The Role of Metapopulations in Conservation

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The role of metapopulations in conservation

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Nothing in the world is single;
All things, by a law divine,
In one another's being mingle.
(Percy Bysshe Shelley (1792–1822), 'Love's Philosophy')

Introduction

Wherever wildlife management concerns the movement of individuals across structured habitat, its scale of operations will encompass metapopulation dynamics. The goal of this essay is to review the potential applications of metapopulation concepts and models in reserve design and conservation management. Our perspective is forward-looking. We show how some key problems of where to direct conservation effort and how to manage populations can be addressed in the context of regional habitat structure and the survival and renewal of habitat patches. We also mention several cases of successful metapopulation management and point out practical problems (for example, see Box 5.1)

We emphasize:

1. that the viability of a population may depend on surrounding populations, in which case metapopulation processes influence or determine reserve design and management options;

2. that understanding the dynamic processes of populations requires models, which make assumptions that need validating;
3. that the principle limitation of metapopulation models is their single-species focus.

Conservation strategies clearly depend on the particular social, economic and ecological circumstances of each region, and concepts such as the metapopulation can seem irrelevant to practical concerns. We aim to show, nevertheless, that an understanding of metapopulation dynamics can be vital to asking pertinent questions and seeking potential solutions. The conceptual framework of metapopulation dynamics tells us what information is needed in order to build case-specific models relevant to any of a wide range of issues. These issues include: the potential disadvantages of habitat corridors, or hidden benefits of sink habitat; the optimal schedule for translocations or reintroductions; the relative merits of reducing local extinctions against increasing colonizations; the optimum distribution of habitat improvement; and the advantages of increasing life spans of ephemeral habitats.

Concepts

We define a **metapopulation** as a set of discrete populations of the same species, in the same general geographical area, that may exchange individuals through migration, dispersal, or human-mediated movement (based on a very similar definition by Hanski & Simberloff 1997). Older, more restrictive definitions of metapopulation (e.g. Hanski & Gilpin 1991) reflect particular approaches to modelling, for example, by requiring that populations have independent (uncorrelated) fluctuations, are all equally connected by dispersal (Levins' 'island–island' model), or that one population is much larger and less vulnerable than the others (MacArthur and Wilson's 'mainland–island' model). Most criticisms of the metapopulation concept (e.g. Dennis et al. 2003) arise from shortcomings of these more restrictive definitions (Baguette & Mennechez 2004). Over the past decade, the trend in metapopulation concepts has moved from abstract models toward real-world applications. Our more general definition has only two requirements: (i) populations are geographically discrete; (ii) mixing of individuals between populations is less than that within them – otherwise the regional assemblage of local populations may be more aptly described as a single panmictic population. Within these limits, the definition encompasses all levels of variation between populations in colonization rates (including the extreme of 'source–sink' systems, detailed later in this essay) and in extinction rates (including synchronous extinctions, detailed later in this essay). We emphasize that a metapopulation is a dynamic system of linked populations, as opposed to simply a patchy habitat, and many of its demographic processes are visible only through the filter of models.

Although the focus of this essay is on species conservation in habitat fragmented by human activities, metapopulations occur in a variety of forms without any human intervention. Many species depend on habitat patches created by natural disturbances such as fires. Other examples of natural metapopulations include species inhabiting discrete water bodies such as ponds and lakes; despite the physical isolation of freshwater habitats, their populations of aquatic plants and invertebrates may be widely interconnected by birds inadvertently transporting propagules between them (Figuerola & Green 2002), and their populations of amphibians are often interconnected by seasonal dispersal through the landscape. Amongst mammals the Ethiopian wolf (*Canis simensis*) is naturally confined to rodent-rich alpine meadows, but is threatened with extinction by the intervening terrain between plateaux becoming too hostile to allow safe passage (Macdonald & Sillero 2004). Mountain sheep (*Ovis canadensis*) populations in southern California inhabit mountain 'islands' in a desert (Fig. 5.1); this species cannot live for long in the desert, but it can migrate through it (Bleich et al. 1990).

A **sink** is a population with deaths exceeding births and extinction only averted by immigrants exceeding emigrants. Conversely, a **source** is a population with a net outflux of individuals. The identification of sources and sinks is complicated by temporal and spatial variability, and density dependence in demography and dispersal (detailed later in this essay).

Habitat corridors are more-or-less linear strips of habitat with a designed or incidental function of increasing dispersal among populations. We focus specifically on human-modified habitat, additional to natural linear features (such as riparian habitat) that may already link populations. Corridors such as field margins supplement hedgerows which were planted to meet needs not directly related to conservation, but which are increasingly nurtured for their conservation value. Corridors may provide a continuous stretch of habitat between populations, or discontinuous patches that improve connectivity in 'stepping-stone' fashion. A corridor for movement in one direction may simultaneously act as a barrier in the
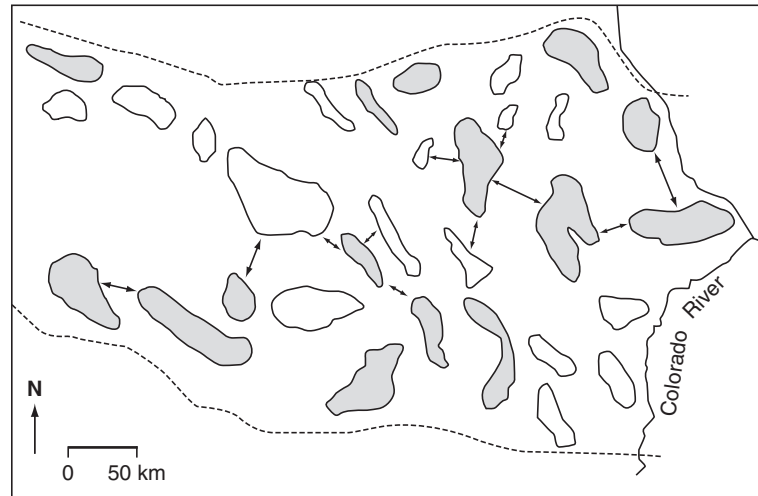
Fig. 5.1 Populations of mountain sheep (*Ovis canadensis*) in southern California. Shaded areas indicate mountain ranges with resident populations, arrows indicate documented intermountain movements; the dotted lines show fenced highways. (After Bleich et al. 1990; reprinted from Akçakaya et al. 1999 with permission from Applied Biomathematics.)

perpendicular direction (such as road verge: Rondinini & Doncaster 2002).

Issues and options

Does conservation need metapopulation concepts?

Animals and plants may occupy metapopulations wherever landscapes are either naturally heterogeneous, or fragmented as a result of human activities such as habitat loss to urbanization, agriculture and transportation routes. Metapopulations are thus relevant to the conservation of any patchy or fragmented habitat. They are also relevant to the conservation of a single population if its dynamics depend on those of neighbouring populations.

One misunderstanding is that the use of the metapopulation concept in conservation requires or implies the conservation or management of species as multiple populations. In some cases, maintaining more than one popu-

lation does increase the persistence of the species as a whole, but this is neither universal, nor a necessary result of using a metapopulation approach. Thus, what conservation needs is not necessarily metapopulations *per se*, but the metapopulation approach and concepts, which permit assessment of the persistence of a species that happens to exist in a metapopulation, either naturally or due to habitat loss and fragmentation. The metapopulation concept is important because species that exist in a metapopulation face particular issues related to environmental impacts, and have conservation options that can be evaluated more completely, or only, in a metapopulation context. These are discussed in the next two sections.

Environmental impacts in a metapopulation context

Metapopulations can be affected by impacts on their entirety or on the individual components. Impacts studied at the regional level include roads and other dispersal barriers that decrease

connectivity of populations, and habitat frag-mentation that divides a homogeneous popula-tion into several smaller populations. The effects of such factors on the overall viability of the species involve interactions among popu-lations (e.g. dispersal and recolonization), and as such they can be assessed or studied only in a metapopulation context.

Impacts such as hunting or fishing may re-duce reproduction or survival of individuals in particular populations. For example, hunting pressure or fishing mortality may differ be-tween neighbouring populations, and failure to incorporate the variation into quotas may result in overexploitation, even if the regional harvest is set at a conservative (precautionary) level (Smedbol & Stephenson 2004). An overall harvest level set for a metapopulation may even lead to a series of local extinctions (or a serial collapse of stocks), if most hunters (fish-ermen) focus on the same few populations with easiest access. After these are locally extinct, the focus shifts to remaining populations with the easiest access. Thus, many local extinctions can occur serially, although the overall (re-gional) harvest quota is precautionary and is never exceeded. Dynamics of these sorts may have contributed to the collapse of the New-foundland cod fishery in 1992 with the loss of 40,000 jobs and no recovery in sight.

Conservation and management in a metapopulation context

Conservation options for species that exist in metapopulations include those that aim to increase the size or persistence of individual populations, as well as those that aim to benefit the metapopulation.

The conservation options at the single popu-lation level include habitat protection or im-provement, regulation of harvest, reduction of predation and removal of exotic species. Even these measures that target individual popula-tions may need to be evaluated in a metapopu-lation context, because the presence of other populations may change the relative effective-ness of alternative options. An example of this is the effectiveness of reducing seed predation for *Grevillea caleyi*, an endangered understory shrub of Australian eucalypt forest. The few remaining populations of this species are found within a small area at the interface be-tween urban development and remnant native vegetation, and are threatened by habitat de-struction, adverse fire regimes and very high seed predation (Auld & Scott 1997). Seed pred-ators include weevils in the canopy and native mammals at the soil surface. Seed germination is triggered by fires, which also kill existing plants. Thus, the frequency and intensity of fires are important components of the species' ecology. A study focusing on a single small population (Regan et al. 2003) concluded that predation reduction improved the chances of long-term persistence of small populations sub-stantially. However, a metapopulation study (Regan & Auld 2004) concluded that manage-ment of fires is crucial for the long-term persistence of *G. caleyi* populations, and that predation management was rather ineffective by itself. The reason for this difference is that the number of seeds entering the seed bank after predation is extremely low for a single small population, and there is a substantial risk that all seeds will be depleted in the seed bank due to viability loss and germination. Reducing predation rates for a small population would therefore substantially reduce its risk of extinction. For the metapopulation, however, its seed bank is large enough to always contain available seeds, and a reduction in predation rates does not have a substantial effect on its risk of extinction. At the metapopulation level it is more important to ensure adequate seed production, regular germination and plant survival in years when there are no fire events (Regan & Auld 2004). Thus, for the regional persistence of *G. caleyi* fire management appears to be a much more important strategy, a conclusion that was not as apparent when only a single population was considered, even though both actions – fire management and

predation control – can target a single popula-
tion or all populations in the metapopulation.

The conservation options at a metapopula-
tion level include reserve design, reintroduc-
tion and translocation, dispersal corridors and
management actions geared to local population
dynamics (such as sources and sinks). We
discuss these below.

RESERVE DESIGN

Reserve design is a complex topic that almost
always involves multiple species, as well as
social, political and economic constraints. Here
we focus on only one aspect: directing conser-
vation effort at a subset of the populations of a
target species, in order to maximize the chances
of its survival. This issue is informed by predic-
tions and observations of generally higher
extinction rates in smaller populations, and
lower probabilities of rescue by immigration in
more isolated patches (Hanski 1994). It was

originally phrased as the 'SLOSS' debate, i.e.
whether a single large or several small
(SLOSS) populations are better to protect the
species. Although simplistic, this formulation
captures the nub of the issue, and underlines
the relevance to conservation of spatial struc-
ture and metapopulation dynamics.

On the one hand, several small populations
may have a lower extinction risk than one large
one if the rate of dispersal is high enough and
the degree of spatial correlation of environ-
ments is low enough. This is because a single
large population will not benefit from uncorrel-
ated environmental fluctuations; if it becomes
extinct, it cannot be recolonized. For example,
an important reason for establishing the wild
dog reserves discussed in Box 5.1 was to provide
a hedge against the possibility of a catastrophic
event hitting the single large Kruger population.

On the other hand, compared with a large
population, each of the small populations will
be more vulnerable to extinction due to
demographic stochasticity, higher mortality of

Box 5.1 Reintroduction of wild dogs in South Africa

Most metapopulations are the regional-scale expression of responses by individuals to patchiness in their habitat.
Persistence at the regional level is enhanced if individuals can retain some ability to move across the matrix to
prevent local extinctions or to recolonize empty patches. Here we describe a particularly extreme example of a
metapopulation, in which the habitat patchiness is caused by fences, and individuals have lost all intrinsic capacity to
mix freely between populations. The persistence of the metapopulation relies entirely on human-induced transloca-
tions, and corridors take the form of transportation vehicles.

A programme was initiated in 1997 to establish a second South African population of the endangered wild dog
Lycaon pictus apart from the only viable one in the Kruger National Park (Mills et al. 1998). As the Kruger population
fluctuates around 300 (Creel et al. 2004) it was thought prudent to bolster the small number of dogs in South Africa
and provide a hedge against the uncertainty of a catastrophic event hitting the Kruger population. At present South
Africa has no other protected area large enough to contain a self-sustaining population of wild dogs, so the strategy
has been to introduce them into a number of small widely scattered reserves separated by hundreds of kilometres
and to manage the various subpopulations as a single metapopulation.

Preliminary modelling of this wild dog metapopulation suggested that periodic, managed gene flow through
translocations should be implemented to reduce inbreeding and the resultant risks of meta- and subpopulation
extinction. The model indicated that by using a frequency of exchange based on the natural reproductive life span of
wild dogs (approximately 5 years) inbreeding could be reduced by two-thirds and population persistence could be
assured (Mills et al. 1998).

The guiding principle in reserve selection was to look for areas that reasonably can be expected to sustain at least
one pack of 10 to 20 animals. The average home range size for a pack is $537\,km^2$ in Kruger National Park (Mills &
Gorman 1997), which comprises a similar savannah woodland habitat to the habitat available in most of the
potential reserves for reintroduction. The range of sizes of the five reserves into which wild dogs have so far been

introduced for the metapopulation is $370-960\,km^2$. All reserves are enclosed with electrical fences, to protect the wild dogs and to minimize conflict with livestock farmers. Fences act as important barriers to the movements of the dogs, so that there is little emigration and even less immigration. The reserves are isolated from each other, with no possibility at present to establish corridors, and almost all movement of wild dogs between the reserves is conducted through artificial introductions and removals.

Apart from protecting the regional viability of the species, an important objective in the wild dog metapopulation management programme is to promote biodiversity conservation. Biodiversity is a broad concept incorporating compositional, structural and functional attributes at four levels of ecosystem organization: landscapes, communities, species and genes (Noss 1990). A biodiversity objective for wild dogs that may be especially difficult to achieve in a small reserve is to restore their ecological role as predator. Wild dog packs can produce large litters and more than double in size within a year, posing a particularly challenging situation for managers because of the rapidly escalating predation pressure, at least in the short term. This is exacerbated by the tendency for wild dogs to use fences as an aid to hunting (van Dyk & Slotow 2003), which may artificially increase kill rate. An important aspect of the programme is to research the viability of interactions between wild dogs and their prey in confined areas.

Following release of the first six to eight animals, the principle management strategy has been to continue to simulate the natural dynamics of wild dog packs by moving single sex groups between reserves as and when necessary, so as to maintain the genetic integrity of the metapopulation and, if necessary, to promote new pack formation as originally recommended (Mills et al. 1998). In the reserves, regular maintenance and daily patrolling of the fences is essential. In spite of this weaknesses do occur. Holes dug by other species such as warthogs (*Phacochoerus africanus*), flood damage along drainage lines and occasions when predators chase prey through a fence are among the ways in which breaches can occur. These are most likely to be exploited during dispersal events by the dispersing animals. Escapes are most likely to happen if there are no suitable dogs of opposite sex available with which dispersers can form a new pack, or if the reserve is too small to allow for the formation of another pack. The obvious solution to dispersers escaping from a reserve is to remove dogs before they break away, but it is difficult to know which dogs to remove and when. The preferred solution would be to remove dogs only after they have naturally split off from the pack. Managers decide on the removal of dogs when they are concerned about the impact of increasing numbers on the prey, or in order to decrease the risk of dogs escaping from a reserve. Behavioural observations may help to predict when a breakaway is about to occur and which dogs are involved, in which case management intervention can thus be applied pre-emptively based on this behavioural research.

Financial costs of the wild dog management programme have as much influence on strategy as do ecological imperatives. Costs include upgrading reserve fences, constructing a holding facility, radio-telemetric apparatus for monitoring the dogs, running vehicles, veterinary costs of capture, vaccination and transportation of the dogs, and liability insurance against escaped dogs causing damage to neighbours' domestic animals. Almost $380,000 was spent on wild dog conservation in South Africa between 1997 and 2001, of which c.75% was spent on establishing the metapopulation (Lindsey et al. 2005).

Despite the complexities outlined above, the extremely artificial nature of this metapopulation's spatial structure, and a general lack of knowledge about the dynamics of this species in small reserves, several aspects of this case are closely related to the metapopulation issues we will discuss in this essay.

dispersers and edge effects (smaller patches have a higher proportion of 'edge' to 'core' habitat). Thus, if they become extinct at the same time, or if the extinct ones cannot be recolonized from others, a metapopulation of several small populations may have a higher extinction risk than a single large population (see Akçakaya et al. (1999) for an example). In some cases, however, the choices are limited. In the wild dog case, for example, available habitat limited the size of the established populations to a maximum of three packs each, resulting in a mixture of several small populations and one large (Kruger) population.

There is no general answer to the SLOSS question. The answer depends not only on the degree of correlation and chances for recolonization, but also on other aspects of metapopulation dynamics, such as the configuration, size and number of populations, their

rates of growth, density dependence, carrying capacities, etc.

Often the monetary or political cost of acquiring a patch for a reserve might not be related to its size; in other cases the size or carrying capacity of a patch might not be directly related to its value in terms of the protection it offers. A small patch that supports a stable population might contribute more to the persistence of the species than would a large patch that is subject to greater environmental variation or human disturbances. Each case requires individual evaluation, using all of the available empirical information to evaluate as many as possible of the potential impacts on the extinction time of the metapopulation. Predictions for individual cases, however, will always depend on a thorough understanding of the underlying dynamic processes of density dependence and interactions with the physical environment that drive the case-specific mechanisms (Doncaster & Gustafsson 1999). Although few of these processes can be observed directly in nature, the wider framework in which they operate is provided by generic models of the conceptual issues.

Wherever possible, design options should consider less extreme alternatives than SLOSS. A mixture of smaller and larger populations can hedge against uncertainty in the scale of future impacts, and it has potential genetic benefits. Unless the small populations act as sinks, they are likely to send out a greater proportion of emigrants as well as receiving more immigrants, than larger populations. For example, collared flycatchers (*Ficedula albicollis*) exhibit this higher turnover in smaller populations, which both reduces genetic drift and slows the evolution of adaptations to local conditions (Doncaster et al. 1997). The combination of small (habitat generalist) and large (habitat specialist) populations pre-adapts the metapopulation for future environmental changes.

A related question for reserve design concerns the optimum distribution of resources between patches. Is the species better protected by a more heterogeneous or more homoge-

neous distribution of resources? Temporal variability tends to stress populations near to extinction thresholds, so reducing their sizes (Hastings 2003). In contrast, spatial heterogeneity is likely to improve the predicament of such species across both population and metapopulation scales (Doncaster 2001). This effect arises because the abundance of rare consumers generally decreases disproportionately with degrading habitat quality, regardless of their particular functional response to limiting resources. For example, oystercatchers (*Haematopus ostralegus*) will abandon beds of mussels (*Mytilus edulis*) below a certain threshold of available shellfish set by their foraging efficiency (Caldow et al. 1999). The counter-intuitive implication for metapopulations is that the regional abundance of a target species can be raised by redistributing resources between patches even without any overall improvement to habitat quality, so that those of intrinsically higher quality are augmented to the detriment of others already below the giving-up density.

TRANSLOCATION AND REINTRODUCTION

Establishment of new populations through translocation and reintroduction actions requires many decisions: how often; how many individuals, of which age classes or sexes; from which population, to which existing population or formerly occupied habitat patch? Each decision is potentially a trade-off, because it may benefit one population while decreasing the size of another one. Metapopulation models can address these questions by finding strategies that maximize the overall viability of the metapopulation. This was especially important in the wild dog reintroduction case (Box 5.1), because almost all movement of wild dogs between the reserves is conducted through artificial introductions and removals. In this case, a metapopulation model with genetic structure would have helped to plan translocations in such a way as to reduce inbreeding and maintain population structure, but in the event a

more needs-driven approach had to be taken in terms of supply and demand of suitable dogs, although always keeping in mind the genetic history of the individuals concerned.

Metapopulation models may be particularly important tools in decisions related to translocation and reintroduction of endangered species, because the status of these species discourages experimentation and makes a trial-and-error approach less desirable. Using a metapopulation model, McCarthy et al. (2004) assessed various options for establishing a new population of helmeted honeyeaters (*Lichenostomus melanops cassidix*) from a captive population. This bird is endemic to remnant riparian forests in southern Victoria, Australia. Extensive habitat destruction in the nineteenth century led to a dramatic decline, and by 1990 the only remaining population included 15–16 breeding pairs. As part of a recovery programme initiated in 1989, a captive colony was established to support the wild population and to establish populations in new areas (Smales et al. 2000). Because of uncertainties about the fates of individuals and the difficulty of integrating the available information from numerous different sources, the optimal release strategy is not immediately apparent. McCarthy et al. (2004) ran simulations to determine how the rate of release from the captive population affects the probability of success of the reintroduction over 20 years. The optimal strategy was to release individuals only when the captive population contained at least four adult males, and then to release 30% of the stock. The simulations suggested that the chance of success of the proposed reintroduction was moderately good, with little chance that the new population will have fewer than 10 males after 20 years (McCarthy et al. 2004). Although there were several factors that could not be modelled explicitly (e.g. whether the released birds would remain where they are released, would establish the same population behaviour, and would have the same vital rates as the current wild population), the modelling exercise provided valuable information that could not

have been obtained in any other way for this extremely rare species.

CONNECTIVITY AND HABITAT CORRIDORS

In addition to human-mediated dispersal through reintroduction and translocation, dispersal can be increased by conservation or restoration of the habitat lying between existing populations, sometimes called the 'landscape matrix'. Matrix restoration can reduce local extinctions by facilitating the 'rescue effect' of colonization, and it can increase the rate of recolonization following local extinction. One implementation of these efforts to increase the overall persistence of the species is the building or maintenance of habitat corridors. To answer the question 'Are corridors useful conservation tools?', we need to answer several subquestions that are intimately bound to metapopulation concepts.

1. Are the habitat corridors used by the target species? Use of a corridor depends not only on its habitat, but also its shape, particularly the width and length. For example, of the mammalian predators native to California, more species use creeks with wide margins of natural vegetation as corridors than use creeks with narrow or denuded margins (Hilty & Merenlender 2004). European hedgehogs (*Erinaceus europaeus*) dispersing across arable habitat use road verges as corridors, particularly on long-distance dispersals of as much as 10 km (Doncaster et al. 2001).

2. If used, do the corridors increase dispersal rate? Perhaps individuals using the corridor would have dispersed anyway; corridors are more likely to affect dispersal rate where dispersal is otherwise limited. For example, if it were possible to build corridors between the widely scattered wild dog reserves discussed in Box 5.1, the lack of natural connections and the pack-forming behaviour of the species suggest that such corridors would have increased dispersal between reserves. Corridors are likely to benefit fast-

reproducing species in the short term and slower reproducers in the long term, so their value depends on the time scale of conservation goals (Hudgens & Haddad 2003). Experimental fragmentation of moss banks has demonstrated rescue effects of artificial corridors for moss-living micro-arthropods. Figure 5.2 shows how corridors between moss fragments arrested declines in the abundance of most species (Gonzalez et al. 1998). It is worth noting that this experiment on an abundant fauna cost little to run, yet has provided invaluable quantification of the positive relation between abundance and distribution in connected landscapes, and of the breakdown of this relation in the ab-
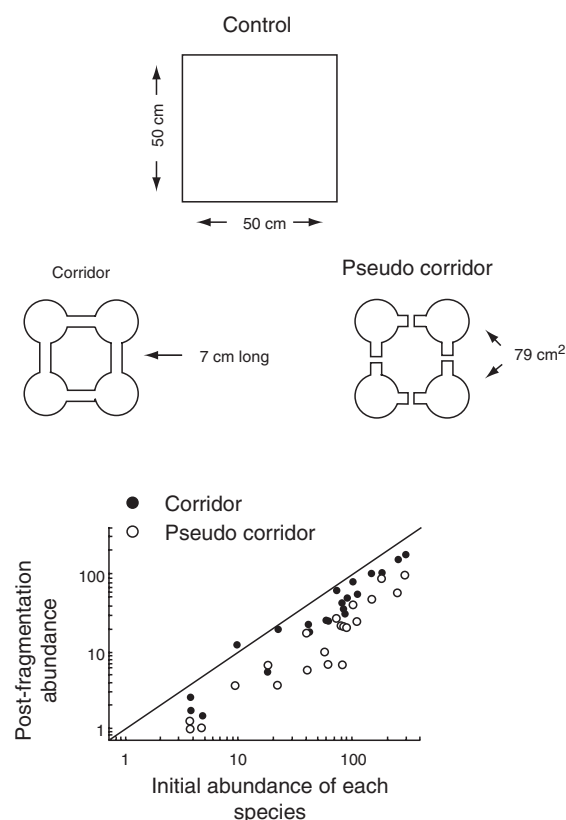

Fig. 5.2 Experimental fragmentation of moss banks into small patches reduces the abundance of micro-arthropods, but most species are saved from substantial decline by corridors connecting the fragments. (From Gonzalez et al. 1998. Reprinted with permission. Copyright 1998 AAAS.)

sence of corridors. Conservation needs more such field tests of metapopulation theory by ecologists.

3. Does an increased dispersal rate increase the overall viability of the metapopulation? Usually it does, by rescuing local populations from potential extinction. Colonists can also bring hybrid vigour to isolated populations that suffer from inbreeding depression (e.g. of *Daphnia*: Ebert et al. 2002). However, increased connectivity may also have 'anti-rescue effects' (Harding & McNamara 2002), with documented examples due to the spread of infectious diseases, or parasites or predators (Hess 1996; Grenfell & Harwood 1997), or gene flow reducing local adaptation (Hastings & Harrison 1994; Harrison & Hastings 1996). High dispersal can increase impacts of catastrophes (Akçakaya & Baur 1996), and losses to sink habitats. In other cases, the effectiveness of dispersal in reducing extinction risks depends on the correlation of environmental fluctuations experienced by different populations. If the correlation is high, all populations decline simultaneously, reducing recolonization rates of empty patches. For example, if a major climatic shift caused a region-wide decline in the prey base of the wild dogs discussed in Box 5.1, all populations would decline or become extinct and it would be difficult to recolonize them even with a well-planned translocation programme. If, on the other hand, the fluctuations are at least partially independent, some patches can act as sources of emigrants (Burgman et al. 1993). Extinction risks are often sensitive to spatial correlation in environmental fluctuations and the pattern of disturbance, as demonstrated by models for a variety of species, including the mountain gorilla (*Gorilla beringei beringei*; Akçakaya & Ginzburg 1991), spotted owl (*Strix occidentalis*; LaHaye et al. 1994) and Leadbeater's possum (*Gymnobelideus leadbeateri*; McCarthy & Lindenmayer 2000).

4. Do corridors have any other effects on metapopulation viability? Negative impacts may include increased mortality due to predation along the corridor. All Dutch highways constructed since 1990 have underpasses for

European badgers (*Meles meles*), and these are also used by other wildlife, including hedgehogs. This benefits the hedgehogs because they too are a frequent casualty of roads, but the benefit is undone because they are also a favoured food of badgers, into whose jaws they are channelled by the underpasses (Bekker & Kanters 1997). Costs such as these need to be weighed against the benefits of dispersal. The Dutch Government spends US$5 million each year on tunnels and fences for wildlife along its highways (Teodorascu 1997), so it makes economic sense to evaluate the combined effect of all changes on metapopulation viability.

5. Are there cheaper alternatives to corridors? These may involve seeding new habitable patches, or improving existing populations by augmenting net growth rates or carrying capacities. In simulations of metapopulations prone to local extinction events, the viability of the system is found to benefit more from reducing local extinction probabilities, particularly on patches with the lowest probabilities, than from increasing colonization probabilities (Etienne & Heesterbeek 2001). Birds using rainforest fragments show evidence of this response (Lens et al. 2002), but more empirical testing is needed of this model, as with most metapopulation models.

Although the importance of corridors has long been recognized, it is only with the use of metapopulation models that their advantages can be quantified, for example, in terms of increased persistence or viability of the species, and compared with advantages of alternative strategies.

SOURCES AND SINKS

When conservation is geared to local populations with dynamics of sources and sinks, management options must consider many interdependent factors. Two general issues arise:

1. How do source–sink dynamics affect metapopulations? The overall effect on metapopulation persistence of dispersal from sources to sinks depends on the cost to source population (increased risk of local extinction), the benefit to sink population (decreased risk of local extinction), and the changes with local population density in dispersal, survival or reproduction. In the presence of density dependence, the excess of deaths to births that is characteristic of a sink can be caused directly by the influx of immigrants rather than being an inherent property of the patch. The viability of such a 'pseudosink' consequently need not depend on the arrival of emigrants from sources. It may even benefit from a reduced influx, in contrast to a true sink which is rescued by immigration (Watkinson & Sutherland 1995). Management options will differ for true and pseudosinks because of this, yet the two types can be hard to distinguish in field surveys. For example, sources and pseudosinks in the highly fragmented Taita Hills forests of Kenya could be identified only from a combination of demographic, genetic and behavioural work (Githiru & Lens 2004). To sidestep these complications, sinks can be defined as populations whose removal would increase the overall viability of the metapopulation. This approach, however, requires modelling of the underlying dynamics of the metapopulation, and therefore more data.

2. Should sink populations be protected? This depends on various factors, the most important being what is meant by 'protected' and its alternatives. If 'protected' means that fecundity or survival may increase to the extent that the sink population can become self-maintaining (i.e. have a low risk of extinction even in the absence of dispersal from other populations), and the alternative is continuation as a sink population, then protection is probably justified (as Breininger & Carter (2003) demonstrated for the Florida scrub jay (*Aphelocoma coerulescens*)). If 'protected' means it is maintained as a sink population and the alternative is that individuals that would have dispersed to the sink end up in a habitat patch with higher survival or fecundity, then protection of the sink is probably not justified (as Gundersen

et al. (2001) demonstrated for root voles (*Microtus oeconomus*)). In the wild dog case (Box 5.1), for example, if mortality exceeds reproduction in one of the reserves as a result of a local decline in the prey base, then it would be justified to attempt to maintain this population by increasing the prey base in that reserve (e.g. by enlarging the reserve or by habitat improvement), but it might not be justified to attempt to maintain this population only by increasing translocations from healthier populations. Other considerations include whether the sink population can increase connectivity (as a 'stepping stone' between other populations), its contribution to total abundance and its function as a buffer against catastrophic events. Where conservation is aimed at culling an invasive alien, its regional decline can be hastened by allocating culls to sinks as well as sources (as for the European hedgehog introduced into the Scottish Western Isles; Travis & Park 2004). The point is that there are a lot of details, and generalizations are difficult if not impossible. The only way to address such questions is to develop case-specific models that incorporate all that is known about the dynamics of the metapopulation, including survival, fecundity and dispersal for all populations whether source or sink, as well as temporal variability and density-dependence in these parameters.

Do metapopulations need models?

The metapopulation concept lends itself to modelling because its core dynamic – of populations colonizing patches (and their potential local extinction) – bridges models of persistence at the levels of the individual and the community: of individuals consuming resources (and their eventual death), and of species colonizing niches (and their potential extinction: Doncaster 2000). Metapopulations encompass landscape-level processes of patches being formed, split and merged in habitat successions and disturbance events. At all of these scales, models

are used to pare away as much of the complexity inherent to nature as is necessary to reveal the underlying patterns and to explore the range of forces that shape these patterns. Models are particularly important to the conservation of metapopulations, because the regional focus and undesirability of experimental manipulations usually rules out any other methods of distinguishing causes of endangerment from secondary effects. Most of the issues and decisions regarding metapopulations concern interdependent factors, such as number of populations, spatial correlation, dispersal and density dependence. Because many of these factors involve interactions between populations, there is no simple way of combining models on dynamics of individual populations into regional-scale decisions. The only way to incorporate all these factors is to simultaneously include all populations and their interactions in one model, in other words, to use a metapopulation model. Models are particularly valuable tools in cases where the endangered status of species makes other (e.g. experimental) approaches difficult or impossible.

Models are also useful in evaluating management actions at large spatial scales, at which experiments may not be feasible. Frequently, management of a metapopulation means management of the species' habitat. Habitat management may take many forms, including controlling the rate and pattern of habitat alteration through the effects of grazers or harvest by humans. For example, Schtickzelle & Baguette (2004) used a structured metapopulation model to study the effect of grazing on the bog fritillary butterfly (*Proclossiana eunomia*) in south-eastern Belgium. This species has a very restricted habitat; both larval and adult stages feed on a single plant species that occurs mainly in wet hay meadows along rivers of some uplands scattered in western Europe. Grazing by large herbivores is sometimes used by conservation agencies to maintain early successional stages in wet hay meadows. The metapopulation model demonstrated that grazing substantially increases the extinction risk

for the bog fritillary butterfly in south-eastern Belgium. Its predictions led to modifications in the management protocol of a nature reserve: several grazing regimes are being tested and half the area is now kept ungrazed.

Controlled timber harvest is another form of habitat management. Regan & Bonham (2004) developed a metapopulation model of the carnivorous land snail *Tasmaphena lamproides* inhabiting native forests in northwest Tasmania. This species is listed as threatened due to its small range, much of which is within timber production forest. The model was designed as a decision support tool for managers to explore the trade-offs between timber production requirements and conservation of the species under various management scenarios. Future use of the area involves converting native forest to eucalypt plantations, or harvesting native forest followed by burning to promote regeneration. Burning is thought to eliminate populations of this snail, but they reinvade native forest areas once the required habitat has formed with adequate level of litter and food sources. The metapopulation model combines geographical information system (GIS) data on the distribution of forests and demographic data on the dynamics of the species, and allows the investigation of alternative harvesting strategies which meet wood production needs in the long term but minimize population declines in the short term.

In aquatic systems, habitat management often involves water regimes and barriers such as dams. Changes in water regime were implicated in the severe decline of the European mudminnow (*Umbra krameri*) along the River Danube during the second half of the twentieth century (Wanzenböck 2004). Water regulation in the Danube has increased flow velocity and caused the river to cut a deeper channel, lowering the groundwater level in the surrounding floodplain. As a result, the original side channel used by the mudminnow has been transformed into a chain of disconnected, groundwater-fed ponds. A simple metapopulation model was used to demonstrate that reversing this declin-ing trend in habitat capacity is critical to the mudminnow's persistence, and to recommend increasing the habitat availability for, and connectivity of, populations. To implement these recommendations, groundwater levels are being raised by opening some of the longitudinal dams bordering the main river and reconnecting some backwaters to the river. These conservation efforts began in the late 1990s, are continuing today, and their impact on the mudminnow is being monitored closely.

There are several different types of metapopulation models, each with their own set of assumptions and restrictions (detailed in Akçakaya & Sjogren-Gulve 2000; Breininger et al. 2002). Patch-occupancy models have the simplest demographic structure, describing each population as present or absent (e.g. within regional distributions of butterflies or other winged insects; Hanski 1994). Intermediate complexity is found in structured (or, frequency-based) models that describe each population in terms of the abundances of age classes or life-history stages (Akçakaya 2000a). These models incorporate spatial dynamics by modelling dispersal and temporal correlation among populations (e.g. of the land snail *Arianta arbustorum*; Akçakaya & Baur 1996). At the other extreme are individual-based models, which describe spatial structure within the location of territories, or of each individual in the population (e.g. of northern spotted owls (*Strix occidentalis caurina*); Lamberson et al. 1996; Lacy 2000). Some models use a regular grid where each cell can be modelled as a potential territory. For example, Pulliam et al. (1992) used this approach in a region managed for timber production to show that population sizes of Batchman's sparrow (*Aimophila aestivalis*) depended more strongly on mortality rates than on dispersal ability. Another approach uses a habitat suitability map to determine the spatial structure of the metapopulation (e.g. of the helmeted honeyeater (Akçakaya et al. 1995) and California gnatcatcher (Akçakaya & Atwood 1997)). All of these approaches have been applied to specific conservation manage-

ment questions (Chapter 9). The appropriate choice depends on the complexity of the problem at hand, the assumptions of the model in relation to the ecology of the species (see below) and the data available.

Current limitations and dilemmas

Single-species focus

Most metapopulation applications focus on a single species, yet much of conservation management concerns communities. Even where a single species is targeted for conservation, its survival and fecundity will often depend on competition within the trophic level or predation from higher trophic levels. For example, in the case of wild dogs (Box 5.1), an important objective is to restore their ecological role as predator, which requires research into the viability of wild dog–prey interactions in confined areas. Metapopulation models tend to focus on single-species dynamics because these are better understood than foodweb and ecosystem processes. Adding an extra species to the system requires at least two extra dimensions in the analysis (to account for both exclusive and shared occupancy of suitable habitat), greatly increasing the number of parameters for estimation and thus model error. The general lack of understanding and data on multispecies interactions means that few empirical metapopulation studies have sufficient parameter estimates to model community dynamics. An astute use of simplifying assumptions, however, can bring theory within the grasp of empirical data.

Simple models have achieved some robust predictions for competitive coexistence by reducing the representation of competition to a binary distinction between competitively dominant and inferior (fugitive) species. For example, habitat destruction is predicted to disadvantage dominant species with slow dispersal to the benefit of fugitive species, and the early loss of dominants has most effect on

community structure because of their potential role as keystone species (Tilman et al. 1997). The dominant–fugitive dichotomy applies particularly to plant diversity in prairie grasslands. The generalized version of this patch-occupancy approach explores the full range of competitive asymmetries in regional coexistence, and without needing extra dimensions in the analysis if it can be assumed that both residents and colonists experience similar effects of density on survival (Doncaster et al. 2003). This model reveals that subdominant species with poor dispersal are the most sensitive to habitat degradation. Their loss from the community provides a useful early warning of regional disturbance and degradation, because it will have less impact on community structure than the subsequent disappearance of dominant and potentially keystone species. In general, faster reproducing communities (e.g. invertebrate assemblages) are both predicted and observed to have higher tolerance for differences in growth capacity, compared with slower reproducing communities (e.g. forest trees), which have higher tolerance for competitive interactions. Coexistence is even possible amongst tree species competing for identical resources in the same metapopulation, if they differ in their threshold conditions for switching from vegetative growth to seed production (e.g. Mexican rain forest trees; Kelly & Bowler 2002). These low productivity communities tend to be the most at risk from human induced disturbance, and therefore the most in need of predictive models.

Where conservation efforts are directed towards a community of species, a practical approach to dealing with the single-species limitation is to select a target species that is representative of the natural community, that is sensitive to potential human impact and whose conservation will protect other species (Noon et al. 1997). One danger here is that the target species and others may have different networks of habitat patches in the same region. For example, from a large-bodied predator's point of view, there may be a few large habitat

patches, but for its small prey, there may be hundreds of distinct patches. Or, the degree of fragmentation may be different for each species depending on their habitat requirements. For example, roads fragment forest habitat for song-birds in direct proportion to their dependence on canopy-level vegetation for nesting and feeding (St Clair 2003). Endangered silver-studded blue butterflies (*Plebejus argus*) and sand lizards (*Lacerta agilis*) both disperse between heathland fragments, but the greater capacity for the butterflies to use areas between habitat patches (also called 'matrix') suggests they will benefit most from climate warming, at least in terms of increased patch connectivity and metapopulation stability (Thomas et al. 1999). The best strategy in such habitat and community studies is often to combine results from different target species (Root et al. 2003).

For addressing most conservation questions involving species in fragmented landscapes, metapopulation models often have less severe limitations than the available alternatives, such as rule-based methods, expert opinion, reserve-selection algorithms and habitat mapping. However, these alternatives have the potential of contributing to the realism of metapopulation models or of complementing them (Akça-kaya & Sjogren-Gulve 2000; Breininger et al. 2002; Brook et al. 2002).

Definition and delineation of populations in a metapopulation

Most metapopulation approaches represent the landscape by discrete habitable patches within a surrounding matrix that may allow dispersal but does not support populations. To the extent that there exist areas where a species can reproduce and those where it cannot, this assumption is not unrealistic. However, it does require the definition of a population, and a method for identifying these areas (patches) in a given landscape.

A general definition of a population presents dilemmas, regardless of the metapopulation

context. Considering the difficulty of defining a species, a much more fundamental concept, this is perhaps not surprising. A biological population can be defined as a group of interbreeding (i.e. panmictic) individuals. Assuming that the distribution of a species is more-or-less continuous across parts of the landscape, the question of delineating a population can be rephrased as: how far apart must two individuals be in order to be considered to be in different populations? This depends on the movement distance, home range, or some other measure related to the possibility of interbreeding. This approach, combined with modelling and prediction of suitable habitat, is used in habitat-based metapopulation models to delineate populations (Akçakaya 2000b, 2005). In the wild dog metapopulation (Box 5.1), populations are easily defined by fenced reserves.

Assumptions of metapopulation models

All models assume certain constants, in order to interpret the dynamics of interest. The usefulness of any model therefore depends on the validity of its assumptions. Below we discuss recent approaches to improving the fit of metapopulation models to data.

COLONIZATION MATCHES EXTINCTION

Some metapopulation models assume that the metapopulation is in equilibrium with respect to the extinction and recolonization of patches (e.g. incidence function type of patch-occupancy models; Hanski 1999). There is little evidence to suggest that metapopulations of any species are in fact at equilibrium (Baguette 2004), and small, highly variable metapopulations are particularly unlikely to be so. However, metapopulations that persist over long time-scales must be under some form of density regulation at the regional scale, often assumed to be in colonization rate, which implies at least a deterministic attraction towards an equilib-

rium density of occupied habitat. Equilibrium models therefore can play a useful role as null hypotheses for analysing the processes that may threaten viability, such as habitat loss, exploitation and alien invasions. A poor fit of equilibrium models to the data can signal the need to account for other factors, such as competitive interference in addition to exploitation (Doncaster 1999), or multiple equilibria (Hanski et al. 1995), or it may result from random fluctuations. Null models test these alternatives parsimoniously by seeking to explain deviations from equilibrium predictions. Note that density regulation of local populations in a metapopulation does not guarantee the existence of an equilibrium at the metapopulation level. The metapopulation may still decline if the rate of local extinctions due to environmental fluctuations and demographic stochasticity exceeds colonization rates, because of factors such as limited dispersal, or Allee effects on small populations, or correlated environments.

The equilibrium assumption is sometimes mistakenly believed to apply to the metapopulation concept in general, yet several metapopulation models and approaches do not make this assumption (e.g. structured and individual-based models, described in Akçakaya & Sjogren-Gulve 2000). These are particularly useful for predicting the extinction probability of small metapopulations which may have unbalanced sex ratios or age structures, or low genetic variability, and which are most prone to environmental fluctuations (e.g. some coral reef fishes: Bascompte et al. 2002), or which may be declining (e.g. California gnatcatcher (*Polioptila californica*); Akçakaya & Atwood 1997).

INDEPENDENT DYNAMICS OF LOCAL POPULATIONS

Some metapopulation models assume that the dynamics of local populations are independent of each other. However, this assumption is violated in many metapopulations where local populations are affected by regional environ-

mental factors that impose a correlation. For example, fecundities of the California least tern (*Sterna antillarum browni*) are correlated across different subpopulations, presumably due to the effects of large-scale weather patterns such as the El Niño–Southern Oscillation that may simultaneously affect the food resources of many populations. The correlation coefficients average 0.32 (range 0–0.6), and decline with increasing distance between the populations (Akçakaya et al. 2003a). When correlations are based on population sizes rather than vital rates such as fecundity, it may be difficult to untangle the relative contributions of correlated environmental factors, dispersal, and trophic interactions to the observed spatial correlation in population dynamics (Ranta et al. 1999). However, it is clear that for many species, subpopulations experience spatially correlated dynamics (Leibhold et al. 2004). In these cases, results of simple models that assume independence may be misleadingly optimistic in their estimation of risks of extinction and decline. However, it is possible to make realistic and unbiased assessments by using models that incorporate dependencies or spatial correlations among populations (e.g. Harrison & Quinn 1989; Akçakaya & Ginzburg 1991; LaHaye et al. 1994).

STATIC HABITAT

Many metapopulation models assume a constant number and location of habitable patches, yet natural landscapes are inherently dynamic. Spatial structure changes according to seasons, climatic fluctuations and succession, as well as human impacts (urban sprawl, global climate change, agricultural expansion, etc.). The viability of a metapopulation will depend on its rate of patch turnover, as well as the static quantity and quality of suitable habitat (Keymer et al. 2000). Under habitat succession or age-dependent disturbance, for example, a metapopulation is predicted to persist for as long as the mean age of its constituent patches

exceeds the average interval between colonization events (Hastings 2003). A metapopulation with a slow turnover of patches thus may persist even with a high extinction rate of local populations, and managers should be wary of underestimating its viability. Equally, management action aimed at increasing the lifespan of patches is likely to do more good than action focused directly on the survival of local populations on the patches.

Some metapopulation models incorporate community succession, which tends to be particularly patchy in time and space at its early stages and determines critical habitat for certain species (Johnson 2000; Hastings 2003). Other models incorporate changes in carrying capacity over time, either deterministically, for example to simulate forest growth, or stochastically to simulate the effects of random disturbances such as fires, or both, e.g. as a deterministic function of time since a stochastic disturbance event (Pulliam et al. 1992; Lindenmayer & Possingham 1996; Stelter et al. 1997; Akçakaya & Raphael 1998; Johst et al. 2002; Keith 2004). A recently developed approach addresses these issues by linking a landscape model and a metapopulation model (Akçakaya et al. 2003b, 2004, 2005).

An example of incorporating habitat change in metapopulation dynamics involves the woodland brown butterfly (*Lopinga achine*), which lays its eggs at the edges of glades of the partly open oak woodland pastures where its host plant *Carex montana* grows. The habitat quality for this species is related to the amount of bush and tree cover within the pastures and the occurrence of its host plant (Bergman 1999). As discussed above, grazing often helps maintain grassland habitats in successional stages that favour certain species. As grazing ceases, the essential habitat of this species (open glades with host plants) becomes overgrown and deteriorates. Using a metapopulation model, Kindvall & Bergman (2004) calculated long-term extinction risks under various landscape scenarios. An important aspect of this analysis was that the landscape

scenarios were dynamic; thus, the study integrated the changes in the habitat (as a result of succession and grazing) with changes in the metapopulation, and demonstrated the importance of landscape dynamics in affecting the viability of this species.

Conclusions

Metapopulation models have been essential to the management of many species. The listing of several species on the Endangered Species List in the USA, as well as the management and recovery plans for a number of species, were based in part on the analysis of their metapopulation dynamics. For example, the draft recovery plan for the Pacific coast population of the western snowy plover (*Charadrius alexandrinus nivosus*) included a metapopulation model (Nur et al. 1999), which highlighted the need for increased management of the species and its habitats. This population is listed as threatened in the USA, because habitat degradation caused by human disturbance, urban development, introduced beachgrass (*Ammophila* spp.), and expanding predator populations have resulted in a decline in active nesting areas and in the size of the breeding and wintering populations. Using a metapopulation structure that allowed estimates for demographic parameters to vary among subpopulations was considered an important aspect of this model. The metapopulation model predicted a high probability of decline under existing conditions, which included intensive management in some areas by area closures, predator exclosures and predator control. The model suggested that recovery at a moderate rate would be possible with a productivity of 1.2 or more fledglings per breeding male, but would require shortterm intensive management and long-term commitments to maintaining gains. Other species for which metapopulation models have been used in recovery planning or listing include northern spotted owl (*Strix occidentalis*

caurina), California spotted owl (*Gambelia silus*), south-western willow flycatcher (*Empidonax traillii extimus*), marbled murrelet (*Brachyramphus marmoratus*), Florida scrub jay (*Aphelocoma coerulescens*) and Florida panther (*Felis concolor coryii*). These cases, and several examples discussed throughout this essay, illustrate our answers to the two questions posed earlier in the essay: conservation needs metapopulation approaches, and metapopulations need models.

Many species live in naturally heterogeneous or artificially fragmented landscapes, and decisions on their conservation and management should consider metapopulation concepts and models. Models make assumptions, however, many of which await evaluation and should not be tested on our most treasured wildlife. The metapopulation literature is full of caveats to the effect that more empirical data are needed to distinguish between alternative processes and mechanisms. These data must come from field experiments, yet too often field ecologists are pulled towards the expediency of mission-oriented conservation with the result that we still lack a well-tried framework for

managing endangerment at the regional scale. The wild dog case (Box 5.1) illustrates how the principal function of metapopulation models in conservation – to evaluate alternative options and scenarios – depends on there being alternatives to choose from. Metapopulation models stimulated the original concept of linked reserves, and contributed to addressing potential problems of inbreeding at the planning stage (Mills et al. 1998). Options at the construction stage were severely limited by the small number of sites and animals available, favouring a pragmatic approach of adaptive management for this large social species with complex behavioural ecology. Population monitoring and autecological studies are now providing data for optimizing population sizes and translocation rates. Models will thus become increasingly important decision tools in the long-term management of the metapopulation. Despite these caveats and limitations, we believe current conservation efforts for many species would benefit from a more explicit and quantitative consideration of metapopulation dynamics.

There is nothing in this world constant, but inconstancy.
(Jonathan Swift (1667–1745), *A Critical Essay upon the Faculties of the Mind.***)**

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