Selective loss of sensitive species

MacArthur and Wilson (1967) suggested that, if there is a large difference in species' dispersal abilities, large islands should hold more species than two smaller islands of the same area - the SLOSS (single large or several small) question. Diamond (1973, 1974), Terborgh (1974), Diamond and May (1976), Forman *et al.* (1976), Davis and Glick (1978), Terborgh *et al.* (1978), Faaborg (1979) and Blondel (1980) extended this to observe that small patches tend all to preserve the same set of "catholic" species: "rats, cockroaches, sparrows". Their proposition was that such species have a good colonising ability and maintain good populations, and thus are both unlikely to go extinct and likely to recolonise should they do so.

> "That is those species most in need of protection were differentially lost..." (Diamond and May 1976).

Size is related to corridors through this selective loss of sensitive species, as very effective corridors may turn a set of small areas into one large one where the sensitive species would be safe (Noss 1987). Burkey (1989) re-examined the SLOSS question with a stochastic simulation model which, like MacArthur and Wilson's model, assumed habitat homogeneity. He suggested that, for a given degree of fragmentation, corridors may be very useful, but there comes a point when additional corridors are of little avail, so that efforts should be put to other ends. However, as fragmentation was increased, the population needed a higher dispersal rate to survive, and hence it required more or better corridors.

The characteristics of sensitive species are of interest because they may allow predictions of which species may require corridors. MacArthur & Wilson (1963) observed that rare species should encounter the highest extinction rates on islands. Their proposition was simply that the small population was more susceptible to some chance factor or disturbance; they were clear that this process could be non-interactive (Wilson 1969). Others seem to consider that the area effect is due largely or solely to interactions between species, such as competition or predation (Wright & Hubbell 1983).

MacArthur and Wilson's (1967) view that species with low populations are sensitive to extinction has been supported subsequently by Terborgh and Winter (1980), Schoener and Schoener (1983), Goodman (1987), Shaffer (1987) and Pimm *et al.* (1988). These authors see little chance of extinction from ordinary stochastic changes of populations numbering more than a few tens or hundreds. Local extinctions have been attributed to three sources of variation (stochasticity): population processes (birth, death and sex ratio); the environment; and genetic factors, as well as more extreme, and less predictable, natural catastrophes (Terborgh & Winter 1980; Wright & Hubbell 1983; Merriam & Wegner 1992; Harrison 1991). Island biogeography and most metapopulation theories deal with population and environmental variation only.

Brown (1971) speculated on the characteristics of mammal species that may make they susceptible to the fragmentation of their habitat. Since then there have been many similar speculations about animals.

Faaborg (1979) considered that species with a small geographic range are susceptible. Others have identified particular trophic roles with susceptibility. Brown (1971), Abele and Connor (1979) and Bennett (1991a) thought that species with a restricted habitat ("specialists") are susceptible, Diamond (1974) adding that the food may be seasonal or patchy in occurrence. Brown (1971), Abele and Connor (1979), Wilcox (1980), and Wilcove *et al.* (1986) concluded that large herbivores and top carnivores were susceptible. Margules and Usher (1981) agreed that species at high trophic levels are susceptible. For birds, Terborgh (1974) and Karr (1982) thought that those that foraged or nested on the tropical forest floor were most susceptible. A long series of authors (see references in Wilcove and Robinson 1990) considered neotropical migrant birds in eastern USA deciduous forests to be susceptible.

Large species were thought to be susceptible by Brown (1971), Terborgh (1974), Abele and Connor (1979) and Bennett (1990) among many others.

In a taxonomic comparison, Wilcox (1980) considered that most mammals and reptiles should be more susceptible than birds and bats, where the ability to fly means that they can cross gaps readily. Despite this Wilcox (1980) and Wilcove *et al.* (1986) suggested that birds and mammals are susceptible, by virtue of their low population densities.

Most of these speculations on animal susceptibility deal with features such as habitat, food, or body size, which may be correlated with population size and thus may merely reflect the effect of low populations. Diamond (1974) for example was explicit when associating birds with large territory requirements with low populations.

A second factor, however, is the variability of the population size; Terborgh and Winter (1980), den Boer (1981, 1990) and Karr (1982b) considered that rarity is not a good predictor of extinction probability, but that population variability is. Some invertebrates may fluctuate in numbers much more than do vertebrates and so be more likely to go to extinction (den Boer 1990).

Pimm *et al.* (1988) reviewed existing mathematical models of susceptibility which extend the original MacArthur-Wilson proposition. Apart from the size and variability of the population, they added short-lived species and those with a low reproductive potential (intrinsic rate of increase) to the susceptible categories. They tested the predictions with data on birds of British offshore islands and confirmed that population size and variability are both important. Length of life and reproductive potential both correlate with body size and they concluded that, below a population size of about seven individuals, small-bodied species are most susceptible. Above this size large-bodies species are susceptible.

Most of these theories focused on the risk of extinction, but some workers on animals examined also the other factor that influences survival on habitat fragments - dispersal ability. Warren and Key (1991) and den Boer (1990) considered that many of Europe's threatened woodland insects have very limited powers of dispersal and that this should be a major consideration when considering a conservation strategy. Turin and den Boer (1988) found that carabid beetle species which had declined over the previous century were those that could not fly and inhabited long-standing habitats.

A related concept is the ancient woodland indicator species of British plants (Peterken 1974) which appear to have poor dispersal powers and which Pollard *et al.* (1974) found to invade hedgerows very slowly; Macdonald and Smith (1990) suggested that these have either poor dispersability or very specific requirements for establishment. Verkaar (1990) suggested that some grassland species share this poor colonising ability and that such species have neither a persistent seed bank nor good dispersability of seeds. He considered these sensitive plants to be those of continuously distributed (plagio) climax ecosystems which have been subject to selection for survival rather than reproduction ("K" selection). Hodgson and Grime (1990) reached a similar conclusion in their review of the dispersal mechanisms of British higher plants; species from impermanent or disturbed habitats tend to have well-defined mechanisms of dispersal in space and/or time, while those from more stable habitats do not. They suggested that the sensitive species commonly have persistent juveniles. Middleton and Merriam (1983) considered many north temperate woodland herbs to be clonal perennials with most of their biomass concentrated underground.

Susceptibility may be summarised in relation to MacArthur and Wilson's (1967) "r-K" spectrum, Southwood's (1977) "Habitat templet" or den Boer's (1990) "founding hypothesis of dispersal". In the context of recolonisation, size threshold or climate change, the species at risk are at the "K" end of the spectrum: those associated with natural habitats of long durational stability. For such species, selection favours competitive ability and longevity, rather than reproductive potential and ability to disperse. In terms of the templet, their natural habitats tend towards homogeneity in space and are climax (or plagio-climax), rather than seral. These factors mean that the species have evolved large size, longevity, decreased fecundity and a poor ability (or behaviour) to disperse widely, but fragmentation of their habitat or climate change has introduced a need for dispersal.

Some susceptible insects appear to be an exception to this rule, by being characteristic of successional habitats (Thomas *et al.* 1992; Webb 1993). The suggestion is that, over centuries of management, this habitat had always been available nearby, so that it was in fact of long durational stability, but that the lapse of management, or fragmentation, has changed this.

In the context of migration many of the attributes of the species are the same as those above, but the habitats vary seasonally in their suitability and so the species are nearer the "r" end of the spectrum.

Few authors have applied these ideas from ecological theory to reach general conclusions on which species may require corridors. Bennett (1991a), however, considers them to be:

1. specialists for a particular, and fragmented, habitat; and

2. "core", rather than "edge" species.

He concludes that neither group is expected to find corridors easy to move through.

Soule and Gilpin (1991) thought large and uncommon species may require corridors for recolonisation. Hobbs and Hopkins (1991) thought those of restricted distribution might require them to avoid the effects of global warming. Harris and Scheck (1991) considered that individual animals with a large home range may require corridors to traverse the necessary minimum area for survival. L.M. Cook (pers. comm.) suggested that some arboreal primates may be particularly in need of corridors to find their seasonally variable food. This review would extend these scattered thoughts by applying Southwood's "habitat templet" as indicated above.

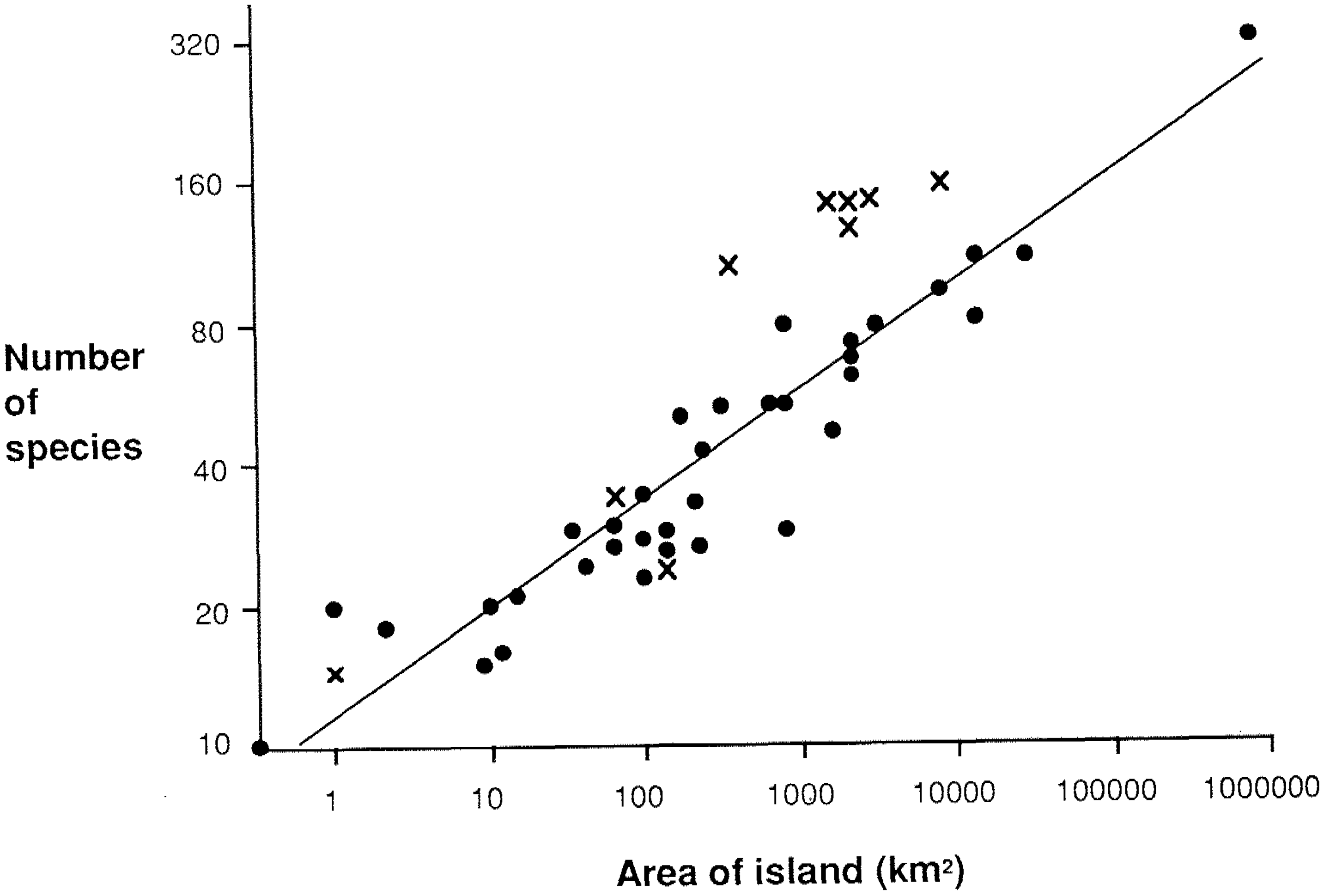
Other factors that may prevent particular species from surviving in small patches are discussed under the "edge effect" below.

The speed of Relaxation back to equilibrium

A slow relaxation to equilibrium after the fragmentation of the habitat (Figure 7) means that many species may be doomed to extinction on the fragments. Corridors are supposed to reduce the effects of relaxation by raising the effective size of habitat patches; large patches are supposed to lose fewer species than do small ones. The question of just when a corridor is good enough to make two patches effectively into one must be answered for each species individually.

Relaxation is supposed to be quicker on small than on large patches, to begin fast and later slow down and to involve the loss of sensitive species. The idea that relaxation generally has far to go and therefore that present-day populations of a species may not be viable is still current (Harris & Scheck 1991).

Figure 7 The number of bird species on islands off New Guinea. The line is fitted through the islands presumed to be at equilibrium (O). The number of species on islands created by rising sea levels (X) is supposed to be above equilibrium, as relaxation is not yet complete (after Diamond 1974).



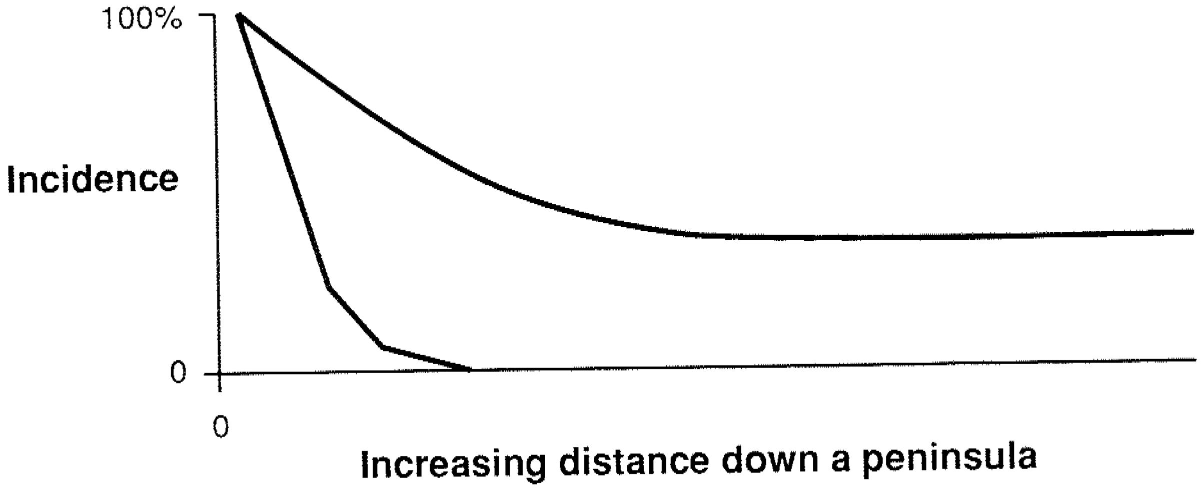
The peninsular effect

Simpson (1964) described a decline in species richness of North American mammals with distance away from the main land mass along a peninsula and suggested that this may be caused by colonisation and extinction on a series of habitat patches along the peninsula. This was brought into the criteria for reserve design by the suggestion that long narrow reserves (peninsulas) will be less rich than compact ones (the continental land mass).

Theory to model the peninsular effect was developed by Taylor and Regal (1978) and extended by Gilpin (1981). The theory has not been applied to corridors, although all that is required to do so is a shift downwards in spatial scale, to make it applicable to smaller features, by considering them to be peninsulas of terrestrial habitat in a sea of less hospitable terrestrial habitat. Where there is a target patch at the end of the corridor, it is analogous to the tip of the peninsula in the theory. Alternative explanations of the peninsula effect (for example that narrow peninsulas suffer from an edge effect) may also be applicable to corridors.

In Gilpin's model species fall into one of two classes: either declining exponentially to zero occurrence with distance down the peninsula from the source, or declining to a plateau of constant incidence (Figure 8). The latter group of species could use the corridor as a conduit, whereas the former could do so only were its length such that incidence does not decline to zero before the target area is reached. Where a corridor is short relative to the dispersal range of a species, Gilpin's model reduces to a limiting case where the only influences left are the probability of entering the corridor and of mortality within it.

Figure 8 The two patterns of incidence of a species down a peninsula, according to Taylor & Regal (1978) and Gilpin (1981). In (a) the species disperses poorly and declines exponentially to zero occurrence with distance whereas in (b) a species with better dispersal ability declines to a plateau of constant incidence.



Metapopulation

The island biogeographic approach was developed from a theory that describes species richness at an equilibrium state on habitat patches, with a "mainland" source for immigration. Many of the seminal works in this field have been on birds of tropical oceanic islands. In contrast, metapopulation theory deals with individual species or simple interactions between a few species and was developed first to describe populations of invertebrates inhabiting small-scale habitat mosaics (Hanski 1989).

The "metapopulation" concept (Levins 1970; Hanski 1989) is a formal mathematical model of an idea first propounded by Andrewartha and Birch (1954); that the numbers of any given species may fluctuate greatly in small patches of habitat, to the extent that, while a species may go extinct on some patches, in a large collection of patches it survives because it re-invades places where extinction has occurred from the other places where it has not. The "populations" occupy individual patches and the metapopulation the whole system of patches. Again the habitat homogeneity assumption is involved; without homogeneity there is no guarantee that recolonisation is available from a nearby patch, nor that the spaces between patches are barriers to dispersal. The rate of establishment of new populations has to exceed the rate of local extinctions for the metapopulation to survive.

Most models assume that all occupied patches are equal sources of recolonisation, ie that there are no distance effects. Comins and Noble (1985) however describe a model in which recolonisation only of adjacent patches permits metapopulation survival. Hanski (1989) stressed that distance may have a major effect on metapopulations; short distances between patches increase the recolonisation rate, but also increase the chance that fluctuations on all patches are correlated. The former tends to increase survival and the latter to decrease it.

"Patch dynamics" (see above) is in fact a metapopulation theory for the special case where the populations occupy contiguous patches and the habitat of the patches comes and goes. Henderson *et al.* (1985) have extended its application to a network of patches and corridors.

The idea behind corridors and close spacing (criterion 3) is that, when a species goes extinct in a patch, it will be replaced rapidly by invasion along the corridor, or across a small gap. Alternatively its population can be supplemented through the corridor so as to avoid extinction in the first place. Species can persist in this way, even if they would go extinct on individual patches (Simberloff & Abele 1976). This "island biogeographic" idea is clearly related to metapopulation theory. Corridors are not necessary for a metapopulation, but movements between patches are (Merriam 1991a).

Although metapopulation theory is almost as old as island biogeography, and it might be better suited to explain the situation where an archipelago of habitat patches acts as a diffuse source of immigrants for any one of their number (Webb and Hopkins 1984), it was only latterly applied to issues of reserve design. den Boer (1981) applied a metapopulation model to invertebrate conservation. Middleton and Merriam (1981) used Andrewartha and Birch's (1954) ideas to account for the behaviour of whitefooted mouse *Peromyscus leucopus* in woodland patches. Gilpin (1980, 1981) and Gilpin and Armstrong (1981) developed the island biogeographic model to deal with individual species, so partially bridging the gap between the two theories. Fahrig and Merriam (1985) developed a metapopulation model of whitefooted mouse populations in woodlands where immigration enhanced population survival. Wilcox and Murphy (1985) reiterated the biotic collapse recommendations, using metapopulation, rather than island biogeographic, models. McLellan *et al.* (1986) applied a metapopulation model to describe an archipelago of habitat patches, and Opdam (1987) and Merriam (1988) applied metapopulation findings to landscape ecology. Merriam (1991a) reviewed several small-scale metapopulation models based upon the populations of small mammals in Canada, as components of a landscape ecology approach (see below). Others have used no explicit model, but clearly describe a metapopulation (Saunders 1989). The word "metapopulation" has now displaced "island biogeography" as the theory cited in most works on habitat fragmentation.

The development of metapopulation theory has led to a resurgence of the debate about the relative merits of single large or several small reserves (SLOSS). Wright and Hubbell's (1983) model of demographic fluctuation did not give a strong preference for either alternative, but Wilcox and Murphy (1985) considered that habitat heterogeneity strongly favoured single large reserves. Wilcove *et al.* (1986) took McLellan *et al.*'s (1986) model to conclude that "even where most of the habitat has already been destroyed, subsequent fragmentation should be minimized, lest a rapid loss of species occur. Furthermore, insularisation can cause extinctions independent of habitat reduction." Similarly Taylor (1991) modelled the incidence of species in habitat patches of differing size to predict that species with large area requirements would never be found in any total area made up solely of small patches. This theory too leads to the recommendation that corridors be used to convert several small patches into fewer large patches.

When genetic effects are modelled, another severe theoretical disadvantage of a metapopulation structure is suggested; Maruyama and Kimura (1980) studied the "genetic effective population size" of metapopulations, to conclude that it can be orders of magnitude less than it is where the same individuals live on a single large habitat patch. This may result in inbreeding depression (Frankel & Soule 1981; Ralls & Ballou 1983). Gilpin (1991) considered this to be a strong reason to prefer single large reserves. However Boecklen (1986) simulated genetic effects in a single large or several small comparison to conclude that subdivided populations are to be preferred; the issue is still open to debate (Saunders *et al.* 1991b).

Subdivision of a single population into a metapopulation may have a different result depending upon whether or not there are important interactions between species; Johnson *et al.* (1992) concluded that subdivision in single-species systems increases the chance of metapopulation extinction, but that in multispecies systems it may promote survival.

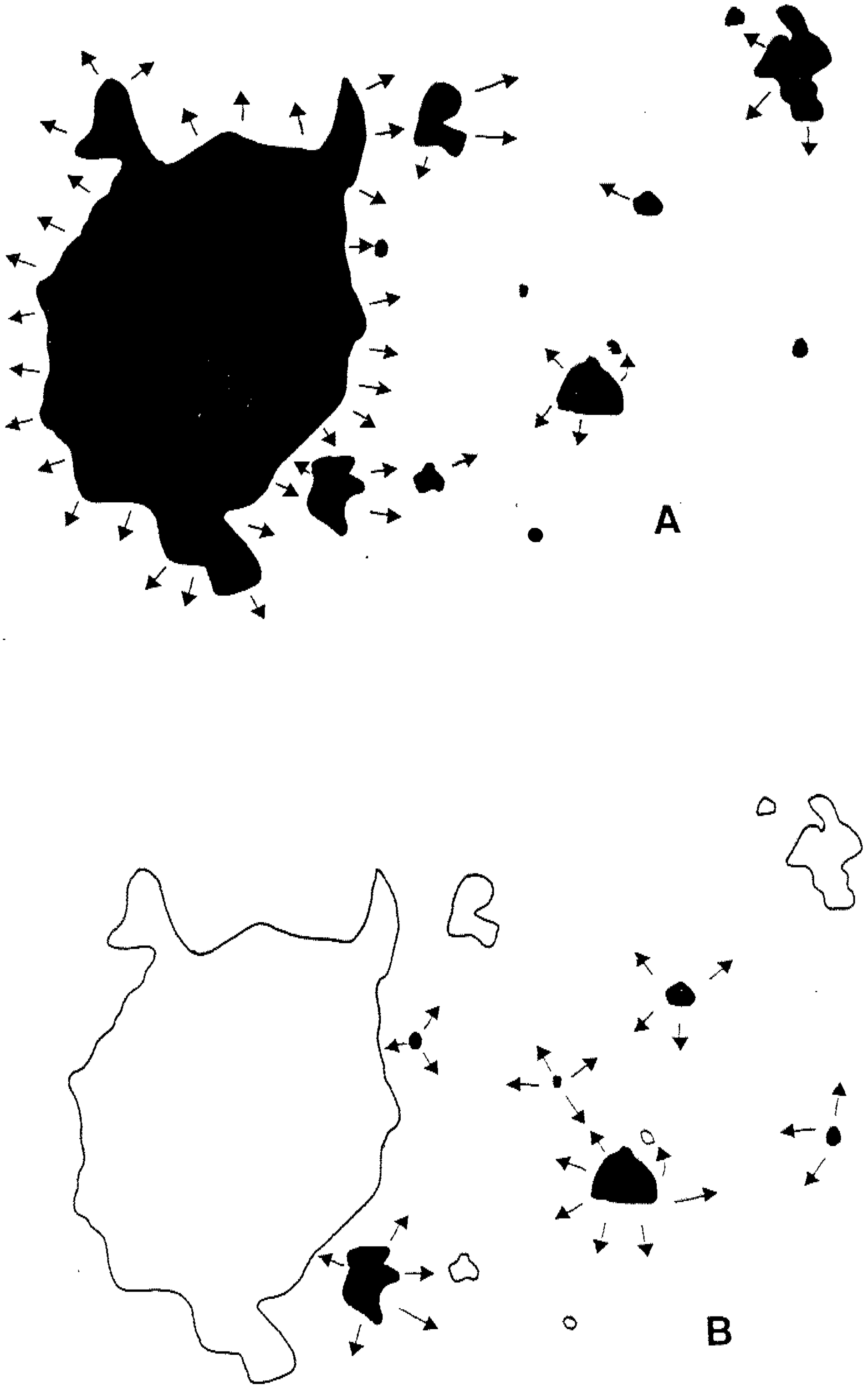
Crowley (1981) examined the mathematical behaviour of a special case of metapopulations: predator-prey interactions, first studied by Huffaker (1958). As is usual in metapopulation models (Hanski 1989, 1991; Taylor 1990), the interacting species survived for longer the more habitat patches there were (an increase by a factor of 10 doubled survival time) and the more random effects there were on the populations of individual patches. However, the probability of survival only increased as dispersal of individuals between patches was increased up to a "low" value of dispersal (around five percent of the population leaving the patch per unit time). After that it decreased with further increases in dispersal because the connection between the patches become so good that population fluctuations in them became synchronous, so increasing the chance that extinctions are synchronous. The initial increase was consistent with the recommendations from island biogeographic theory, but "...the stability and thus the persistence of the whole population may hinge on keeping dispersal rates low enough to avoid complete synchrony" (Crowley 1981).

Metapopulation theory then seems to indicate that corridors should be sufficient to damp stochastic population fluctuations on habitat patches so that local extinction and its drastic genetic effects are rare, but corridors should not be so effective as to synchronize population fluctuations on all habitat patches. It is a moot point whether these two conditions can coexist.

Source and sink

In practice few habitat patches are homogeneous, as assumed in island biogeography and metapopulation theories (Figure 9, Hanski & Gilpin 1991). Rather, some are inferior to others and require replenishment of species from them - the "buffer effect" (Kluyver & Tinbergen 1953; Brown 1969; Fretwell & Lucas 1970; Hanski 1982), "donor habitats" (Hansson 1977), or "source" and "sink" populations (Pulliam 1988; Terborgh & Winter 1980). Pulliam (1988) defined the source as a net exporter of individuals and the sink as a net importer. Organisms occupying a series of habitat patches may occur in a mixture of source and sink populations, each of which may be as much or more influenced by the type and proximity of other patches as by the resources and other conditions of the patch where they are found.

Figure 9 In the MacArthur-Wilson model (a) the mainland and all the smaller patches are of identical habitat, and dispersal occurs equally across the edge of any patch so that large patches are the main sources of dispersal. In contrast, in the source and sink model (b), the sources are of superior habitat, so that they are net exporters of individuals and the sinks are of inferior habitat and are net importers of individuals. This means that small patches can act as significant sources of dispersal to larger patches.



Detailed knowledge of the population processes in the areas concerned is needed else areas may be given quite the wrong value; conserving a sink without its source would lead to local extinction.

Recent papers on corridors have concluded that they may act as population "sinks" and so do more harm than good to the source populations and be of no value to the recipient population (Soule & Gilpin 1991; Panetta 1991; Merriam 1991a). The extreme case described by these authors does not do justice to the range of possible circumstances. The movement between source and sink may be a consequence of population pressure in the source lowering success there to the extent that success is equal or greater in the less populated sink (Pulliam 1988). If good sites in the source are rare and the poor sites in the sink are common, only a small fraction of the population will occur in areas where local reproduction is sufficient to compensate for local mortality. Thus, many natural populations may occur in sinks under circumstances where they may contribute significantly to metapopulation survival and even if the individuals in the sink are not fully self-sustaining, they are members of its community, and contribute to biodiversity there.

Corridors may thus be part of a network that links sources and sinks and where: "the risk of local extinction can be reduced by movement from the more productive patches to supplement growth of populations in less productive, small patches" Merriam (1991b).

Minimum viable population

Recent work on the conservation of threatened species has involved the concept of a "minimum viable population" (Terborgh & Winter 1980; Shaffer 1981, 1987; Shaffer & Sampson 1985; Gilpin & Soule 1986; Burgman *et al.* 1988), an attempt to synthesise the ways in which a low population may avoid extinction. This can be approached empirically or with either a population genetics or a stochastic population model. The models are species-specific and the work seems as yet not to have resulted in general principles that can be applied to corridors, beyond those covered elsewhere in this review (Soule & Simberloff 1986; Saunders *et al.* 1991). An issue illustrated well by this work, however, is that assuring survival is a probabilistic concern which requires decisions on the risk of extinction over a defined time period.

Mortality on the journey

The theories reviewed above all focus on the survival of populations, rather than of individual plants or animals. They do not distinguish between two causes of low rates of colonisation: failure to leave the source and mortality on the journey. Corridor theorists, however, point out that a poor corridor may act as a "lethal cul-de-sac" to a relatively sedentary or a vulnerable species (Soule & Gilpin 1991). The corridor itself is believed to act as a "sink" (see above).

Conversely, however, corridors are often advocated to avoid mortality at a barrier, or in the unfriendly matrix (Grove & Schermeister 1990; Reh & Seitz 1990; Harris & Scheck 1991). The provision of conduits for animals to pass under major roads is often advocated for this reason (Langton 1989; Bennett 1991b; Cox 1993). In the extreme, mortality can prevent effective migration or recolonisation, but it may also have deleterious, if sublethal, effects on the population without actually preventing all movement.

The edge effect

The original development of corridor theory assumed homogeneous habitat, but an important later development incorporated the heterogeneity between the middle and edges of habitat patches. Species that appear to occur only in large patches of habitat may do so because they require special habitats that exist only in the core of a patch, or they suffer competition from species which thrive at the edge of the patch, or in the "ecotone" (Forman & Godron 1981; Mader 1984; Start 1991; Merriam & Wegner 1992). If the habitat of a patch does differ between its edge and core, this violates the homogeneity assumption of the MacArthur-Wilson or metapopulation model (Hart & Horwitz 1991) and may make the source and sink (Pulliam 1988) model more apposite.

Small or narrow patches may not contain any "core" habitat, free from all the physical and biotic influences of the surrounding matrix (Forman & Godron 1981). Only for species that do not perceive any difference between the edge and core of a patch can small patches be considered equivalent to samples from the matrix of larger patches. Many authors consider the size effect in biogeography to be caused, at least in part, by the edge effect (Willis 1984; Goldstein-Golding 1991; Usher 1991).

The reserve design criterion that calls for compact nature reserves, can be derived from this edge effect as well as from the peninsula effect (Usher 1991). The edge of a habitat patch may differ from its core in several respects (Noss 1983); in its microclimate and soil (Start 1991); and it may harbour species which belong to the surrounding habitat, or to the edge itself (Galli *et al.* 1976). This may invalidate comparison of species lists from samples of large homogeneous source habitat with those from habitat patches, unless the edge species are excluded from the comparison (Galli *et al.* 1976; Webb & Hopkins 1984). Edge species may be "weedy" (Panetta & Hopkins 1991), may be predators on, or exclude or compete with core species. This reduces the effective area of the patch (Noss 1983; Williamson 1975; Start 1991) so small habitat patches lose their core species (Dawson 1991).

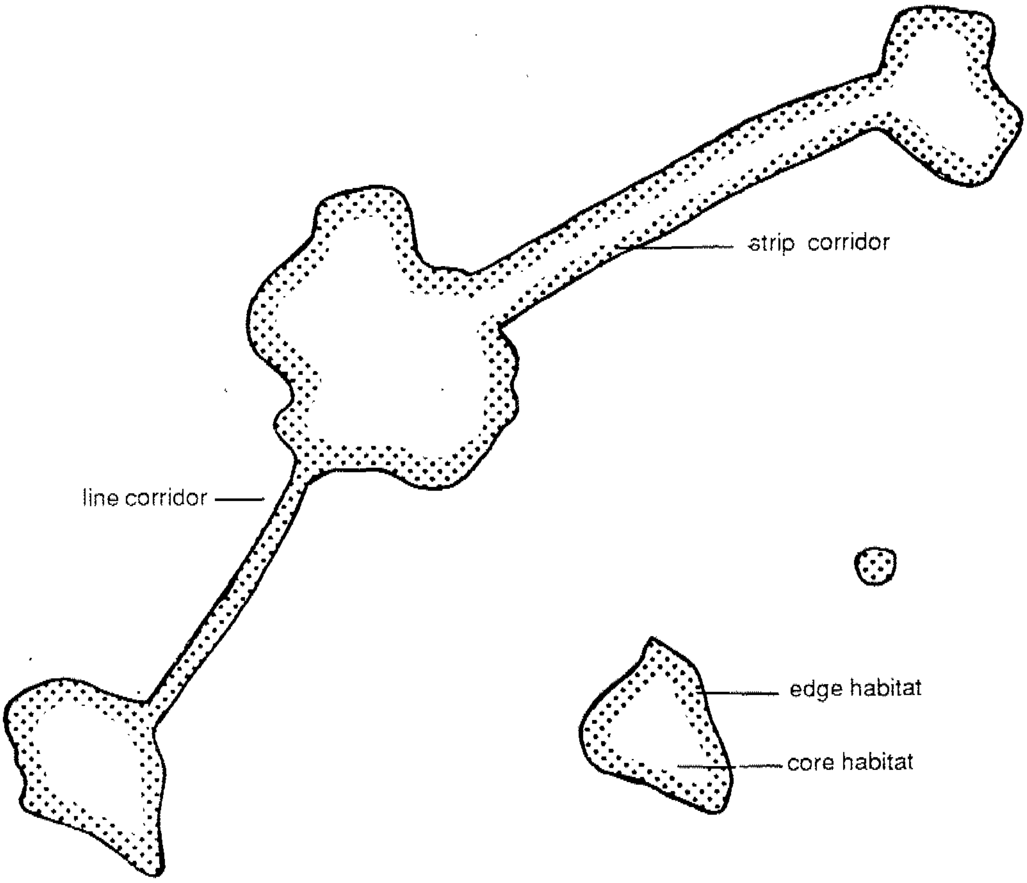
The extent of the effect clearly depends upon the habitat concerned and the taxon of interest. For New Jersey Piedmont forest birds Galli *et al.* (1976) considered plots of less than 0.2 hectares to be entirely edge. Elsewhere the "edge effect" was estimated to vary in width from 12 m to more than 180 m (Goldstein-Golding 1991 and Hansson & Anglestam 1991). Mader (1984) considered that core species were outnumbered by edge species in forest patches in Germany of less than 2 to 5 hectares for carabid beetles and less than 10 hectares for "wandering" spiders.

Edge effects weigh against thin corridors, that may be considered to be very largely, or entirely, edge (Figure 10, "line corridors", Forman & Godron 1981) and hence not suitable for sensitive species to reside in, or pass through (Noss 1987; Soule & Gilpin 1991). Lovejoy *et al.* (1986) and Bridgewater (1987) suggest, however, that corridors may allow motile species an acceptable dispersal route even when they would not reside there. K. Porter (pers. comm.) also suggests that some edges may hold concentrations of food, such as nectar and berries, that serve to lead animals along them.

Blyth (1991) considered that edge effects on corridors may become more significant as climate changes and that their width should therefore be sufficient to guard against this. Effective width may decline with time due to a progressive encroachment by weeds, fire, road building and exotic animals (Noss 1987; Friend 1991).

Thin corridors, therefore, are least suitable for species which are specialists for the habitats found in the core of patches and which need to reside along their length, or which do not find them acceptable habitat to move through.

Figure 10 A "strip corridor" is wide enough to retain some habitat in its core for species that find the edges of habitat patches inhospitable. A "line corridor" is so narrow that it has no such core (after Forman & Godron 1981). For species that respond in this way, the source and sink model is appropriate, as the habitat is less hospitable the smaller the patch.



Minimum area

Individual animals may have a "home range", that is an area over which they range to find its daily needs for food, shelter and a place to breed (Hayne 1949; Brown 1962). Excursions beyond this range are rare or of a dispersal or migratory nature (Bennett 1990). In a given kind of habitat the size of a species' home range varies little between individuals. A defended home range is termed a "territory" (Moffat 1903; Howard 1920; Moore 1957). Animals may be tied down to one place at times (for example to a nest site when breeding), and then another body of theory applies: the theory of "central place foraging". In this it becomes increasingly uneconomic for an animal to forage, the further it goes from its central place (Covich 1976; Stephens & Krebs 1986). Such animals may be likened to a ball attached to a point by an elastic band in that they rarely move far from the central place and return regularly to it.

Corridors, by linking patches of suitable habitat, are sometimes supposed to enable individual animals to find sufficient habitat over which to range to find their needs - the larger the home range of the individual the more corridor links it may need (Sullivan & Shaffer 1975; Simberloff & Cox 1987; Lyle & Quinn 1991).

Migration routes

Whitcomb *et al.* (1977), Diamond (1981), Shafer (1990) and Harris and Scheck (1991) considered that barriers and the fragmentation of habitat jeopardised the migration routes of large herbivores and predators, such as the African ungulates, Arctic caribou and the North American elk. Karr (1982a & b) suggested that many tropical birds need to migrate between places offering different resources, and that fragmentation of their habitat may prevent this. Two other cases involve the migration between clearly distinct habitat types; many amphibia move between breeding, summering and hibernating sites (Wilcove *et al.* 1986; Reh & Seitz 1990) and some insects use different plant species at each stage of their reproductive cycle.

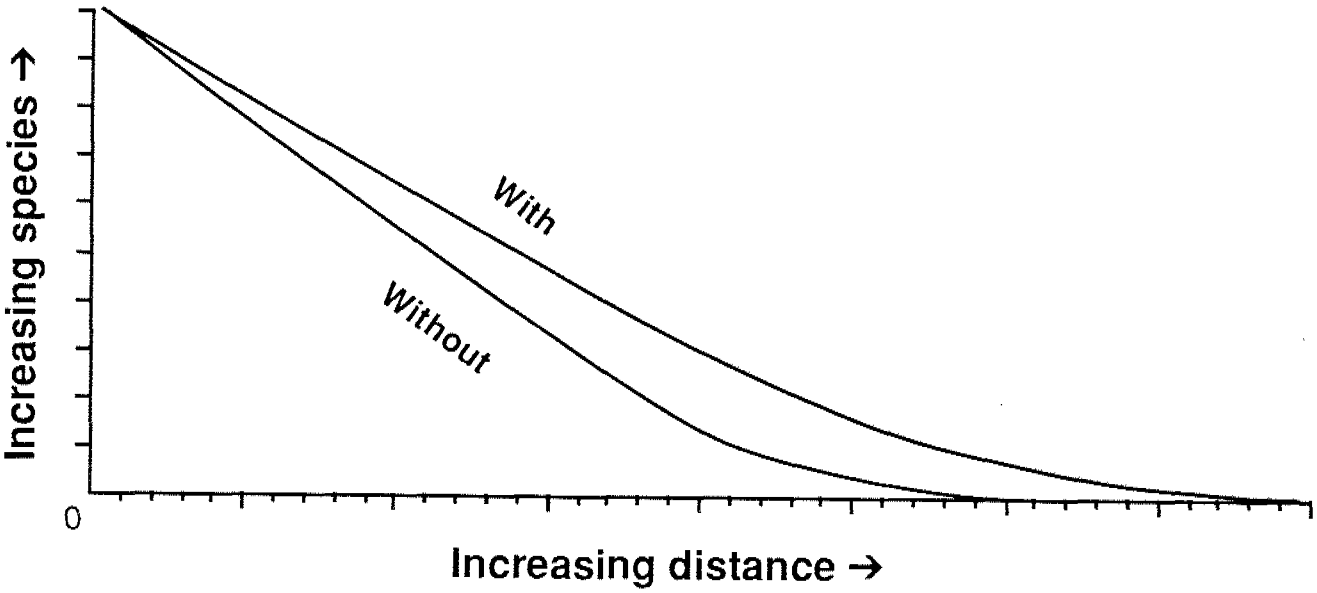
Corridors have been advocated to permit such migrants to continue their movements after the fragmentation of previously continuous habitats.

Stepping stones

Gilpin (1980) built on MacArthur and Wilson's theory by allowing that individual species differ in their ability to survive on small "stepping stone" islands, using a similar model to that for the peninsular effect (see above). He considered that, in the absence of stepping stones, most species would be present all the time on the "target" island or not at all, and his theory suggested that stepping stones would influence very largely a small group of intermediate species: those that sometimes occur on the target island (Figure 11). This is considerably less than the benefit MacArthur and Wilson (1967) predicted from their simpler and less realistic model.

To the extent that this theoretical development applies also to corridors, it suggests that corridors too serve only a small group of species: those with intermediate dispersal powers.

Figure 11 The predicted number of species occurring at various distances from a source patch, with and without a stepping stone patch to assist movement from the source to a target patch, according to Gilpin's (1980) model.



Evolved dispersal powers

Those advocating the preservation or provision of corridors may argue that the natural, primary habitats of most terrestrial areas were better connected before people developed those areas, than they are today. They see corridors as a desirable minimum connection to approach this natural state (Noss 1983, 1987; Adams & Dove 1989; Harris & Scheck 1991; Lyle & Quinn 1991). This implies that each species has evolved a dispersal ability appropriate to past conditions that may not be sufficient to allow the species to cross modern barriers well enough to carry out its natural role in habitat patches.

Others have put forward the contrary view that extensive tracts of habitat without human disturbance were nevertheless composed of a mosaic of habitat types, or subject to periodic disturbance, and species evolved good dispersal powers to cope with this (Middleton & Merriam 1981, 1983; Forman & Godron 1986, "resource patches"; Harrison 1991).

The historical aspect of this theory is difficult to test and its predictions on dispersal ability are covered elsewhere in the review.

Landscape ecology

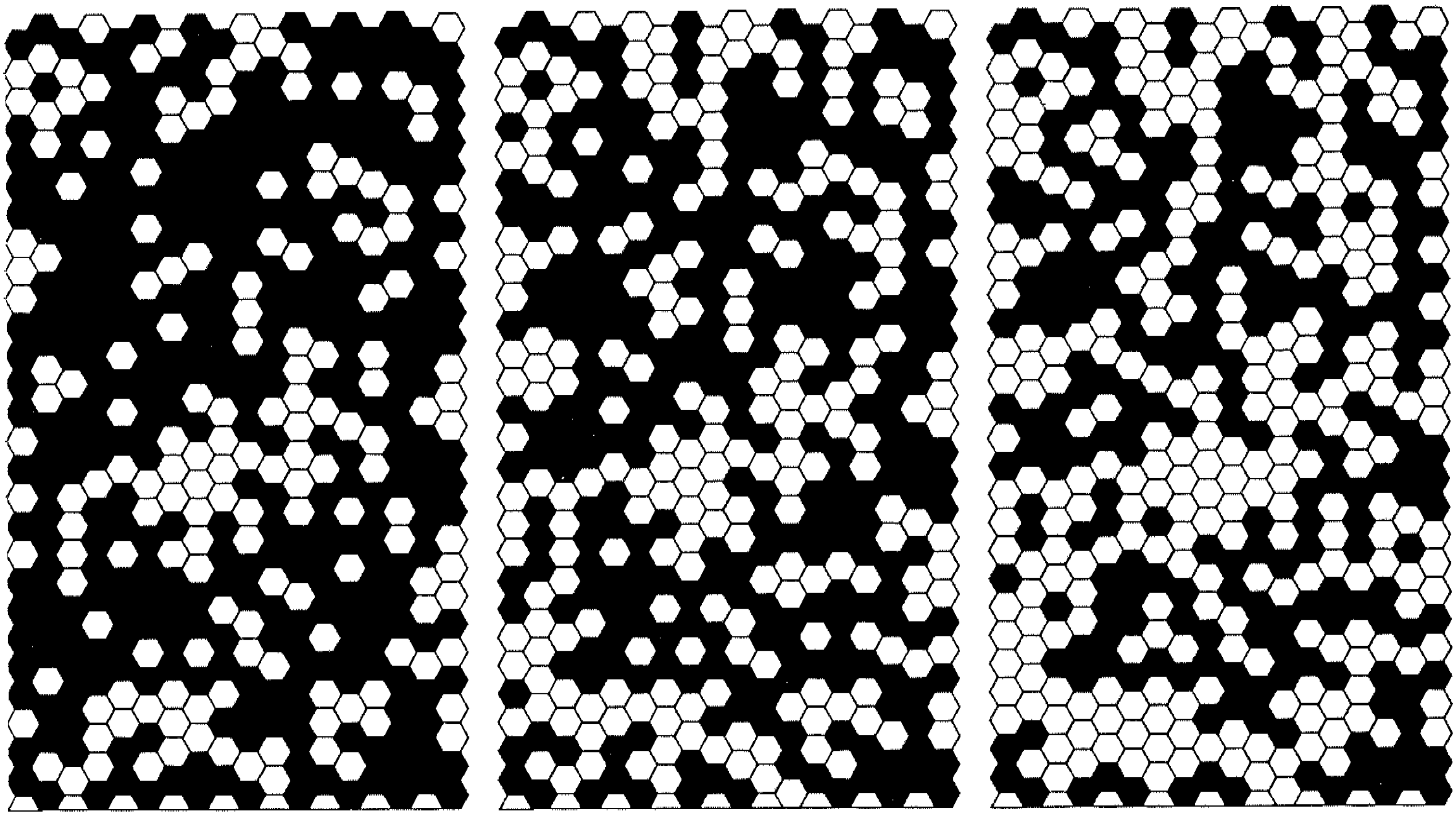
Landscape ecology deals with the effects of landscape (spatial) patterns on ecological processes (Turner 1989). It is an holistic approach (Hansson 1977; Noss 1983; Forman & Godron 1981, 1986; Hansson & Angelstam 1991) bringing together ideas from ecology, biogeography and a structural description of landscape for application particularly to human influences on landscape and its management. It deals with large scale processes such as occur over kilometres rather than tens or hundreds of metres (Forman & Godron 1981). At this scale, a patterning emerges that is not seen at a smaller scale (Turner 1989), and most of the deductions involve an integration of results obtained at small-scales to broad scales.

It is difficult to introduce adequate realism into theoretical models of landscapes, and so simplifying assumptions may be used in "neutral models" of landscape structure to illustrate the way in which small scale pattern can integrate on a landscape scale (Turner 1989; Forman 1991; Johnson *et al.* 1992). Figure 12 illustrates one such model. This shows how the removal of small habitat patches hardly affects regional connectivity at first, but that, as connectivity decreases, the route through the landscape becomes more and more tortuous until a catastrophic decline in connectivity occurs as a critical percentage is approached, after which there are no connections left.

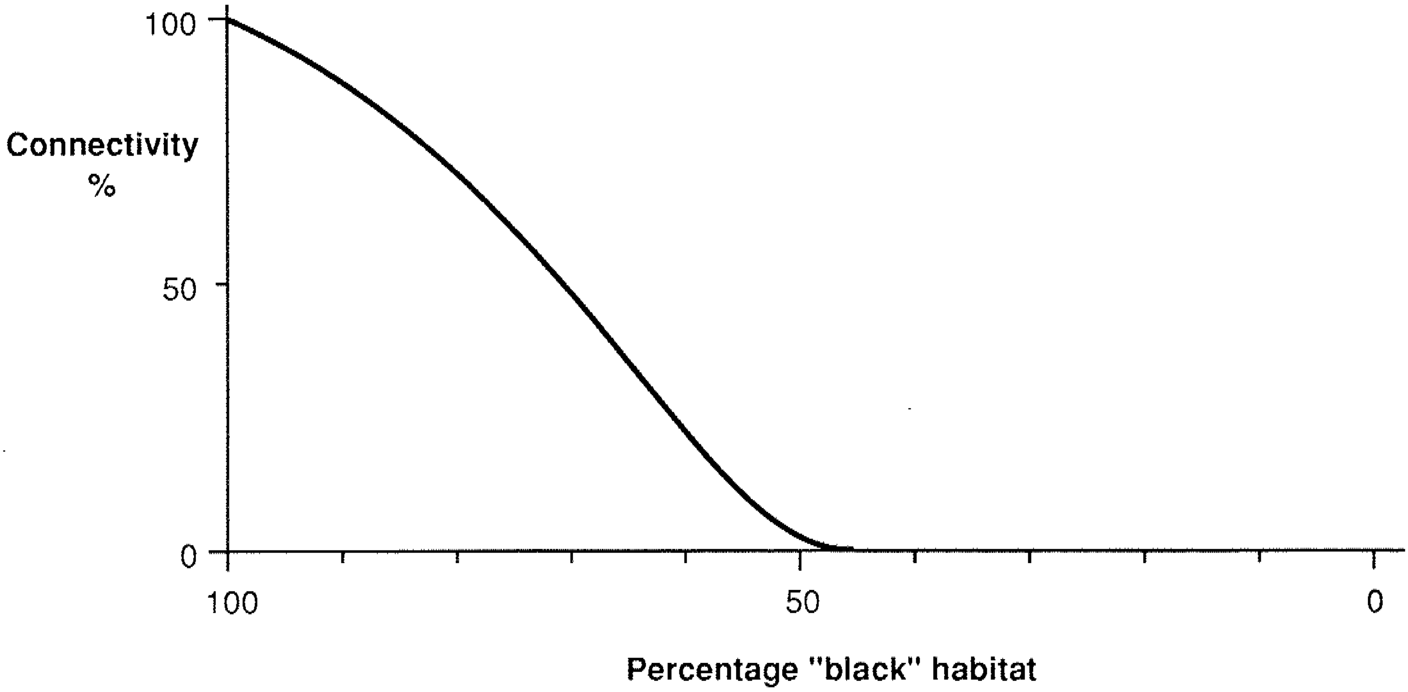
Landscape ecology is largely descriptive, rather than deductive (Hanski & Gilpin 1991) and much of its deductive basis is covered elsewhere in this review; for example it uses ideas from island biogeography, including sensitive species, area effects, relaxation and edge effects, often uncritically (Forman & Godron 1981; Turner 1989) and also from metapopulation theory (Merriam 1991a).

Various measures of isolation had been developed to describe the situation where an archipelago of patches acted as the source of immigrant species for one of their number (Askins *et al.* 1987; Van Dorp & Opdam 1987). Landscape ecologists took up this subject and corridor links (or "connectivity" Forman & Godron 1986; Baudry 1984; Merriam 1984; Noss & Harris 1986) play an important part in landscape ecology recommendations.

Figure 12 A "neutral model" of a landscape composed of equal-sized patches of two different habitat types. Species that occupy the black habitat, but for which the white is a barrier, find the landscape well connected at first (a). When white is substituted for about 25% of black an accelerating loss of connectivity occurs until about 40% has been substituted (b), after which black occurs only as unconnected fragments, which progressively decrease in size (c). Below, an index of connectivity (the percentage of top patches which are connected with the bottom of the landscape) is graphed against the percentage of the landscape which is composed of favourable habitat (black patches).



a 70% black **b 60% black** **c 50% black**



Baudry and Merriam (1988) distinguished connecting landscape elements ("connectiveness") from behaviourally determined species-specific "connectivity", a similar distinction to Webb's (1993) biotope and habitat patches, although Forman's (1991) review of the theoretical basis did not make this distinction. Opdam (1991) used Forman and Godron's (1986) phrase "landscape resistance" to describe the inverse of density of corridors and stepping stones.

Another landscape concept is Mader *et al.*'s (1990) suggestion that linear landscape barriers to movement, such as roads and railways, may reduce the net distances moved by terrestrial animals by leading them off their direct route of travel.

Hansson and Anglestam (1991) considered that the greatest problems with fragmented habitats should be expected for those biological communities that developed in environments which were relatively uniform and stable over time. This parallels the views on sensitive species reviewed above. They also considered that the loss of "keystone" species may lead to loss of other species which depended upon them, and their replacement by less specialised species, so that the community becomes more like that of the surrounding matrix. This again is one of the original island biogeographic views interpreted in a landscape context.

Landscape ecology models may suggest that local extinctions accumulate to regional extinctions and finally global extinctions (Merriam 1991a; Opdam 1991; Merriam & Wegner 1992). Turner (1989), for example, suggested that: "Habitat fragmentation may progress with little effect on a population until the critical pathways of connectivity are disrupted; then, a slight change near a critical threshold can have dramatic consequences for the persistence of the population."

Forman and Godron (1981), Noss and Harris (1986) and Merriam (1991a) suggested therefore that elements of a well-connected landscape mosaic may act as rest stops for species moving between patches, and that corridors may link patches into a network of habitat permitting movement through the landscape. Noss and Harris (1986) recommended retaining a hierarchy of landscape elements at different spatial scales to provide for organisms with differing requirements.

Corridors and barriers

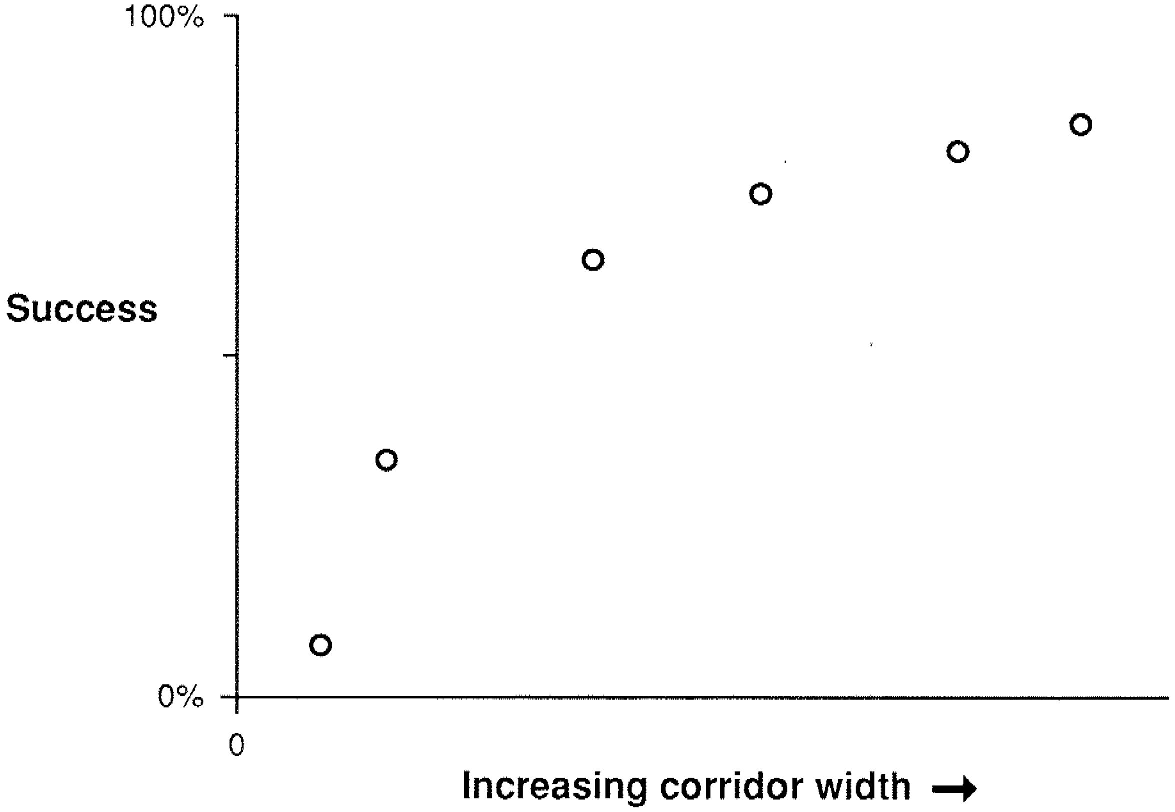
The landscape ecology approach has produced the interesting insight that a corridor link across an inhospitable matrix for one species or group of species could equally constitute a barrier to species which find their habitat in the matrix (Forman & Godron 1981; Adams & Dove 1989; Verkaar 1990; Woiwod & Thomas 1993). For example, in Figure 12, a landscape that is well connected for the black habitat has isolated fragments of the white. Many writers on corridors have as their model a natural habitat, subject to fragmentation by human development and, in this situation, the species to be conserved are those of the natural habitat, not the developed land (Harrison & Scheck 1991; Saunders & Hobbs 1991b). However, in some situations, such as lowland Europe, development took place so long ago that no genuinely natural habitat remains. Here there may be no such clear guide to the habitats or species to be conserved.

Corridor theory

This review so far has shown that there is no comprehensive theory of the conduit function of corridors but quite enough theoretical basis, albeit scattered, to show that they may be worthy of critical examination.

Soule & Gilpin (1991) described the preliminary results of a computer simulation of movement of individual animals through corridors. This described movements and mortality only and suggested that the optimal width would depend upon how fast the species moves and how wide and adverse it finds the edge habitat. Wide corridors were better than narrow ones (Figure 13). Their simulations treated the matrix habitat outside the corridor as always lethal to the animal and modelled a variety of animal behaviour. They found that straight corridors were superior to crooked ones and funnel shapes inferior to parallel-sided corridors. Despite their claim that some simulations were of "relatively intelligent animals", in fact the rules they employed for movement were very rudimentary; Johnson *et al.* (1992) found that such simple rules consistently underestimate real movement ability. Soule and Gilpin (1991) did not model plant dispersal, nor surprisingly did they refer to Gilpin's earlier (1980, 1981) theoretical treatment of stepping stones and peninsulas.

Figure 13 The effect of the width of a corridor on the success with which animals use it for movement, after simulations by Soule & Gilpin (1991).



Soule and Gilpin (1991) also provided a useful checklist of factors that may affect corridor capacity for animals. These include features of the corridor itself: its dimensionality and patchiness, and the type, diversity and quantity of its habitat. They also included aspects of the target animal species: its mortality in the edges and along the corridor; the rate, timing and nature of its movement; its life history stage and interactions with animals of the same and other species.

Merriam and co-workers, reviewed in Merriam (1991a), have made metapopulation models of patches connected by corridors that successfully reproduce details of whitefooted mouse population processes. These are more relevant to minimum area than to recolonisation, since their findings show that this species recolonises quickly and readily.

Johnson *et al.* (1992) suggested that theoretical advances in this field could be made with a combination of mathematical or simulation models and studies of microcosms which serve to scale landscape processes down to a tractable size.