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**ECOLOGICAL CORRIDORS:
AN ASSESSMENT**

by
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ECOLOGICAL CORRIDORS: AN ASSESSMENT

by

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ABSTRACT

Five main types of corridors are assessed and reviewed. They (1) connect similar reserves and may reduce extinction rates from reserves, increase recolonisation rates after local extinction, and permit gene flow between reserves. They also (2) allow an interchange of wildlife between different habitat types, (3) allow wildlife to migrate, (4) let species change environments in response to environmental change (e.g., global warming), and (5) link geographically separate regions. The type of habitat within a corridor is crucial to its functioning well, and creating new corridors needs careful consideration.

Conservationists should include ecological corridors among their management options, although only in some circumstances will they solve a specific problem. A system of corridors has been designated in north Westland and maintains a link between the Paparoa Range and the Victoria Range. This system is assessed and considered successful, although a few small additions are recommended. Models for corridors are examined. Other areas in New Zealand should be considered for potential corridor designation, and further research is suggested. Current literature on the subject is reviewed, and an extensive list of references is provided.

1. INTRODUCTION

Small, isolated islands tend to contain relatively small numbers of species compared with larger islands of the same habitat types (Preston 1962, MacArthur and Wilson 1963, 1967). This caused concern among conservationists. They drew an analogy between islands surrounded by water and nature reserves surrounded by human-modified landscapes, and feared for the survival of "protected" species within already-designated reserves. Consequently, Diamond (1975a) and Wilson and Willis (1975) developed design principles for nature reserves, mostly guided by MacArthur and Wilson's (1963, 1967) theory of island biogeography. One of their recommendations was that reserves would be more effective if they were connected to other reserves by strips, or corridors, of habitat that would allow organisms to move between reserves. It was thought that this would allow gene flow

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between populations in different reserves, and that species would be able recolonize reserves following occasional local extinctions. Although there were no clear examples of how corridors worked at the time, the recommendation seemed intuitively sensible. Populations fluctuate in size, and inevitably they sometimes become extinct (section 2). However, it is unlikely that all populations of a given species will become extinct in all reserves at once. In the absence of connections, reserves that have lost their populations may never be recolonized, and eventually each of the reserve populations will become extinct. By providing corridors between reserves, conservationists hoped that recolonization would be facilitated, and that ultimate failure (the extinction of all populations at once) would be averted.

In New Zealand, Best and Harrison (1967) adopted this recommendation. They suggested that ecological reserves in North Westland should be connected by corridors that would permit the passage of wildlife from one reserve to another. It was also thought that the corridors might permit seasonal movements of animals between low and high elevation habitats, and that the corridors would themselves provide valuable additional lowland habitat (Best and Harrison 1967, Imboden and Crook 1977, Best *et al.* 1986, O'Donnell 1991). Over the following years, there was considerable argument in New Zealand concerning the value of Diamond's (1975a) and Wilson and Willis's (1975) reserve design principles (Hackwell and Dawson 1980, Hackwell 1982, Morse 1981, Dawson 1984, King 1984), although only limited consideration was given to the possible role of corridors. Eventually, the Government accepted that many of the existing reserves in North Westland should be enlarged and that intervening areas be reserved as wildlife corridors (see Figure 7.1). The consequences for wildlife of any forestry proposals in the designated corridors were to be reviewed by 31 December 1991.

In this document, I summarize some of the international literature on the theory and practice of ecological corridors. I then suggest which corridor functions are likely to be of greatest importance in the existing North Westland corridor system.

2. PROBLEMS FOR POPULATIONS IN SMALL, ISOLATED RESERVES

Small, isolated populations are susceptible to extinction for various reasons (including chance demographic and genetic variation, and changes to the environment). In most circumstances, habitat fragmentation decreases population sizes and so exacerbates these problems. For completely isolated reserves, population sizes of several thousand individuals are usually required to ensure long-term persistence, although populations of a few hundred individuals may persist in some circumstances. When detailed information is unavailable, a geometric mean population size of at least 5,500 individuals may be used as a "safe" guideline for the long-term protection of key bird and mammal populations. This recommendation may be useful for the preservation of existing vertebrate populations (e.g., in reserve design) and as a recovery target for populations that are now well below these levels. Smaller populations should not be abandoned as "hopeless" because recovery may be possible and because some small populations survive for many generations.

Ecological corridors may mitigate some of the problems of habitat fragmentation by decreasing the isolation of reserves and by increasing their effective sizes.

2.1 Island Biogeography

Guidelines for the design of nature reserves arose from the equilibrium theory of island biogeography. The major principles of this theory are as follows. More species can be found in large areas than in small areas, and on large islands than on small islands (Preston 1962). MacArthur and Wilson (1963, 1967) proposed that the number of species colonizing an island balances the extinction of species that were previously present on the island. Hence, the total number of species on an island is roughly constant, although the identity of those species may vary from time to time. MacArthur and Wilson (1967) considered that colonization rates would be relatively low for islands far from the mainland, and that extinction rates would be high on small islands: at equilibrium, small, isolated islands were predicted to contain relatively few species. MacArthur and Wilson (1967) suggested that fragmented terrestrial habitats were analogous, and that small, isolated fragments would also contain relatively few species.

These principles were applied to the design of nature reserves (Diamond 1975a, Wilson and Willis 1975, IUCN 1980). The most important recommendations were that reserves should be as large as possible, and that they should not be isolated from one another. The provision of corridors was recommended to minimize the isolation of reserves, and so to increase the number of species present at equilibrium. However, application of the principles of island biogeography to the design of nature reserves requires some modifications of the original theoretical model.

2.1.1 Species Equivalence.

The first principle relates to the equivalence of species. For island birds in the New Guinea region, Diamond (1975b) found that some are restricted to large islands, some to a broader range of island sizes, and others to small islands. This partially undermines the MacArthur-Wilson hypothesis which treats each species as equivalent: in reality, the species present on an island of a particular size do not represent a random selection of all species present on all islands. Since many of the species that are restricted to large, species-rich islands require large areas of undisturbed habitat to persist (Diamond 1975b), they are likely to be of high priority to conservationists. The same result has been found for birds in forest fragments in the North Island of New Zealand (for example, kokako are restricted to the largest forest remnants, Hackwell 1982), and for birds inhabiting chaparral remnants in California (Soulé *et al.* 1988). Therefore, large fragments are important for conservation, but more because they tend to have species of high conservation value that cannot survive in small fragments, than because they necessarily have high equilibrium diversities. Ecological corridors are expected to increase the effective sizes of reserves (section 3), so corridors should facilitate the survival of these high priority species in reserve networks when individual reserves are too small to support independent populations.

2.1.2 Species Turnover.

The second modification concerns species turnover, the rate at which new species become established, and established species become extinct. MacArthur and Wilson's (1967) model predicts that islands close to a mainland will have relatively high species turnover rates, but the limited data available are not consistent with this.

For example, Brown and Kodric-Brown (1977) modified the MacArthur and Wilson model to include the "rescue effect", whereby endangered populations on islands close to the mainland are bolstered up by fresh immigrants from the mainland. Under the modified model, populations on islands near to the mainland would be relatively unlikely to become extinct and these islands would have relatively low turnover rates. Ecological corridors are predicted to increase immigration rates: thus, corridors would enhance the rescue effect, and reduce species turnover in habitat fragments. Minimization of turnover is convenient for conservation managers, and essential when "mainland" habitats no longer exist.

Some island populations persist for long periods, despite the turnover predicted by equilibrium models. To explain this, Williamson (1981) and Schoener and Spiller (1987) proposed that turnover does occur but involves a subset of populations. They suggested that many other populations, particularly large ones, are practically permanent. This is also an explanation of events when the biota of an island is at equilibrium, and most landscapes are not now at equilibrium. In most parts of the world, natural habitats have been fragmented recently, and many of these surviving fragments now contain an excess of species. Extinction rates of organisms from these fragments can be expected to exceed colonizations. It is usually species that are ecological specialists or large that are most susceptible to habitat fragmentation (Diamond 1975b).

At present, communities occupying isolated patches contain some large, *practically permanent populations*; a subset of *fugitive populations* (populations that are transient in any one place, Williamson 1981, 1989); *naturally small populations* with high turnover rates (Schoener and Spiller 1987); *populations which will eventually become extinct*, most of which are now at small numbers, and in small fragments. The latter formerly existed as practically permanent populations in unfragmented landscapes, but they are no longer able to persist in small patches because population sizes are now too small. These populations may have occurred at low density naturally, or may have occurred at much greater densities before other habitat modifications (e.g., introduced predators) reduced natural densities to their present levels (cf. Soulé *et al.* 1988). Finally, the communities contain *seasonal populations* that are relatively mobile and would have occupied the community only periodically. These species would be unable to persist in a small fragment if it were to be completely isolated. Some of these populations would be expected to become extinct very soon after fragmentation, but other populations would continue to find and use the remaining fragment as long as alternative resources were available within commuting distance.

The recommendations that reserves be large and close together (Diamond 1975a, Wilson and Willis 1985) is often (but not always) prudent conservation because extinction rates are likely to be minimized and because area-sensitive habitat specialists and some seasonally mobile species can be maintained. Conservationists are most concerned with designing reserve systems and managing them to minimize the number of species likely to fall into the last two categories discussed above, either small and isolated fragments or isolated seasonal populations. When this approach is taken, the original arguments concerning equilibrium numbers of species are no longer relevant.

The focus of conservation biology has shifted from a biota or diversity approach, to which island biogeographic theory was relevant, to a focal species approach whereby conservation managers attempt to maintain Minimum Viable Populations (MVPs) of key species (Gilpin and Soulé 1986). Because MVPs can be determined for only a small percentage of species in a particular reserve system, the empirical observation that large, near islands have more species than do small, isolated ones still has relevance in conservation planning, even if the theoretical basis of the relationship is dubious (Dawson 1984).

2.2 Population Extinction

Populations of all animals and plants fluctuate in size, often very widely. The smaller a population, the more likely it is to become extinct during one of its normal troughs in population numbers. All things being equal, a population in a large island or reserve is likely to be larger and more extensive than a population in a small island or reserve, and the population in the small area is more likely to become extinct.

Shaffer (1981: 131) divided factors that contribute to extinction into four categories: *Demographic stochasticity* arises from chance events in the survival and reproductive success of a finite number of individuals (May 1973, Roughgarden 1975). For example, the larger a population the lower the chance that all individuals will be of one sex in a particular generation. Environmental stochasticity is due to temporal variation of habitat parameters and the populations of competitors, parasites and diseases (May 1973, Roughgarden 1975). *Natural catastrophes*, such as floods, fires, droughts may occur at random intervals. *Genetic stochasticity* results from changes in gene frequencies due to founder effect, random fixation (genetic drift), or inbreeding (Berry 1971, Soulé 1980).

Soulé and Simberloff (1986) added *social dysfunction* - behaviours that become maladaptive at small population sizes. For example, flocking species might have impaired predator avoidance behaviours when population size is too low. This category can be expanded to include a wider range of negatively density-dependent processes that occur in small populations (see Bianchi *et al.* 1989). These are known collectively as the *Allee effect* (Lande 1988, Simberloff 1988).

Since 1980, there has been considerable discussion of the relative importance of these different factors in causing extinction, particularly of the roles of demographic and genetic stochasticity at low population levels (Lande 1988, Simberloff 1988). All of these factors (except natural catastrophes, sometimes) have particularly deleterious effects when populations are at low numbers, and they often act in concert. These problems exacerbate one another: for example, a population might hit a trough through environmental stochasticity (e.g., disease in the population), the ensuing loss of genetic variation may reduce survival and/or reproductive output, and hence prolong the time that a population takes to recover, so extending the period over which the population is sufficiently small to be susceptible to extinction from demographic stochasticity. Gilpin and Soulé (1986) presented several, similar negative feedback scenarios, which they called "extinction vortices". Below certain levels it may be increasingly difficult for populations to recover, for all reasons given above.

2.2.1 Demographic Factors.

Demographic extinction is usually only a threat to very small populations (Soulé and Simberloff 1986). In undivided, non-territorial populations, demographic fluctuations are unlikely to cause extinction unless the population drops below about 20 individuals (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972). However, naturally biased sex ratios and some population structures may reduce the *effective demographic size* N_d to a level much lower than the actual count of individuals N . For example, in a matriarchal animal society, dispersing males may be unlikely to return or other males to immigrate (because remnant populations are isolated), so there may be only a few males present at once. These populations could become extinct through demographic stochasticity, regardless of the number of females still present. In highly subdivided populations, an extreme example of which is when each patch supports one territory, demographic extinction may occur at much higher total population numbers (Lande 1988). If the population is distributed in one contiguous area, demographic stochasticity is likely to be swamped by environmental stochasticity above a population level of about 100 individuals (Leigh 1981, Goodman 1987).

2.2.2 Genetic Factors. Genetic models have been used to assess the extent to which genetic variation is likely to be lost from small populations. These models are based on the *effective population size*, N_e , which is low relative to N whenever some individuals contribute many more genes to subsequent generations than do others. The actual population count that gives a particular N_e is commonly three or four times larger than N_e itself (Soulé 1980; cf. Franklin 1980). Precise calculation of N_e is difficult (see Harris and Allendorf 1989).

Models of genetic drift predict a loss of genetic variation from small populations. "In the absence of factors acting to maintain genetic variation, such as mutation, immigration, or selection favouring heterozygotes, the expected rate of loss of heterozygosity ... is $1/(2N_e)$ per generation" (Lande 1988). Thus, the smaller the population and the longer a population is at a low level, the greater will be the loss of heterozygosity. Small populations inhabiting small, isolated reserves are likely to possess little genetic variation. This was shown for lizard populations inhabiting islands of different sizes: lizards on islands smaller than five to ten hectares showed far less variation than did populations on larger islands (Soulé 1980). In northern elephant seals, genetic variation was apparently lost at a time when hunting reduced the population to about 20 individuals. Because these seals have a polygamous mating system (a few males obtain most of the matings), N_e would have been lower still at that time. Although the population recovered to over 30,000 individuals, a study of enzymes detected no remaining variation: any variation that was present was presumably lost during the population bottleneck (Bonnell and Selander 1974).

A loss of heterozygosity can have severe consequences for the fitness of a population, although this is not always the case (reviewed by Mitton and Grant 1984, Allendorf and Leary 1986; see Triggs 1988). Benefits to heterozygous individuals have been found in most outbreeding species for various fitness components, such as "growth rates, scope for growth, viability, longevity, morphological symmetry, metabolic efficiency, frequency of disease and abnormality, and survival during stress" (Soulé and Simberloff 1986). Another problem arising from small population size is inbreeding depression, caused by the mating of related

individuals. Such populations may suffer sterility and inviability after several generations. During inbreeding, deleterious alleles that are normally kept rare by selection against them in large populations can become fixed by chance (Lande 1988). A third problem arising from the loss of genetic variation is a loss of evolutionary potential in the face of changing environmental conditions or disease, for example (Simberloff 1988).

A final genetic effect of concern is outbreeding depression, which is a reduction in offspring fitness (usually in the F2 generation) following mating between very dissimilar individuals, often from different races or subspecies. This is of relevance in zoo management, in the transfer of individuals between isolated reserves to restore heterozygosity, and in the choice of individuals transferred to found new populations on unpopulated reserves. Outbreeding depression is unlikely to be of great concern in the present context: corridors are intended to permit normal levels of gene flow, not to increase gene flow beyond the levels that would have occurred before habitats were fragmented.

Effects of population fragmentation are considered by Boecklen (1986), who modelled genetic variation in an intact (undivided) population and in subdivided systems. Up to the 30th generation modelled, the intact population maintained greater heterozygosity than did any of the systems divided into two subpopulations. Beyond generation 30, the intact population did not *always* maintain more heterozygosity than subdivided populations. This may be a function of the design of the model rather than a reflection of what would happen in real systems. Extinction of subpopulations was not permitted in Boecklen's simulations: subdivisions would be likely to become extinct beyond generation 30 for non-genetic reasons (each simulated subdivision had only 6 to 50 individuals).

Maruyama and Kimura (1980) modelled a system in which extinctions and recolonizations were frequent. Under these circumstances, subdivision produced an effective population size considerably lower than the effective size of a freely-mixing, undivided population. Since the retention of genetic variation is related to the effective population size, subdivided populations will retain less heterozygosity. Because models and empirical data show that small populations are more likely to become extinct than are large ones (for non-genetic reasons), any subdivision that reduces subpopulation sizes to a point at which the chance of local extinction is increased will also result in lowered heterozygosity in the system.

The effects of fragmentation on the total number of alleles maintained by a species are more complex. The total number of alleles maintained may sometimes be increased by fragmentation, even when heterozygosity declines within each population. This is because different alleles can become fixed in different populations (reviewed by Simberloff 1988). This consideration is probably of greater importance in the management of zoo populations, and in the artificial transfer of animals and plants between reserves, than in the present context.

2.2.3 Social Dysfunction - Allee Effect. Species that exhibit group feeding and/or colonial nesting behaviours may be particularly susceptible to social dysfunction. It has been hypothesised that social dysfunction was a major contributing factor in the final extinction of

North American passenger pigeons (Soulé 1983). Bianchi *et al.* (1989) give several examples of organisms, not all of which are social, that modify their environments in a manner that is beneficial to themselves. At very low numbers, their inability to enhance the quality of their own environments may increase the probability of extinction.

2.2.4 Environmental Stochasticity and Natural Catastrophes.

These are different from one another only in degree (Soulé and Simberloff 1986, Simberloff 1988). For example, a drought might be classified as either environmental stochasticity or as a natural catastrophe depending on the frequency of droughts and their usual severity. The effects of both types of event are likely to be less severe for large populations occupying large areas than they are for small populations in small areas. All things being equal, the larger the area, the less likely is an event to eliminate all of the suitable habitat: there is a greater chance that some suitable microsites will survive. For example, the ability of a butterfly population to survive drought conditions in a large patch of serpentine grassland in California was attributable to the variety of aspects and microhabitats (Weiss *et al.* 1988). Even if an area is homogeneous, large areas and large populations may still fare better: the larger the original population size, the greater a percentage loss may be sustained before the population size drops to a level at which demographic and genetic problems are encountered.

Although the effects of some kinds of environmental variation may be modelled (Shaffer and Samson 1985), some of these events are relatively unpredictable, and models may be quite wrong (Simberloff 1988). The effects of patchiness and disturbance regimes have attracted particular attention: a reserve must be big enough to allow each transient habitat type (and the species that rely on it) to be present somewhere on the reserve at all times (Pickett and Thompson 1978, Foster 1980). Seagle and Shugart (1985) modelled patch dynamics and showed that large areas are more likely to contain a wide variety of habitat types than are small patches. However, the model is unrealistic because it assumes that the landscape is divided into identically-sized units which act independently of one another. Real landscapes are more complex. Baker (1989) found no consistent patch sizes or temporal consistency for fires in Minnesota: in that region, there was no scale of the environment that replicated itself (cf. Pickett *et al.* 1989). Thus, it would not be possible to choose a reserve that would contain all of the natural forest dynamics of the region unless the whole region was a reserve!

Grizzly bear population dynamics in the Yellowstone region have been modelled, including effects of environmental variation on birth and death rates (Shaffer and Samson 1985, Suchy *et al.* 1985, Harris *et al.* 1987). For populations starting in the range of 125 to 225 individuals at the beginning of the simulations, there was an approximately 5% probability of extinction in 100 years. Simberloff (1988) reviews other models that include the effects of environmental and catastrophic variation. As might be expected, generalizations are rare because of the inherently unpredictable nature of some of these events.

2.3 Minimum Viable Populations [Summary]

There is no single population size that guarantees the persistence of animal populations. This is partly because extinction is probabilistic and partly because each minimum viable population must be estimated separately. Some generalizations can be made on the basis of existing models, but existing guidelines have been based rather more on theory than on observations of natural population dynamics.

Models have identified many *factors* likely to be important in conservation biology; now is the time to re-examine *data* from wild populations. We need to identify empirically the extent to which population variability is determined by attributes of the organisms themselves.

[This topic is discussed in detail by the author in *Conservation Biology*. The article is reprinted in full, by permission of the journal's editors, as Appendix 1 to this report.]

3. ECOLOGICAL CORRIDORS: CLASSIFICATION AND EVIDENCE

It was originally suggested that corridors of natural habitat that connect nature reserves may enhance the conservation value of reserves by decreasing rates of extinction and by increasing rates of recolonization. More recently, the term "corridor" has been used to describe a number of additional phenomena:

Corridors that *function* as conduits, barriers and habitat.

Corridors that *connect* various habitats: they may connect like habitats and permit the movement of organisms between habitat patches (often reserves), or they may connect unlike habitats and permit the transfer of organisms from one habitat type to another. They may permit seasonal and migratory movements between habitats where resources are available at different times of the year or they may allow gradual population migration along environmental gradients in response to environmental change. They may connect different biotas and permit the long-term exchange of species between biogeographical regions.

Corridors that *contain* various habitats that permit organisms to pass along them (transit corridors) or live in them (inhabited corridors). Linear habitats (e.g., riparian habitats) are also described as corridors, but these do not necessarily act as conduits or barriers.

Examples of most of these are known. A particular corridor system may function in different ways for different organisms. In the late 1970s it was predicted that corridors would have important genetic and demographic consequences for populations inhabiting fragmented landscapes. A few experimental tests and many corroborative examples now confirm this view, although information on gene flow through corridors is still limited.

Corridors that connect small reserves by strips of continuous breeding habitat are likely to be particularly beneficial to wildlife. Migratory corridors that permit animals to use seasonally

available resources are also important. On the basis of theory and empirical examples, there is no doubt that corridors can work, and that corridors can be useful in conservation planning. However, some corridor types have undesirable effects in some situations, so each corridor proposal must be assessed independently. Decisions must be made by balancing the potential advantages and disadvantages in each case.

3.1 Classification of Corridors

The term has been used in many different ways in the ecological and landscape literature, and different corridors can be expected to have different functions (Forman and Godron 1986). This section classifies different uses of the term and considers evidence appropriate to each type of corridor, using the three-part classification mentioned above. A given reserve and corridor system may function in several ways, and fall into several of the categories listed below. In many cases, the classification of a particular corridor is organism-specific: one connected reserve system may perform quite different functions for populations of different species.

3.1.1 Function. D

Diamond (1975a) and Wilson and Willis (1975) recommended that reserves should be linked together by strips of habitat that act as ecological corridors between reserves. In reserve planning, corridors were predicted to have five major benefits.

Corridors increase the effective area of reserves by making one larger reserve out of several smaller ones, and thereby decrease the probability of extinction of species requiring large areas.

Corridors permit an increased rate of recolonization of one reserve from others following local extinction in one of the reserves. With a corridor, recolonization may sometimes be instantaneous.

Corridors provide a "rescue effect", whereby continuing migration from one reserve (the source) to another (the recipient) may prevent particular species from becoming extinct when they are at a low ebb in the recipient reserve. (See Brown and Kodric-Brown 1977; they also included instantaneous recolonization under the term "rescue effect", grouping instantaneous recolonization with prevention of extinction because it is often hard to distinguish between the two. I restrict use of the term "rescue effect" to the prevention of extinctions.)

Corridors permit seasonal movements of animals between temporarily available resources.

Corridors permit gene flow between reserves.

These effects are expected to be beneficial because they increase colonization rates and decrease extinction rates, according to biogeographical models, increase the equilibrium number of species on reserves (Simberloff and Cox 1987). The effects apply equally to single species: they are predicted to increase the likelihood that a reserve system will maintain MVPs of key species. The attributes above (partly excepting the first one) emphasise one function -

that corridors act as conduits for organisms between otherwise separate areas. However, corridors can be expected to perform three general functions (Forman and Godron 1986).

They may act as conduits: organisms may pass through the corridor from one habitat patch to another (e.g., a forest bird may pass from one forest patch to another via a forested corridor).

They may act as barriers to organisms that live in the matrix through which the corridor passes (e.g., hedges act as barriers to livestock in agricultural landscapes).

They may provide habitats in their own right.

In this report, we are concerned principally with the first and third functions.

3.1.2 Types of Habitat Connected

Type A: Connecting like habitats.

Most ecological uses of the term corridor refer to one patch of a given habitat type being connected to another patch of the same habitat type by a corridor that permits dispersal and gene flow between the patches. This category can be subdivided into three sections depending on the sizes of habitat patches being connected. I consider a habitat patch "large" if it can support MVPs of all organisms being considered. (The physical size at which habitat patches are classified as small or large may vary over orders of magnitude, depending on the taxa being considered.) MVPs are not magic numbers that ensure survival, but estimates of the population sizes likely to produce some chance of survival for a given period (e.g., 95% probability of survival for 500 years; section 2).

Type Ai: Small to Small.

POTENTIAL CONSEQUENCES. In this category, none of the connected patches are large enough to support MVPs, when patches are considered in isolation. When corridors connect small patches, some additional species reach their MVP sizes in the connected reserve network. In these networks, reciprocal recolonizations and rescue effects are likely to be important (section 2.1.2). Species that use patchily-distributed or seasonally-available resources may be able to persist only in connected systems. Reciprocal gene flow between connected patches may maintain heterozygosity.

The retention of species in connected reserve networks may have additional, indirect effects: any reserve that loses species may experience cascading effects (e.g., in plant composition following the loss of key seed dispersal agents or pollinators; cf. Gilbert 1980, Soulé *et al.* 1988). Corridors connecting small patches may increase foraging group sizes of animals that would show social dysfunction at small population sizes (section 2.2.3). The habitat contained in corridors between small patches may be important in providing additional habitat (because corridors make up a relatively high percentage of the total area when patches are small) and in acting as buffers against population fluctuations (section 3.1.3).

Potentially, some pest species might persist in small habitat fragments only if the fragments are connected to one another, but this has not been documented in this category (see Small to Large, last two paragraphs).

EVIDENCE. a) In an experimental system, Forney and Gilpin (1989) showed that connected subpopulations of laboratory *Drosophila* flies that had a transfer rate of roughly one fly per generation became extinct at a significantly lower rate than did unconnected populations.

b) Chipmunks that inhabited woodlots connected by hedgerows periodically became locally extinct and were recolonized by chipmunks from other woodlots (Middleton and Merriam 1981, Henderson *et al.* 1985). Since chipmunks usually moved along hedgerows in this agricultural mosaic, hedgerow corridors probably increased the rate of recolonization (and hence the chance of chipmunk persistence), although some recolonization might still have occurred (at a lower rate) in the absence of hedgerows (Wegner and Merriam 1979, Henderson *et al.* 1985).

c) Temporary local extinctions from woodlots also occur in *Peromyscus* mice and, again, these animals move predominantly along connecting hedgerows (Taylor 1978, Middleton and Merriam 1981). This situation was modelled by Fahrig and Merriam (1989). Their model predicted that population growth rates during summer would be higher in connected woodlots than in isolated woodlots: their prediction matched the field data. Populations in isolated woodlots were then expected to be more likely to become extinct overwinter because autumn numbers were lower.

d) Corridors have been advocated as a conservation measure for Florida panthers *Felis concolor coryi* because remaining habitat fragments are too small to maintain viable populations, whereas if all potential patches were connected there might be sufficient space to maintain a viable population (Cristoffer and Eisenberg 1985, Noss 1985, 1987, Noss and Harris 1986). At present, panthers are restricted to one contiguous area of habitat of 1 million ha, and are absent from smaller patches (Harris 1988). Since only 20 to 50 individuals persist in the one populated area (Noss 1987), even 1 million ha is apparently too small to maintain a MVP this species. This corridor proposal has been criticized by Simberloff and Cox (1987) because of the cost of providing extensive corridor systems in a heavily populated part of the USA (see section 3.2 for further criticisms): Simberloff and Cox suggested that the artificial transfer of individuals would be cheaper. However, all authors agree that the fragmented nature of remaining habitat threatens the survival of the Florida panther.

e) Carnaby's cockatoos apparently require corridors of habitat to survive in the landscape of small habitat fragments that they now inhabit in Western Australia: the birds forage along roadside habitat corridors, and often reach new habitat fragments by following the corridors (Saunders and Ingram 1987, Saunders and Hobbs 1989). The species is locally extinct in areas without roadside corridors.

f) For a hypothetical system in which extinctions do not take place, genetic models predict that greater heterozygosity will be maintained for 30 generations in a fully connected system than in subdivided populations (Boecklen 1986; see section 2.1.2 for details). The extinction of some subdivisions followed by recolonization from others will result in a further loss of heterozygosity (Maruyama and Kimura 1980). If extinctions take place in subdivided systems (which they do), the provision of linkages is likely to increase heterozygosity by reducing the chances of extinction, and by permitting recolonization from more than one source. However, connections do not always result in the maintenance of additional genetic variation (reviewed by Simberloff 1988).

When all habitat patches are small, corridors can increase the chance of population survival,

particularly by providing routes that permit recolonization of locally-extinct patches, enhance the rescue effect, and enable wide-ranging species to forage in several small patches.

Type Aii: Small to Large.

POTENTIAL CONSEQUENCES. The large patch is sufficient to support MVPs of species of interest, but the small patch is not. In this case, the large patch increases the representation of various species in the small patch, but the small patch has little effect on the large one. The effect of a corridor connecting the two will vary, depending on the type of corridor. If the corridor is wide and fully populated by the species of interest, then the population in the small fragment becomes part of a larger population. If the corridor allows for only limited movement, but nonetheless increases the rate of dispersal between the patches relative to no corridor, then corridors may still increase the ability of populations to persist in the small patch. A population in the small patch will benefit by gene flow, which prevents genetic drift, by the rescue effect, and by recolonization from the large patch, which will balance occasional local extinctions from the small patch. Small patches may be able to maintain animal populations for most parts of a year, or even in most years, but occasionally the population may have to visit the larger patch to forage when resources are temporarily unavailable in the small patch. Although the small patch does not itself maintain viable populations of some species, the presence of these populations through being connected to the large patch may allow natural community processes (e.g., fruit dispersal, predation) to take place, and so avoid cascading community processes resulting from missing species.

A potential problem is that some introduced pests or diseases may be present only in large areas. Populations of some "desirable" species may be able to persist only in unconnected patches that are too small to support these pests or diseases.

EVIDENCE. a) Willis (1974) studied birds on Barro Colorado Island in Panama, which is an island that was created when surrounding land was flooded to create the Panama Canal. He recorded the extinction of several bird species that follow swarms of army ants and capture insects that the ants dislodge. Willis hypothesized that ant-birds might persist in small reserves if they were connected to large reserves by corridors. In Amazonia, Lovejoy *et al.* (1986) showed that three ant-bird species persisted in a 100 ha reserve that was connected by a forest strip to a large region of forest, but became extinct soon after the corridor was severed. Subsequent partial regeneration of the corridor resulted in a reinvasion by one of these ant-bird species from the nearby, large forested region (in Simberloff and Cox, 1987).

b) In the southeastern United States, Harris (1988) gives examples in which relatively small areas would be unlikely to maintain MVPs of black bears (two cases) and red-cockaded woodpeckers (two cases). At present the smaller patches are still connected to larger patches that probably can maintain MVPs of these species, and Harris urges that the connecting corridors be protected.

c) Gottfried (1979) found that *Peromyscus* mice in a hedgerow/woodlot landscape had decreasing population densities in woodlots with increasing distance from a large forest. Because most *Peromyscus* movements are along hedgerows (see above), it seems likely that densities would decline more rapidly with increasing distance from the forest if the hedgerows were absent, but this has not been tested directly.

d) Peninsulas are small areas connected to large areas (mainlands) by a corridor. A review of peninsula effects (section 4) shows that peninsulas act in a way that is consistent with the hypothesized functioning of ecological corridors.

e) Small to large corridors may be detrimental if large areas maintain pest or disease populations. Ogle (1987) reported the *Paryphanta* snails may be able to survive only in relatively small (but not very small) unconnected forest fragments in northern New Zealand because the snails are susceptible to predation by introduced pigs, and feral pigs are present only in the largest forest patches.

f) In New Zealand, mistletoes have been virtually eliminated from some large forest tracts by introduced vertebrate browsers (possums), but persist in isolated trees and small groups of trees (Ogle and Wilson 1985). Presumably, mistletoes would not benefit if these groups of trees were to be connected to larger areas of forest by corridors.

Small patches that are connected to large patches probably often have more species than they would have in the absence of a connecting corridor, but this has been shown experimentally only for ant-birds. Cases are also known where this type of corridor would be detrimental. The pig/snail and possum/mistletoe type of problem, described above, is probably most frequent on oceanic islands and in continental habitats that are susceptible to invasion by exotic species. Because of this potential problem, retention of existing corridors is likely to be more valuable than the establishment of new corridors in this category.

Type Aiii: Large to Large.

POTENTIAL CONSEQUENCES. Because each large patch contains a MVP, demographic consequences are relatively trivial. However, since estimates of MVP size are probabilistic, there is always some chance that a population occupying a large patch will become extinct (e.g., a 5% chance in 500 years). In this case, connected large patches will act in the same way as connected small patches and may decrease the probability of overall extinction. The connection may have costs, however, because contagious events, such as fire or disease, may be able to spread from one patch to another and so adversely affect both populations (Simberloff and Cox 1987). Conversely, the corridor may permit normal levels of gene flow, and beneficial genes (e.g., for disease resistance) arising in one patch may be able to spread into the other only in the presence of a corridor. The same may be true of learned behaviours such as foraging skills (e.g. Fisher and Hinde 1949, Dawson and Foss 1965, Lefebvre 1986) and song dialects (Krebs and Kroodsma 1980, Cunningham 1985). Most justifications for preserving connections between very large areas fall into subsequent corridor categories.

EVIDENCE. a) Waldbauer *et al.* (1988) studied gene flow between two subspecies of butterfly in the Great Lakes region of North America. Where there was only a narrow strait of water separating the subspecies, considerable gene flow was detected, whereas there was little or no gene flow where the lake shores were more widely separated. In this case, the strait is a partial corridor.

b) In the Andes Mountains in Colombia, there is a relatively low elevation pass (the Dagua pass) which provides a corridor of habitat between the western slopes of the mountains and a valley in the centre of the mountains (the Cauca valley). In the Dague pass, races of a low- to mid-elevation species of butterfly, *Heliconius cydno*, meet and interbreed, and clines in gene frequency exist away from the pass (M. Linares pers.comm.). The races are isolated from one another except for this natural ecological corridor. Not only does this show a natural genetic corridor in action, but Linares believes that such connections may result in the generation of novel recombinants of potentially great evolutionary significance.

c) The same phenomenon occurs for a number of butterfly species in the Meseta Central in Costa Rica (e.g., for *Heliconius ismenius*), where a mid-elevation valley connects the faunas on the Pacific and Atlantic sides of the mountains, and permits gene flow between them (De Vries 1987).

Predicted and observed effects are principally genetic. The above examples (particularly the last two) could perhaps come under Type E corridors because the connections are between different races that may have become connected in the present interglacial. In these examples, gene flow is obvious because geographic races differ in appearance, and hybrids are readily identified. Nonetheless, they demonstrate that natural gene flow is likely to occur through similar corridors of recent anthropogenic origin.

Type B: Connecting Unlike Habitats.

POTENTIAL CONSEQUENCES. Narrow strips of one habitat into another may facilitate the transfer of organisms between the two habitats. I term these corridors "ecotone enhancing" because they work by increasing the interface between two habitat types. The strips of habitat act as resources themselves and as conduits. This category is a mixed blessing. Town planners use corridors to increase the penetration of wildlife into suburban areas, although some of this wildlife may then become troublesome (e.g., foxes in some British cities). In agricultural landscapes, corridors may be beneficial by acting as barriers to livestock, by reducing soil erosion, and by permitting beneficial organisms (e.g., predators of crop pests) to gain access to agricultural landscapes. Conversely, corridors may enable agricultural pests to gain access to crops. Wildlife may benefit from these corridors by gaining access to resources in the wider (nonreserved) landscape, but this will be beneficial only if the wildlife is safe there. When survival and/or reproductive success are relatively low in the wider landscape, the transfer of individuals can act as a drain on populations in reserves. A further potential problem is that ecotone enhancing corridors may also enable plants and animals of disturbed landscapes, and human hunters, to gain access to reserve networks (Simberloff and Cox 1987; see section 3.2).

EVIDENCE. This category is of limited interest in the present context, so just two examples are given (see Forman and Godron 1986, for further examples).

a) Kemp and Barrett (1989) studied the effects of grass and successional corridors in soybean fields. They designed an experiment in which there were three types of plot -solid soybeans, soybeans separated by strips of grass, and soybeans divided by strips of successional habitat. They found significant effects and, as predicted, some of these were beneficial and others detrimental to soybean yields. In the plots with successional strips, pest levels were relatively high and yields were low. Part of the reason may have been the movement of some species of predators out of the crop into the successional corridors. Conversely, plots divided by grassy corridors had yields greater than those in undivided plots. Plots with grassy corridors contained lower numbers of one herbivore species early in the season, and levels of a fungal disease of green cloverworm (a lepidopteran pest of soybeans) were relatively high in these plots.

b) Mice, birds and insects are all known to move from hedgerows into fields (Pollard and Relton 1970, Pollard *et al.* 1974, Saint-Girons 1976).

Ecotone enhancing corridors can increase transfers between habitat types (Kemp and Barrett 1989).

Type C: Migratory Corridors.

Many species of animals migrate between areas where resources are available at different times of the year. Sometimes migrations take place in response to conditions that occur less frequently. Migratory pathways may be continuous routes that must be followed (e.g., fish swimming up a river) or a series of staging posts along a given route (e.g., waterfowl and waders stopping-off at a few foraging/resting sites during migration). The more continuous the route, the more relevant are ecological corridors as a means of allowing animals to move in an uninterrupted manner between resources that are available at different times of year.

POTENTIAL CONSEQUENCES. The consequences depend on the extent to which the animals in question are able to pass through hostile or unnatural environments. At worst, severing a natural migratory route will eliminate the population. At best, the animals will simply pass through or over the damaged habitat along the route and be none the worse for it. Usually the consequences can be expected to be intermediate: the organism may abandon its migration and persist all year round, at lower numbers, at each end of its former range, or it may continue to migrate, but at lower numbers or with a lower chance of surviving the journey.

EVIDENCE. For populations following a strict pathway, evidence is scarcely needed - if the pathway is broken, the migration is prevented. Many of the examples are simply descriptions of where migratory corridors have been preserved to prevent this calamity. Examples without citations are given by Harris (1988).

a) Migrating wildebeest died in their thousands where fences cut a migratory route that was used occasionally, in times of drought, in the Kalahari desert (Owens and Owens 1985). The connected nature of the Serengeti plains permits seasonal migration of various ungulates (Sinclair and Norton-Griffiths 1979).

b) Fish ladders have been used widely in order to allow movement of migrating fish around hydro-electric dams and power generating plants (Harris 1988).

c) Pipelines in Alaska are elevated to permit migrating caribou to pass.

d) Highways in Wyoming and Colorado, USA, include underpasses to allow migrating elk to pass beneath them.

e) The Queets River corridor is designed to allow the protected passage of migratory fish, elk and deer between the high elevation Olympic National Park in Washington State, USA, and the Pacific Ocean and coast.

f) La Zona Protectora Park in Costa Rica connects a low elevation forest reserve and a high elevation national park, allowing at least 35 species of vertebrates to use it for their altitudinal migrations (Pringle *et al.* 1984).

g) Karr (1982) attributed many extinctions of bird species from Barro Colorado Island to their need for different resources and habitats at different times of year. When the island was created by the formation of the Panama Canal, links with other habitats were broken.

The severance of natural migratory pathways is sometimes calamitous. Normal seasonal migrations are relatively easy to accommodate in corridor design, but irregular

migrations made in response to unusual conditions are harder to predict and accommodate.

Type D: Environmental Gradient Corridors.

The distributions of many species are sensitive to changing climatic conditions (Davis 1986, van Devender 1986, Huntley and Webb 1989). When conditions ameliorated at the beginning on the present interglacial, populations of many animals and plants moved polewards (Bennett 1985, 1986, Davis 1986, van Devender 1986, Huntley and Webb 1989). Changes in species ranges and elevations in the first half of the present century also coincided with a gradual warming of the climate (Hustich 1958, Pollard 1979, Ford 1983, Hengeveld 1985, Payette and Filion 1985, Kullman 1986, Grove 1988). Responses of species ranges to changes in long-term rainfall patterns and other climatic variables are less well documented, but these changes are likely to be equally important. Most scientists are now agreed that a warming of several degrees in the world's average is likely to take place over the next 100 years, so we are almost certainly faced with corresponding changes in species distributions and community compositions. Conservationists must be prepared.

POTENTIAL CONSEQUENCES. Peters and Darling (1985) painted a gloomy picture of the effects of climatic change on conservation, in which we will find that many of our reserves will be in the wrong places for the species that the reserves are supposed to protect. Although it may be possible to move some species from one reserve to another, this is not practical for most of the world's invertebrates. Linked networks of reserves provide a possible solution in some circumstances: species unable to move across human-modified landscapes would be able to migrate along natural corridors, from one reserve to another, in response to climatic change (Graham 1988, Hunter *et al.* 1988). Relatively broad corridors could be placed along environmental gradients. This will be relatively easy in mountainous country (where many reserves are already situated, and include a variety of altitudes): species may respond to climatic warming by migrating upslope. It is unlikely that it will be feasible to create man corridors along north-south and mesic-arid gradients in generally agricultural landscapes, but existing uncultivated corridors along these gradients may warrant increased protection.

If exotic species are able to migrate across modified landscapes to reach reserves that have become unsaturated in species, failure to provide corridors for the use of native animals and plants may permit exotics to invade reserves, and further decrease their value.

EVIDENCE. Many examples are known of species changing distributions. Trees are known to have spread at rates of 10 to 100 km (maximum recorded 200 km per 100 years in response to climatic warming at the beginning of the present interglacial (Davis 1981, Huntley and Birks 1983). Animals are known to be able to spread more rapidly (Grove 1988): changes of over 100 km in a butterfly species (Pollard 1979) to 1,000 km in cod (Ford 1983) have been reported for poikilothermic (cold-blooded) animal species in response to relatively minor warming over periods of only two decades. If current climatic predictions are fulfilled, populations and species will be faced with extraordinarily fast distributional changes. It seems likely that corridors of natural habitat would facilitate some of these distributional changes.

Type E: Geological or Geographical Links.

In response to geological events at various frequencies, new links are made between different biotas, and old links are broken. For example, rising waters at the beginning of the present interglacial separated the New Zealand mainland into the present North, South and Stewart islands. Similarly, increasing elevations of vegetation zones can forge new connections through mountain passes, allowing species and populations on different sides of the mountains to intermingle (see Type Aiii). When connections are made, transfers of organisms take place. When old links are broken, the newly separated populations can potentially diverge and eventually evolve into separate species.

POTENTIAL CONSEQUENCES. No ecologist is suggesting that ecological corridors should be provided between mainlands and offshore islands, that peninsulas should be severed from the mainland, or that faunas and floras from one region should be provided permanent access to another. Yet these things have been done by humans, and we have to live with the consequences. Potentially, artificial severances (including ones induced by human-caused changes to the world's climate, and hence vegetation zones) simply leave populations to evolve separately. For some species, for example those restricted to a few connected mountain-tops, the severed populations may be too small and some species could become extinct. Artificial connections may have more dramatic consequences. One biota, complete with its diseases and predatory capacities, may wreak havoc with another.

EVIDENCE. a) Separate subspecies of many bird species are now found in the North and South Islands of New Zealand, although the islands were connected by a land bridge in the last glacial period. Presumably, at least some of these populations have diverged into subspecies in the present interglacial (see Bull and Whitaker 1975).

b) Many species moved from the Red Sea into the Mediterranean following the completion of the Suez Canal, displacing some of the native Mediterranean species (Por 1971). The consequences were probably relatively minor in that case because the connection was between a temperate and a tropical sea. The consequences of the proposed Central American sea level canal, which would connect two tropical oceans, would be far greater and could result in hundreds or even thousands of extinctions.

c) The fauna and flora carried around the globe by humans is analogous to the connection of continents and islands by corridors. The long lists of extinctions caused by introduced rats, cats, dogs, goats, predatory snails, etc. show that the forging of new corridors is likely to have major consequences.

Geological/geographical corridors are of great evolutionary significance, and humans should be wary of creating new corridors or severing existing ones. The creation of new Type E corridors is likely to be especially deleterious.

3.1.3 Corridor Habitat.

This classification is similar to that in Forman and Godron (1981, 1986) and Forman (1983). Forman and Godron described three corridor types. *Line corridors* are thin strips, such as hedges, roads and ditches, dominated by edge species. Other species are present in line corridors only in transit. *Strip corridors* are wider, with a central interior environment which possesses substantial numbers of interior species. Their third category is *stream corridors*. This is simply one type of linear habitat and is treated as a subset of that category, below. Although, Forman and Godron's line versus strip classification is of great value to landscape

ecologists (theirs is a community-based classification), it is of limited value to conservation biologists because it does not describe the reactions of key species to particular landscape components. Therefore, I give below an organism-specific classification. Forman and Godron, Forman and Baudry (1984) and Noss and Harris (1986) also refer to corridor networks, but these are composites of the corridor types already described.

Type 1: Transit Corridors.

Transit corridors are routes that may be used for dispersal between habitat patches, but they provide few, if any, resources for the organism in transit. They may provide safety from predation and shelter. Because most of these corridors are thin, transit corridors usually fall into the line corridor category used by Forman and Godron. However, the two categories are not synonymous because the width of habitat strip that acts as a transit corridor will depend on the characteristics of the species considered. For species that will not enter habitat edges, a transit corridor must be a little wider than double the width of the edge: the core is wide enough to allow transit, but inadequate to provide sufficient resources for occupancy. Such a corridor would be included in Forman and Godron's strip corridor category because it would contain some habitat-interior species. Transit corridors function only as conduits and barriers.

EXAMPLE. Many organisms move along transit corridors without establishing populations. Examples include snakes (Pollard *et al.* 1974) and rodents (Wegner and Merriam 1979) moving along hedgerows.

Type 2: Inhabited Corridors.

These corridors are used by populations that exist in habitat patches and in corridors. Typically, they contain some habitat interior and so fall into Forman and Godron's strip corridor category. They act as conduits, barriers, and as habitat in their own right. These corridors can be subdivided further:

Permanently populated strips provide all resources that are necessary for a population to persist. As such they are linear extensions of breeding habitat between patches, and they allow dispersal and gene flow along the corridor.

EXAMPLE. A forested corridor that connected a small, otherwise isolated, forest patch to a forest mainland (Corridor Type Aii) supported breeding territories of several forest-interior bird species that occurred in both the small patch and in the mainland (MacClintock *et al.* 1977).

Resource strips provide some but not all resources that are needed to support a permanent population. They are occupied at some times of the year only, or for only some of the time throughout the year.

EXAMPLE. In Western Australia, Carnaby's cockatoos forage along roadside corridors. However, the corridors do not provide sufficient resources to maintain permanently resident birds (Saunders and Ingram 1987, Saunders and Hobbs 1989).

Buffer strips provide sub-optimal habitat that may be used when areas of greater habitat suitability are already fully populated. These corridors may act as conduits and barriers, but their primary function is as "overflow" habitat.

EXAMPLE. Great tits are insectivorous birds that occupy British hedgerows when higher quality habitats (woodlands) are fully occupied. Experimental removal of a territory holder from a wood resulted in its replacement by another great tit from the adjoining hedgerow (Krebs 1971).

Type 3: Linear Habitats.

Any long, narrow habitat will support populations of some organisms regardless of whether it is attached to habitat patches at either end. The primary function is as a habitat, although linear habitats may also act as Type 1 and 2 corridors when attached to other habitat patches. Examples are riparian strips (stream corridors), seashores, rivers, some cliff edges, and many ecotones. These habitats may require conservation in their own right. Other wise, their significance is covered by previous categories.

Further consideration of habitat types within corridors is given in section 5.

3.1.4 Other Corridor Types.

"Corridor" has become something of a buzzword in conservation planning (cf. Noss 1987) and has been used in all manner of circumstances. The above three-part classification (function, habitats connected, habitats in the corridors) is intended to categorize many of these uses and facilitate discussion of different sorts of corridors. The classification is not intended to impose any one strict use of the term corridor (which would be impossible), and additional uses of the term may be found. A common use of corridors is in urban planning, sometimes called "greenbelts". These "corridors" may be areas surrounding urban developments, or sometimes habitat within a generally urban environment. A reader should not assume that they know what is meant by a corridor unless it is specified.

3.2 Criticisms of Ecological Corridors.

The diverse nature and functioning of ecological corridors (above) means that each case must be judged on its own merits (Soulé and Simberloff 1986, Simberloff and Cox 1987). It is clear from the above examples that ecological corridors can work, and that they should be considered seriously along with other options that may be available to conservation planners. The difficulty is in determining corridor desirability in a particular case.

Simberloff and Cox (1987) have been outspoken in their criticisms of corridors because they feared that enthusiasm for the idea might be premature, and that disadvantages tend to be ignored. I will deal with these criticisms in turn, although most of their comments have already been addressed by Noss (1987). Some of the disputes become irrelevant once a particular corridor has been classified adequately. For example, Simberloff and Cox (1987) suggested that the extinction of bird species (by introduced predators, among other factors) from all but the most isolated and least modified islands in the Seychelles demonstrates the potential undesirability of corridors. Were the islands connected to one another, these remnant populations would also have been lost. True. But, the connection of these islands (and the introduction of predators) would fall into the "new links" part of the Type E corridors category. There is no argument. New Type E links have not been advocated as desirable by conservationists. This does not in any way detract from the desirability of retaining naturally existing Type E links as well as other types of corridor.

- Gene flow may disrupt adaptations to local conditions and cause outcrossing depression (reduced fitness of offspring, often in the F2 generation, following mating between very dissimilar individuals). Corridors are intended only to maintain existing links and to re-establish links that existed until recently: these are aimed at permitting relatively *natural* levels of gene flow. In Type Ai and Aii corridors (above), benefits from increased heterozygosity (and from the rescue effect and recolonization) are likely to outweigh any slight problems arising from possible outbreeding depression. For other corridor types, populations are sufficiently large that outbreeding depression is unlikely to pose any threat. Simberloff and Cox (1987) suggested that the translocation of a few individuals each generation might be a feasible alternative to corridors for a few focal species, but the transfer of individuals is more likely to cause outcrossing depression than are natural corridors (cf. Simberloff 1988).

- Corridors may facilitate the spread of diseases, exotics, and other undesirable species into reserves, and throughout the landscape. Simberloff and Cox (1987) gave the inappropriate Seychelles example in support of this contention. The possible inability of snails and mistletoes to survive in connected fragments in New Zealand, because of pig and possum predation respectively (section 3.1.2, Type Aii), show that this criticism of corridors is sometimes valid for some taxa. While this may happen in some circumstances, the majority of introduced animals and plants, and the diseases they may harbour, are confined to, or more abundant in, human-modified environments. Therefore, this criticism has greatest validity when corridors are narrow and in environments that are particularly susceptible to invasion by exotic species. Wide, inhabited corridors will most often be beneficial in that they permit organisms to pass between reserves without coming into contact with the external matrix that contains these hostile species.

- Corridors may facilitate the spread of abiotic disasters, such as fire. While true, it is possible to argue that corridors also provide an escape route for animals when a disaster strikes one reserve in a linked system, and that corridors provide a recolonization route after the disaster has passed. One of New Zealand's most endangered bird species, kokako, was eliminated from the Omahuta forest by logging. As the forest gradually recovered from this human-caused disaster, kokako moved back into the Omahuta forest from the contiguous Puketi forest, 40 years later (Ogle 1982). Kokako fly so weakly that they would be extremely unlikely to recolonize isolated forest remnants.

- Corridors may increase the exposure of wildlife to hunters, poachers, and other predators. In Western Australia, Carnaby's cockatoos are subjected to increased "predation" by motor cars in roadside corridors (Saunders and Ingram 1987, Saunders and Hobbs 1989). This sort of problem may occur in some corridors, but, if the alternative is for wildlife to cross farmland, they may be much safer in a corridor. Johnson and Adkisson (1985) found that even narrow corridors could provide protection from natural predation: hedgerows provided jays with cover from hawks that were migrating through a predominantly agricultural landscape. In countries such as New Zealand, where there are many introduced vertebrate pest species, increased access for hunters may be beneficial.

- Riparian strips, which are often recommended as corridor sites, might not enhance dispersal or survival of upland species. This is certainly true, but it is a matter of corridor design (section 5). For species that will only move through their own habitat type as the reserves. Before this criticism was made, Forman and Godron (1981, 1986, Forman 1983) had already proposed that at least one side of a river should have a wide strip that contains and permits the movements of non-riverine, habitat-interior species as well as river bank species. This design would permit the passage of additional species, although not of upland species that will only use upland corridors.

- The costs and conflicts with other land uses may not be worthwhile, especially when the inherent quality of the corridor is low. If a certain amount of money is to be spent, or a certain area is to be designated as conservation land, it may be better to obtain further isolated patches of habitat of greater intrinsic value than to connect existing reserves with corridors that contain mediocre habitat. This criticism deserves serious attention. However, in many cases the preservation of a corridor area does not prejudice the preservation of another patch of isolated habitat of greater intrinsic value, or *vice versa*, particularly if the land is already in public ownership.

3.3 Conclusions

There are many different types of ecological corridor. Each corridor type has somewhat different functions. Empirical support is found for most types of corridor function. Many of the consequences of corridors are beneficial to wildlife, but there may also be detrimental consequences. Therefore, each corridor proposal must be appraised separately on the basis of its individual advantages and disadvantages. The retention of existing corridors will usually be beneficial, but the creation of new corridors requires more careful consideration.

4. CORRIDORS AND PENINSULAS

Peninsulas are analogous to reserves connected to larger areas of habitat by a corridor. Of 28 examples of the fauna or flora on peninsulas, only ten show a consistent decline in species number from the base to the tip of the peninsula. This phenomenon is known as the "peninsula effect". Usually, environmental gradients and other habitat changes are responsible for changes in species number and composition from peninsula base to tip: i.e., species are absent because conditions are unsuitable rather than because they cannot gain access to the peninsula. These findings are consistent with the hypothesis that peninsulas act as corridors for species from mainland to peninsula tip. The results also have implications for the design of corridors (section 5). The peninsulas considered here are mostly considerably larger than ecological corridors linking nature reserves, so the analogy between linked reserves and peninsulas should be treated with caution.

4.1 Introduction

For several taxonomic groups, the number of species decreases from the base to the tip of a peninsula (e.g., Simpson 1964, Cook 1969, Kiester 1971, Taylor and Regal 1978a, b), although this is not the case for all taxa on all peninsulas (Seib 1980, Busack and Hedges 1984, Brown

1987, Schwartz 1988). The decline in species number from base to tip of a peninsula is termed the "peninsula effect". When a peninsula effect does occur, four hypotheses have been invoked to explain the decline in species number (Means and Simberloff 1987, Schwartz 1988). These are:

The historical hypothesis. Past climatic or other environmental events have eliminated some species from part or all of the peninsula, and too little time has elapsed for species to reinvade the now-suitable habitat (cf. Orr 1960, Means and Simberloff 1987: 552).

The environment hypothesis. The present environments and habitats on peninsulas are unsuitable for some mainland species (Taylor and Regal 1978a). "According to a hybrid of the historical and environment hypotheses, some species for which the present habitat is suitable do not have access [usually because of some environmental barrier] and have not yet colonized." (Means and Simberloff 1987).

The immigration-extinction hypothesis. Increased local extinction and decreased immigration, due to the geometry of peninsulas, result in a decline in species number along the length of a peninsula (Simpson 1964, MacArthur and Wilson 1967, Cook 1969).

The area hypothesis. Several peninsulas become narrower towards their tips, resulting in reduced numbers of species from area effects (Schwartz 1988). In the pure form of this hypothesis, the decline in species number with peninsula area is the same as would be observed from sampling areas of the same sizes on the mainland. However, this hypothesis is only partially distinct from the preceding two hypotheses. Schwartz (1988) considered that the area effect in two Alaskan peninsulas was due to either environment or habitat effects - smaller areas near the tips resulted in lower habitat diversity and hence lower species numbers), and supporters of the immigration-extinction hypothesis invoke reduced area at the tips of peninsulas as one of the factors influencing immigration and extinction rates.

4.2 Relevance to Ecological Corridors

Peninsulas are analogous to islands (reserves) connected to the mainland (large area of unmodified habitat) by a corridor (corridor Type Aii; section 3.1.2). Therefore, if there is usually a decline in species numbers towards the tips of peninsulas, doubt is cast on the efficacy of corridors at maintaining large numbers of species in reserves. Two kinds of information are relevant to testing the efficacy of corridors in this respect.

First, if the connectedness of peninsulas to the mainland results in increased species number, the ends of peninsulas should hold more species than do islands of the same size. Although no specific tests of this hypothesis are available in the literature, information is available for species-area relationships of islands, mainlands and a few peninsulas. If the species-area relationships of mainlands and peninsulas are more similar to one another than either are to the relationships for islands, then peninsulas are not necessarily depauperate in species.

Second, of the four hypotheses given above to explain the peninsula effect, only the second one says that species number is reduced on peninsulas due to reduced environmental diversity or due to an environmental gradient or barrier somewhere along the length of the peninsula. If this explanation is correct, then the geometry and other features of peninsulas do not automatically reduce the flow of species along them. If this hypothesis is usually or always the explanation for the peninsula effect, then corridors may be effective, provided they are designed properly.

In this section, I review support for each of the four hypotheses. I also compare species-area relationships for mainlands, peninsulas and islands.

4.3 The Occurrence and Cause of Peninsula Effects

The studies considered are presented in Table 4.1. Reports of peninsula effects when fewer than five species were examined were not included. Of the 28 cases considered, only 10 showed a true peninsula effect, whereas 11 showed no effect, two showed a \cap -shape distribution (more species in the middle of the peninsula than at either end), four showed a U-shape (fewer species in the middle than at either end), and one case showed a reverse trend with more species at the tip than at the base. The overwhelming explanation given has been that environmental changes along peninsulas are the major causes of changes in species numbers and composition (19 out of 28 explanations). There were five cases in which the historical hypothesis was invoked, but all of these were on two peninsulas, Baja California and Iberia. Baja California falls in a temperate-tropical transition zone, and so the end of the peninsula is effectively a tropical island with a temperate connection. The base of the Iberian peninsula is the Pyrenees mountains, and so this peninsula is also "island-like". For both peninsulas, the historical events concern changes over very long time scales. Furthermore, for four of these five cases, historical factors are invoked to explain changes in species composition (not species number) from base to tip of the peninsulas. The remaining case is heteromyid rodents on Baja California. This widely-cited peninsula effect (a decline from nine to five species) is not statistically significant (two-tailed binomial test, $p = 0.22$; my calculation). In three cases, area is invoked to explain variation in species numbers beyond that explained by environmental causes. In each case the area effect may represent reduced sampling, further environmental effects, or support for the immigration/extinction hypothesis. Only one study (Milne and Forman 1986) invoked the immigration/extinction hypothesis directly, and then it explained only 5% of the variation in species richness. Since Milne and Forman (1986) did not attempt to correlate their residual variation with area before correlating it with distance along peninsulas, even this small amount of variation may be an effect of area rather than of distance.

With the exception of a few taxa on the Baja California and Iberian peninsulas, almost all changes in species number or composition from bases to tips of peninsulas can be attributed to environmental gradients or other habitat changes. The historical explanations concern changes in species compositions, not changes in species numbers. Area may be an important subsidiary effect, but the immigration/extinction model receives little if any support. Provided that corridors contain suitable habitats/environments for the species of interest, evidence from these peninsulas suggests that corridors can be effective.

Table 4.1: Examples of various forms of the peninsula effect, hypotheses supported, and location of examples.

Effect	Hypothesis supported				Location and species
	Historical	Environment	Immigration/ extinction	Area	
reverse	-	+	-	-	Baja California: bats ¹
yes	+	+	-	-	heteromyids ¹
no	-	-	-	-	murids ¹
no	-	-	-	-	carnivores ¹
yes	-	-	-	-	birds ²
no	-	+	-	-	lizards ^{3,4}
no	-	+	-	-	snakes ^{3,4}
U-shape	+	+	-	-	butterflies ⁵
∩-shape	+	+	-	-	scorpions ⁶
yes	-	+	-	-	Florida: birds ⁷
yes	-	+	-	-	reptiles ⁸
yes	-	+	-	-	amphibians ⁸
U-shape	-	+	-	-	woody plants ⁹
no	+	+	-	-	Iberia: lizards ⁴
no	+	+	-	-	snakes ⁴
U-shape	-	+	-	-	Yucatan: lizards ^{4,10}
U-shape	-	+	-	-	snakes ^{4,10}
no	-	-	-	-	Lake Manitoba: small mammals ¹¹
no	-	-	-	-	carabid beetles ¹¹
∩-shape	-	+	-	-	Italy: plants in beech woods ¹²
yes	-	+	+	-	Maine: woody plants ¹³
yes	-	-	-	+	Seward, Alaska: woody plants ⁹
yes	-	+	-	+	Aleutians: woody plants ⁹
yes	-	+	-	-	SW England: butterflies ¹⁴
yes	-	+	-	+	Kent: butterflies ¹⁴
no	-	-	-	-	Northland NZ: butterflies ¹⁴
no	-	-	-	-	East Cape NZ: butterflies ¹⁴
no	-	-	-	-	Cape Palliser NZ: butterflies ¹⁴

¹ Lawlor 1983 ² Taylor & Regals 1978a ³ Seib 1980 ⁴ Busack & Hedges 1984
⁵ Brown 1987 ⁶ Due & Polis 1986 ⁷ Wamer 1978 ⁸ Means & Simberloff 1987 ⁹ Schwartz 1988 ¹⁰
Lee 1980 ¹¹ Taylor & Pfanmuller 1981 ¹² Peoli & Lagonegro 1981 ¹³ Milne & Forman 1986
¹⁴ C.D. Thomas, unpublished

4.4 The Species-Area Relationship

The relationship between the number of species (S) and area (A) is approximated by the equation

$$S = cA^z$$

There has been much controversy over the biological meaning of the two constants, c and z. Most debate has concerned constant z, which is the slope of the line when log S is plotted against log A. Preston (1962) and MacArthur and Wilson (1967) showed that high z values are characteristic of islands (usually between 0.2 and 0.4), whereas lower values are characteristic of samples within continents (usually 0.12 to 0.19). They argued that continents were relatively saturated in species, and hence the number of species does not increase so rapidly with increasing area. Although not all island and continental samples fall into the predicted range of z values (Connor and McCoy 1979), on average, island biotas are characterized by higher z values than are continental biotas.

It is unnecessary to repeat here the arguments over whether the many published z values are consistent with theory. In the present context, suffice it to say that island z values are usually higher than continental values, and this may be due, in part, to reduced species saturation of small islands. We are concerned here whether values for peninsulas fall closer to those of islands or continents. According to the immigration-extinction hypothesis, peninsulas could be expected to have z values that are intermediate between island and continental values. Conversely, if peninsulas act as adequate corridors for species from the mainland to the end of the peninsula, peninsular z values are predicted to be similar to continental z values. Few species-area relationships have been calculated for peninsulas. Estimates are available for lizards and snakes on the Florida, Baja California and Yucatan peninsulas. The values of z on these peninsulas range from 0.01 to 0.06 (n = 6, mean = 0.04), and these compare with values of 0.04 to 0.08 (n = 4, mean = 0.06) for the same taxa on nearby continental areas (Busack and Hedges 1984). These z values are low (see above), and give no indication that peninsulas are intermediate between continental and island values. Only on the Iberian peninsula, which has the Pyrenees mountains as a barrier at the base of the peninsula, are values intermediate between island and continental scores. On the Iberian peninsula, z values were 0.16 for anurans (normal for continents), 0.215 for salamanders, 0.22 for snakes, and 0.23 for lizards (Busack and Jaksic 1982, Busack and Hedges 1984). For butterflies on the South West peninsula of England, z = 0.175, which is typical of mainland values (C.D. Thomas unpublished). Peninsulas and continents usually have similar values of z. This is consistent with peninsulas functioning adequately as ecological corridors.

The constant c almost certainly has meaning in the species-area relationship, but its biological significance is even less well understood (Connor and McCoy 1979). For a given value of z, a higher c means that there are more species in a given area (Gould 1979). Furthermore, a region that has a species-area relationship with both higher c and higher z values than those obtained for a second region has a higher diversity than the second region for any area greater than the unit sample size (i.e., the lines do not cross). If we take the criterion of the lines not crossing as indicating a consistent difference in species richness, it is then possible to re-examine Busack and Hedges' (1984) data to assess whether peninsulas are

depauperate. For Florida snakes, the peninsula has a higher c but lower z compared to adjacent mainland, so the lines cross. For Florida peninsular lizards, the c and z values are both slightly higher than on the mainland, so the peninsula is actually relatively rich. For snakes and lizards on the Baja California and Yucatan peninsulas, c and z values are all the same as or lower than the values for mainland Mexico, so these peninsulas are depauperate for these taxa. In summary, two peninsulas are depauperate and one is not by this criterion. The U-shape and -shape distributions of species richness of some taxa on both depauperate peninsulas (see above, Brown 1987, Lee 1980, Busack and Hedges 1984) indicate that these patterns cannot be explained solely by the immigration-extinction hypothesis.

The values of the constants in the species-area relationship are not very different for mainlands (continents) and peninsulas. This is consistent with, although it does not prove, the hypothesis that the basal sections of peninsulas act as adequate ecological corridors between mainlands and peninsula tips. A better test of whether peninsulas act as corridors would be to compare species-area relationships for peninsulas and islands, for the same taxa in the same region. As far as I am aware, this has not been done.

5. CORRIDOR DESIGN

This section considers corridors between reserves of like habitats, designed so that the corridors are likely to be permanently populated by wildlife. Habitat quality, corridor geometry and edge effects are particularly important. Section 5.4 outlines design guidelines in summary form.

5.1 Introduction

Because there are so many types of corridor, no single rule governs corridor design. This section concentrates on design principles that may be relevant to the North Westland corridor. The species of greatest concern in the region rely on undisturbed forest habitats (O'Donnell 1991; section 6): these are usually habitat-interior species. Corridors should permit the passage of habitat-interior species between ecological reserves, which, it is assumed in this section, contain like habitats (Type A corridors, section 3.1.2). In unknown circumstances, corridor design should be conservative: this entails the establishment of continuous breeding habitat between ecological areas (i.e., an inhabited corridor, Type 2i, section 3.1.3).

The need to be conservative in unknown cases can be illustrated. Even if animals are sometimes seen to cross open areas, a populated link may still be required to ensure population persistence in an otherwise isolated forest fragment. The ant-birds studied by Lovejoy *et al.* (1986, see section 3.1.2, Type Aii) were known to fly across cleared areas on occasion, but they still became extinct from an isolated forest patch when the connecting corridor was severed.

Unless detailed ecological information demonstrates that other types of corridor will be effective for the species of interest, the safe target is to ensure that reserves are connected by permanently inhabited corridors. Corridor lengths and widths need to be considered.

However, the design consideration of greatest relevance is corridor width because length is usually determined by existing distances between reserves.

5.2 Habitat in Corridors

To ensure that a corridor is permanently inhabited, suitable habitat should occur throughout the length of the corridor. It is possible to argue that continuously suitable corridors are not necessary, and that stepping stones of suitable habitat may be adequate. This can sometimes work for migratory corridors, but, even then stepping stones cannot be guaranteed to ensure natural rates of movement. Kareiva (1982) experimentally manipulated a system in which flea beetles were feeding on collards. He found that movements along rows of collards were much more frequent than movements between rows separated by only a narrow strip of other vegetation. He also found that the closer together he placed collards (i.e., the more continuous the habitat strip), the faster the rate of movement. Lines of collards were effective corridors for beetle movement, provided the collard habitat was continuous.

The ability of species to reach the tips of the peninsulas considered in section 4 is usually determined by the habitat, and by environmental gradients along the length of the peninsula. For Baja California, a habitat barrier in the centre of the peninsula prevents some species from reaching the tip. This is analogous to a corridor system joining the tip of the peninsula to the mainland: the corridor does not work for habitat specialists that cannot pass through a different habitat in the corridor. Any habitat breaks in a corridor are potentially disruptive to the corridor's function.

All natural habitats are patchy in distribution, and the patch size, or grain, of the environment should be considered in corridor design. When patches are large, corridors must be wide enough to accommodate each habitat type throughout the corridor. For example, suppose that there are two habitat types, A and B, that both habitat types occur as square blocks 100 metres across, and that habitat patches are arranged in a chequer-board fashion. If a corridor is 10 metres across, then it would usually contain alternate 100 m long bands of habitat A and B, and would prevent the movements of habitat-specific organisms that could not cross 100 m of the wrong habitat. Only once the corridor was over 100 m wide would each section of the corridor be sure to contain both habitats, and only when the corridor was 300 m wide would each section be sure to contain a complete patch of each habitat. In this unrealistic system (and in others with more habitat types, also in a chequer-board arrangement), the minimum width to contain a full patch of each habitat in each corridor section is $w(n+1)$, where w is the width of each habitat square, and n is the number of habitat types.

This example is not to be taken literally, but to illustrate that corridors must be relatively wide when there are many habitat types, and habitat patches are large. In reality, habitat patches are not square, they are not regularly spaced, and not all habitat types will be of equal concern.

Some habitat types and populations are not static. It has been advocated that reserve systems should be sufficiently large to ensure the persistence of all of these dynamic habitat types and populations (Pickett and Thompson 1978). For example, breeding pockets of one species of British butterfly were as small as 0.1 ha. Breeding pockets occurred in suitable microhabitats

within heathlands, but the pockets were transient, and the butterfly persisted only in heathlands of over 5 ha: only these provided continuity of habitat (Thomas 1985). In this case, the minimum area of heathland for persistence was at least 50 times greater than the minimum breeding area. Corridors may need to be considerably wider than minimum breeding areas to permit patchy, transient populations to exist within them.

Patchiness and habitat longevity also have bearing on the exploitation of corridors. For example, suppose that an initially pristine forest corridor between reserves was to be logged on a sustainable yield, and that a forest species was restricted to mature forests. Suppose that there were no edge effects (see below), and that the forest species concerned could exist in patches that were 200 m wide. Suppose also that cut patches were 200 m wide, and that the duration of the cycle permitted a specialist on mature forest to use the corridor habitat in only the last quarter of the logging cycle. An uncut, continuous corridor would be adequate for these imaginary species if it was 200 m wide, but would need to be at least four times as wide (800 m) under this imaginary logging scheme if each section of the corridor was to contain some populated habitat. Because edge effects occur in reality (see below), some habitat specialists would persist only if patches were very much larger (and hence corridors much wider). This scenario is intended only for illustration: any activity that reduces the quality of some or all of the habitat within a corridor may greatly increase the width needed to ensure proper corridor functioning.

5.3 Edge Effects and Minimum Patch Size Models

An important determinant of corridor width is likely to be the extent to which habitats are affected by their proximity to the corridor edge. Edge effects were reviewed in a special section in the December 1988 issue of *Conservation Biology*, and in other recent papers (Wilcove *et al.* 1986, Lovejoy *et al.* 1986, Reese and Ratti 1988). If corridors are too narrow, they may be completely "edge", and so fail to act as permanently populated strips between habitat patches.

Several studies have shown that major vegetational changes at habitat edges are often apparent for only 10 to 30 m into a forest (Wales 1972, Ranney 1977, Gates and Mosher 1981), where edges are permanent. Freshly created patches may possess wider edges: these can result in reduced humidity, and in increased tree mortality and increased leaf-fall inside forest (Lovejoy *et al.* 1983, 1986). Indirect effects of edges on the vegetation may take place over distances at least two orders of magnitude greater. The creation of many edges has long been practised as a management technique for increasing deer numbers in North America. This appears to have produced strong impacts of deer browsing (including elimination of some plant species) from <1 km to at least 8 km from edges (Bratton 1979, Alverson *et al.* 1988).

For birds, edge effects have been found at least 25 m (Strelke and Dickson 1980) and up to 600 m into forest habitats (Wilcove 1985). Lovejoy *et al.* (1986) found fewer forest interior birds at 50 m compared to 1 km into Amazonian forest, but, unfortunately, intermediate distances and distance over 1 km were not examined. Deer edge effects are measured in kilometres (Alverson *et al.* 1988). Butterfly edge effects have been recorded for 200 to 300 m into Amazonian forest fragments (Lovejoy *et al.* 1986). Webb and Hopkins (1984) found an

increasing proportional representation of heathland spider species with increasing area of heathland fragments, up to about 150 ha (reading off their Figure 3). Webb and Hopkins also reported edge effects directly. If fragments were circular, edge effects would penetrate for about 700 m from the habitat edge.

Studies that considered species abundances as well as composition have usually found edge effects of about one order of magnitude greater than studies that consider only the presence or absence of species. Although edges often contain some habitat-interior species (at relatively low density), the above data suggest the (unproven) possibility that edges act as population sinks for some habitat-interior species.

Most animal edge effects show changes over distances of a few hundred metres to one kilometre. Although measured plant edge effects are generally smaller (except for animal-induced changes), most studies are in woodlands that have not been isolated for more than one of a few tree generations: longer-distance, long-term edge effects that involve population changes of trees may not have been completed yet.

For habitat-interior species, a corridor that is to provide permanently populated habitat must contain a core of populated habitat as well as an edge on either side. Determination of the minimum core width is less easy than is determination of the width of edges. The percentage of area that is core habitat declines dramatically with habitat fragmentation (Temple and Cary 1988): in their model example a decline in total forest area of 73.9% resulted in a 97.1% loss of core area, and a 90.4% total loss resulted in a 99.8% loss of core area. On the same principle, the narrower a corridor becomes, the lower the proportion of core habitat.

Temple (1986) found that bird species presence and abundance was more closely correlated with core area of forest fragments than with total area of each fragment. The minimum core diameter of a patch that will support a given habitat specialist should be adequate for the core width of a populated corridor. In Temple and Cary's (1988) model, there were edges of 100 m (which they designated poor quality habitat), areas from 100 to 200 m from an edge (intermediate quality), and core habitat (good quality). Habitat-interior species persisted in a moderately fragmented system in which cores were rarely more than 400 m wide (i.e., double the edge effect), but in these simulations the population stabilized at only 15% of the landscape's carrying capacity. In a severely fragmented system, core width was up to 200 m to extinction of habitat-interior species was rapid, unless supplemented by immigration. The model values were designed to match real values for Wisconsin birds and forest fragments. A corridor occupancy of 15% seems undesirably low, unless connected reserves are very large. Corridor cores in excess of double the width of an edge seem warranted.

Several other studies have considered area: perimeter or edge-to-size ratios for reserves (e.g., Game 1980, Beuchner 1987a, b, Stamps *et al.* 1987). These are based on the concept that small reserves, with a high ratio of edge, are more likely to be disrupted by the emigration of "desirable" species out of them, and from the immigration of "undesirable" species. It may be possible to adapt these models to consider length: width ratios for corridors. Long thin corridors possess a higher edge: centre ratio than do short wide corridors. Thus, long thin corridors may be more likely to pass out of the corridor if it is long and thin, and undesirable species outside may be relatively likely to penetrate these corridors.

At present, minimum patch models simply provide an analogy. They are most useful in identifying important parameters. The following is based on models by Buechner (1987a, b) and Stamps *et al.* (1987). The first important parameter is the edge-to-size ratio itself. The probability of emigration for habitat-interior species is lower when the edge-to-size ratio is low (i.e., species are unlikely to emigrate from large patches, or wide corridors). Edge permeability and habitat preference also affect emigration. If edges are "hard" (recognizable boundaries) organisms are relatively unlikely to emigrate, and if habitat preference is strong organisms are unlikely to emigrate. Therefore, habitat-interior species are least likely to leave habitat patches if they are large, have easily detected edges, and if those species have a strong preference for the interior habitat. The parameters also interact. Habitat preference and edge permeability are relatively important when there is a high proportion of edge, but not when the proportion of edge is low (Beuchner 1987b, Stamps *et al.* 1987). This means that relatively short-wide corridors (with a low proportion of edge) will be adequate for all habitat-interior species, but long-thin corridors will be adequate only for species with a strong habitat preference and if the corridors have easily-detected edges.

Models by Buechner and by Stamps *et al.* are based on the proportion of home ranges that are adjacent to the edge, not on measured distances. If realistic, this implies that minimum core area (and core width of a corridor) is likely to be directly proportional to home range area. In Buechner's model (1987b, her Figure 3), at least two-thirds of dispersing animals stayed in the reserve (even when animals did not show habitat preference and when patch edges were permeable) when there was four times as much core as edge. A cross section of a corridor designed in this way would possess an edge of one unit at either side, with a core eight units wide. In fact, habitat boundaries are rarely completely permeable, and habitat-interior specialists usually do show habitat preference (i.e., they would be more likely to move along a corridor than out of its side), so this result may be unduly pessimistic. Even so, cores would usually need to be several times wider than the width of each edge. In summary, according to minimum patch size models, we can predict that core widths would usually need to be between two and eight times as wide as an edge to ensure that a corridor will be permanently populated.

Edge effects also have implications for alternative land-uses and management of corridors. Natural (e.g., rivers) and artificial (e.g., roads) breaks in a corridor may provide substantial barriers to habitat-interior species: these species are faced with a barrier of two edge effect widths plus the width of the actual break. Some types of management may convert the entire corridor to "edge". For example, selective removal of only a few percent of the trees from a forest may create sufficient openings to ensure that the forest is entirely edge habitat. This may prevent habitat-interior species from using the area as a corridor.

5.5 Corridor Design Guidelines

Far too few real examples of corridors have been studied to be able to give definite recommendations for the design of corridors. These guidelines are tentative, based on limited current knowledge, and should be used only with caution and with regard to specific local conditions (as with Diamond's (1975a) and Wilson and Willis' (1975) reserve design

guidelines. These corridor design guidelines are specific to corridors linking like habitat patches (section 3.1.2, Type A) with permanently inhabited corridors (section 3.1.3, Type 2i). These corridors are intended to function both as conduits and as habitat for habitat-interior species.

Habitat in the corridor should be similar to, or the same as, habitat in the patches that are being connected.

When several habitat types exist, corridors should be wide enough to encompass each habitat type in each segment of the corridor, as far as possible.

When the spatial distributions of habitats and species populations are patchy, and the positions of patches change over time, corridors must be sufficiently wide to enable natural patch dynamics to take place in them. Corridors should usually be wider than the mean inter-patch distance.

Corridors should be sufficiently wide that they are not entirely edge. In forest, edge effects are commonly found for up to 500 m.

Habitat breaks across corridors (e.g., roads) should be minimized or eliminated since they may constitute a habitat barrier of two edge widths (plus the width of the break) across the corridor, and impair its function. Habitat modification (e.g., selective logging) that creates many edges should be minimized or eliminated as these activities may impair corridor functions for habitat-interior species.

The longer a corridor, the wider it should be in order to ensure that the corridor is continuously populated, and that organisms can pass from one end to the other.

In long corridors, the core width should usually be at least several times wider than the combined width of the two edges. For example, if one edge effect is 500 m, then the corridor should be at least 3 km wide -two edges plus at least 2 km of core. (If some sections of corridor are narrow or disrupted, adjacent sections should be wider than this.)

Corridor habitat is often partially modified at the time of corridor designation, and habitat restoration may be needed. Damaged habitat that can be restored in the long-term may be adequate for corridor designation since most corridor benefits are expected to occur in the long-term.

When these design criteria cannot be met, less complete designs may still fulfil useful corridor functions, but their benefits are less predictable. Existing, connecting strips should not be abandoned if they do not meet all of these design criteria.

6. PROS AND CONS OF CORRIDORS

Noss (1987) provided a list of some potential advantages and disadvantages of ecological corridors. The following is an elaboration of his scheme.

6.1 Possible Advantages

- Increase immigration rates into reserves, which could:
 - increase or maintain species richness
 - provide a "rescue effect" for populations at low levels
 - allow recolonization following local extinction
 - reduce genetic drift, maintain heterozygosity, and avoid inbreeding depression
 - allow "beneficial" genes to spread from one population to another
 - permit the spread of "beneficial" learned (cultural) behaviours from one population to another.
- Permit two separate reserves to become effectively one, providing the first and fourth benefits listed above, and
 - reduce the probability of population extinction by increasing populations size
 - increase the foraging area for wide ranging species
 - prevent social dysfunction
 - provide a mixture of habitats and/or resources to permit seasonal use of different resources or use of different resources by different stages of the life cycle.
- Corridors may provide organisms with access to resources outside reserve systems, and in other habitats.
- Resources are provided within corridors.
- Corridors may provide suboptimal habitat than can buffer populations on reserves against population fluctuations.
- Corridors may provide predator-escape cover for movements between patches.
- Corridors may enable human managers to gain access to wildlife (e.g., for census) and pests (for control).
- Corridors allow migratory movements.
- Corridors permit distributional changes (e.g., latitudinal, altitudinal) in response to environmental change.
- Corridors enable escape from disasters.
- Natural corridors act as barriers to livestock, and may limit the spread of agricultural pests.

6.2 Possible Disadvantages

- Corridors will increase immigration rate into reserves, which could:
 - facilitate the spread of diseases/pests etc. between reserves
 - disrupt genetic adaptations to local conditions (outbreeding depression), reducing genetic differences between populations
 - disrupt cultural adaptations to local conditions.

- Small, isolated patches may support desirable species that are eliminated from large or connected patches by predators or diseases. (It may be easier to eliminate aliens/undesirable species from small, isolated reserves.)
- Corridors may permit wildlife to become pests in agricultural and other habitats. Wildlife entering other habitats via corridors may survive poorly/encounter hunters, predators, etc. Wildlife may transfer disease to livestock/crops, and vice versa, via corridors. Exotic species may invade corridors and then gain access to reserves.
- Corridors may provide sub-optimal habitat, which can act as a population sink, reducing population densities on reserves.
- Corridors may provide external predators access to prey in the habitat corridor and may provide hunters/poachers access to wildlife in corridors.
- Corridors may permit the spread of contagious disasters (e.g., fire) from one reserve to another.
- New corridors between geologically/geographically separate regions may produce many extinctions. However, conservationists have not proposed creating new corridors of this type.
- Poorly designed corridors (e.g., containing habitat barriers) may fail to act as conduits.
- Resources spent on corridors might be better spent on preserving other habitat fragments of higher intrinsic value, elsewhere. As corridors have relatively high ratios of edge to interior habitat, it may be more useful to preserve a roughly circular patch of the same total area, if interior habitat is of greater value than edges. Corridors with a high proportion of edge may be hard to police.

7. THE NORTH WESTLAND CORRIDOR

The North Westland corridor system connects ecological areas that would otherwise be too small to contain viable populations of most key forest bird species. The corridors also allow unimpeded seasonal migrations between upland and lowland forests. In the long-term, these corridors may permit population migrations in response to environmental change (e.g., global warming). The Reefton Saddle area may also represent a natural biogeographical link between the Paparoa Range and the Southern Alps. There are many potential advantages of the North Westland corridor system. Most potential disadvantages can be eliminated or reduced by suitable management.

Commercial forestry activities are not compatible with the conservation of key forest-interior species in the corridors. Past commercial forestry activities have damaged some corridor segments, but these areas could be restored by allowing natural regeneration to take place.

Some relatively small additions to the corridor system are recommended. It is concluded that the corridors in North Westland are likely to increase the long-term value of existing reserves in the region.

7.1 Introduction

Assessment of the value of the North Westland corridor given in this report is based on general corridor principles outlined in the previous sections. This report does not consider the intrinsic values of the corridor habitats. The designation of reserves (Ecological Areas - EAs) and corridors are shown in Figure 7.1 and Table 7.1. Approximately one-fifth of the total area of 50,000 ha is designated as wildlife corridor (Table 7.1).

7.2 Minimum Population Size

At present, a single area of nearly 50,000 ha exists, connected at each end to mountainous ranges of much greater areas. If the 10,000 ha of corridors were eliminated, seven separate reserve blocks would exist, each of the area shown in Table 7.2. Two of these are small pakihis (blocks B, G), and will not be considered further. The remaining areas are forest, although some past forestry activities have taken place in some of these. Would any of these areas be able to support populations of key species if they were to be isolated?

O'Donnell (1991) identified key bird species of interest in the North Westland area. Of the 16 forest species in the region that are endemic to New Zealand, eight are forest specialists, and four of these are nationally threatened or rare (O'Donnell 1991). These four species are great spotted kiwi, kaka, yellow-crowned parakeet and yellowhead. The following summarizes and elaborates on O'Donnell's findings for these four species.

Great spotted kiwi may occur at a density of only one bird per 70 ha, resulting in an estimated population size of about 712 if all corridors and ecological areas were connected. This connected value is adequate for the long-term maintenance of birds of normal demographic variability (section 2.3), provided gene flow with adjacent areas is assured. However, it is unknown whether great spotted kiwi exhibit normal variability. If corridors were eliminated, and assuming the same density, the largest block of contiguous ecological area (Table 7.2) would contain fewer than 250 birds. This is lower than recommended MVP levels. Assuming the same density, the whole Paparoa Range (150,000 ha) may hold a population of about 2,000 great spotted kiwi. This population size is not sufficiently large to ensure persistence if populations have unusually high demographic variability (section 2.3), so the maintenance of the existing corridor between the Paparoas and the Southern Alps would seem to be a prudent conservation measure for this flightless bird.

Kaka densities are poorly known, but the total connected area of 50,000 ha is unlikely to contain more than one hundred to a few hundred birds (O'Donnell 1991). Parakeet densities are even less well known, but they have been recorded at the same density as kaka elsewhere on the mainland (Kikkawa 1966). For these two parrot species, even the whole Paparoa Range of 150,000 ha may hold populations of only a few hundred to a thousand. The linking of ecological areas and connection of the Paparoas to the Southern Alps seem likely to be important for the conservation of these species.

Fig. 7.1 Map of areas mentioned in the text. See Table 7.1.

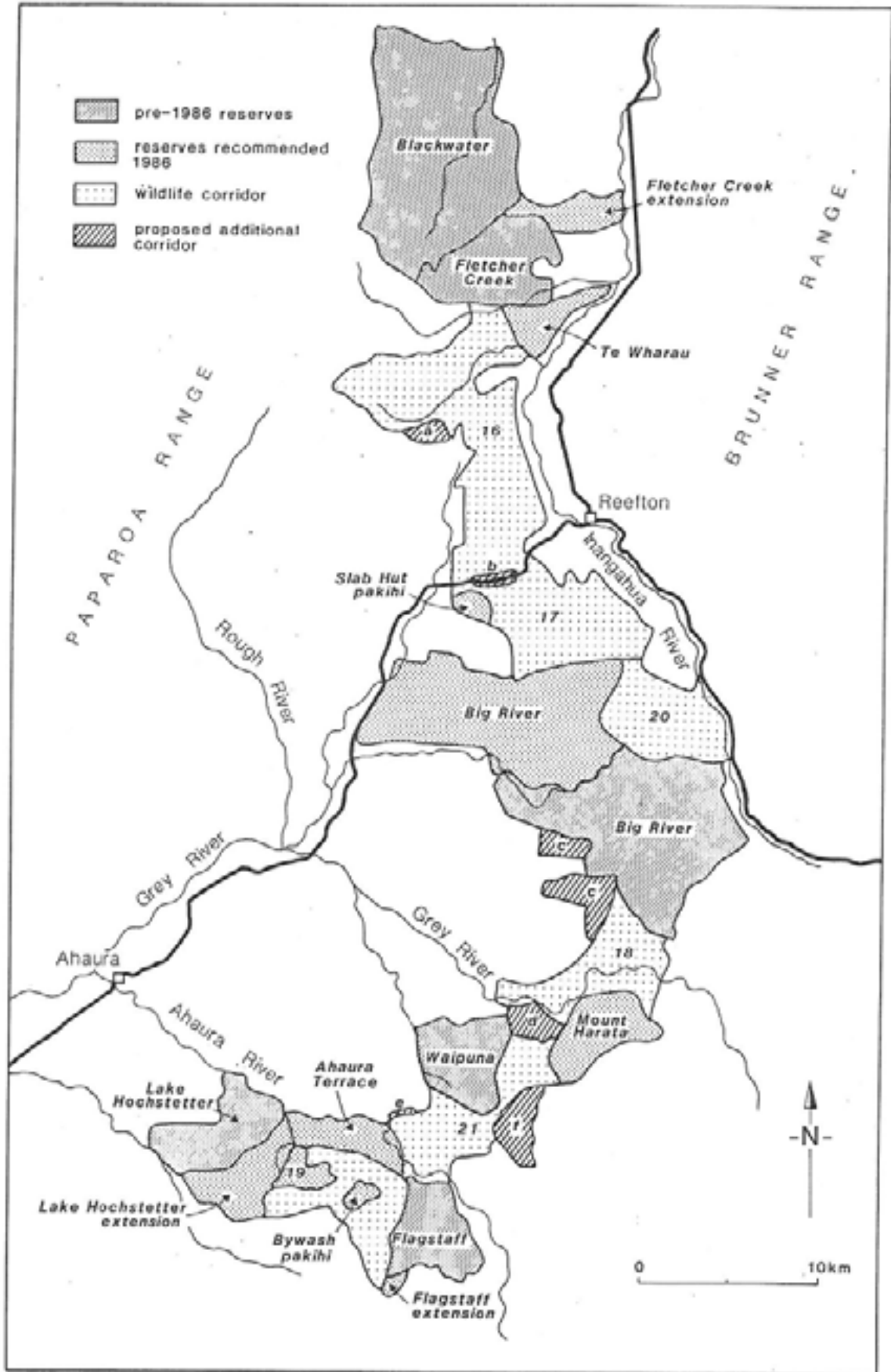


TABLE 7.1 Reserves agreed upon in the vicinity of the North Westland Wildlife Corridor (from O'Donnell 1991). Numbered areas refer to Figure 7.1.

RESERVES IN EXISTENCE PRE-1986	Area (ha)
1 Blackwater Ecological Area (EA)	9,105
2 Fletcher Creek EA	2,586
3 Big River EA	6,733
4 Waipuna EA	1,910
5 Lake Hochstetter EA	1,803
6 Flagstaff EA	1,622
Total	23,759
NEW RESERVES RECOMMENDED IN 1986	
7 Fletcher Creek EA extension	504
8 Te Wharau EA	300
9 Slab Hut Pakihi EA	120
10 Mount Harata EA	1,590
11 Big River EA extension	10,000
12 Ahaura Terrace EA	1,110
13 Bywash Pakihi EA	127
14 Flagstaff EA extension	475
15 Lake Hochstetter EA extension	526
Total	14,752
Wildlife Corridors (areas 16-21 combined)	10,246
Amenity Reserves	1,087
GRAND TOTAL	49,844

TABLE 7.2 Areas of contiguous reserve blocks in the absence of corridors. Area numbers correspond to those in Table 7.1 and Figure 7.1.

Block	Areas included	Total area (ha)
A	1, 2, 7, 8	12,495
B	9	120
C	3, 11	16,733
D	10	1,590
E	4	1,910
F	5, 6, 12, 14, 15	5,536
G	13	127

Yellowheads are practically extinct in the corridor system already (Gaze 1985).

Unfortunately, little information is available on population sizes of other animal groups in the area, and the spatial dynamics of the forest are little understood. For key bird species, existing corridors should certainly be maintained. For birds, there would also be a strong argument for the conservation of any additional lowland forest that is not designated as conservation land already.

7.3 Corridor Type and Function

The North Westland corridor system was intended to function as a conduit and as habitat in its own right. Different sections of the corridor system may be classified in different ways.

Corridor Type Ai. These corridors connect small areas, potentially increasing the survival of various species in the system. This type of corridor is applicable in corridor segments 19 and 21, which link otherwise isolated and relatively small ecological areas (Figure 7.1). For very low density species, such as kaka, the Paparoa Range may represent one small area, and the Victoria and Brunner Ranges another: for these species, the Reefton Saddle (corridor segments 16, 17, and ecological area blocks A-C in Table 7.2) would represent an ecological corridor of this type, connecting the ranges.

Corridor Type Aii. These connect small areas to large areas. Corridor segment 21 acts in this way, connecting the Waipuna, Flagstaff, Ahaura and Hochstetter EAs to Granville State Forest. Segment 19 connects Bywash Pakihi EA to block F, and segments 16 and 17 connect Slab Hut Pakihi to blocks A and C. Some of these smaller areas can expect to contain or be visited by key species that would be absent were the ecological areas to be isolated.

Corridor Type Aiii. These connect large areas. The Reefton Saddle (corridor segments 16, 17, and ecological area blocks A-C) connects the Paparoas with the Victoria Range. For species with viable populations in both ranges, the corridor is likely to represent a link that permits gene flow between populations in the two ranges.

Corridor Type C. Migratory corridors. Corridor segments that connect low and high elevation forest are considered of particular importance to various bird species that exhibit altitudinal migrations (reviewed by O'Donnell 1991).

These corridors may also permit the movement of species to infrequently-available resources. Many tree species in the area fruit only infrequently, and corridors may be important in allowing bird species to exploit these fruit. As an extreme example, extension 14 of the Flagstaff ecological area contains a large stand of silver pine. Silver pine produces seeds in large quantities only very infrequently (about once a decade), but may be an important food source for some species when it does (e.g., for parakeets).

Although this example is speculative, such resources would be unlikely to be found unless they were linked into a reserve system.

Corridor Type D. Environmental gradients. Several corridor segments contain a range of elevations, and abut higher elevation land. In the face of global warming, these could potentially be important in allowing low elevation species to survive by gradually moving upslope. Northwest Nelson contains many endemic species, and other species reach their southernmost limits there and in the Paparoas (see McGlone 1985). Should some of these species spread southwards in response to global warming, the Reefton Saddle could constitute an important future route for these species to the Southern Alps.

Corridor Type E. Geographical links. The Reefton Saddle (corridor segments 16, 17, and ecological area blocks A-C) connects the Paparoas with the Victoria Range. This saddle may well represent an important biogeographical link between ranges, pre-dating recent deforestation by humans. On all other sides, the Paparoa Range is isolated by the Tasman Sea, and by the Buller, Inangahua and Grey Rivers. The Reefton Saddle represents the only uninterrupted connection to the Southern Alps. Deforestation has accentuated the isolation of the Paparoas, and increased the importance of the remaining link.

Corridor Type 2. Inhabited corridors. All corridor segments contain important low elevation habitats that support a rich fauna and flora. These habitats are used seasonally by a number of forest bird species. The loss of the corridor habitats would be likely to reduce numbers of these birds at higher elevations at other times of the year (e.g., Dawson *et al.* 1978, Wilson *et al.* 1988, O'Donnell 1991). Unfortunately, some areas have suffered from clear-felling and selective logging and are no longer permanently populated by some habitat-specialist species (see below).

The North Westland corridor system falls into several categories. At least some of the potential benefits of these different types of corridor are likely to be realized.

7.4 Corridor Design

There is no single "best design" for a corridor system, but existing corridor segments in the North Westland area would be largely adequate to fulfil the above functions, had some areas not been subject to forestry activities in the past.

7.4.1 Potential Additions.

There are a few holes in the corridor. Some of these are due to past human disturbance, and require restoration (see below), but others are holes in ownership (Fig. 7.1).

(a) The northern end of the Reefton Saddle is extensively modified. Adjacent to this is a small additional area (Jacks Creek, GR K30 0702) of only partially modified forest. Including this in the corridor would improve the quality of the northern link.

(b) In the centre of the Reefton Corridor, along the main Reefton to Greymouth road, is a thin strip of land under private ownership, most of which is now pasture. Eventually, it would be desirable for this to become part of the corridor, and for the pastures to be restored to forest.

(c) Snowy River. Much of section 3 of Big River EA is at relatively high elevations. There is only a very limited low elevation link between the lower elevation parts of Big Rive EA (mostly in section 11) and low elevation corridor segment 18. At present this constitutes a partial gap in the low elevation forest, separating the reserve network into northern (Blackwater to Big River) and southern (Alexander River to Flagstaff/Hochstetter) halves. To improve this link, it would be desirable for the area north of the Alexander Water race, including part of the Snowy River valley, and for part of the Brown river valley south of the water race, to be incorporated in the corridor. This would then link up with Waiuta Amenity Area and a small section of Victoria State forest (which should also be included), and hence

connect with the lower elevation parts of Big River EA. Much of this proposed link has been selectively logged already, but could be restored (below).

(d) A relatively large section of private ownership exists between corridor segments 18 and 21. Eventually, it would be desirable for this to be incorporated into the corridor, and restored.

(e) A small area of Forest Corp land, at Big Gully (GR K31 0565), is surrounded by corridor and other DoC lands. This should be incorporated into the corridor.

(f) If the area around Granite Creek (GR L31 1163) were to be zoned as corridor (rather than as production forestry), the value of the southern portion of the reserve system would be greatly enhanced. This would strengthen the link between the small, southern ecological areas and Granville State Forest.

In total, these additions would add about 5% to the reserve and corridor area.

7.4.2 Forestry in Corridors.

Some key bird species are unable to persist in selectively logged forests (reviewed by O'Donnell 1991). Kaka are normally eliminated by logging. Although some key bird species can return to logged-over forests after some decades, rotational selective logging in corridors would result in corridors being poor or useless for these bird species for most of the rotation. O'Donnell (1991) presents a table showing comparative densities of six forest bird species in logged and unlogged forest: I have tested these results statistically. To do this, I pooled two of O'Donnell's three categories. I then compared whether a given bird species occurred at lower (including absence) or higher density in logged or unlogged forest, using two-tailed binomial tests. All six species were significantly more likely to occur at higher densities in unlogged forests ($p = 0.0002$ for kaka, $p = 0.003$ for parakeets, $p = 0.02$ for rifleman, $p = 0.0005$ for brown creeper, $p = 0.013$ for tomtit, and $p = 0.013$ for robin).

Dugdale (1974) found that the number of arthropod species in samples was lowered by about a third in cut-over forests compared to uncut indigenous forest. Because some species that are characteristic of edges and open country would presumably be represented in the samples from cut-over forests, the effects on forest-interior species would have been more detrimental than the overall loss of one third of the species.

Selective logging that removes only a few percentage of the trees is likely to convert most of the forest to edge habitat. This would be detrimental to most habitat-interior specialists. Forestry activities are not compatible with the conservation of key bird species in these corridors, and information is limited on other groups.

7.4.3 Habitat Restoration.

Various human activities have disrupted parts of the existing corridor system, and these sections require restoration. Over extensive areas, selective logging has removed some of the timber (mostly mature podocarps), leaving the remaining forest as a jungle of edges. Natural regeneration should eliminate most of these edges in a hundred or so years, although there would still be a lack of ancient podocarps. Once this succession has taken place, most of the corridor would be operating as projected.

Other areas may require more specific attention:

At the northern end of the Reefton corridor, extensive induced pakihis sever all but two or three thin links between the Paparoas and the rest of the Reefton Saddle. Succession will eventually restore the pakihis to forest (provided fires are prevented), but additional planting might be desirable. Replanting should be of seedlings grown from seed collected locally. Some pakihis areas could be kept open for pakihispecialists.

The bottomlands in one of the valleys in corridor segment 16 have been cleared, and may require some replanting to speed restoration.

The road and railway from Reefton to Greymouth form a break in the corridor. In some places, scrub exists between the two and could be allowed to regenerate to forest. Some replanting may be needed. (see also 7.4.2, above).

In this last area, and also in various other sites (e.g., in sections 15 and 19, Figure 7.1), exotics have been planted. It would be desirable to remove these before they seed heavily. Otherwise, extra work will be needed to ensure that exotics do not regenerate after the present crop has been harvested. Again, replanting with native trees and shrubs may be needed.

7.5 Possible Problems

Although the spread of diseases etc. along corridors is a potential problem, those species of greatest concern (i.e., those with small population sizes) are more likely to be endangered by severing the links than by keeping them: if links were severed, the resulting isolated populations would be too small to be viable in the long-term.

Problems may arise in connected reserve systems if exotic pests can become established. For example, deer, goats and pigs may cause problems for the native fauna and flora, and be impossible to eliminate because of the connected nature of a reserve system. Deer (and perhaps also goats) thrive in edge habitats that are created by logging activities (section 5.3). Therefore, connected systems in which commercial forestry activities do not take place may in fact maintain relatively low pest densities. Since, the New Zealand landscape contains many isolated fragments, species that cannot persist in large reserves (because of browsing/predation by these large exotic vertebrates) can probably be preserved elsewhere. Where pigs are known to threaten populations of large native snails, it may be possible (although expensive) to fence key areas and exclude pigs from them (pig exclosures are used in Hawaii Volcanoes National Park, USA). If present corridor segments were to be used for commercial forestry, they would still contain these introduced vertebrates (probably at increased densities).

There could be problems arising from the transfer of native organisms out of reserves, and of alien organisms and diseases into reserves systems, via corridors. Some introduced animals have already entered this reserve system, and exotic plants (mainly pines and eucalypts) have been planted. Ensuring that the corridor remains in a condition of unmodified habitat should

minimize these problems, and physical removal of planted exotic trees will be needed. It is unknown whether modified habitats in corridors now act as population sinks for wildlife in reserves. Habitat restoration will again solve this potential problem.

Corridors may provide access for hunters/poachers. Usually, this will be beneficial since the quarry is mostly feral vertebrates. However, possum trapping can severely reduce populations of kiwi, and probably also of some other birds. Since possums cause extensive damage to native vegetation, some possum control is desirable: strict policing of trapping (to ensure that traps are not placed flat on the ground) and the use of poison and disease as alternatives to trapping may be required.

Contagious disasters will not necessarily be prevented if habitats between reserves were to be logged rather than kept as corridors. For example, logged forests contain more ground-level fuel, so uncut corridors would in fact decrease the likelihood of problems from fire.

At present, parts of the corridor have been logged, and may pose habitat barriers to forest-interior species. Again habitat restoration will solve this, along with a few additions to the corridor system (section 7.4.1).

If 10,000 ha are to be preserved somewhere, careful consideration should be given to whether the corridor segments under consideration are the best available areas of forest to preserve. The corridor segments considered here do have substantial intrinsic value (and will have greater value after restoration): corridor segments contain areas of rich lowland forest, which is still under-represented in New Zealand reserve systems.

In summary, there are many potential benefits from the North Westland corridors: additional evidence is given by Best *et al.* (1986) and O'Donnell (1991). A number of birds species, and undoubtedly some other wildlife, cannot be preserved adequately unless large or linked reserves are provided for them. Although the list of potential disadvantages is nearly as long as the list of potential advantages, most of the disadvantages can be eliminated or reduced by adequate management and restoration of corridor habitats. The maintenance of unmodified corridors and restoration of those that have been damaged would appear to be important conservation measures in the North Westland region.

8. FUTURE RESEARCH NEEDS

Few major research projects concerning the functioning of corridors could be completed by 31 December 1991. The research suggestions listed below are areas in which the international literature is of limited value, and areas of particular interest to the North Westland corridor system. Assuming that funds are limited, my recommendation is that they should be assigned to the first four topics listed below. Although several authors have emphasised that few specific tests of corridor theory have been published, international interest in corridors has increased rapidly in the past five years. The two studies that were designed as specific tests of corridors have been published this year (1989), and it is likely that many more studies will be published over the next five years. Therefore, it is probably of greater value to DOC to undertake research on the applications of corridors in New Zealand than to test the theoretical validity of corridors directly.

Forestry practices: Study the effects of various forestry practices on vertebrates other than birds, invertebrates and plants to assess the permissibility of these activities taking place within designated corridors and other forested areas.

Identify key species and groups of species (apart from birds) that are of greatest concern in North Westland and which might benefit from the corridor system.

Species studies: Undertake major, long-term studies (and increase existing studies) of all key species that have declined in the present century (e.g., kaka, parakeet, yellowhead, carnivorous snails, and others identified under topic 6). Are these species still declining and, if so, at what rate and why? For birds, rates of decline (or increase) could be assessed initially by a programme of repeating bird counts that were carried out in the past, in the same areas, and under the same conditions. However large an area is preserved, and however many corridors are provided, these species will not be protected in the medium- to long-term unless the causes of decline within large areas of undisturbed habitat are identified, and checked. For species that continue to decline even within "suitable habitat", connected reserve systems may prolong the time to extinction, but they do not prevent extinction. Such reserve systems do, however, give biologists a few extra years to undertake the work needed to solve the underlying problems and establish recovery programmes for these species. Furthermore, unless unmodified reserve networks are available, recovery may never be possible. Research must start before species are on the point of total extinction. Now!

Identify other areas in New Zealand for potential corridor designation, for the preservation of endangered populations and species in reserve networks (e.g., for kokako, see McSweeney 1989) and to enable species to undertake distributional changes in response to predicted climatic changes.

Genetics: Empirical studies have provided little information on the role of corridors in permitting gene flow between otherwise isolated areas. A comparison of heterozygosities and genetic distances in connected and unconnected systems would be very hard to undertake in the field (because of the problem of replication), although the results of such a study would be of international significance (O'Donnell 1991). A large research effort would be required to do this properly, and the study system would have to be chosen or created carefully. This sort of study could not be completed easily in the North Westland area, nor by 1991.

Edge effects: Study the effects of edges on population densities and reproductive success for a variety of forest-specialist species of animals (e.g., snails, insects, birds) and plants in North Westland. This information could be used in estimating minimum corridor width, and in assessing the potential conservation values of other isolated patches of forest of various shapes and sizes.

Habitat restoration: Investigate ways of enhancing regeneration in modified habitats in existing corridors and ecological areas.

Modelling: Investigate the effects of different levels of timber extraction on the proportion of edge habitat in a forest, and on different species with different degrees of reliance on core (non-edge) habitat.

Undertake studies of the relationship between bird counts and actual bird densities (using banding, etc.), in different habitats and in different seasons, so that bird count data can be of much greater use in conservation planning and monitoring. Bird densities estimated by O'Donnell (1991; see section 7) are only "educated guesses". If bird counts could be converted to real densities (with estimated errors), assessment of minimum areas would be less difficult.

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Appendix 1: Minimum Viable Populations article in full.

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