Support for a metapopulation structure among mammals

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ABSTRACT

1. The metapopulation metaphor is increasingly used to explain the spatial dynamics of animal populations. However, metapopulation structure is difficult to identify in long-lived species that are widely distributed in stochastic environments, where they can resist extinctions. The literature on mammals may not provide supporting evidence for classic metapopulation dynamics, which call for the availability of discrete habitat patches, asynchrony in local population dynamics, evidence for extinction and colonization processes, and dispersal between local populations.

2. Empirical evidence for metapopulation structure among mammals may exist when applying more lenient criteria. To meet these criteria, mammals should live in landscapes as discrete local breeding populations, and their demography should be asynchronous.

3. We examined the literature for empirical evidence in support of the classical criteria set by Hanski (1999), and for the more lenient subset of criteria proposed by Elmhagen & Angerbjörn (2001). We suggest circumstances where metapopulation theory could be important in understanding population processes in mammals of different body sizes.

4. The patchy distribution of large (>100 kg) mammals and dispersal often motivate inferences in support of a metapopulation structure. Published studies seldom address the full suite of classical criteria. However, studies on small mammals are more likely to record classic metapopulation criteria than those on large mammals. The slow turnover rate that is typical for medium-sized and large mammals apparently makes it difficult to identify a metapopulation structure during studies of short duration.

5. To identify a metapopulation structure, studies should combine the criteria set by Hanski (1999) and Elmhagen & Angerbjörn (2001). Mammals frequently live in fragmented landscapes, and processes involved in the maintenance of a metapopulation structure should be considered in conservation planning and management.

Keywords: asynchrony, conservation, discrete local populations, dispersal, population turnover, vacant habitats

INTRODUCTION

Claims for the existence of metapopulations are dominated by descriptions of population networks of insects (e.g. Leisnham & Jamieson, 2002; Massonnet, Simon & Weisser, 2002; Caudill, 2003; Thomas & Hanski, 2004; Rabasa, Gutiérrez & Escudero, 2007), birds (e.g. Esler, 2000; Inchausti & Weimerskirch, 2002; Githiru & Lens, 2004), reptiles (e.g. Semlitsch & Bodie, 2003; Rodrigues, 2005), amphibians (e.g. Alford & Richards, 1999; Marsh &

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Trenham, 2001; Smith & Green, 2005; Werner *et al.*, 2007) and small mammals (e.g. Lima, Marquet & Jaksic, 1996; Lawes, Mealin & Piper, 2000). Few studies have addressed population networks in large mammals (>100 kg in body mass), and those that do apparently provide little support for metapopulation structures (Elmhagen & Angerbjörn, 2001).

Habitat fragmentation and loss often reduce the distributional ranges of large mammal species (e.g. Brashares, 2003; Cardillo *et al.*, 2005). Anthropomorphic alterations of landscapes for agricultural or conservation purposes fragmented many populations; some may even be confined to a fraction of their former ranges (Ceballos & Ehrlich, 2002). This may reduce individual survival and increase extinction risk (Cardillo *et al.*, 2006). The metapopulation concept caters for species that live in fragmented landscapes (Hanski, 1999). It focuses on populations that consist of local populations that exchange individuals through migration and dispersal, even when human mediated (Hanski & Simberloff, 1997; Akçakaya, Mills & Doncaster, 2007). It also integrates extinction, dispersal and colonization in patchy environments. It thus has appeal when designing conservation networks to overcome the effects of fragmentation (Önal & Briers, 2005).

The detection of population networks as metapopulations requires that (i) dispersal occurs between local populations; (ii) extinction and colonization take place; (iii) the dynamics of local populations are in asynchrony; and (iv) habitat patches support local breeding populations with colonizable vacant habitats (Hanski, 1999). Based on these criteria, Elmhagen & Angerbjörn (2001) found evidence for metapopulation dynamics among small mammals, but little support among large mammals. Based on Hanski's (1999) criteria, Elmhagen & Angerbjörn (2001) deduced two more lenient criteria for large mammals – first, breeding local populations should be discrete rather than inhabiting discrete habitat patches. Second, local populations should have dissimilar growth rates, i.e. some local populations may increase while, at the same time, others decrease. Such temporal fluctuations in growth rates imply demographic asynchrony among local populations (Elmhagen & Angerbjörn, 2001).

The use of the term 'metapopulation' has broadened substantially since it was proposed by Levins (1969). It now includes a variety of spatial population structures and definitions (see Hanski & Gilpin, 1991; Harrison, 1994; Pannell & Obbard, 2003; Akçakaya *et al.*, 2007). However, this broadening of the original concept may detract from its meaning (Pannell & Obbard, 2003). As far as we are aware, only Hanski (1999) (for all species populations) and Elmhagen & Angerbjörn (2001) (for mammal species populations) recommended specific criteria that have to be met by a population for it to be classified as a metapopulation.

Here, we examine the empirical support for metapopulation dynamics among mammals. We determine the frequency of the application of the concept to mammal populations by searching literature published from 1991 to 2007, and recording proof for or against the classic criteria (Hanski, 1999) and the more lenient criteria proposed by Elmhagen & Angerbjörn (2001). We determine if body size influences the application of the criteria, and speculate on the value of the concept. Our study adds to the contribution of the review by Elmhagen & Angerbjörn (2001), and may assist in the formulation of conservation plans based on the restoration of spatial axes to regain spatial–temporal dynamics (Thomas & Kunin, 1999) that enhance persistence and overcome local impacts on other species (e.g. van Aarde & Jackson, 2007). We appreciate that the metapopulation concept is based on mathematical abstraction rather than empirical observation, but argue that this abstraction has value when it describes population processes that can be manipulated to enhance conservation initiatives (van Aarde, Jackson & Ferreira, 2006).

MATERIAL AND METHODS

We collated empirical evidence for the existence of metapopulation dynamics among mammals by searching for relevant publications in the following electronic databases: Agricola, Biological Abstracts, Blackwell Synergy, Ecological Abstracts, Google Scholar (first 1000 'hits' from http://www.google.com/scholar), JSTOR, Science Direct, Scirus, Scopus, and Wildlife and Ecology Studies Worldwide. We based the search on the keywords 'metapopulation and mammal*'. We recorded the number of studies that dealt with metapopulation dynamics in mammals for every year from 1991 to 2007. We included only papers in which the authors either described the metapopulation or stated that the population could potentially function as a metapopulation. We also included papers that did not explicitly test Hanski's (1999) or Elmhagen & Angerbjörn's (2001) criteria for metapopulations, but that casually may have deduced such dynamics. For instance, if authors stated that they classified their studied population based on evidence using the definition of Hanski & Gilpin (1991), which defines a metapopulation as 'a set of local populations which interact via individuals moving among populations', we assumed that the criteria of dispersal, discrete habitat patches or discrete local populations were met. We then recorded the specific criteria used by authors to infer a metapopulation structure for a species. For populations assessed more than once, we used the most recent publications. We distinguished among studies based on the body weight of the species that were studied and noted whether the apparent metapopulation existed in a natural, or 'intact' landscape (e.g. rocky cliffs) or in an anthropomorphically altered, or 'disturbed' landscape (e.g. artificially fragmented forests).

For each study, we recorded evidence for the populations meeting the criteria set by Hanski (1999) or the subset of criteria proposed by Elmhagen & Angerbjörn (2001). We noted whether the authors (i) found evidence, (ii) found no evidence, (iii) did not asses the specific criteria, and (iv) stated or assumed that a condition could be fulfilled, but did not provide supportive evidence. We then recorded the number of criteria used in each study to describe metapopulations. Furthermore, we noted the incidence at which specific criteria were used to describe metapopulations.

We distinguished between small mammals ($\leq$5 kg), medium-sized mammals ($>5 \leq 100$ kg) and large mammals (>100 kg), and used contingency table analyses to test for the influence of body size on the frequencies at which criteria were met, as well as for the influence of the type of landscape in which the mammals were studied. Statistical significance was set at $\alpha = 0.05$.

RESULTS

The number of publications we found on metapopulation dynamics in mammals between 1991 and 2007 ranged from one to nine per year. In total, we included 63 studies, representing 75 species. Studies by Lima *et al.* (1996) on five and McShea *et al.* (2003) on nine species of small mammals were included as single studies and analysed as each representing one species, as the authors did not consider metapopulation criteria separately for every species. Conversely, the study by Gerlach & Hoeck (2001) was included and analysed as two studies, as the authors considered metapopulation criteria separately for two species. The studies included mammals ranging in body size from 0.002 to 5000 kg (see Appendix), and size classes were evenly distributed across intact and disturbed habitats ($\chi^2 = 5.12$, d.f. = 2, $P = 0.077$). The three studies on mammals >500 kg took place in landscapes fragmented by humans.

Not all the studies met the criteria recommended by Hanski (1999). In 90% of them ($n = 57$), dispersal was recorded between local populations, 16 (25%) experienced extinction and colonization events, while 33 (52%) exhibited asynchrony in population dynamics. Thirty (48%) occurred as breeding local populations in discrete habitat patches, with additional
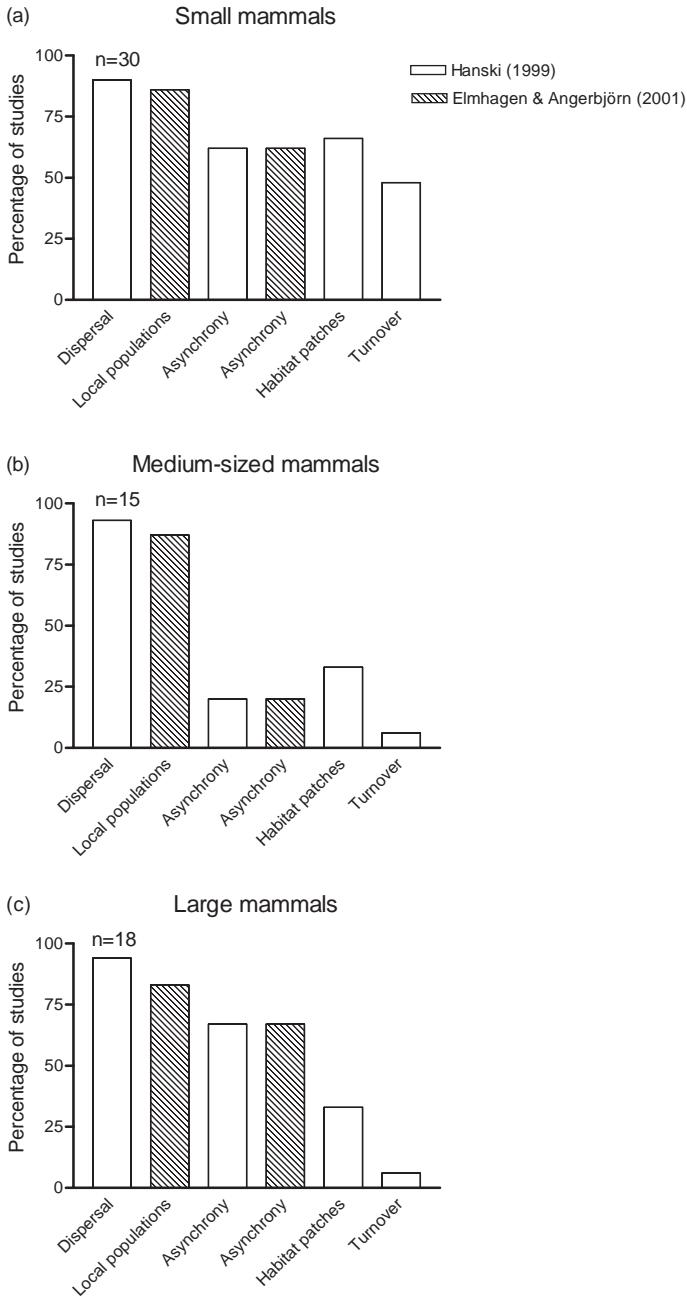
Fig. 1. The percentage of (a) small, (b) medium-sized and (c) large mammal species populations, in which the criteria of Hanski (1999) and Elmhagen & Angerbjörn (2001) were used to describe metapopulation dynamics in mammals. Open bars indicate the classic criteria of Hanski (1999), shaded bars indicate the more lenient criteria described by Elmhagen & Angerbjörn (2001). Sample sizes are numbers of studies.

vacant habitats that could be colonized (Fig. 1). One of the criteria recommended by Elmhagen & Angerbjörn (2001) was met in 84% ($n = 53$) of studies; species occurred as discrete breeding local populations. Thirty-three (52%) exhibited asynchrony in dynamics (Fig. 1). For 32% ($n = 20$) of studies, only one of Hanski's (1999) criteria was used to describe
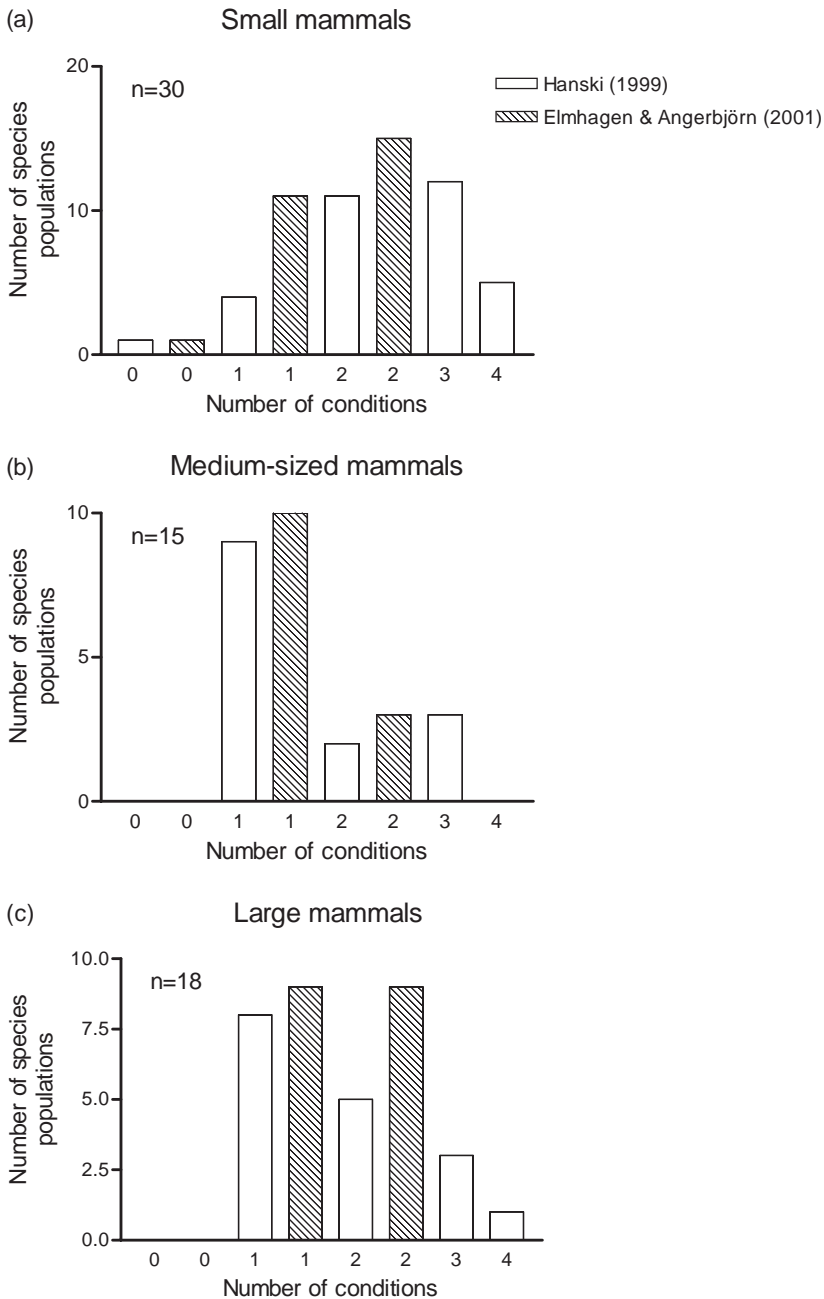
Fig. 2. The number of criteria that researchers applied to describe (a) small, (b) medium-sized and (c) large mammal species populations as metapopulations based on papers published from 1991 to 2007. Open bars indicate the classic criteria of Hanski (1999), shaded bars indicate the more lenient criteria described by Elmhagen & Angerbjörn (2001). Sample sizes are numbers of studies.

a metapopulation structure, while 46% ($n = 29$) of studies met one or the other of Elmhagen & Angerbjörn's (2001) two criteria (Fig. 2). Both the criteria of Elmhagen & Angerbjörn (2001) were noted for 41% ($n = 26$) of the studies, while 66% ($n = 42$) met more than one of Hanski's (1999) criteria (Fig. 2).

Table 1. An assessment of the classical criteria of metapopulations (Hanski, 1999) reported in studies on small (≤5 kg; *n* = 30), medium (>5 ≤ 100 kg; *n* = 15) and large (>100 kg; *n* = 18) mammal species (total *n* = 63)

Metapopulation criteria		Small mammals	Medium mammals	Large mammals
Individual dispersal	Yes	26	14	17
	No	3	1	1
	Not assessed	1	0	0
Population turnover	Yes	14	1	1
	No	0	0	0
	Not assessed	16	14	17
Asynchrony in dynamics	Yes	18	3	12
	No	0	0	0
	Not assessed	12	12	6
Habitat patches with breeding sub-populations	Yes	19	5	6
	No	0	0	0
	Not assessed	11	10	12

Table 2. An assessment of the more lenient criteria of metapopulations (Elmhagen & Angerbjörn, 2001) reported in studies on small (≤5 kg; *n* = 30), medium (>5 ≤100 kg; *n* = 15) and large (>100 kg; *n* = 18) mammal species (total *n* = 63)

Metapopulation criteria		Small mammals	Medium mammals	Large mammals
Breeding sub-populations are discrete	Yes	25	14	15
	No	0	0	0
	Not assessed	5	1	3
Asynchrony in dynamics	Yes	18	3	12
	No	0	0	0
	Not assessed	12	12	6

Body size influenced the patterns noted above. For small (≤5 kg), medium (>5 ≤ 100 kg) and large (>100) species, dispersal was the condition most frequently assessed (Fig. 1). Dispersal between local populations was also assessed at similar frequencies among body size classes ($\chi^2 = 0.396$, d.f. = 2, $P = 0.821$). Population turnover was recorded for 14 of 30 studies on small mammals, but for only one of 15 on medium sized and one of 18 on large mammal species. The frequency of reporting asynchrony in population dynamics differed with body size ($\chi^2 = 8.476$, d.f. = 2, $P = 0.014$). The reporting of incidences of habitat patches that supported breeding local populations did not differ with body size ($\chi^2 = 5.670$, d.f. = 2, $P = 0.059$) (Table 1). The occurrence of discrete breeding local populations was similar for small, medium-sized and large mammals ($\chi^2 = 0.095$, d.f. = 2, $P = 0.953$) (Table 2).

In most (60%) of the 63 studies published on metapopulation dynamics, authors stated that they evaluated criteria before classifying the population as a metapopulation, while 15% (*n* = 9) classified populations as metapopulations, but did not evaluate any criteria. In about 16% (*n* = 10) of studies, authors suggested that the studied population would function as a metapopulation if suitable conservation measures were put into place, while a further 7% (*n* = 4) of studies dealt with artificially created metapopulations where metapopulation processes and criteria were mimicked by management strategies. In two studies (3%), the population used to function as a metapopulation, but did not anymore. In one case, the studied

population was found not to be a metapopulation. For small mammals, 9 out of 30 (30%) studies mentioned that metapopulation processes could contribute to the conservation of the studied species populations, while for large and medium-sized mammals, 22 out of 33 (67%) studies invoked metapopulation processes for conservation purposes.

DISCUSSION

Metapopulations are not always easy to identify (Hanski & Simberloff, 1997; Thomas & Kunin, 1999). Our analysis suggests that the use of the concept is not always supported by empirical information that may meet the criteria of Hanski (1999), or even the more lenient subset of criteria proposed by Elmhagen & Angerbjörn (2001). Most of the 63 studies that we assessed provide some evidence for a metapopulation structure, and nearly all authors concluded that the population they studied functioned as a metapopulation. However, much of the evidence for metapopulations stems from the inconsistent application of the concept and the use of a range of definitions that ignores some of the original criteria. For instance, in only one (Hayward *et al.*, 2004) of the 29 studies published since 2001 is it stated explicitly that the criteria recommended by Elmhagen & Angerbjörn (2001) were evaluated.

The criteria of Elmhagen & Angerbjörn (2001) seem easier to apply than those of Hanski (1999). For example, in most (84%) of the 63 studies that we reviewed, the species comprised discrete breeding local populations, and thus met one of the two criteria set by Elmhagen & Angerbjörn (2001), while in only half (48%), the studied species inhabited discrete habitat patches with additional vacant habitats that can be colonized, as expected by one of the four criteria of Hanski (1999). However, most (83%) of the studies that recognized discrete habitat patches, as recommended by Hanski (1999), or discrete breeding local populations as recommended by Elmhagen & Angerbjörn (2001), used dispersal to deduce metapopulation dynamics. Therefore, no matter the criteria, where species illustrate dispersal, studies deduced metapopulation structures.

Our analysis furthermore suggests that the size of mammals influences the criteria that may be used to support metapopulation dynamics. For instance, for small mammal species (≤5 kg), the criteria of Hanski (1999) were met with the same frequency as those of Elmhagen & Angerbjörn (2001). Small mammals were also more likely to adhere to the full set of criteria proposed by Hanski (1999). For instance, extinction and colonization events were recorded in 46% of small mammal species populations compared with only 7 and 6% in medium-sized and large mammals respectively.

Case studies that support the classical metapopulation structure are rare (Elmhagen & Angerbjörn, 2001). This is also supported by our review. Only five of 75 species populations adhered to classical metapopulation criteria – these are all small mammals and comprise the four-eyed opossum *Philander opossum*, American pika *Ochotona princeps*, black-tailed prairie dog *Cynomys ludovicianus*, field vole *Microtus agrestis* and the round-tailed muskrat *Neofiber alleni* (Adler & Seamon, 1996; Moilanen, Hanski & Smith, 1998; Roach *et al.*, 2001; Banks *et al.*, 2004; Schooley & Branch, 2007). Few studies thus provide support for the full set of criteria for the classical metapopulation. Meeting these criteria depends on case-specific spatial conditions to which populations will respond. From the review of Krohne (1997), it is apparent that fragmentation, dispersal barriers and dispersal corridors are all species population specific, and that species' responses to these depend on body size, habitat, physiological responses to stressful environments and social factors. We therefore agree with Clinchy, Haydon & Smith (2002) that evidence of metapopulation processes rather than spatial occupancy should be used to provide evidence of metapopulation dynamics.

For studies on small mammals, we propose that the full complement of metapopulation criteria (Hanski, 1999) can be applied to yield new perspectives on population regulation. Metapopulation processes could also be used to parameterize models that emphasize small mammal characteristics (see Lambin *et al.*, 2004). Metapopulation processes can also be incorporated into management and conservation paradigms. For instance, McShea *et al.* (2003) suggest that a timber harvest management paradigm based on metapopulation processes would conserve small mammal species populations more effectively than a traditional approach that only focused on the proportion of available habitat.

Our review suggests that the application of the metapopulation concept differs between small and other-sized mammals, but is similar for medium and large mammals. Authors consider dispersal between discrete local populations of large mammals as the key condition for a metapopulation structure and tend to ignore the other criteria. For instance, in 31 of the 33 studies on large mammal populations, all criteria except dispersal are ignored by authors, labelling their studied population as a metapopulation. The limitations in evaluating the other criteria may induce this bias. Criteria associated with extinction and recolonization events may not be used, because the time span of these events usually exceeds that of most studies, possibly due to the relatively long generation times and slow reproductive rates of large mammals (Murphy, Freas & Weiss, 1990). It may therefore prove futile for studies on larger mammals to focus on population turnover as a condition to be met for metapopulation dynamics. Even so, our results suggest that a metapopulation structure can exist in mammals, but that the longevity and slow turnover typical of medium- and large-sized mammals may make it difficult to find support for the full set of classical criteria for a metapopulation structure. Despite this detraction, the metapopulation concept can be applied to large mammal species populations.

Our review suggests that most (31 of 33 studies, 94%) medium and large mammal species populations that occurred as discrete breeding local populations also dispersed between local populations. Furthermore, the dynamics of nearly half (15 of 31, 48%) of these populations were asynchronous. Such asynchrony could reflect on habitat heterogeneity, lack of dispersal between local populations, variation in community processes and trophic interactions, and environmental variation that can induce source–sink dynamics (Pulliam, 1988; Bjørnstad, Ims & Lambin, 1999). Alternatively, synchrony in population dynamics can result from high dispersal rates or correlated changes in environmental conditions (Ranta, Kaitala & Lundberg, 1998).

Dispersal alone may not be a good indicator of metapopulation dynamics. We propose that both dispersal, the focus of much of the literature we reviewed, and asynchrony in dynamics between discrete local populations, need to be included in the evaluation. Because turnover is difficult to record in medium to large mammals, the illustration of dispersal and asynchrony alone may serve as evidence for a metapopulation structure.

Determining the spatial structure of a population is essential when formulating conservation guidelines, because it presents a conceptual tool for dealing with the interactions between, within and among populations (Githiru & Lens, 2004). The application of metapopulation theory may be more important for large than small mammals for the simple reason that large mammals usually operate at spatial scales at which they are exposed to landscape fragmentation. Consequently, large mammals are more frequently exposed to human-induced disturbances than small mammals (Crooks, 2002; Cardillo *et al.*, 2005), and are often restricted to national parks and wildlife reserves (e.g. Brashares, 2003).

Spatial population patterns maintain processes that have implications for persistence (Thomas & Hanski, 2004). Emphasis therefore should shift from observing spatial patterns to recording spatial processes (e.g. Thomas & Kunin, 1999; Hanski & Gaggiotti, 2004). We

therefore suggest that metapopulation theory should be applied to populations of mammals when constructing conservation plans to ensure population persistence and to contribute to the forces that stabilize populations regionally.

Most (22 of 33, 67%) of the studies we included in our review, which explicitly deal with medium and large mammals, suggest that conservation will benefit from the inclusion of metapopulation processes. For instance, Singh & Kumara (2006) recognized that for a wide-ranging animal such as the Indian grey wolf *Canis lupus pallipes*, sanctuaries could only protect one or two wolf packs. They suggest that the conservation of forest patches of varying sizes in a landscape matrix could facilitate the dispersal of wolf packs that then may become part of a large metapopulation. Similarly, Sweanor, Logan & Hornocker (2000) and Hellgren, Onorato & Skiles (2005) showed that cougars *Puma concolor* and black bears *Ursus americanus* persist if conservation initiatives are implemented on a regional scale. The most artificial application of the metapopulation concept in conservation comes from the advocacy that removing individuals from one isolated population mimics dispersal. Translocations of wild dog *Lycanon pictus* and black rhino *Biceros dicornis* from one conservation area to another in Africa (Amin *et al.*, 2006; Akçakaya *et al.*, 2007) serve as good examples.

We caution against implementing conservation strategies based on metapopulation dynamics if habitat discreteness, likelihood of dispersal and potential of asynchrony have not been evaluated. The application of metapopulation theory to cases or species that do not meet the criteria to exist as a metapopulation may lead to conservation actions that neglect important life histories, with consequences for species persistence (see Grimm, Reise & Strasser, 2003). For instance, the metapopulation concept can motivate the development of movement corridors without evidence that corridors would be used, or forestall extinction (Boitani *et al.,* 2007). Such actions are expensive and could detract from efforts to protect particular populations that require specific refuges (Simberloff *et al.*, 1992; Boitani *et al.,* 2007). However, the correct and consistent application of metapopulation theory and the implementation of metapopulation processes in mammal populations may improve the persistence of mammals in fragmented habitats.

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APPENDIX

Table A1. Studies in which mammals have been described as metapopulations or as possibly functioning as metapopulations

Species population	Body mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding sub-populations	Metapopulation Type	Reference
Bank vole *Clethrionomys glareolus*	0.002–0.003	Anthropogenic	Yes	Yes	Yes	N.A.	Yes	Source-sink	van Apeldoorn *et al.* (1992)
Euro *Macropus robustus*	90	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Not described	Arnold *et al.* (1993)
Greater glider *Petauroides volans*	0.002–0.003	Anthropogenic	Yes	Yes	N.A.	Yes	N.A.	Modelled	Possingham *et al.* (1994)
Pine vole *Microtus duodecimcostatus*	0.002–0.003	Natural	Yes	Yes	Potential	N.A.	Yes	Source-sink	Paradis (1995)
Four-eyed opossum *Philander opossum*	0.24–0.4	Natural	Yes	Yes	Yes	Yes	Yes	Boorman–Levitt	Adler & Seamon (1996)
Leadbeater's possum *Gymnobelideus leadbeateri*	0.12–0.16	Anthropogenic	Possible	Yes	N.A.	Yes	Yes	Not described	Lindenmayer & Possingham (1996)
Vancouver island marmots *Marmota vancouverensis*	0.25	Natural	Yes	N.A.	N.A.	Yes	Yes	Not described	Bryant & Janz (1996)
Lower Keys marsh rabbit *Sylvilagus palustris hefneri*	2.5–3	Natural	Yes	Yes	Yes	N.A.	Yes	Not described	Forys & Humphrey (1996)
Leaf-eared mouse *Phyllotis darwini*; olive grass mouse *Akodon olivaceus*; elegant fat-tailed opossum *Thylamys elegans*; Degu *Octodon degus*; long-tailed pygmy rice rat *Oligoryzomys longicaudatus*	0.005–0.01	Natural	N.A.	Yes	N.A.	N.A.	Yes	Not described	Lima *et al.* (1996)
White-tailed deer *Odocoileus virginianus*	300–600	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Not described	Seagle & Close (1996)
Leaf-eared mouse *Phyllotis darwini*	0.007–0.01	Anthropogenic	Possible	Yes	Yes	N.A.	Yes	Partially coupled	Torres-Contreras *et al.* (1997)
Polar bear *Ursus maritimus*	300–600	Natural	Yes	N.A.	N.A.	N.A.	Yes	Not described	Ferguson *et al.* (1998)
Iberian lynx *Lynx pardinus*	13–25	Anthropogenic	Yes	Potential	N.A.	Yes	Yes	Source-sink	Gaona, Ferreras & Delibes (1998)
Puku *Kobus vardoni*	74–77	Natural	Yes	N.A.	N.A.	Yes	Yes	Not described	Goldspink *et al.* (1998)
American pika *Ochotona princeps*	0.5–1.0	Natural	Yes	Yes	Yes	Yes	Yes	Classical	Moilanen *et al.* (1998)
Woodland caribou *Rangifer tarandus caribou*	170–300	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Rettie & Messier (1998)
Tiger *Panthera tigris*	205–227	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Smith, Ahearn & McDougal (1998)
Harbour seal *Phoca vitulina*	~130	Natural	Possible	N.A.	Potential	N.A.	Yes	Not described	Swinton *et al.* (1998)
White-footed mouse *Peromyscus leucopus*	0.023	Anthropogenic	Yes	N.A.	Yes	Yes	Yes	Not described*	Krohne & Hoch (1999)
Greater glider *Petauroides volans*	1.6–1.9	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	McCarthy & Lindenmayer (1999)
Nubian ibex *Capra ibex nubiana*	~50	Natural	Yes	N.A.	N.A.	N.A.	Yes	Not described	Shkedy & Saltz (2000)
Yellow-necked mice *Apodemus flavicollis*	0.016–0.032	Anthropogenic	Yes	N.A.	N.A.	Yes	N.A.	Patchy	Szacki (1999)
Long-furred woolly mouse opossum *Micoureus demerarae*	0.13	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Not described	Pires & Fernandez (1999)
San Joaquin kit foxes *Vulpes macrotis mutica*	7–8	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Koopman, Cypher & Scrivner (2000)
Samango monkey *Cercopithecus mitis liabiatus*	7–9	Anthropogenic	No	N.A.	N.A.	N.A.	Yes	Transient non-equilibrium	Lawes *et al.* (2000)
Tree hyrax *Dendrohyrax arboreus*	~3	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Mainland–island	Lawes *et al.* (2000)
Blue duiker *Cephalophus monticola*	4–5	Anthropogenic	Yes	N.A.	N.A.	Yes	Yes	Mainland–island	Lawes *et al.* (2000)
Bighorn sheep *Ovis Canadensis*	170–302	Natural	Yes	Yes	Yes	Yes	Yes	Not described	Singer, Bleich & Gudorf (2000)
Cougar *Puma concolor*	~75	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Sweanor *et al.* (2000)
Silvery gibbon *Hylobates moloch*	~8	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Andayani *et al.* (2001)
Mountain pygmy possum *Burramys parvus*	0.045	Natural	Yes	N.A.	Yes	N.A.	Yes	Not described	Broome (2001)
Artic fox *Alopex lagopus*	3.1–3.8	Anthropogenic	Yes	N.A.	Yes	Yes	Yes	Not described	Elmhagen & Angerbjörn (2001)
Rock hyrax *Heterohyrax brucei*	~3	Natural	Yes	N.A.	Potential	Yes	Yes	Not described	Gerlach & Hoeck (2001)
Rock hyrax *Procavia johnstoni*	~3	Natural	No	N.A.	Potential	Yes	Yes	Not described	Gerlach & Hoeck (2001)

Table A1 (*Continued*)

Species population	Body mass (kg)	Fragmentation type	Dispersal	Turnover	Asynchrony	Discrete habitat patches	Discrete breeding sub-populations	Metapopulation Type	Reference
Black-tailed prairie dog *Cynomys ludovicianus*	0.7–1.5	Anthropogenic	Yes	Yes	Potential	Potential	Yes	Not described	Roach et al. (2001)
Grey seal *Halichoerus grypus*	200–350	Natural	Yes	Yes	Yes	Yes	Yes	Not described	Gaggiotti et al. (2002)
Florida panther *Puma concolor*	~75	Anthropogenic	Yes	N.A.	N.A.	N.A.	N.A.	Not described	Maehr et al. (2002)
Spanish ibex *Capra pyrenaica*	~50	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Pérez et al. (2002)
Steller sea lion *Eumetopias jubatus*	~300	Natural	Yes	N.A.	Yes	N.A.	Yes	Not described	Ruam-Suryan et al. (2002)
Kodkod *Oncifelis guigna*	11–14	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Mainland–island	Acosta-Jamett et al. (2003)
White-footed mouse *Peromyscus leucopus*; deer mouse *Peromyscus maniculatus*; northern short-tailed shrew *Blarina brevicauda*; Eastern chipmunk *Tamias striatus*; Southern red-backed vole *Clethrionomys gapperi*; woodland jumping mouse *Napaeozapus insignis*; smoky shrew *Sorex fumeus*; masked shrew *Sorex cinereus*; pygmy shrew *Sorex hoyi*	0.01–0.05	Natural	Yes	Yes	Yes	Yes	N.A.	Not described	McShea et al. (2003)
Field vole *Microtus agrestis*	0.01–0.03	Natural	Possible	Yes	Potential	N.A.	Yes	Not described	Banks et al. (2004)
Water vole *Arvicola amphibius*	0.16–0.35	Natural	Yes	Yes	N.A.	N.A.	Yes	Not described	Lambin et al. (2004)
Indus river dolphin *Platanista minor*	170–301	Natural	No	N.A.	N.A.	N.A.	Yes	Not described	Gachal & Slater, 2004
Tundra vole *Microtus oeconomus*	~0.05	Experimental population	Yes	N.A	Yes	Yes	Yes	Not described	Ims & Andreassen (2005)
Amur tiger *Panthera tigris altaica*	215–270	Anthropogenic	Yes	N.A.	Yes	N.A.	N.A.	Not described	Carroll & Miquelle (2006)
Quokka *Setonix brachyurus*	2.5–5.0	Anthropogenic	No	Yes	Yes	Yes	Yes	Not described	Hayward et al. (2004)
European bison *Bison bonasus*	450–1000	Anthropogenic	Possible	N.A.	Potential	Yes	Yes	Not described	Perzanowski, Olech & Kozak (2004)
Ethiopian wolf *Canis simensis*	~20	Natural	Yes	N.A.	N.A.	N.A.	N.A.	Not described	Sillero-Zubiri et al. (2004)
Fisher *Martes pennanti*	2.1–7.0	Natural	Possible	N.A.	Potential	Yes	Yes	Not described	Wisely et al. (2004)
Black bear *Ursus americanus*	170–303	Natural	Yes	N.A.	Potential	Yes	Yes	Mainland–island	Hellgren et al. (2005)
Brown bear *Ursus arctos*	130–700	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Preatoni et al. (2005)
Gaint panda *Ailuropoda melanoleuca*	100–115	Anthropogenic	Possible	N.A.	N.A.	N.A.	Yes	Not described	Ran et al. (2005)
Ili pika *Ochotona iliensis*	0.5–1.0	Natural	No	N.A.	N.A.	N.A.	N.A.	Not described	Li & Smith (2005)
Amur tiger *Panthera tigris altaica*	215–270	Anthropogenic	Yes	N.A.	Yes	Yes	N.A.	Not described	Carroll & Miquelle (2006)
Black rhino *Diceros bicornis*	~1000	Anthropogenic	Yes	N.A.	Potential	Yes	Yes	Not described	Amin et al. (2006)
Mountain caribou *Rangifer tarandus caribou*	170–300	Anthropogenic	Yes	N.A.	Yes	N.A.	Yes	Not described	Apps & McLellan (2006)
Indian gray wolf *Canis lupus pallipes*	18–27	Anthropogenic	Yes	N.A.	N.A.	N.A.	Yes	Not described	Singh & Kumara (2006)
Mountain vizcacha *Lagidium peruanum*	~3	Natural	Possible	N.A.	Potential	Yes	Yes	Not described	Werner, Ledesma & Rodrigo (2006)
European hare *Lepus europaeus*	2.5–6.5	Anthropogenic	Yes	N.A.	Potential	N.A.	N.A.	Not described	Bray et al. (2007)
Wild dog *Lycaon pictus*	24–28	Anthropogenic	Yes	N.A.	Potential	Yes	Yes	Not described	Akçakaya et al. (2007)
Peccary *Tayassu pecari*	20–40	Anthropogenic	Possible	N.A.	N.A.	N.A.	N.A.	Not described	Mendes Pontes & Chivers (2007)
Elephant *Loxodonta africana*	5500–6000	Anthropogenic	Yes	N.A.	Yes	N.A.	N.A.	Source–sink	van Aarde & Jackson (2007)
Round-tailed muskrat *Neofiber alleni*	0.2–0.4	Natural	Yes	Yes	Potential	Yes	Yes	Source–sink	Schooley & Branch (2007)

N.A., not assessed.
The empirical support for this classification or lack thereof, as described in the studies, is shown for each species.
*Metapopulation described as type C' from Krohne (1997).