LETTER

Extinction risk and tradeoffs in reserve site selection for species of different body sizes

Justin Kitzes, & Adina Merenlender

Department of Environmental Science, Policy, and Management, University of California, Berkeley, California

Abstract

Designing reserve networks often requires a tradeoff between maximizing patch sizes to decrease local extinction rates and clustering patches to increase colonization rates. Here we use stochastic metapopulation models to evaluate how this tradeoff affects landscape wide extinction risk for idealized terrestrial mammals with body sizes from 10 g to 100 kg. In simple two-patch networks, clustering patches decreases extinction risk only when interpatch distances are within 0.5–1.25 times a species' maximum observed dispersal distance. In an empirical landscape in which a fixed total area can be protected, this finding accurately predicts that, relative to a network that maximizes mean patch area, clustering patches most decreases extinction risk for intermediate-sized species. These results demonstrate that there is no globally optimal level of patch clusterin that will best protect all species and highlight rules of thumb for reserve network design based on the interaction of species' body size and landscape scale.

Introduction

As global habitat loss and fragmentation continues, species' populations are becoming increasingly restricted to remnant habitat patches surrounded by relatively inhospitable matrix (Fahrig 2003; Lindenmayer & Fischer 2006). A major challenge in spatial ecology and conservation biology is to predict the extinction risk faced by these newly fragmented populations and to use this knowledge to prioritize the conservation of remaining patches to best minimize this risk.

As suggested by island biogeography and metapopulation theory (MacArthur & Wilson 1967; Hanski 1999), the two first-order factors that control diversity in patchy landscapes are patch areas (primarily by influencing the probability of local patch extinction) and patch isolation (primarily by influencing the probability of the recolonization of a locally extinct patch). Land managers and policy makers with a fixed budget for conservation have thus long been advised to prioritize protection of the largest available habitat patches in a landscape and, presuming a relatively homogeneous matrix between patches, to simultaneously ensure that these patches are as close together as possible (Diamond 1975; Williams et al. 2004). In any real landscape in which a fixed area of habitat can be protected, however, it will generally be impossible to simultaneously maximize mean patch area and minimize interpatch distance, barring the coincidental case in which the largest available habitat patches form the tightest cluster. Managers are thus frequently faced with a tradeoff between these two considerations, and the appropriate balance between the two should ideally be set by examining the risk of a species' extinction in each potential reserve network.

Many methods have been proposed for estimating a species' extinction risk in patchy landscapes and selecting a network of patches to minimize this risk. Using detailed empirical data, spatially explicit stochastic patch occupancy models (e.g., Moilanen & Cabeza 2002; Cabeza & Moilanen 2003; Drechsler et al. 2003; Nicholson et al.

2006) and age or stage structured demographic models (e.g., Carroll *et al.* 2003; Akçakaya 2004; Newbold & Siikamäki 2009) can be constructed to predict extinction risk in any patch network. These models lack generality, however, in that they are parameterized for a particular species in a particular landscape, and the extent of their broader applicability is often unclear. More general, theory-based approaches have reached overarching conclusions about extinction risk as a function of species and network characteristics (e.g., Frank 2005; McCarthy *et al.* 2005, 2006; Drechsler & Johst 2010). These approaches, however, often do not consider the population dynamics of individual patches, are fully or partially spatially implicit, use aggregate constants to represent species' life history traits, and assume relatively simple statistical distributions for model parameters.

A desirable method for patch selection should be broadly applicable and flexible enough to be used to explore the effects of different modeling assumptions, while also being detailed enough to directly incorporate key differences between species and landscapes. One promising approach to achieving this balance involves the combination of empirical allometric relationships, known patterns in the relationship between body size and life history traits (Sutherland *et al.* 2000; Jones *et al.* 2009; Blueweiss *et al.* 1978; Damuth 1981), and dynamic population models (Belovsky 1987; Wilson *et al.* 2010). Here, we construct and explore one such set of models for idealized terrestrial mammal species of different body sizes and use it to analyze the tradeoff between patch size and patch clustering in protected area networks. The models are first used to examine extinction risk by body size in two-patch networks, across a range of patch areas and interpatch distances, to identify general patterns in the relationship between extinction risk, body size, and network characteristics. The analysis is then extended to an empirical landscape in northern California, where the patch networks that best minimize extinction risk for species of different body sizes are identified and compared.

The results demonstrate that, at any spatial scale, selecting clustered patch networks does not benefit all species equally and that the species that may benefit from clustering can be identified by matching dispersal distances to interpatch distances. In principle, there is no globally optimal network design that best minimizes extinction risk for species of all body sizes, and the selection of priority patches for conservation should be made with the explicit knowledge of which species are advantaged and disadvantaged by any network design. These general findings, as well as the full allometry-based models themselves, could be extended to other taxonomic groups and landscapes and may be particularly useful for the prac-

Table 1 Life history parameters, including yearly reproductive output, *y* (maximum female young per adult female per year), population density, *s* (females per hectare), and maximum observed dispersal distance, *x* (km) for idealized terrestrial mammals of different body sizes (see "Methods" section). Each species' characteristic range, CR (km), is calculated as 0.5–1.25 times *x* (see "Results" section)

Body mass (kg)	*y*	*s*	*x*	CR
0.01	2.26	6.91	0.28	0.14–0.35
0.1	1.96	1.26	1.35	0.67–1.69
1	1.70	0.23	6.46	3.23–8.08
10	1.47	0.04	31.0	15.5–38.6
100	1.28	0.01	148	74.0–185

tice of conservation planning in landscapes where little is known about resident species of conservation concern.

Methods

Metapopulation models

We constructed stochastic, demographic metapopulation models to evaluate extinction risk in patchy landscapes for idealized terrestrial mammal species with adult body masses of 10 g, 100 g, 1 kg, 10 kg, and 100 kg. The models required knowledge of individual patch areas and locations and three life history parameters that could be estimated from a species' body size: maximum female offspring per adult female per year, *y*, mean female population density, *s*, and maximum observed dispersal distance, *x*. For a species of a given body size, the values of *y* and *s* were estimated from log–log regressions using data for global mammals (Jones *et al.* 2009), and the value of *x* was taken from a log-log regression reported by Sutherland *et al.* (2000). The values of these parameters for each body size are given in Table 1. Two additional parameters, θ and p_e, were used to set the level of environmental stochasticity in each landscape and were assumed. The parameter p_e gives the mean per capita probability of surviving a "catastrophe" event, while θ is a shape parameter.

The mathematical details of the metapopulation models are described in the Supporting Information. For each species, the models began by calculating a carrying capacity, K_i, for each patch *i*, which was set to the patch area multiplied by mean female population density multiplied by 10. Each patch was initialized with a population equal to one half its carrying capacity. Local populations in each patch then underwent birth and recruitment, death due to demographic stochasticity, and death due to environmental stochasticity. All simulations were discrete time and are carried out for 100 years. The fraction of network-wide extinctions by year 100 was

used as a measure of extinction risk in all subsequent analyzes.

The models described births in each patch as Poisson distributed, with a mean birth rate for each patch i equal to the sum over all patches j (including $i = j$) of the product of y, the current population of patch j, and the probability that an individual born in patch j recruited to patch i. The probability of an individual born in patch j recruiting to patch i was calculated using a Gaussian dispersal kernel with a variance set by assuming that 99% of individuals recruit to a distance lower than the maximum observed dispersal distance reported by Sutherland *et al.* (2000).

The number of deaths in each patch due to demographic stochasticity was drawn from a binomial distribution with the number of trials equal to the postbirth population of each patch. A density-dependent per capita survival probability was calculated to ensure that (1) the lowest mean per capita death rates occur when populations were small and (2) at a patch's carrying capacity, the expected number of deaths was equal to the expected number of births.

Death due to exogenous environmental "catastrophes" was modeled for each local patch using a beta-binomial distribution, parameterized using $\theta = 1$ and a variable level of p_e (Bolker 2008), which gives a strongly U-shaped distribution in which the most likely outcomes are local patch extinction or survival of all individuals. The value of p_e, the mean per capita survival probability, was varied to change the frequency of catastrophic events.

In general, the overall conclusions of our analysis, however, were found to be a function only of the parameter x (Figure S1). In particular, the parameter p_e was found to affect absolute extinction risk for each species and network but not the relative extinction risk of different network types (Figure S2).

Network comparison and reserve design

First, we used these metapopulation models to evaluate extinction risk for each species in two-patch networks. Patch areas from 1 to 200 hectares and interpatch distances of 1–50 km were examined, with the parameter $p_e = 0.85$, in 1,000 replicate simulations. This analysis was used to examine general patterns in the relationship of extinction risk to body size, patch area, and interpatch distance.

Second, we applied these models in an empirical, fragmented landscape to select a set of patches with a fixed total area that minimized network-wide extinction risk for each species. The long computation times associated with the metapopulation simulations precluded true op-

timization, and instead a first-in greedy heuristic (Church *et al.* 1996) was used to select reserve networks. At each step, the mean number of occupied patches in year 100 for a candidate reserve network was used to determine which additional patch to add to the network (see Supporting Information). This approach was applied to an empirical landscape near Santa Rosa, California consisting of 57 patches of remnant low-elevation mixed oak savannah (Clark 1937) interspersed with urban and agricultural development (Merenlender *et al.* 2005). Similar to the two-patch analysis, 1,000 replicate simulations were conducted with $p_e = 0.7$. Habitat quality within patches was assumed to be equal, and the matrix between habitat patches was assumed to be homogeneous. Complete reserve networks containing up to 66% of the total available area were selected 10 times for each species.

Finally, we calculated and compared the absolute extinction risk using 2,000 replicate simulations for each species in two networks, a reference network consisting of the four largest available patches in the empirical landscape and a clustered network including three of these four patches and several smaller patches nearby (Figure 3, inset). For comparability between species, the value of p_e for each species that gave a 50% probability of extinction in the reference network in year 100 was used.

Results

In two-patch networks, extinction risk varies greatly as a function of body size, patch area, and interpatch distance (Figure 1). These results show that each species exhibits a unique and limited "characteristic range," defined here as the range of interpatch distances within which interpatch distance substantially influences persistence probability, that is indicated by the steeply sloping isoclines in Figure 1. The steeply sloping portion of these isoclines define a range of interpatch distances within which a greater patch area is needed to maintain a constant extinction risk as the interpatch distance is increased, implying that within this range the interpatch distance has a large effect on extinction risk.

Visual examination of these results show that the characteristic range for each species falls from approximately 0.5–1.25 times a species' maximum observed dispersal distance. Only within this characteristic range do changes in interpatch distance substantially increase or decrease a species' extinction risk, while outside of this range, interpatch distance is largely irrelevant to extinction risk. Broadly speaking, this range is defined by a lower threshold below which a species can nearly equally disperse between patches at all distances and an upper threshold
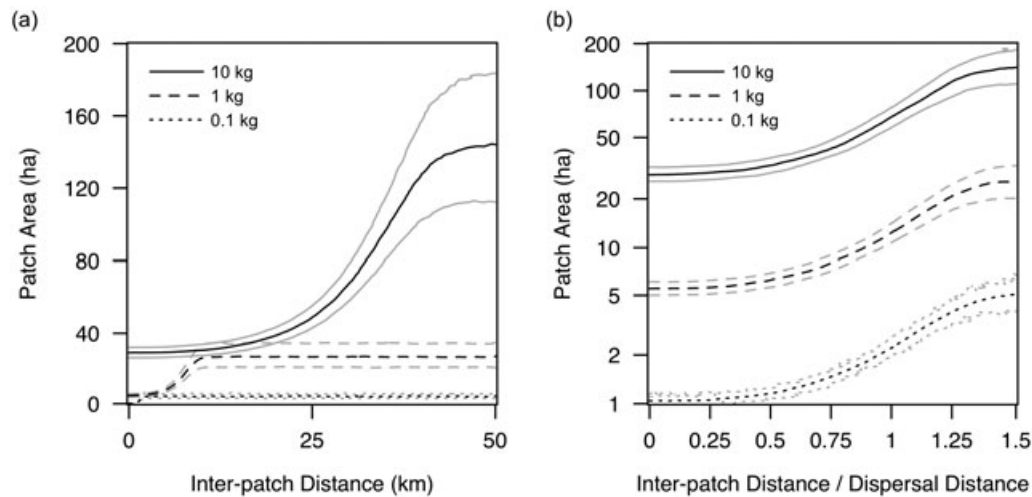
Figure 1 Isoclines of persistence probability for species in two-patch networks with different patch areas, A_i (hectares), and interpatch distances, d_{ij} (km). Black lines show combinations of A_i and d_{ij} that give a 35% probability of persistence to year 100 for species with adult body masses of 0.1 kg, 1 kg, and 10 kg, with gray lines showing 25% and 45% probabilities. (a) Each species has a unique characteristic range, indicated by steeply sloping portions of the isoclines, within which interpatch distance substantially affects extinction risk. (b) As in (a), but with the ratio of interpatch distance to maximum observed dispersal distance on the x-axis and a log scale for area. The characteristic range for all three species falls at approximately 0.5–1.25 times the species' maximum observed dispersal distance.

above which a species cannot disperse between patches regardless of distance. This characteristic range can be shown to be only a function of a species' maximum observed dispersal distance x, and not other model parameters (Figures 1 b and S1). The characteristic range for each species is given in Table 1.

In a multipatch network of fixed total area, clustered patch networks will generally have shorter interpatch distances, more patches, and lower mean patch areas than a reference network selected to maximize mean patch area. In general, the first two of these factors have the potential to lead to lower extinction risks in clustered networks, while the third has the potential to lead to higher extinction risks in clustered networks. The analysis of the differences between a clustered network and a reference network is thus reminiscent of the long-standing single large or several small (SLOSS) debate in conservation biology (reviewed in Ovaskainen 2002), where here the relationship between interpatch distance and dispersal is explicitly modeled.

Considering specifically the importance of local patch extinction and recolonization, the two-patch network results lead to an initial hypothesis regarding which species might experience reduced extinction risk in a multi-patch network that is clustered at any scale. Relative to the reference network that maximizes mean patch area, clustering may specifically benefit, via increasing recolonization rates, those species whose characteristic range matches the scale of the patch cluster. If, however, this cluster-

ing also results in a decrease in mean patch area, all species may potentially experience an additional "cost" associated with an increase in local patch extinction risk. As a first approximation, any given scale of patch clustering might thus be expected to most reduce network-wide extinction risk for species whose characteristic range matches the cluster scale.

This hypothesis is tested in an empirical, multipatch landscape, where networks are selected to minimize extinction risk for each species given that the entire set of patches cannot be protected (Figure 2). In this landscape, many pairwise interpatch distances are on the order of 1–10 km, a spatial scale that overlaps most substantially with the characteristic ranges of the 0.1 kg species and 1 kg species (Tab. 1). As predicted, the chosen reserve network for the 0.1 kg species qualitatively displays clustering at small spatial scales within this landscape, the 1 kg species network displays clustering across larger scales, and the networks selected by both larger and smaller bodied species are similar to the reference network. Several large, core patches are selected in all networks and would represent important first targets for protection in this landscape. In a hypothetical landscape in which interpatch distances are artificially increased by a factor of five, the pattern of patch clustering selected here by the 1 kg species is selected by the 10 kg species, also as predicted (Figure S3).

Figure 3 compares, for each species, extinction risk in a reference network consisting of the four largest available
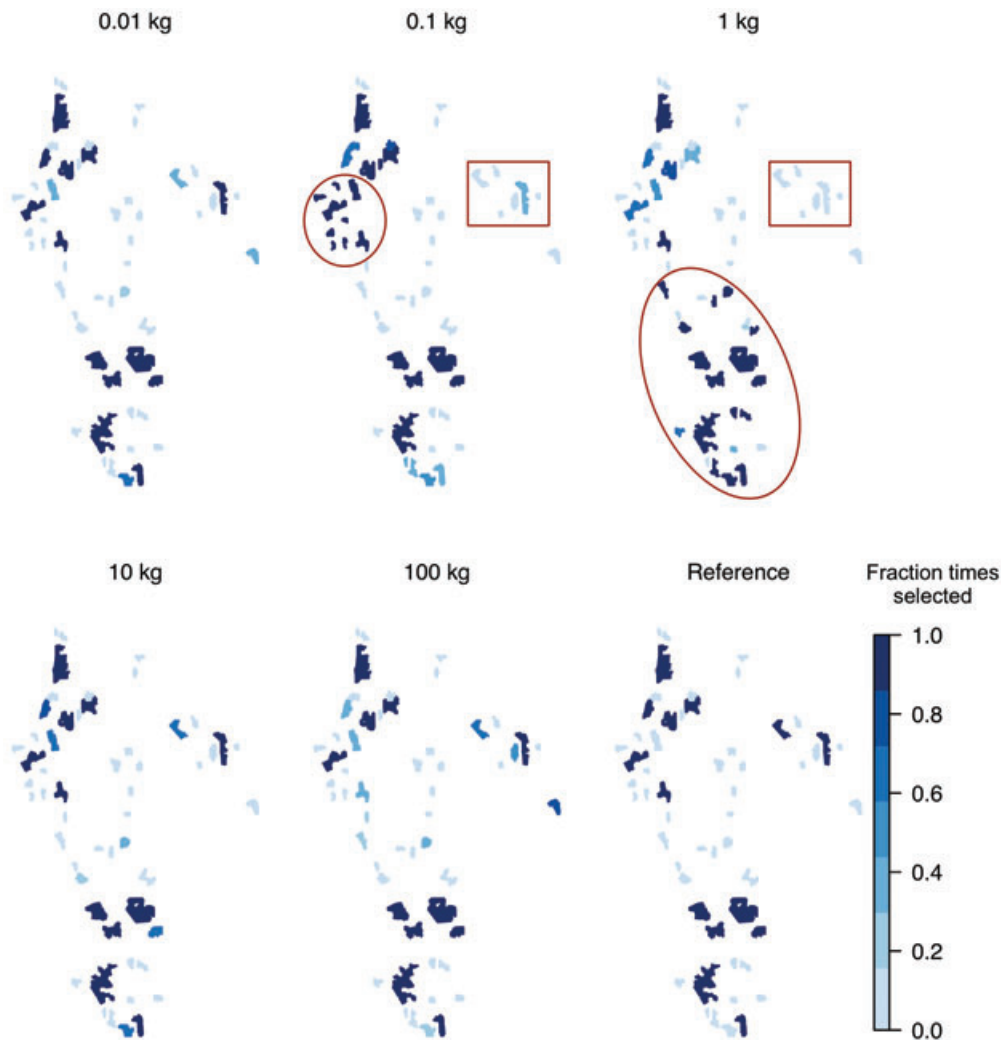
Figure 2 Reserve networks selected from a 57 patch empirical landscape for species of different body sizes, and a reference network that maximizes mean patch area. Color scale gives the fraction of replicate reserve network design simulations in which a patch was selected. Networks for the 0.01 kg, 10 kg, and 100 kg species are very similar to the reference network, which lacks any specific site clustering. The network for the 0.1 kg species displays a tight cluster of many small reserves in the northwest, and the network for the 1 kg species includes a looser cluster of reserves in the south (red circles). The 0.1 kg and 1 kg networks also exclude patches in the west (red squares) that are included in the reference network. The characteristics of each species' reserve network are predicted by the match of interpatch distances to that species' characteristic range.

patches and extinction risk in a clustered network of the same total area consisting of three of these patches and a set of smaller nearby patches. At a species-specific level of p_e chosen such that each species has a 50% probability of survival to year 100 in the reference network, probabilities of survival to year 100 are 6%, 33% 49%, and 20% greater in the clustered network for the 0.01–10 kg species, and 20% lower in the clustered network for the 100 kg species (results for other values of p_e are shown in Figure S2). As expected from the qualitative results, the species that most benefits from a clustered network design is the intermediate-sized 1 kg species, with the benefits of clustering decreasing for successively larger or smaller body sizes.

Discussion

This analysis finds that each idealized terrestrial mammal species has a unique characteristic range, found from approximately 0.5–1.25 times a species' maximum observed dispersal distance, within which changes in interpatch distance substantially influence extinction risk. In real landscapes, interpatch distances will fall within the characteristic range of only a subset of all resident
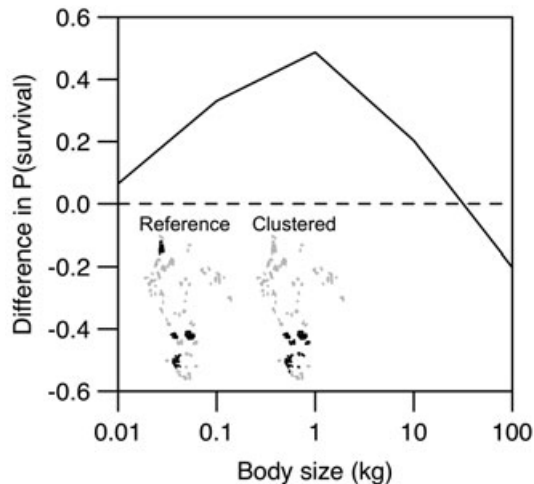
Figure 3 Difference in probability of persistence to year 100 between a clustered reserve network and a reference network for species of different body sizes. p_e for each species is chosen to give a 50% probability of persistence in the reference network and ranges from 0.58 to 0.77. Medium-bodied species have substantially higher persistence probabilities in the clustered network, while the largest-bodied species has a lower persistence probability in the clustered network.

species. These species may experience lower extinction risks in clustered patch networks due to increased recolonization rates, while species whose characteristic range does not match the scale of interpatch distances may experience higher extinction risk due to the inevitable decrease in mean patch area associated with selecting a clustered patch network.

We believe that these findings violate two assumptions commonly made by conservation planners, which are that a clustered network of patches (1) most benefits the largest bodied species in the landscape (which has the highest probability of local extinction and hence supposedly will most benefit from increased recolonization rates) and (2) will not substantially harm the probability of survival for any species in the landscape. These intuitions are likely behind the many qualitative and quantitative attempts to increase patch clustering in reserve network designs (e.g., Önal & Briers 2005; Marianov *et al.* 2008; Williams 2008; Groeneveld 2010).

The results presented here, however, demonstrate that the decision to select a clustered or nonclustered network necessarily represents an implicit decision to favor the protection of some species over others. Given these findings, we propose that conservation planners are left with three reasonable options when attempting to design a reserve network to decrease extinction risk for multiple species of different body sizes. First, network design decisions may be made for the largest bodied species present in the landscape, which will generally have the

highest absolute extinction risk in any network. Second, if the basic body size structure or dispersal characteristics of species in the landscape are known, an explicit decision may be made to cluster or not to cluster patches based on the overlap between the characteristic ranges of the species present in the landscape and the scale of interpatch distances. Third, a detailed simulation such as the one presented here could be conducted for any target species of concern in any real landscape.

Several limitations of the modeling framework presented here are important to note. With regard to the metapopulation model structure, the models are single stage, and presume that individuals reach reproductive maturity after a single year and have equal fecundity and an equal probability of death (a Type II survivorship curve) at all ages. While adding additional complexity in reproduction and surviorship may affect estimates of absolute extinction risk, they are unlikely to affect the choice of different patch networks, which is controlled only by dispersal distance. Additionally, like many general models of population dynamics in patchy landscapes (e.g., Ovaskainen 2002; McCarthy *et al.* 2005; Nicholson *et al.* 2006), these models do not include spatial correlation in environmental stochasticity, which, to the extent that populations physically closer together in space tend to have correlated dynamics, would likely increase predicted extinction risk for clustered network designs, as nearby sites would be less likely to serve as a source of colonists in the event of a local extinction.

Other simplifications relate to the modeling of dispersal. The metapopulation perspective used here allows movement between patches only during natal dispersal. Additional adult movements between patches, including those that would allow an individual to combine multiple patches into a single home range, are not incorporated. Dispersal is modeled here using a Gaussian kernel in which the probability of long distance dispersal events is negligible compared to other "fat tailed" kernels (Clark *et al.* 1998; Getz & Saltz 2008). Increasing the probability of long distance dispersal events would effectively increase the characteristic range for each species, decreasing the body size of the species expected to benefit from reserve clustering. Finally, these models presume that the matrix between patches is homogeneous and no specific features such as corridors or impermeable barriers are present between patches (Hilty *et al.* 2006).

With regard to model inputs and validation, the results for each body size should be interpreted in light of substantial variation around the allometric regressions used to parameterize the models used here (Figure S4), especially with regard to predicted reproductive rates. The predictions of these models could be validated through comparisons with the predictions of more detailed

population models (Akçakaya 2004), and we note that previous work has suggested that simple conservation "rules of thumb" based on vertebrate body size and tropic level can be a reasonable proxy for more informed population models (Possingham and Andelman, unpublished data). The predictions could also potentially be compared to long-term empirical data from populations inhabiting fragmented landscapes (Hanski 1999; Debinski & Holt 2000; Terborgh *et al.* 2001).

Three additional extensions to these models could aid their application to empirical problems in conservation planning. First, the framework presented here could be applied to other taxa with well-characterized allometric relationships, such as birds. Second, modifications could be made to this modeling framework in the event that specific knowledge of a species' life history traits or the characteristics of a specific landscape are known. Third, the extinction-based approach described here could be combined with a representation-based reserve selection approach, such as that implemented in the popular conservation software packages MARXAN (Ball *et al.* 2009) or Zonation (Moilanen 2007), to select networks that would represent the greatest number of species in a reserve network at a future time horizon, rather than at present.

The allometry-based models presented here provide a novel approach for estimating the extinction risk faced by species of different body sizes in any network of habitat patches. The results suggest that species may have a lower extinction risk in a clustered network of patches when interpatch distances are approximately 0.5–1.25 times that species' maximum observed dispersal distance. Other species, however, may experience elevated extinction risks in this clustered patch network due to the likely associated decrease in mean patch area. The decision to select any particular design for a reserve network must thus be made carefully in light of the unavoidable trade-off between the extinction risks of different species. Beyond these general findings, these models also provide a quantitative site-selection method that can be used to provide a first-pass design for reserve networks based explicitly on species' extinction risk, even in the absence of detailed empirical data on the species and landscape in question.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

S1: Influence of model parameters on extinction risk for a 1 kg species in two-patch landscapes with different patch areas, A_i (hectares), and interpatch distances, $d_i j$ (km). Each subfigure shows isoclines of 35% probability of persistence to year 100 in black lines, with 25% and 45% isoclines in surrounding gray lines, for three different levels of (a) yearly reproductive output y, (b) population density s, (c) maximum dispersal distance x, and (d) environmental stochasticity parameter p_e. In the first three subfigures, model parameters were set to 0.2, 1, and 5 times the value drawn from the allometric regressions. Note that the lowest absolute extinction risk occurs for an intermediate level of y in these models, as very high reproductive rates have the potential to lead to overshoots of carrying capacity followed by population crashes (see Eqs. S1 and S7).

S2: Probability of persistence to year 100 for species of (a) 0.1 kg, (b) 1 kg, and (c) 10 kg, and (d) 100 kg body masses in a reference network (solid line) consisting of the four largest patches in the empirical landscape and a clustered network (dashed line) (see Figure 3, inset). The three smaller bodied species have a higher probability of persistence in the clustered network across all values of p_e, while the 100 kg species has a higher probability of persistence in the reference network for all p_e. So long as survival is neither ensured nor impossible in both networks, the preferred reserve network design for each species is thus independent of the chosen level of environmental stochasticity. Results for the 0.01 kg species are not shown (persistence probabilities in the two networks are very similar for all levels of p_e for this species).

S3: As in Figure 2, but with all interpatch distances increased artificially by a factor of five (distances not shown to scale). Color scale gives the fraction of replicate reserve network design simulations in which a patch was selected. As predicted by the match between characteristic range and interpatch distances, the reserve network selected for the 10 kg species now demonstrates a clustered design similar to that of the reserve network formerly selected for the 1 kg species, and the network selected for the 1 kg species is now more similar to the reference network.

S4: Allometric relationships for terrestrial mammals based on data from Jones *et al.* 2009 (Ecological Archives E090-184-D1). (a) Maximum yearly reproductive output, y (female young per adult female per year), calculated as one-half the product of litter size and litters per year, as a function of body mass, m (g), for terrestrial

mammals (n D 813). The shape of the log-log relationship between y and m has substantial scatter and is arguably not linear, and a reasonable alternative would be to set log10y for all species to a global mean near 0.5. As characteristic range is relatively insensitive to y, this change would affect absolute probabilities of extinction for each species, but not preferred reserve networks (see Figure S2a). (b) Population density, s (females per hectare), as a function of body mass, m (g), for terrestrial mammals (n D 927).

References

Akçakaya, H. R. (2004). *Species conservation and management: case studies*, Vol. **1**. Oxford University Press, Oxford, UK.

Ball, I., Possingham, H. & Watts, M. (2009). Marxan and relatives: software for spatial conservation prioritisation. Pages 185-195 in A. Moilanen, K. Wilson, & H. Possingham editors. *Spatial conservation prioritisation: quantitative methods and computational tools*, Chapter 14. Oxford University Press, Oxford, UK.

Belovsky, G. E. (1987). Extinction models and mammalian persistence. Pages 204 in M. E. Soule, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, UK.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. & Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia* **37**, 257-272.

Bolker, B. M. (2008) *Ecological models and data in R*. Princeton University Press, Princeton, NJ.

Cabeza, M. & Moilanen, A. (2003). Site-selection algorithms and habitat loss. *Conserv. Biol.* **17**, 1402-1413.

Carroll, C., Noss, R. F., Paquet, P. C. & Schumaker, N. H. (2003). Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecol. Appl.* **13**, 1773-1789.

Church, R. L., Stoms, D. M. & Davis, F. W. (1996). Reserve selection as a maximal covering location problem. *Biol. Conserv.* **76**, 105-112.

Clark, H. W. (1937). Association types in the north coast ranges of California. *Ecology.* **18**, 214-230.

Clark, J., Fastie, C., Hurtt, G., Jackson, S. & Johnson, C. (1998). Reid's paradox of rapid plant migration. *BioScience.* **48**, 13-24.

Damuth, J. (1981). Population density and body size in mammals. *Nature.* **290**, 699-700.

Debinski, D. M. & Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* **14**, 342-355.

Diamond, J. (1975). The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* **7**, 129-146.

Drechsler, M., Frank, K., Hanski, I., O'Hara, R. B. & Wissel, C. (2003). Ranking metapopulation extinction risk: from patterns in data to conservation management decisions. *Ecol. Appl.* **13**, 990-998.

Drechsler, M. & Johst, K. (2010). Rapid viability analysis for metapopulations in dynamic habitat networks. *Proc. R. Soc. B* **277**, 1889-1897.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol., Evol. Syst.* **34**, 487-515.

Frank, K. (2005). Metapopulation persistence in heterogeneous landscapes: lessons about the effect of stochasticity. *Am. Nat.* **165**, 374-388.

Getz, W. M. & Saltz, D. (2008). A framework for generating and analyzing movement paths on ecological landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 19066-19071.

Groeneveld, R. A. (2010). Species-specific spatial characteristics in reserve site selection. *Ecol. Econ.* **69**, 2307-2314.

Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford, UK.

Hilty, J. A., Lidicker Jr., W. & Merenlender, A. M. (2006) *Corridor ecology: the science and practice of linking landscapes for biodiversity conservation*. Island Press.   Q1

Jones, K. E., Bielby, J., Cardillo, M., *et al.* (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648.   Q2

Lindenmayer, D. B. & Fischer, J. (2006) *Habitat fragmentation and landscape change*. Island Press, Washington, D.C.

MacArthur, R. H. & Wilson, E. O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Marianov, V., ReVelle, C. & Snyder, S. (2008). Selecting compact habitat reserves for species with differential habitat size needs. *Comput. Oper. Res.* **35**, 475-487.

McCarthy, M. A., Thompson, C. J. & Possingham, H. P. (2005). Theory for designing nature reserves for single species. *Am. Nat.* **165**, 250-257.

McCarthy, M. A., Thompson, C. J. & Williams, N. S. G. (2006). Logic for designing nature reserves for multiple species. *Am. Nat.* **167**, 717-727.

Merenlender, A. M., Brooks, C., Shabazian, D., Gao, S. & Johnston, R. (2005). Forecasting exurban development to evaluate the influence of land-use policies on wildland and farmland conservation. *J. Conserv. Plan.*, **1**, 40-57.

Moilanen, A. (2007). Landscape Zonation, benefit functions and target-based planning: unifying reserve selection strategies. *Biol. Conserv.*, **134**, 571-579.

Moilanen, A. & Cabeza, M. (2002). Single-species dynamic site selection. *Ecol. Appl.* **12**, 913-926.

Newbold, S. C. & Siikamäki, J. (2009). Prioritizing conservation activities using reserve site selection methods and population viability analysis. *Ecol. Appl.* **19**, 1774-1790.

Nicholson, E., Westphal, M. I., Frank, K., *et al.* (2006). A new method for conservation planning for the persistence of multiple species. *Ecol. Lett.*, **9**, 1049-1060.

Önal, H. & Briers, R. A. (2005). Designing a conservation reserve network with minimal fragmentation: a linear

integer programming approach. *Environ. Model. Assess.*, **10**, 193-202.

Ovaskainen, O. (2002). Long-term persistence of species and the SLOSS problem. *J. Theor. Biol.* **218**, 419-433.

Sutherland, G. D., Harestad, A. S., Price, K. & Lertzman, K. P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conserv. Ecol.* **4**, 16 .

Terborgh, J., Lopez, L., Nuñez, P., *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923-1926.

Williams, J. C. (2008). Optimal reserve site selection with distance requirements. *Comput. Oper. Res.*, **35**, 488-498.

Williams, J. C., ReVelle, C. S. & Levin, S. A. (2004). Using mathematical optimization models to design nature reserves. *Front. Ecol. Environ.*, **2**, 98-105.

Wilson,K. A., Meijaard, E., Drummond, S., *et al.* (2010). Conserving biodiversity in production landscapes. *Ecol. Appl.* **20**, 1721-1732.

Q3

Queries

Q1 Author: Please provide publisher location for reference Hilty *et al.* (2006).

Q2 Author: If reference Jones *et al.* (2009) is not a one-page article please supply the first and last pages for this article

Q3 Author: If reference Sutherland *et al.* (2000) is not a one-page article please supply the first and last pages for this article.