They did not consider the rescue effect, and their analysis suffered from the exclusion of some species, failure to present confidence limits, and regression using dependent and independent variables which were both subject to the same measurement errors.

The ideas on the risk of extinction have therefore not advanced much from the time of MacArthur and Wilson. Some of the species and taxa which are considered to be "sensitive" are indeed habitat specialists (Bennett 1991a), so that their requirements will need to be met in the design of a reserve network. The ideas on susceptibility are well summarised with reference to Southwood's (1977) "Habitat templet".

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Methodology and alternatives

Applications of theories have been criticised by Connor and Simberloff (1978), Simberloff and Abele (1976), McCoy (1982), Haila et al. (1982), Haila (1986), Verner (1986), Boecklen and Simberloff (1986), Van Dorp and Opdam (1987), Burgman et al. (1988) and Bierregaard (1990). They considered that a fashionable bout of studies fitted their data to the theories, often with scant regard for the relevance of the theory to the study, the validity of the theory, confounding factors, the need for appropriate null hypotheses, the necessity to compare equally complete lists of resident species only, adequate sample-sizes, or statistical confidence intervals. Such problems affect most work in this field. The critics suggest that autecological studies will prove more valuable in guiding the preservation of species than will application of general principles (Kitchener 1982; Simberloff & Abele 1984; Soule & Simberloff 1986). Much of the recent work in this field has concentrated on metapopulation models of single species in response to this suggestion.

Opdam (1990) agreed with these critics, observing also that few studies examined the assumptions that, apart from area and isolation, all other things are equal, and that the populations are in balance with the landscape, rather than reflecting their differing histories.

Another difficulty has been that many studies have (and still do: Bellamy et al. 1993) lumped together species with quite different requirements for habitat and area and which find the gaps between habitat patches a barrier to greatly differing degrees (Simberloff & Gotelli 1984; Opdam 1991). The findings of such studies do not inform the debate. Some studies have broken with the requirement that the subject species are specialised for the habitat of the patches and rarely use that of the barriers between, for example in dealing with long distance migrants, which obviously are not impeded by small gaps (Willis 1974; Butcher et al. 1981; van Dorp & Opdam 1987). Any biogeographic patterns found in such studies should not be forced into a theory that assumes movement between patches to be difficult (Haila 1993).

Much of the work has been on birds and in forested habitats (Abele & Connor 1979; Wilcove et al. 1986; Verner 1986; Opdam 1991; Bellamy et al. 1993). This may limit the applicability of the findings to other taxa and habitats.

Recent theoretical developments are also subject to problems. For example the application of metapopulation theory by Wilcove et al. (1986) depends upon particular assumptions about the incidence of species with isolation or area and ignores habitat diversity, and their model does not appear to have been tested against departures from these assumptions. It is strange therefore to find recent papers (Goldstein-Golding 1991; Harris & Scheck 1991) repeating essentially the same recommendations for reserve design as were promulgated in the early 70s, without adequate reference to the critical re-examination and refinement these criteria have received in the last 20 years.

Such problems as are discussed in the preceding paragraphs mean that studies and recommendations require critical examination, but this does not mean that general principles are without utility. Such principles, even if imprecise, are of relevance to the design of reserves now, before the completion of the multitude of autecological studies that would be required to provide detailed recommendations for all species of concern in all possible habitats (Shafer 1990, Soule & Gilpin 1991; Merriam 1991b). Hobbs and Hopkins (1991) reach a similar conclusion in the context of global warming. The point is whether design principles are soundly based, rather than whether they give any particular precision. The review, therefore concentrates on criticisms of the applicability of the theoretical models rather than the precision of their estimates.