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Are habitat corridors conduits for animals and plants in a fragmented landscape? A review of the scientific evidence

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ARE HABITAT CORRIDORS CONDUITS FOR ANIMALS AND PLANTS IN A FRAGMENTED LANDSCAPE?

A REVIEW OF THE SCIENTIFIC EVIDENCE

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PREFACE

This report on habitat corridors was prepared for English Nature as part of its Commissioned Research Programme at the instigation of George Barker. It is one of a series of inter-related reviews looking at issues connected with habitat fragmentation and how any deleterious consequences for wildlife may be overcome. Further information on the work of EN's habitat fragmenetation group can be obtained:

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SUMMARY

A critical review was carried out of the theoretical basis and empirical evidence for a function of habitat corridors which enables species of animals or plants to move to, and thrive in, places where they otherwise might not do so.

Corridor theory has been developed as part of a general consideration of fragmented habitats and barriers to dispersal. The function was first suggested from island biogeographic theory, but most recent work has been in relation to metapopulation theory and landscape ecology. Other important theoretical precursors have been niche, source and sink, home range and central place foraging theories. Most of the theories are founded in population ecology, but genetic theories are playing an increasing role.

There is a very substantial body of research suggesting this conduit function of corridors, and some suggesting circumstances where it does not apply, but little of it comes near to meeting the formal requirements of hypothesis testing; many of the findings are consistent with alternative explanations, and the few conclusive studies confirm a conduit function in a limited range of circumstances. Suggestions are made to remedy the paucity of good work.

The studies show that corridors:

1. Sometimes allow individual animals to survive by allowing them access to sufficient habitat to meet their needs;

2. May maintain populations of some animal and plant species by replenishment; however, most species probably either fail to use a corridor or can cross the gaps between patches of habitat adequately without its aid; and

3. Can serve the needs of some migratory animals in their seasonal movements.

It is doubtful whether good corridors can be found in many geographic regions to allow sensitive species to move in response to global warming. The idea that a network of small corridors enables large-scale movement is attractive but untested.

Decisions on the allocation of land and resources cannot await the completion of the many careful studies that would be required to confirm the conduit function across a useful range of circumstances. Recommendations are therefore made on the basis of the present limited knowledge:

1. Corridors should be preserved, enhanced and provided, where this can be cost-effective, as they do permit certain species to thrive where they otherwise would not;

2. Corridors should be as wide and continuous as possible; and

3. Their habitat should match the requirements of the target species.

INTRODUCTION

This report was prepared under contract to the English Nature to assist with the formulation of policies for the conservation of animals, plants and their habitats. It examines a concept that has been very popular in nature conservation, to see what basis exists in ecological and biogeographic theory, and in the results of scientific studies. The aim was to provide practical conclusions for those who must decide whether to keep, enhance or provide corridors.

Unfortunately the publications on this subject are numerous, scattered and disparate, so the review is long and heavy-going in places, and the conclusions limited. Suggestions are made for further research. Those who are happy to accept the scientific reasoning will find the introduction and conclusions will meet their needs. The main part of the review is divided into two parts. First, is the theoretical basis for corridor recommendations. Second, is a critical examination of these theories and the empirical studies that bear upon them.

A parallel review "Linear features. Linear habitats and wildlife corridors" (Spellerberg & Gaywood 1993) covers a wider topic. It was prepared before this one and was a valuable starting point for it.

The concept of habitat corridors to enable animals and plants to cross inhospitable barriers, and hence to survive where they otherwise might not do so, has had great currency in the last 20 years. A very large number of published works have advocated the retention or creation of such links (Diamond 1974, 1975; Wilson & Willis 1975; Diamond & May 1976; Forman & Godron 1981; Noss 1983; Wittig & Schreiber 1983; Bridgewater 1987; Burgman, Akcakaya & Loew 1988; Adams & Dove 1989; Saunders & Hobbs 1989; Grove & Schermeister 1990; Moore 1991; European Economic Community 1992). Early practice was reviewed by Harris and Scheck (1991); see also Helliwell (1975).

The interest in corridors arises in part from concern that natural habitats are being depleted, fragmented and isolated from each other (Moore 1962; Diamond 1975; Diamond & May 1976; Mader 1984; Wilcove, McLellan & Dobson 1986; Noss 1987; Opdam 1990; Webb 1993; Peterken 1993); that the links between them are being lost (Hooper 1971); the separation of the fragments is increasing (Wilcove *et al.* 1986) and that this leads to the extinction of species and a reduction in biodiversity (Noss 1983; Robbins *et al.* 1987; Goldstein-Golding 1991; Harris & Scheck 1991).

More recently there has been widespread concern over the effects of predicted global warming on animals and plants. The fear that many species may become trapped and die in isolated natural areas as warming makes their environment unsuitable has renewed the interest in corridors (Wilcox 1980; Peters & Darling 1985; Peters 1988; Grove & Schermeister 1990; Warren & Key 1991; Moore 1991; Hobbs & Hopkins 1991).

These ideas are fraught with difficulty, because many practitioners have adopted ideas that have been based more on theoretical reasoning than on empirical research. Despite this uncertain basis, some of these ideas have been very popular (Harris & Scheck 1991) and have appeared in the most prestigious publications (IUCN 1980). However papers that have criticised the concept (Helliwell 1975; Simberloff & Cox 1987) have led others to conclude that it may have no basis.

Purpose of this review

This review attempts to find what is well-founded, and to extrapolate reasonably from existing knowledge without building on unsound foundations. The theoretical basis for suggesting that terrestrial habitat corridors may act as conduits and the empirical evidence for this is reviewed.

The review is solely on the concept of habitat corridors as conduits (Bennett 1990; Forman 1991; Peterken 1993). These have also been called "travel corridors" (Johnson & Beck 1986), "biotic corridors" (Spellerberg 1989) and "movement corridors" (Merriam 1991b). Corridors may, and do, serve aesthetic, recreational and other functions (Forman & Godron 1986; Noss 1987; Forman & Moore 1990; Low 1991; Forman 1991; Hobbs 1992; Spellerberg & Gaywood 1993), and they may deserve recognition as elongated patches of habitat regardless of any connecting function (Adams & Geis 1983; Arnold 1983; Osbourne 1984; Forman & Godron 1986; Simberloff & Cox 1987; Noss 1987; Adams & Dove 1989; Lynch & Saunders 1991; Merriam 1991b, "habitat corridors").

The evidence for beneficial corridor effects is examined critically. This is necessary for two reasons:

1. The negative effects of corridors could conceivably outweigh the positive (Simberloff & Cox 1987), and

2. Those responsible for keeping, creating or managing corridors need to know how beneficial they are and how to maximise any benefit, so that this may be balanced against the various costs of doing so. This must be compared with the costs and benefits of other actions such as habitat improvement, species reintroduction or the enlarging of biological reserves (Simberloff & Cox 1987; Opdam 1990; Moore 1991; Nicholls & Margules 1991; Maunder 1992).

The purposes of corridors

Corridors have been advocated for five differing purposes, all of which require them to promote movement.

1. They allow a species on a single habitat patch to be saved from, or to recolonise after, local extinction (Diamond & May 1976; Forman & Godron 1981; Adams & Dove 1989; Bennett 1990; Soule & Gilpin 1991; Merriam 1991b; Hobbs 1992). This is called "recolonisation" below.

2. They are seen as permitting an individual mobile animal to find the necessary minimum quantity of habitat for its existence in two or more connected patches where a single isolated patch would be too small (Sullivan & Shaffer 1975; Forman & Godron 1981; Simberloff & Cox 1987; Goldstein-Golding 1991; Merriam 1991a, 1991b; Hobbs 1992). This is called "size threshold" below.

3. Migratory animals may use corridors to facilitate their regular, seasonal movement between places where they reside (Adams & Dove 1989; Merriam 1991b; Hobbs 1992).

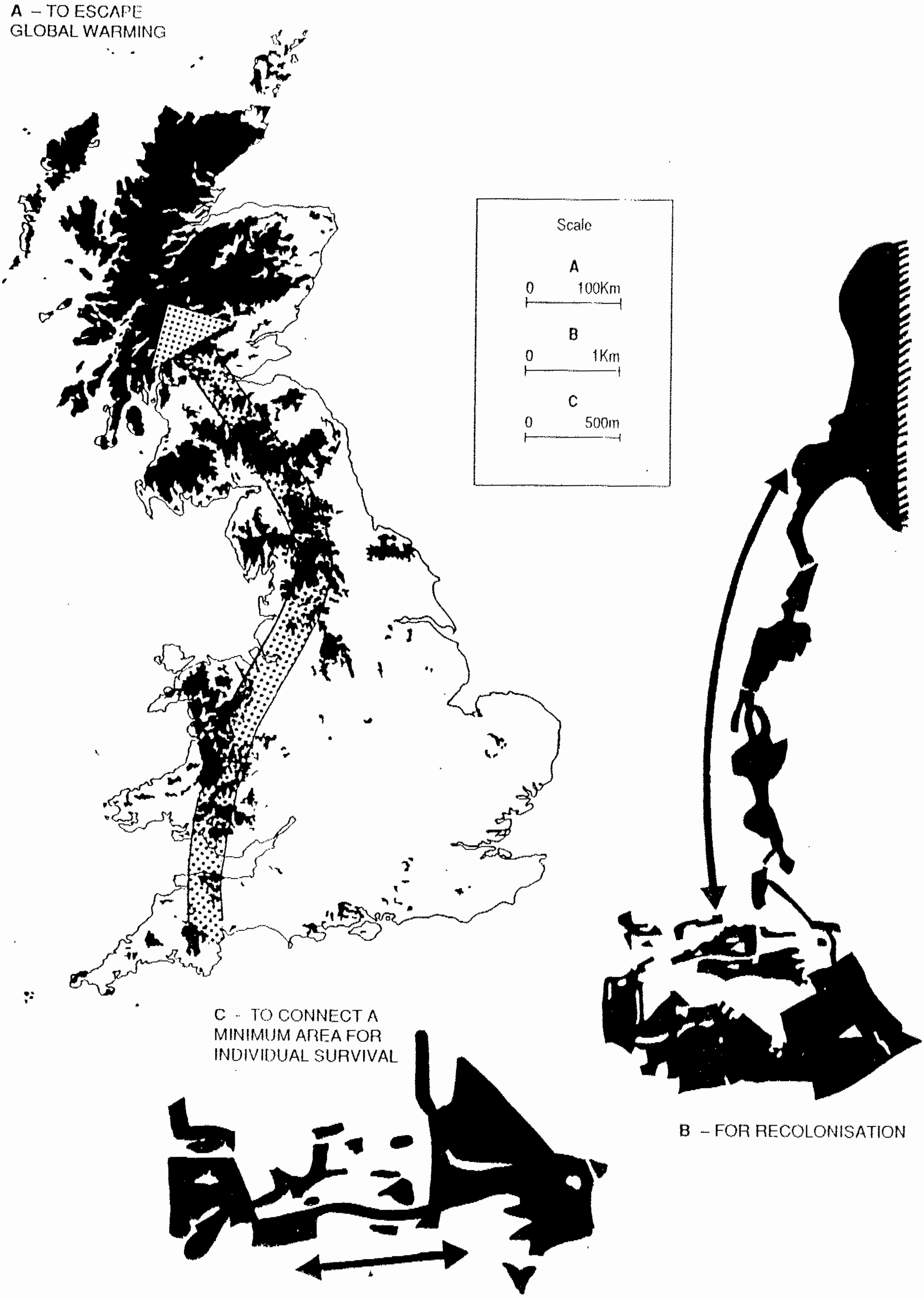
4. They may provide a means to escape the effects of global warming (see above).

5. They may facilitate gene flow across the landscape (Forman & Godron 1981; Merriam 1991b).

These purposes require corridors at a variety of spatial scales (Figure 1).

Some of the ambiguity in the literature stems from a confusion of, or grouping together of, these separate functions. For example a textbook by Forman and Godron (1986) describes a conduit function but does not distinguish between these purposes. Most of the literature on corridors has been on the recolonisation function, and so too is most of this review.

Figure 1 Corridors have been suggested to promote movement at various spatial scales: (a) to escape climate change may require hundreds of kilometres; (b) for recolonisation an intermediate distance may be required; and (c) for putting together a minimum area for survival tens or hundreds of metres may be required. The needs of different migrants span the whole range of distances.



The review also focuses largely on population rather than genetic processes. This is again because most of the work has been on the presence or absence, or simple enumeration, of organisms, rather than the more detailed work required by genetic studies. Theoretically, if populations become too small they may suffer increased homozygosity, genetic drift, inbreeding depression and a lessened ability to adapt, all of which could be reduced by movement along corridors (Soule & Simberloff 1986; Noss 1987). However, if previously isolated, viable populations are brought into contact by corridors they may suffer outbreeding depression and loss of adaptation (Templeton 1987; Simberloff & Cox 1987). In practice viable population sizes for survival may be similar whether one considers population or genetic processes and the empirical result, of local survival or extinction, is common to the two processes.

There is a distinction between the requirements of an individual species and those of a whole taxonomic group. At one extreme there are studies that examine species richness only and at the other are studies of the requirements of individual species. Many papers deal with an intermediate situation: treating rare and threatened species as a group (Noss 1983) or analysing habitat specialists only (Opdam 1991).

Clarification of terms

There is some semantic confusion in the literature over movement. "Dispersal" is used for movement away from the place where an organism's parents were to be found (den Boer 1990) and "migration" for regularly repeated (usually seasonal) movement between places of residence and back again. Some insects, however, do not show the return movement. It is clear that only motile organisms face a choice between staying where they were born (philopatry) and moving elsewhere (Macdonald & Smith 1990) and that this choice is not available to plants and many sessile animals, for which it is only propagules (seeds, fragments or passive plankton) that disperse from the parent. Animals that drift in the wind or have poor powers of flight often disperse further than those with good powers of flight (den Boer 1990). Thus some organisms choose to use corridors and others chance to do so.

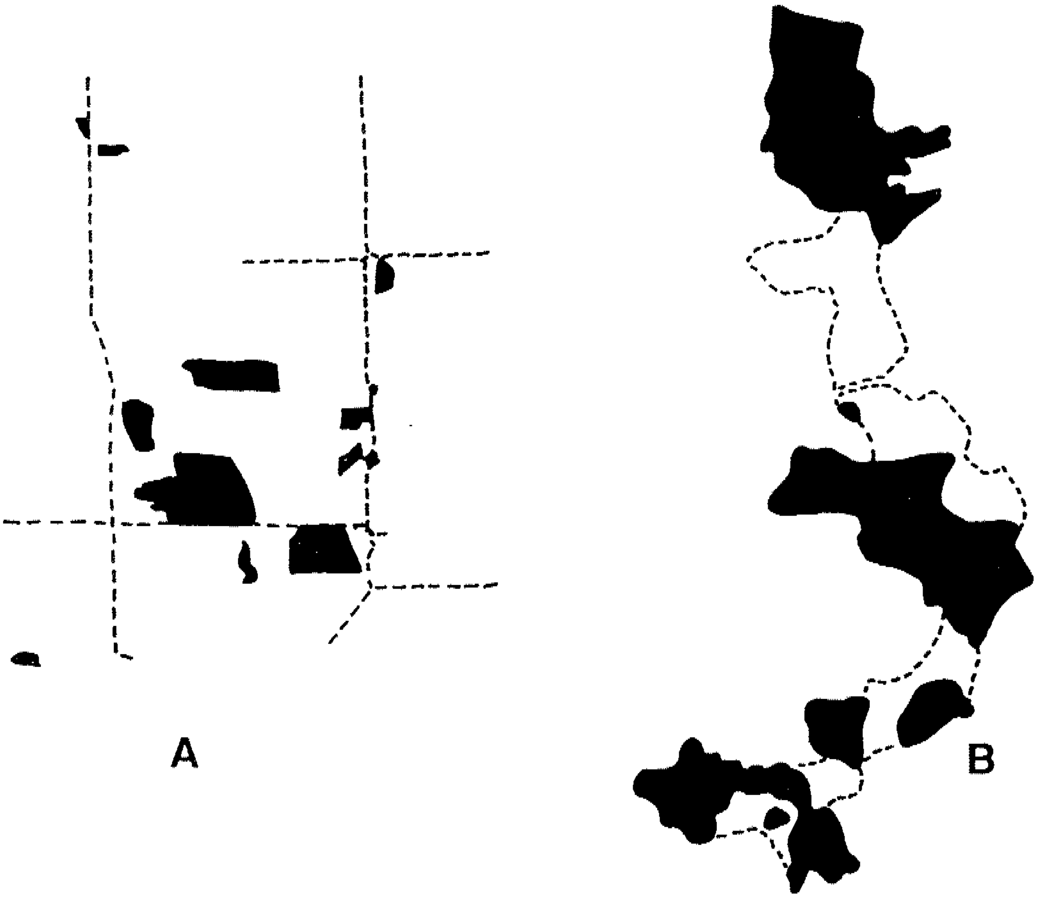
The term "wildlife" corridor is avoided in this review because it is defined so differently in different places. To most North Americans, for example, it includes vertebrate animals, but not invertebrates or plants. Australians include both flora and fauna (Watson 1991).

Most of the work on corridors has been on linear habitat strips, like hedgerows (Forman & Godron 1986; Adams & Dove 1989). Most definitions of the word "corridor" (for example those in various chapters of Saunders & Hobbs 1991a) require them to be both narrow and connect habitat patches. This review, however, includes all situations where the links are thinner or poorer than the pieces they connect (as do Forman & Godron 1981 and Merriam 1991a, 1991b, and see also Western & Ssemakula 1981 for "dispersal areas"), and does not require them to have a destination. A corridor can lead animals and plants into its length even where there is no larger habitat patch at its end (Henderson *et al.* 1985).

Corridors are usually considered together with patches of habitat. These patches may be little larger than the corridors, which may therefore effectively make several patches into one (Noss 1987), or they may dwarf them (Figure 2).

All these features fit the dictionary meaning of "corridor". The addition of the word "travel" or "movement" to qualify the word "corridor" is therefore unnecessary, and it is those who use the word "corridor" to describe elongate patches of habitat in other contexts who must qualify the word to indicate a departure from the dictionary meaning.

Figure 2 Corridors may be (a) very much thinner than the patches they accompany, or (b) comparable to them in their dimensions. (a after Nicholls & Margules 1991 and b after O'Donnell 1991).



There is a related concept of "stepping stones" (MacArthur & Wilson 1967; Hooper 1971; Gilpin 1980; Burel 1989), which suggests that movement across a barrier may be facilitated by "islands" of suitable habitat in the unsuitable matrix of the barrier. This concept is included in the review as, at some level of detail, many so called corridors may lack total continuity of suitable habitat (Lyle & Quinn 1991; Merriam 1991b); a possible route through suitable habitat may entail small gaps. It is also clear that corridors do not need to lead in any particular direction and may link up in a complex network (Forman & Godron 1981).

THE THEORY

Harris and Scheck (1991) reviewed a number of works published from the mid twentieth century on that advocated "travel corridors" for animals. However theory for the idea that habitat corridors may act as desirable conduits for plants and animals seems to have been put forward first by Preston (1962). It has been developed from several overlapping or related ecological theories. The historical development of these theories is outlined below in sufficient detail to identify the key assumptions made in their elaboration and the elements (some of which are common to more than one theory) that may be required for corridors to have a beneficial effect. Much of the theory covers the broad issues of habitat fragmentation as well as corridors *per se*. Few works are specific to corridors, but many include corridors among other considerations, or address the general theories from which corridor recommendations are made. Corridor ideas were often seen as a special application of the MacArthur-Wilson (1967) theory of island biogeography and much of their elaboration has been on that basis.

Niche and habitat theory in relation to corridors

The "niche" concept (Grinnell 1904; Elton 1927; Hutchinson 1965; MacArthur 1972; James *et al.* 1984; Verner, Morrison & Ralph 1986) or "habitat selection" (Lack 1933) concept is that any given species of animal or plant may survive in only a certain range of conditions and not outside this range (Thomas 1991). Such conditions may include the influence of predators, competitors, disease, climate and the physical and biological habitat. It is the latter, habitat factors that are involved in the idea of corridors; the assumption is that the biosphere is seen by any particular species as being composed of pieces that satisfy its needs (the "headquarters habitat" of Elton 1966), and others that do not. This can be likened to a map in black and white or, more realistically, shades of grey because usually a habitat may be more or less suitable for a species. The individual patches of suitable habitat may be connected by corridors that are suitable, to enable movement between patches. In this review the word "habitat" means what suits each particular species, or a group of species with similar requirements.

It should be realised that patches of habitat as perceived by people ("biotope patches", Webb 1993) may be either larger or smaller than those where different species find their niche. Species with special requirements may be confined to one small part of a biotope patch and those with broad requirements may find several biotope patches comprise their habitat patch. Throughout this review the habitat patches are meant in the sense of the species' niche, rather than biotope patch, but a confusion of the two exists in some published studies.

Niche theory is fundamental to all reasoning on corridors, as other theories require that some areas are suitable habitat for a species while others may be such poor habitat as to constitute barriers to movement or dispersal. The key point is that the corridors must enable movement from one suitable habitat patch to another; in some cases this may involve successful reproduction along the length of the corridor (often, for example, in higher plants, Burel 1989), but also in other taxa (Henderson *et al.* 1985; Bennett 1990). In other cases the corridor enables movement only, and reproduction occurs in the habitat patches (Merriam 1991a).

The corridors of this review are therefore habitat corridors.

Island biogeography

The theory of island biogeography deals with patches of habitat on a large, even a continental, scale. According to this theory, a patch of habitat (or "island") will hold more species if it is near to a source of possible colonists (other patches, or the 'mainland') and if it is large, than if it is distant or small.

MacArthur and Wilson (1963, 1967) described an equilibrium theory of "island biogeography" to provide an explanation of two empirical biogeographic trends. The first is the well established relationship between the size of the area studied (A) and the number of species (s) of a particular animal or plant group to be found in it (Preston 1962; reviewed by McGuinness 1984); they modelled the relationship between the two and described it by the equation:

$s = bA^k$, where b and k are empirical constants, the latter less than one. This relationship is a curve, in which the number of species increases rapidly with increasing area at first but much more slowly later. The curve becomes a straight line if plotted on logarithmic axes (Figure 3).

The second biogeographic trend is that island faunas become progressively "impoverished" (have fewer species than an equivalent area of mainland) with distance from the nearest land mass (Figure 3; Mayr 1940; Preston 1960; Moore 1962).

Before MacArthur and Wilson, one explanation for remote patches having fewer species than near ones was that there had been insufficient time for the species to colonise the patch; given enough time, the remote places would fill up as much as near ones. The number of new immigrants should decrease as the number of species already on the patch increased. MacArthur and Wilson added a second process to the theory: extinction of established species. The number of established species going extinct on the island should increase, the more species were there.

The fundamental prediction of the model is that the number of species to be found on a patch of habitat reflects an equilibrium between these two processes; the equilibrium comes about because, when fewer than the equilibrium number are present, immigrants should outnumber extinctions and vice versa. Extinctions are lower on an equivalent area of "mainland source" simply because it is not isolated from the surrounding habitat; its immigration rate is higher and some of its species are maintained by this surrounding habitat (Preston 1962).

This theory can 'explain' the species-area and species-distance relationships if it can be shown that near patches do have a greater rate of immigration than far ones and that small patches have a greater rate of extinction than large ones (Figure 4). It also accounts for a steeper species-area curve the greater the isolation of the habitat patches (Diamond & May 1976). MacArthur and Wilson (1967) extended the theory to the situation where a "stepping stone" patch enhances the immigration rate of species from a source to a target patch beyond the stepping stone. "..even minute islands (stepping stones) can significantly enhance biotic exchange provided they are able to support populations of the species in the first place". This is the first theoretical treatment of a corridor proposition.

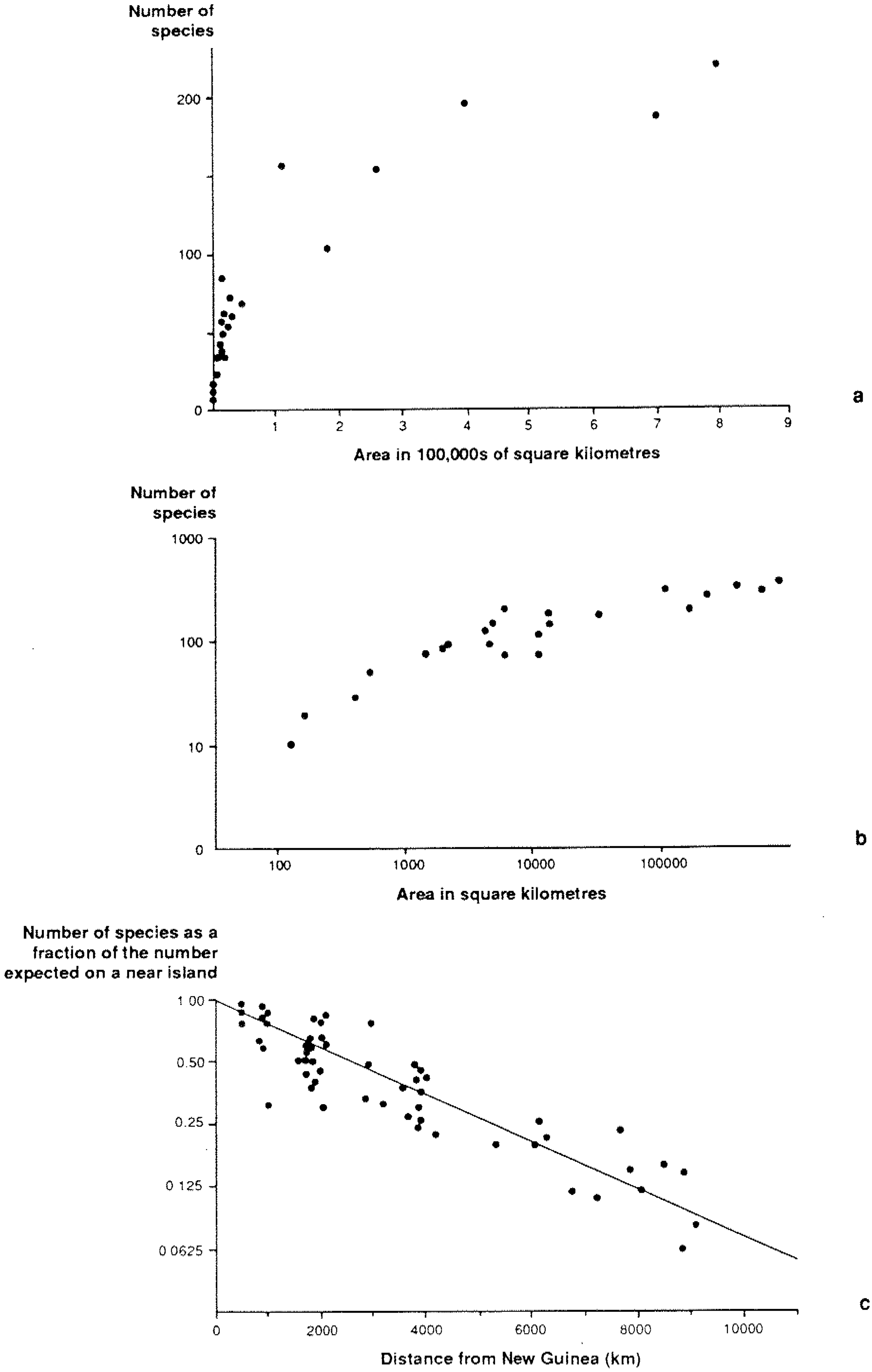
MacArthur and Wilson made several other detailed predictions from the model, but for our purposes only three are relevant, there is:

1. a chance fluctuation about the equilibrium;

2. a turnover of species as some go extinct and others replace them as immigrants; and

3. if a patch is not at equilibrium it will take time to return ("relax", Diamond 1972) to a new equilibrium.

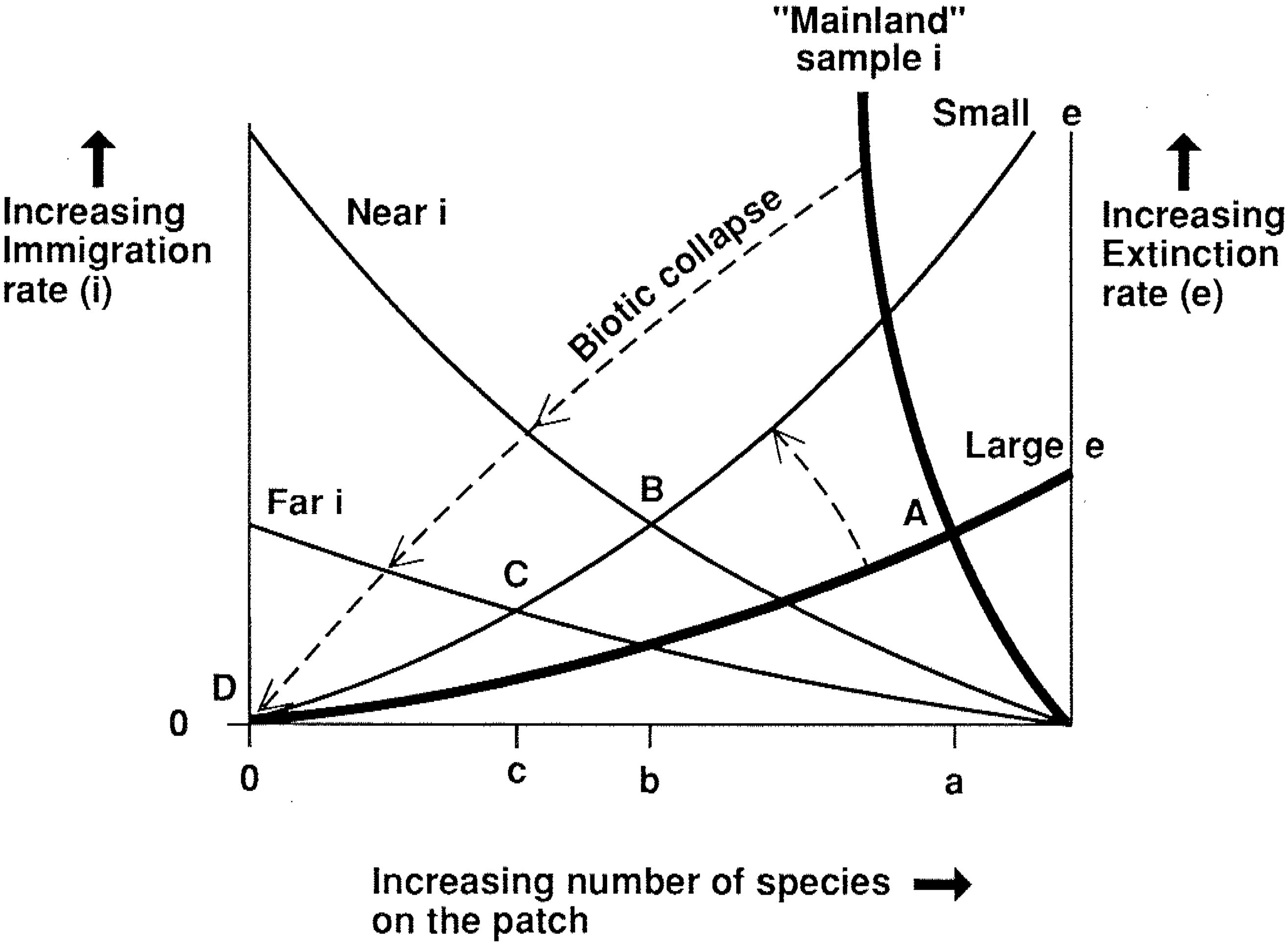
Figure 3 Typical species-area curves: (a) arithmetic axes; (b) the usual log-log plot and (c) a typical distance effect. All are for the numbers of land and freshwater bird species on various islands (a and b of the Sunda Group, after MacArthur & Wilson 1963 and c islands off New Guinea after Diamond 1975).



In a subsequent modification of the theory, anticipated by Preston (1962) and Wilson and Willis (1975), Brown and Kodric-Brown (1977) described a "rescue effect" whereby extinction is less likely on near patches than on far ones, because recurrent immigration boosts the gene pool and population of species already there. This elaboration increases the effect of isolation on species richness. Some animal communities, like Brown and Kodric-Brown's arthropods on thistles and fish on coral reef patches (Molles 1978), are maintained very largely by colonisation from external sources.

A special case of the MacArthur-Wilson theory was first used by Brown (1971) and developed by Diamond (1974); this extended the application to a subset of species that they considered cannot cross the gaps, so no distance effects are observed. Here one is concerned with extinction, as in the MacArthur-Wilson model, but by definition no new species of this kind arrive. The situation is one of disequilibrium: a slow approach towards extinction of all such species (Figure 4).

Figure 4 According to MacArthur & Wilson (1967) the number of species on a patch of habitat at equilibrium is given by the intersection of curves describing the rates at which species immigrate and go extinct there. Immigration is affected by the isolation of the patch and extinction by its area. The biotic collapse theory is that natural habitats (A) had many species, but that habitat fragmentation reduced the area of patches and isolated them (arrows), so that a new lower equilibrium number of species (B or C) is approached. Relaxation (Diamond 1972) is the approach over time to this equilibrium. In the extreme case of biotic collapse the immigration rate is zero and the equilibrium number is therefore also zero (D).



That an equilibrium between immigration and extinction does occur is very difficult to demonstrate (Burgman *et al.* 1988) but experiments, such as those of Simberloff (1976) on mangrove islands and Strong & Rey (1982) on saltmarsh islands off Florida, come close to a demonstration of the model (Gilbert 1980).

The theory deals with "ecologically uniform areas". This is the important assumption of habitat homogeneity that is discussed further below.

Patches of habitat

MacArthur and Wilson (1967) recognised that their theory applied to plants as well as animals and could apply wherever patches of uniform habitat, not just islands, could be recognised that were different from the inhospitable matrix in which they stood (see also Kilburn 1966).

These patches have variously been termed "habitat islands" (Preston 1962; Janzen 1968; Simberloff 1974; Diamond & May 1976; Terborgh & Winter 1980; Webb & Hopkins 1984; Wilcove *et al.* 1986), "virtual islands" (Diamond 1974; 1975; Diamond & May 1976), "insular refugia" (Terborgh 1974), "terrestrial islands" (Galli *et al.* 1976), "island-like ecological enclaves" (Myers 1979), "isolates" (Wilcox (1980), "fragmented remnants" (Terborgh & Winter 1980) and "remnants" (Saunders *et al.* 1987b). They are called "patches" of habitat in this review to avoid confusion with actual islands; this is also the terminology advocated by Forman & Godron (1981) for landscape ecology and Hanski & Gilpin (1991) in their review of metapopulation ideas. Simberloff's (1974) description of them relates them clearly to niche theory:

> Any patch of habitat isolated from similar habitat by different, relatively inhospitable terrain traversed only with difficulty by organisms of the habitat patch may be considered an island; in this sense much of the biotic world is insular, for habitats are often not homogeneous but rather are arranged as patches in a crazy quilt.

Preston (1962) described the populations inhabiting such habitat patches as "isolates" in contrast to the "samples" from the regional flora or fauna that are found where dispersal between patches is easy. There the number of species decreases also as smaller samples are considered, but at a slower rate than for isolates.

It was this extension beyond islands that was used by Hooper (1971), Diamond (1973, 1974, 1975), Willis (1974), Kolata (1974), Terborgh (1974, 1975), Fleming (1975), Wilson and Willis (1975), Forman *et al.* (1976), and Helliwell (1976a), when they developed an application of the theory to the design of biological reserves.

> ..the total area occupied by natural habitats and by species adversely affected by man is shrinking at the expense of area occupied by man-made habitats and by species benefited by man. Second, formerly continuous natural habitats and distributional ranges of man-intolerant species are being fragmented into disjunct pieces. If one applies the island metaphor to natural habitats and to man-intolerant species, island areas are shrinking, and large islands are being broken into archipelagoes of small islands (Diamond 1974).

The assumption was that reserves, and other patches, were uniformly much better than the habitat between them, ie that they were habitat islands in the sense of Simberloff (1974). Following MacArthur and Wilson they acknowledged that the habitat composition of the reserves would influence their species richness but, at least at first, considered habitat to have a minor influence in comparison with the area of the patch *per se* (Diamond 1973).

Some authors (eg Verner 1986; Spellerberg 1989; Bellamy *et al.* 1993) wrongly contended that MacArthur & Wilson's (1967) theory applied to the extreme habitat differences to be found between terrestrial islands and the water of oceans and thus should not be applied to habitat patches.

Biotic collapse

Diamond (1972) and Terborgh (1975) studied birds on oceanic islands that were cut off from the mainland as sea levels rose after the last glaciation and concluded that relaxation to a lower number of species was still in progress (see also Wilcox & Murphy 1985). They considered that both these land bridge islands and recently fragmented terrestrial habitats were in a state of disequilibrium as a result of the drastic lowering of immigration rates. If this is so, it follows that many species will go extinct before a new lower equilibrium number is reached.

This theory was developed within the framework of the MacArthur-Wilson theory and shared with it an assumption of habitat homogeneity. However it depended on particular assumptions about immigration and extinction rates and the speed of relaxation and is thus a special case, that can be falsified without necessarily falsifying the general model. The focus was on habitat patches as "islands" and not on the much larger "mainland" of the theory. It thus either ignored the source region, or regarded the other patches of habitat in the archipelago as the source of colonists for any one patch. The latter approaches a metapopulation model (see below).

Application of the biotic collapse theory

This application of the theory to patches of terrestrial habitat also involved an extension of the theory of stepping stones to corridors. Corridors were advocated because, at best, they could link together several small areas into one large one, and at worst they would perform the same function as stepping stones, or close placement of patches, in promoting immigration. The final equilibrium number of species would be higher than in the absence of corridors and relaxation to it would be slower (Figure 5).

According to Diamond (1974) the theory leads to four criteria for reserve design (Figure 6):

1. large patches will conserve more species than small ones; as a general rule a 90% reduction in area will cause a halving of the species complement (as first suggested by Preston 1962);

2. the same total area of homogeneous habitat will conserve more species if it is in one large patch rather than several small ones (the "SLOSS" question, from single large or several small);

3. the same total area of homogeneous habitat will conserve more species if the patches are close together, or linked with corridors or stepping stones, than if they are far apart or not linked; and

4. a single patch of given size will conserve more species if it is compact than if it is elongate (this is to minimise the "peninsular effect", Diamond & May 1976).

Island biogeographic theory should be most applicable where there is a clear contrast between the habitat patches ('islands') and the matrix ('sea') in which they are found (Johnson 1975; Diamond 1981; Karr 1982a), and where the species considered are restricted to those that are normally confined to the habitat of the patches and do not readily cross the matrix (Kitchener 1982; Mader 1984; Usher 1991).

While the reserve design criteria are expressed in terms of species richness, the prime interest was in conserving rare or threatened species and the authors argued that rich assemblages of species were most likely to have such species. Criterion 3 has been most cited by those advocating the creation or retention of corridors, although the other three criteria are also relevant. The set of criteria are related in that they rely upon just five propositions: barriers to dispersal, size effects, relaxation, sensitive species and the peninsular effect.

Figure 5 If a corridor increases the immigration rate to a patch of habitat, the number of species relaxes to a new higher equilibrium (it goes from A to B).

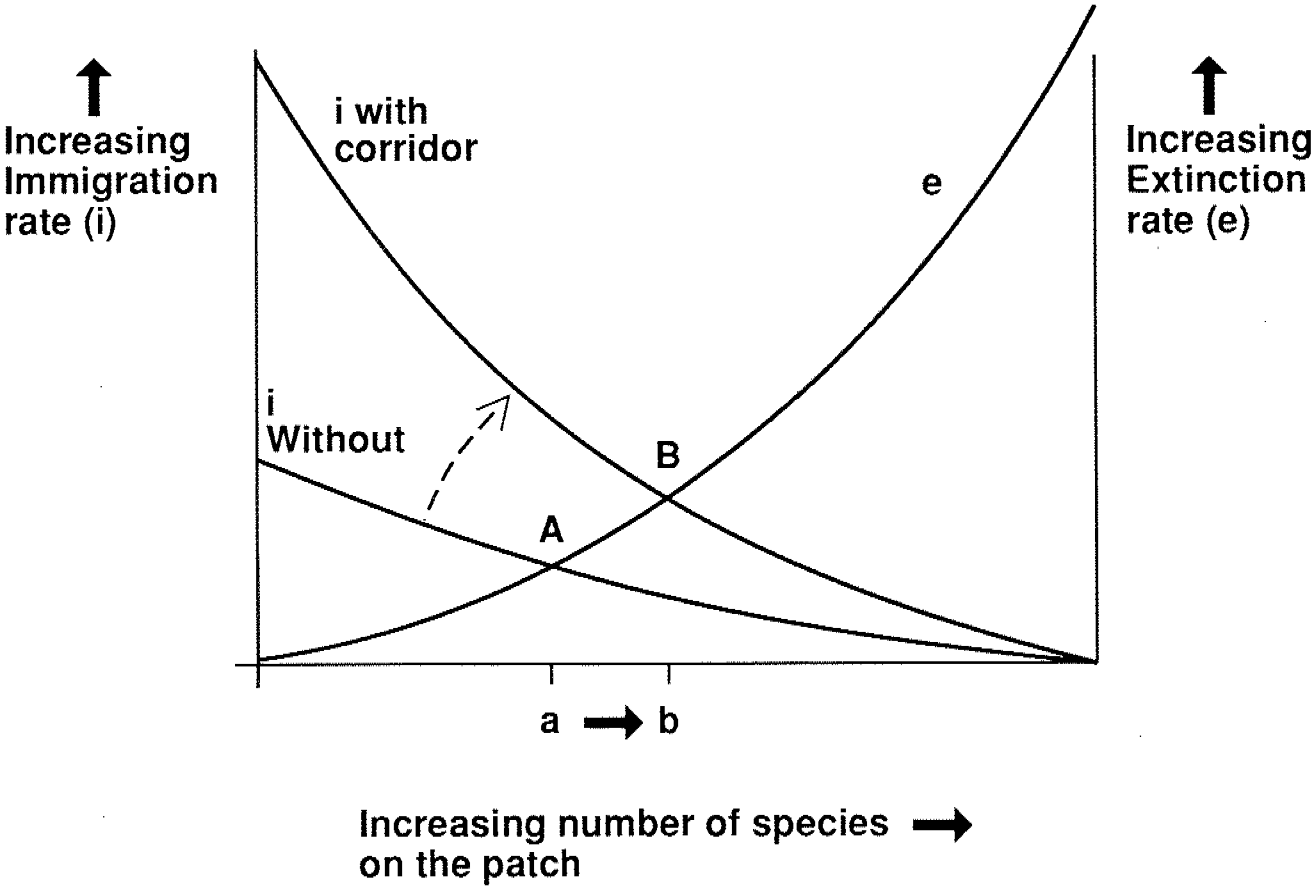
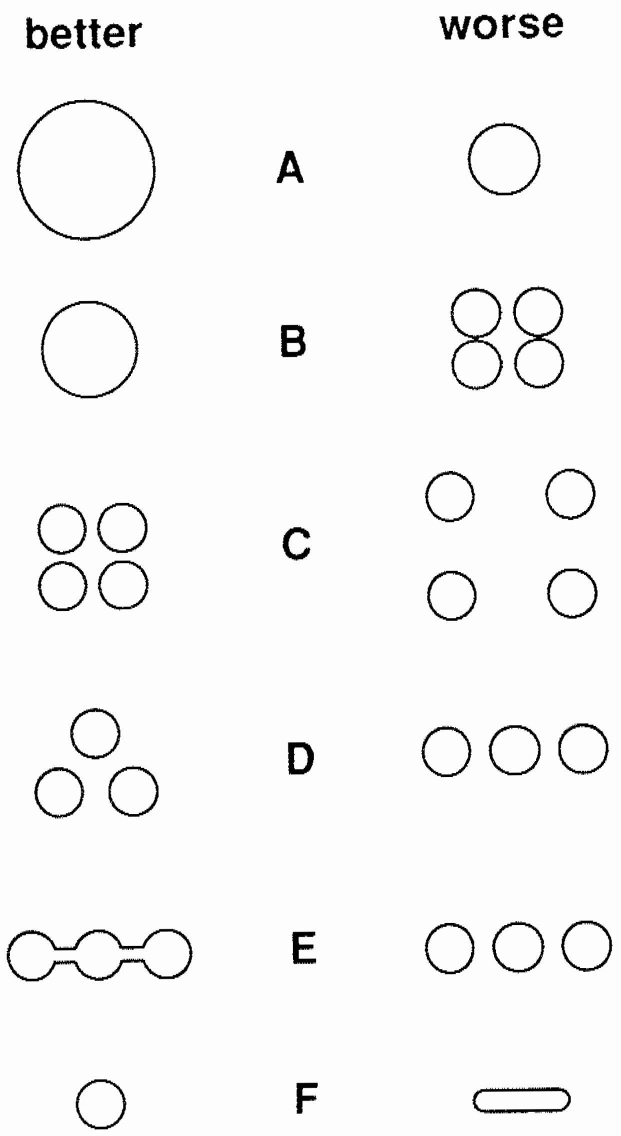


Figure 6 The principles for design of reserves advocated by the biotic collapse theorists of the mid 1970s (after Diamond 1974). In each case species' extinction rates are supposed to be lower for the alternative on the left.



Isolation and barriers to dispersal

Isolation is seen as reducing the immigration rate and hence the equilibrium number of species. In particular, the lower the immigration rate the greater the selective loss of the sensitive species (Diamond & May 1976), so corridors, by increasing the immigration rate, may allow sensitive species to recolonise (Terborgh 1975). Simberloff and Cox (1987) also pointed out that corridors should lower the extinction rate, through the operation of the rescue effect.

Most proponents of corridors seem to assume that they facilitate movement between patches, but not sufficiently to make several patches into one. This partial independence of patches may have a theoretical advantage for the survival of populations in metapopulation theory, in comparison with either a single large patch or several disconnected patches (see below).

Harris & Scheck (1991) listed the many aspects of man-modified landscapes that may be a barrier to terrestrial animal movement, some of which they considered would be as effective as the sea.

Suggestions that certain taxa cannot cross the present-day gaps between their habitat patches have been made for some heathland animals (Moore 1962), woodland ground flora (Hooper 1971), "boreal" small mammals (Brown 1971), poorly flighted birds (Ouellet 1967), and many tropical forest bird species (Diamond 1974).

Barriers may work in two ways: a species may not be able to survive the passage across it; or an animal may have the ability to cross the barrier, but behavioural factors mean that it does not do so. Diamond (1974) and Saunders (1989) provided examples of birds, in the tropics and Australia respectively, that were believed to fall within this latter category. den Boer (1990) concluded that strong-flying arthropods similarly choose not to disperse.

Corridors are unnecessary where there is no barrier to dispersal (Merriam 1991a). However demonstration of a barrier is not proof that a putative corridor will be effective as a conduit.

Large versus small single patches

If a single large area holds more species than a single small area there are two implications for corridors. The area of habitat that comprises a corridor will add to that of the patches it joins and thus increase their area (Forman & Godron 1981; Merriam 1991a). If large area is desirable for particular species, then corridors that are made up of a large area of habitat themselves may be better as conduits.

Pickett and Thompson (1978) developed a theory which helps to account for the significance of area by relaxing the habitat homogeneity assumption (see also den Boer 1990). Their theory is related to Webb's (1993) distinction of biotope and habitat patches. Each biotope patch may consist of habitat patches, within each of which a species may go extinct and later re-establish from other patches. Study of these internal dynamics should establish the "minimum dynamic area", which is the area of biotope patch necessary to retain enough such habitat patches to prevent extinction. These habitat patches may reflect natural heterogeneity, or be the result of rotationally managed or disturbed habitats. Corridors, by extending the area of a biotope patch, could assist in providing this minimum area.

Pickett and Thompson were concerned with species with a low immigration rate, so that extinctions would be the major factor. They recommended that nature reserves should be considerably larger than the largest disturbance patch; include internal recolonisation sources; include different ages of disturbance-generated patches; be large enough to have large populations in habitats not made unsuitable by disturbance; and contain separate minimum dynamic areas of each included habitat type. This theory is related to metapopulation and minimum viable population ideas that are discussed below.

Merriam (1991a) considered that a network of habitat patches and corridors might constitute such a minimum dynamic area. He advocated the rotating of habitats of different successional ages through space, over time, at a landscape scale (see below).

Size is related to the "edge effect", which is discussed below.