

**Dispersal and the distributions of mammals:
moving towards improved predictions**

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Abstract

Climate change is predicted to become a major cause of species loss in the coming century. Shifts in distribution as a response to changing conditions have already been observed for many terrestrial organisms. A species' capacity to respond to climate change will depend greatly on its ability to track suitable conditions; those unable to track optimum conditions will be under increased threat of local extinction. There is, therefore, a need to include dispersal parameters in models that forecast the impact of climate change on species distributions, but this is limited by a paucity of dispersal data for many species. In this thesis I develop predictive models of dispersal ability to improve estimates of both distance and rate of dispersal in mammals. Chapter 2 presents a database of empirically derived dispersal distances for mammals and an analysis of the probability distribution of those distances, aimed at describing the 'tail' of the kernel, important in understanding long distance dispersal. Chapter 3 assesses the explanatory power of species' life history and ecology, within a phylogenetic framework, to predict dispersal distances. Chapter 4 examines the roles of dispersal and colonisation ability in mediating the extent to which a species can fill its potential environmental niche and quantifies the effects of model accuracy and projection extent on this approach. Chapter 5 utilises a new technique for identifying patterns of geographic and phylogenetic constraint to examine the dual roles of evolutionary history and environment in determining a species' ability to fill its potential environmental niche. This thesis helps to clarify controls on range limits and to incorporate such controls into species distribution models. By providing more accurate predictions of the impacts of climate change on species range size and location, this work helps us to better understand the threat to species diversity from global change.

Declaration

All work presented in this thesis is my own, with the following acknowledgements:

Most datasets used in this thesis, apart from the database of dispersal distances, were compiled by others, and I cite the data sources throughout and reference published software and code where appropriate.

I also made use of some programming code kindly provided by others: Emmanuel Paradis kindly provided R code used in chapter 1 to analyse dispersal kernels. Lynsey McInnes provided R code for model simplification and model selection in chapter 2. Susanne Fritz and David Orme wrote the ArcInfo macros to extract species' grid cell occurrences for range filling analyses in chapters 3 and 4. Rob Freckleton and Natalie Cooper provided R code for the joint analysis of spatial and phylogenetic signal in range filling in chapter 4.

Chapter 3 is formatted for submission to the Journal of Animal Ecology and was co-authored with my thesis supervisor David Orme. While the submitted version will use 'we', I have converted these to 'I' for the thesis chapter.

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Chapter 1: Introduction

Climate change is predicted to become one of the major drivers of species loss in this century (Millennium Ecosystem Assessment 2005). Range shifts and altered phenologies attributed to changes in temperature have already been reported for many animal and plant groups (Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006). Climate change is different from most other threatening processes due to its global nature, relatively slow-acting time-scale and varied impacts. Climate change may create new habitats and communities through biotic mixing and new combinations of environmental conditions (Mace and Purvis 2008). In addition, the impacts of climate change are predicted to be most severe at high latitudes, a markedly different pattern from that seen in most other threatening processes, such as land-use change, which dominate at low latitudes (Jetz et al. 2007). A species' ability to respond to changes in habitat or environmental conditions can take several forms: adaptation (whether through phenotypic plasticity or evolution); dispersal to return to optimal conditions; persistence at a new reduced optimum phenotype; or local extinction (Watkinson and Gill 2002; Berg et al. 2010; Franklin 2010).

There is robust evidence for elevational and latitudinal shifts in species' distributions consistent with predictions from climate change models (Walther et al. 2002; Rosenzweig et al. 2008) but see (Lenoir et al. 2010). However, not all species seem to respond equally (Walther 2010; Chen et al. 2011). In a recent study examining the impact of climate change on small mammal communities in Yosemite National Park, Moritz et al (2008) found evidence for both upward range expansion in low-elevation species and range contractions of high-elevation species which were broadly consistent with predictions under climate change. Responses of closely related species in the Yosemite study were "idiosyncratic", but did correlate weakly with life

history and ecological traits in predicting which species were likely to shift in distribution. Indeed, the number of studies which identify dispersal and colonisation ability as good predictors of range shifts is increasing (Perry et al. 2005; Hughes et al. 2007; Pöyry et al. 2009; Lenoir et al. 2010) but see (Angert et al. 2011). A recent framework, constructed to identify the threats and benefits of climate change for individual species, highlighted dispersal as an exacerbating factor important in identifying species at risk (Thomas et al. 2010).

The importance of dispersal ability in mediating the effects of climate change is perhaps unsurprising. Dispersal is frequently cited as being correlated with vulnerability to local extinction (McKinney 1997; Purvis et al. 2000), a rationale which has its roots in the theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Brown 1995). Small and isolated populations have an increased probability of local extinction from both demographic and environmental stochasticity and to inbreeding depression and loss of genetic variability (Smith 1993). High rates of immigration, conferred by the ability to disperse, may help to stabilize population fluctuations and, in extreme cases, even prevent local population extinctions (the 'rescue effect': Brown and Kodric-Brown 1977; Gutierrez and Harrison 1996). As such, dispersal ability is an important parameter in many population and conservation models (e.g. Henein et al 1998). There is also an increasing awareness of the role of dispersal in the context of habitat fragmentation, and biological invasions (Ronce 2007), in the design of nature reserves and habitat corridors (Simberloff 1988; Van Vuren 1998) and in species distribution modelling (Akçakaya et al. 2006; Araújo and Guisan 2006; Franklin 2010). Dispersal may therefore be vital in allowing species to colonise newly available climatically suitable habitats beyond their current range limits but it is often poorly parameterised

in models and predictions due to a lack of data availability. In this introductory chapter, I aim to provide a rationale as to why a better understanding of species' dispersal ability would aid predictions of the impacts of climate change on biodiversity. Firstly however, I give a brief overview about our current understanding of dispersal in vertebrates generally, and with specific reference to mammals, the study group of this thesis.

1.1 Defining and describing dispersal

Individual organisms may make many types of movement in their lifetime; the majority are local in scale and often confined within or near the home range or territory (Greenwood 1980; Stenseth and Lidicker 1992). Occasionally, movements are undertaken on a larger scale and such movements are broadly classified based on their characteristics into three categories: exploration, migration and dispersal (Lidicker 1975; Wolff 1994).

Exploration

Exploration can be thought of as any short-term movement outside the home range, followed by a subsequent return to the range. These exploratory movements can sometimes be a precursor to dispersal, allowing the individual to gather information about habitat quality and population density in nearby patches (Lidicker 1975; Holekamp 1984).

Migration

Migration is “the relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time and is usually followed by a regular return event” (Endler 1977).

Dispersal

Dispersal, in vertebrates, is defined as “the movement an animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate” (Howard 1960). Processes vary from gradual range shift to one-way movements over great distances. Dispersal can be broken down into two subgroups: natal dispersal – the movement of an individual between its birthplace or natal group and its first breeding site or group; and breeding dispersal – the movement between consecutive breeding sites or groups of adult breeders (Greenwood et al. 1979; Shields 1982).

Dispersal ability is, however, also often used as a general term to describe the vagility of an individual or species, i.e. the capacity or tendency of an organism or a species to move through a given environment and consequently colonise empty habitat patches (Bowman et al. 2002). Vagility can be measured by distance travelled, the ability to cross heterogeneous or fragmented habitats and by gene flow (Mallet 2001). It is important to note that all definitions of movement type are highly dependent on the time-scale over which an individual is observed. For example, individuals observed for only short periods of time may become categorised as dispersers, when in fact they are instead visiting a part of the home range which is rarely used (McShea and Madison 1992). Definitions can also vary depending on the biological discipline and taxon in question. For example, if the start and end points of movement are the same (as in exploration or migration for many species) there is a great deal of movement but little or no gene flow between groups. Population geneticists, therefore, define migration as “the movement of alleles between semi-isolated subpopulations” – a process which by definition involves gene flow between subpopulations (Shields 1987).

1.2 Mammals as a model system

Dispersal occurs in most species of mammal and often shows sex biases in both frequency of individuals dispersing and distances dispersed (Handley and Perrin 2007). Which sex disperses depends on the social and breeding system of the species in question. For example, female-defence polygyny, common in mammals, leads to male-biased dispersal (Handley and Perrin 2007). In a minority of mammals, dispersal rate is equal between the sexes and is female biased in only a few cases (Greenwood 1980). Sex bias in the distance dispersed is less common (Greenwood 1980; Van Vuren 1998). Dispersal is typically undertaken as natal dispersal by juveniles but breeding dispersal has also been documented (Van Vuren 1998). While such variety in the expression of dispersal ability in mammals makes them a challenging study group, data availability is relatively high. Variation in observed dispersal ability across the group is also high; differences in dispersal distances vary over several orders of magnitude (Van Vuren 1998), which may mean that intra-species differences can be more readily identified. Furthermore, mammals are a charismatic group, of high conservation interest. Population declines and extinction in mammals are of particular concern to conservation biologists for several reasons. Mammals play a key role in shaping ecosystem structure and function through processes such as seed dispersal, regulation of herbivores via predation and control of resources through interspecific competition (McNaughton et al. 1988; Sinclair 2003; Terborgh et al. 2001; Wright et al. 2000). Mammals are also valued as they are hunted for food and fur and can often provide income in the form of ecotourism (Gaston & Spicer 1998). Mammals can act as flagship or umbrella species serving as a fundraising tool for conservation organisations and helping protect the habitats and ecosystems in which they are found (Leader-Williams & Dublin 2000). For all these

reasons, the study of mammalian responses to climate change is likely to gain public interest and therefore accurate predictions are important if the field is to maintain credibility.

1.3 Modelling dispersal

It has proved difficult to generalise drivers or proximate causes of dispersal as individuals of the same sex and age or cohort may disperse at different times and for different reasons (Stenseth and Lidicker 1992). The stimulus for dispersal may be endogenous (e.g. body condition), exogenous (e.g. increased negative interactions with conspecifics or predators) or a combination of both (Gaines and McClenaghan 1980). Landscape structure is also thought to affect dispersal behaviour, with more complex patch dynamics driving increasingly complicated dispersal behaviours in species which are able to make decisions about when to stay and when to leave the natal range (Van Dyck and Baguette 2005; Prevedello et al. 2010). New research also shows that individuals can gain information about suitable habitats from encounters with conspecifics passing through the natal territory, although this has yet to be demonstrated in mammals (Clobert et al. 2009). Likewise, a number of pathways to settlement of an individual at the end of dispersal phase have also been identified. Preference for a post-dispersal habitat similar to the pre-dispersal habitat (habitat imprinting) and conspecific attraction, where the presence of conspecifics greatly increases the probability of settlement in aggregating and territorial species, have both been observed in a range of taxonomic groups (Stamps 2001) and are thought to be low-cost ways of gaining information about the suitability of a site for settlement and breeding (Danchin et al. 2001).

Given the apparent high costs associated with dispersal (e.g. increased levels of predation during transit, reduced body condition as a result of higher energetic

costs and risk of failure to find suitable habitat or breeding partners upon arrival: Ronce 2007), significant effort has been spent in trying to understand the ultimate causes for the evolution of dispersal. Kin competition and the avoidance of inbreeding have been shown to promote dispersal even in stable environments (Hamilton and May 1977; Lambin et al. 2001). Spatial and temporal variation in access to resources, such as suitable habitat, food and mating opportunities, have also been identified as likely drivers (Gadgil 1971). Johnson and Gaines (1990) summarise those mammal species for which an ultimate cause for the evolution of dispersal has been hypothesised.

Recent modelling studies have focussed on the evolution of dispersal at range margins during periods of range expansion or introduction to new suitable habitats (Holt 2003; Burton et al. 2010). Evidence for morphological changes and increased dispersal rate have been documented, most famously for cane toads (*Bufo marinus*) in Australia after human introduction and for cricket species in Great Britain after recent climate warming (Simmons and Thomas 2004; Phillips et al. 2008). These studies highlight the evolutionary dynamic nature of dispersal, but direct evidence with which to test model predictions is still limited for most groups (but see Hughes et al. 2007; and Stevens et al. 2010 for good evidence of dispersal evolution in butterflies).

The dispersal kernel

The likelihood that a dispersing organism will travel a certain distance before it settles can be described by a dispersal kernel: the probability density function of dispersal distances for a group of individuals, population or species (Turchin 1998; Nathan 2001). In mammals, population and species' dispersal distances are commonly described as a leptokurtic probability function, with a tail of infrequent long-distance dispersal events (Kot et al. 1996; Turchin 1998). The functional form describing the

shape of the kernel is dependent on the dispersal mode of the species and the landscape: populations inhabiting homogeneous landscapes may be well described by a Gaussian or negative exponential distribution (see Figure 1.1) but more patchy habitats may drive individuals to undertake more frequent long distance dispersal and therefore the kernels display a ‘fatter tail’ (Turchin 1998; Murrell et al. 2002; Paradis et al. 2002). Short distance dispersals are probably sufficient for avoiding inbreeding or kin competition, but long distance dispersal events are needed to colonize new territories and to escape intraspecific competition (Perrin & Goudet 2001).

As the rate at which species’ can advance their range limits depends on the distribution of dispersal distances coupled with the population’s rate of increase, accurate quantification of the tail of the dispersal kernel is key to modelling the rate of population spread. The distance travelled by dispersers is difficult to quantify however, and both the rate of long-distance dispersal and maximum dispersal distance are often under-reported (Koenig et al. 1996; Nathan et al. 2003; Phillips et al. 2008). Phenomenological studies relating rates of population spread and shapes of observed dispersal distances to theoretical models of redistribution and dispersal are also rare for actively dispersing animals, especially in a comparative framework (Trakhtenbrot et al. 2005). Where models have been fitted they frequently underestimate rates of population spread, often by more than a factor of two (Turchin 1998; Paradis et al. 2002). This has proved to be a major limitation in the development of theories and tools for forecasting the effects of landscape alteration on connectivity between habitats and subpopulations of animals (Nathan 2001; Nathan 2005). To address this data limitation, in chapter 2 I describe the creation and development of a new database of mammalian dispersal distances. Also in chapter 2, I analyse mammalian dispersal kernels for evidence of a ‘fat tail’ and assess the ability of several different probability

density functions to adequately describe the distribution of dispersal data seen across different species.

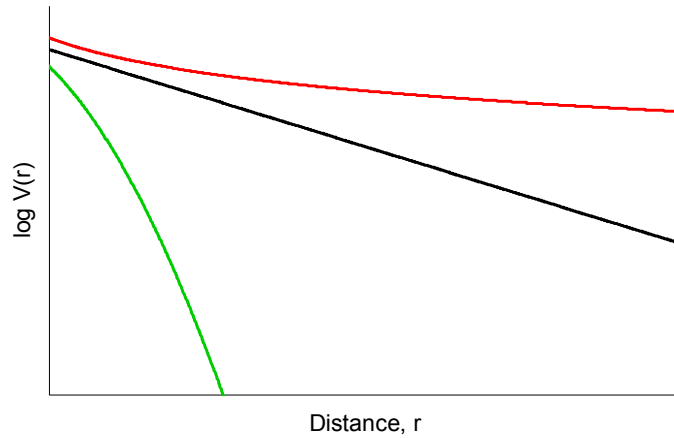


Figure 1.1: Dispersal tails: black line – exponential ($V(r)=\exp(-r)$); green line - Gaussian (declining faster than exponential, $V(r)=\exp(-r^2)$); and red line - Power (declining more slowly than exponential, $V(r)=r^{-2}$). Taken from Turchin (1998).

Identifying significant correlations between dispersal distance and biological or ecological traits may also help us to estimate dispersal ability when data is scarce. Linear relationships have been established between dispersal distance and body mass (Van Vuren 1998; Sutherland et al. 2000; Jenkins et al. 2007) and dispersal distance and home range size (Bowman et al. 2002; Ottaviani et al. 2006) for selected subsets of mammals and birds. Relationships between dispersal distance and a wider variety of life history traits have so far only been explored for birds and these relationships did not persist independently of body size and phylogeny (Paradis et al. 1998).

1.4 The importance of including dispersal estimates in species distribution modelling

Species distribution modelling (SDM) techniques are currently the most popular methods for predicting species range change and subsequently extinction risk due to climate change (Guisan and Zimmermann 2000; Thomas et al. 2004). Methods differ, but the general aim is to characterise the environmental conditions that are suitable for a species, and to then identify where suitable environments are distributed in space (Pearson 2007). SDMs have been used to predict the distribution of species under current, past, and future climatic conditions by inferring a species' environmental requirements from localities where it is currently known to occur (Hijmans and Graham 2006). The potential impact of climate change is measured by the amount of environmental space that is retained, lost or gained by a species or number of species into the future.

The ability of SDMs to accurately predict future species distributions has been questioned because they do not attempt to describe cause and effect between the model parameters and response (Guisan and Zimmermann 2000). The model may incorrectly assume that, if a set of climatic conditions does not currently occur within the species envelope, then the species cannot tolerate them. In addition, SDMs rarely account for biotic interactions (unless they are captured indirectly by the environmental variables of the SDM) or factors such as dispersal ability (Araújo and Rahbek 2006; Botkin et al. 2007). Lack of clarity about species movement and dispersal ability can lead to confusion over what aspect of a species' niche is being modelled. Figure 1.2 illustrates how determinants of species' distribution can be conceptualised as comprising three interacting factors: abiotic, biotic and movement (Soberón and Peterson 2005; Soberón 2007; Barve et al. 2011). Circle A denotes the

suitable abiotic conditions needed for the species to survive and reproduce. Circle B represents the biotic conditions needed for the species to persist, for example: food resources, presence/absence of competitors, the influence of predators and mutualists. Circle M represents area of the world accessible to the species by dispersal. The realised or occupied range (G_O) is denoted in grey, where environmental and biotic conditions are favourable and habitat is accessible to the species (e.g. no barriers to dispersal). A failure to understand the role of dispersal in aiding or limiting species movements may result in a miscalculation of the fundamental niche (G_A), defined by Hutchinson (1957) as an n-dimensional hypervolume, where the dimensions are environmental conditions that define the range in which a species can persist. Area G_I illustrates how dispersal limitation may mean that a species is frequently absent from suitable environments regardless of the presence of suitable biotic conditions. Likewise, individuals may be present in sink populations (open circles) outside suitable environmental space. Population growth rate in sink habitats is < 1 and populations persist only through dispersal from source populations (filled circles) within the realised niche.

The absence of a species from areas which are deemed environmentally suitable by species distribution models may also help shed light on the relative ability of species to disperse in both space and time (Kokko & Lopez-Sepulcre 2006). When a species' ecological niche has been modelled, its potential distribution and actual distribution can be compared, any unfilled environmental space can be inferred to be due to something other than limits on a species environmental tolerances. Several recent studies which compare ratios of realised and potential distributions have inferred that these mismatches between observed distribution and environmentally suitable space are due to dispersal limitation, although direct evidence is so far

proving elusive (Svenning and Skov 2004; Schurr et al. 2007; Munguía et al. 2008). In chapters 4 and 5 I expand this method to test the ability of range filling to predict dispersal ability in mammals. In chapter 4 I correlate range filling with the dispersal distance data described in chapter 2. Chapter 5 expands this method to look at the relative roles of geographic location and phylogenetic relatedness in driving patterns of range filling.

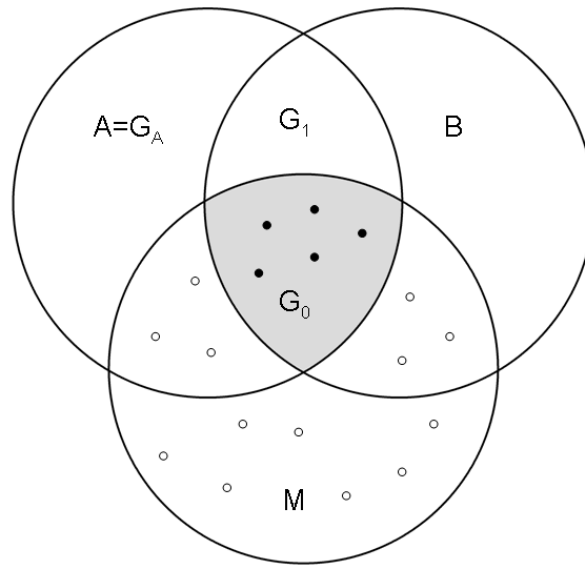


Figure 1.2: Dispersal limitation and source-sink dynamics may confound our understanding of a species' bioclimatic niche. Closed circles denote source populations and open circles denote sink populations. Figure reproduced from Barve (2011) and adapted from Soberon and Peterson (2005).

1.5 Conclusions

Accurately modelling dispersal is of major importance if we are to understand if species can track suitable environmental space at the rate required to keep up with a changing climate (Watkinson and Gill 2002; Thuiller et al. 2008; Loarie et al. 2009). Currently, the majority of studies do not adequately take dispersal into account, using the assumption of full or nil dispersal with the caveat that in reality species will fall

somewhere in-between the two (Broennimann et al. 2006). Such broad assumptions of migration capacity naturally lead to a wide range in projections of species extinction risk (Thuiller et al. 2005). For example, Thomas et al (2004) predicted an extinction risk range between 21 – 52% for the worst case climate change scenario, depending on the dispersal scenario applied. While these sorts of analyses can provide estimates of extinction under extreme scenarios, they tell us nothing about rates of change or range dynamics under climate change (Early and Sax 2011). The recognition of the inadequacy of these estimates has led to the development of a new wave of species distribution models which incorporate migration limits and dispersal estimates into models, but so far these models have only focused on plant species (Engler and Guisan 2009; Thuiller et al. 2009b). Better predictions of dispersal distance and comparative estimates of dispersal ability are now very much needed to inform these new models. This thesis was developed with the explicit aim of improving dispersal estimates for mammals in order to fulfil this need.

1.6 Thesis aims and summary

Chapters 2 and 3 of this thesis examine the predictability of dispersal kernel shape and dispersal distance in mammals. Chapter 2 presents, to my knowledge, the first cross species analysis of dispersal kernels in mammals. In chapter 3, I detail the broadest test to date, both in taxonomic scope and predictors used, of the ability of life history traits to predict dispersal distance. Both distance travelled and number of dispersing individuals can then be used to create more biologically accurate distribution models which take into account the ability of species to move with the changing climate. As such analyses require large quantities of data chapter 2 also details the data collection methods and some of the broader issues encountered in the collection of dispersal data. Chapters 4 and 5 turn the question around. Rather than asking how dispersal

data can inform species distribution modelling I ask: what can distribution modelling tell us about dispersal ability in a comparative framework?

Although chapter 2 deals largely with the data collection process and general descriptions of the data, the end of this chapter is given over to an analysis of the mammalian dispersal kernel. Using data on the distribution of dispersal distances throughout populations, I ask if the shape of these dispersal kernels is consistent across species and if so which probability density function best describes the observed data? I compare the empirically derived data with three density functions: exponential, Weibull and half-Cauchy. Using model AIC as a measure of model performance I then test which of these shapes best fits the data. I find that generally, the Weibull distribution performs best at describing the data, although AICs between models are often very similar. Finding general predictability across species in terms of model fit means that climate change models for mammals can be further parameterised by use of a simple two parameter distribution function.

Chapter 3 takes a model averaging approach to test for life history correlates of natal dispersal distance. I test physiological and ecological traits such as body mass, home range, trophic level and population density plus measures of life history speed such as gestation length and weaning age. I also examine the relationship between average and maximum dispersal distances and I use cross-validation to test the ability of the trait-based relationships to predict dispersal distances. I find that no one trait can be identified as a ‘best’ predictor of dispersal ability. Indeed, many combinations of traits can produce a significant relationship with dispersal distance, although home range size, body mass and geographic range stood out as having higher weighting in the model averaging process compared to most other traits analysed. Geographic range size was only a highly weighted term in models

correlating with maximum dispersal distances, possibly hinting at the influence of long-distance dispersal on range size through allowing access to new areas and exploitation of suitable habitats after periods of climatic change. Cross validation showed that the relationships identified were broadly able to predict dispersal distances for species removed for testing purposes, giving us confidence in creating estimates of dispersal for species where such information is lacking and subsequently to parameterise species distribution models to make them more biologically realistic.

Chapter 4 uses the empirically derived dispersal distances to examine the role of dispersal ability in allowing species to fill all suitable environmental space. The availability of range maps for many groups means that one simple way in which comparative estimates of species dispersal ability can be gained, is to examine their relative ability to fill their potential range. A number of studies have attempted to correlate dispersal ability with range filling extent, with little success to date. In chapter 4, I also examine some of the methodological reasons as to why earlier studies may have failed to find a relationship. By modelling range filling as a proportional variable and accounting for the impacts of limiting study extent, I find significant relationships between dispersal and colonisation ability and range filling extent. While relationships were significant, predictive power was fairly weak and I suggest that further investigation of the causes of limited range filling, including the landscape context of the species in question are needed before range filling can confidently be used as a measure of comparative dispersal ability.

Chapter 5 expands on the analysis in chapter 4 by estimating range filling extent for more than 600 mammal species, using global projections of potential environmental climate space, with the aim that a better understanding of range filling may improve our understanding of the role of dispersal limitation in controlling this

trait. I examine the relative roles of space and phylogeny in determining these estimates of range filling. By using two new methods which co-estimate spatial and phylogenetic signal of range filling by assuming different modes of the evolution of spatial differences, I test relative support for the hypotheses that variation in range filling is explained by a model where spatial distances between species have coevolved with phylogeny against a model where variation in range filling is largely independent of phylogeny and controlled largely by differences in the geographic location of species. I find that a model where spatial effects are estimated independently of phylogenetic effects has greater success in explaining variation than the contrasting model where spatial and phylogenetic effects are interrelated. I also find that the effects of space on determining range filling extent are estimated to be much greater than the effects of phylogeny. Therefore when using range filling as a proxy for dispersal limitation we must always consider the environmental and geographic context of the species being analysed.

Summary of thesis aims

The over-arching aims of this thesis are to improve estimates of dispersal distance, dispersal rate and to test methods to identify dispersal ability in mammals within a comparative framework. To achieve this I develop predictive models of dispersal ability and analyse the role of dispersal in shaping species range limits. Bearing in mind the limited data availability of this trait, I examine ways in which these estimates can be gained with no direct knowledge of the dispersal ability of the species in question. This is to allow estimates of dispersal distance to be incorporated into species distribution models and also to help identify dispersal limited species, which may be at risk of extinction when the effects of climate change mean they are unable track changing environmental conditions and to move to new areas.

Chapter 2. Data collection and kernel analysis

2.1 Introduction

Analyses in Chapters 3 and 4 utilise data from a database I compiled which contains empirically derived dispersal distance data plus ancillary information. This chapter details the data collection methods and describes other data sources used in this thesis, (i.e. life history trait data), which were also supplemented by further data collection. This information is broadly referred to in chapters 3 and 4 but only described in detail here.

2.2 Quantifying dispersal ability

As previously outlined, dispersal is notoriously difficult to measure and while a variety of techniques have been employed, no one technique has yet proved superior. Methods employed to date include:

- a. Distance travelled by individuals – individual movement distances or distribution of dispersal distances for a population or populations both experimental and natural (Van Vuren 1998; Sutherland et al. 2000);
- b. Rate of emigration – proportion of individuals leaving the natal habitat (Waser et al. 1994);
- c. Range expansion in new environments – where documented instances of colonisation or introduction exist measuring range spread from year to year or averaging range spread based on date of introduction and current distribution (Caughley 1963);
- d. Indirect measures of gene flow between populations – measures of genetic differentiation within a population such as Wright's F_{ST} (a measure of variance

- in allele frequency among populations) correlate broadly with N_m (number of individuals migrating into a population) and have been shown to correlate with dispersal ability (Wright 1965; Bohonak 1999);
- e. Quantification of traits thought to promote dispersal such as mode of dispersal, wing length, size and shape and limb length (Jones et al. 2003; Phillimore et al. 2006; Gove et al. 2009; Van Bocxlaer et al. 2010);
 - f. Ability to cross boundaries such as major rivers, seas and mountains (McInnes et al. 2009) or gaps in habitat such as forest clearings (Moore et al. 2008);
 - g. Expert opinion – dispersal ability ranked using questionnaire or similar consensus method e.g. 0 = sedentary and 10 = extremely mobile (Kotiaho et al. 2005); and
 - h. Score based indices – presence and absence of traits and behaviours thought to be linked to dispersal and evidence of dispersal are scored. Scores are combined to give a ranking (Bohonak 1999; Isaac et al. 2009).

All methods have strengths and limitations. For example, observational and experimental data are often limited by the spatial scale of the study area and may fail to capture long distance dispersal. These methods, however, do give an idea about the shape of the dispersal kernel and actual distances travelled. Likewise, rate of emigration tells us much about the number of individuals leaving but gives no indication of distance travelled and while range expansion rates in new environments would be ideal to predict movements under climate change but records are scarce, they may tell us little about movements in native environments and they assume a linear rate of spread.

An indirect approach to inferring levels of migration is through estimating levels of genetic variance between populations. Low levels of gene flow can have a

large impact on the amount of genetic differentiation between populations, so identifying a pattern of genetic differentiation which correlates with some measure of the geographic structure of the populations in question, such as the linear distance between populations, indicates that there are low levels of dispersal between these populations (Palumbi 2003). If geographic structure is found between populations, dispersal distances can be estimated from the slope of an isolation by distance (IBD) regression (Kinlan and Gaines 2003). Research in this area is enabled by ever improving techniques for sampling and analysing genetic data. However, moving beyond estimating genetic variance to inferring dispersal rates from genetic information relies on a set of assumptions about the relationship between genetic structure and the rate of gene flow. A key part of the theory is that the ecological properties of the populations in question match the properties in the theoretical model upon which that relationship is based. This includes assumptions of no selection on the loci under investigation, random migration, no mutation within populations and constant and equal immigration and emigration rates between populations. These tenets are clearly not applicable to many real populations and species, with the consequence that dispersal rates are miscalculated (Whitlock and McCauley 1999, but see Bohonak 1999). Data availability is currently also a key limiting factor for broad scale studies using meta-analytical techniques (Kisel and Barraclough 2010). However, as models and data availability improve, genetic differentiation as an indicator of dispersal distance may prove useful as relatively small sampling effort can give dispersal estimates for whole populations and can quantify infrequent dispersal between populations that is often missed through observational studies.

As an alternative, using traits that are thought to approximate dispersal ability can be a useful way of assessing a large group or set of groups when data is scarce.

For example, when assessing comparative extinction risk across taxa, traits such as body size may give a good enough indication of relative dispersal ability. These proxies do not tell us much about how far the species disperse, however, or the proportion of individuals undertaking long-distance dispersal. Expert opinion and score based indices also require making *a priori* assumptions about which traits and behaviours promote dispersal. Again these may be useful in a comparative study but tell us little about actual dispersal distances. I explore using such traits to predict actual dispersal distance in Chapter 3. As there is no single best measure, a range of life history traits are employed throughout the thesis based on the best measure for each analysis in question.

2.3 Database creation

I searched primary and secondary literature sources to gather values of migration, movement and dispersal distance for extant mammalian species. Marine species and bats were excluded, as their mode of locomotion and thus costs of dispersal are very different from most other mammals. Data were gathered from systematic searches of relevant peer reviewed journals including all issues of Mammalian Species, all online issues of Journal of Zoology and all issues of Journal of Mammalogy from 2000 onwards. In addition, electronic search engines from ISI Web of Knowledge, JSTOR and Google Scholar were searched using the search terms; “natal dispersal”, “breeding dispersal”, “dispersal distance” and “migration distance”. Data came from experimental and observational studies and from reports of individual movement distances. Papers reporting previous meta-analysis of dispersal data were also utilised (Van Vuren 1998; Sutherland et al. 2000; Harris et al. 2009), as was a database created for the Regional Redlist Assessment of Central Asian Vertebrates which contains estimates of migration distance for mammal species from Kazakhstan,

Kyrgyzstan, Tadjikistan, Turkmenistan, and Uzbekistan (for a full description see Milner-Gulland et al. 2006).

An Access database was created to hold and manage the collected data. The data entry module was designed to provide maximum information about each reported dispersal distance in an easy to access format, whilst ensuring identical methods of data entry, thereby improving data quality and minimising data duplication. A reference for each data point was stored in Endnote X and linked to an electronic copy of the original data source where possible. Where no electronic source was available a hard copy of the data was retained. A copy of the formatted reference from Endnote was then linked back into the database. Data fields were chosen to collect information about average and maximum dispersal distances reported and the range and frequency of dispersal distance (i.e. the shape of the dispersal kernel). Ancillary information describing the dispersing individuals, density of the study population, study location and data quality were also recorded.

2.4 Data entry protocols

Taxonomy – Order, Family, Sub-family, Genus, Species and taxonomic authority drop-down lists were created plus a free text field to record sub-species where given. Sub-family and Sub-species were optional fields only entered if the information was available. All species names were recorded under their original taxonomy and subsequently converted to the Wilson and Reeder (2005) taxonomy using the conversion file and method detailed in Jones et al. (2009).

Geography – A free text field was created to store a brief description of the location of the population (e.g. ‘Superior National Forest, Minnesota’). Geo-referencing information was entered in degrees, minutes, seconds and subsequently converted to

decimal format for analysis. For large study areas, a mid-point value was entered. Fields were created to record whether the study location was reported in lat-long format in the original publication or inferred from geo-referencing websites such as Fuzzy Gazetteer or Google Earth. Biogeographic realm and country data were recorded and stored in drop-down menu format. A check-box was created to record dispersal distances reported for locations in which the species was not native (i.e. dispersal distances for introduced, alien or invasive species) as these species may show different dispersal distances when outside the natural distribution.

Data descriptors – A drop down field was created to record the sex of the individuals for each data point. Options were: ‘Male’, ‘Female’, ‘Both’ or ‘Unspecified’. Similarly, a drop down field was created to record at which life stage individuals in the record were recorded dispersing; ‘Adult’, ‘Sub-adult’, ‘Juvenile’, ‘Mixed’ (if dispersal distance of individuals from more than one age class are reported together), and ‘Unspecified’.

Dispersal data fields – Data are reported in the literature in a variety of formats including raw data (i.e. dispersal distances for every individual), mean or median dispersal distance and min/max dispersal distance. Numerical fields were created for ‘mean data value’, ‘standard deviation of the mean’, ‘median data value’, ‘lower data range’, ‘upper data range’. A drop down field was created to record the data units: ‘metres- Linear’, ‘km-Linear’, ‘miles – Linear’. For numeric fields where no data was available, the constraints of Access meant that “-999” was entered as a numerical equivalent of NA, and to differentiate from fields which had not been assessed. “-999” was subsequently converted into NA in R (R Development Core Team 2010). All

dispersal distances were recorded in the reported units and subsequently converted to kilometres.

Dispersal type descriptor - Where the type of dispersal taking place was explicitly identified a descriptor was recorded:

‘Natal dispersal’ – the transition movement from the natal site or natal home range to a home range where an animal (Kenward et al. 2002).

‘Breeding dispersal’ – the transition between separate nuptial sites or nuptial home ranges (Kenward et al. 2002).

‘Migratory’ - the relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time and is usually followed by a regular return migration (Endler 1977).

‘Movement distance’ – where movement outside the home range with no return to that area is reported but there is not enough information provided to specify dispersal type.

Study descriptors – Numerical fields were created for ‘sample size’ defined as the number of individuals contributing data to the dispersal data value/s and for ‘study area size’. A drop down field was created for study area units: ‘Sq Metres’, ‘Hectares’, ‘km sq’, ‘Acres’, ‘Sq Miles’, ‘Metres – Linear’, ‘km – Linear’, ‘Miles – Linear’ and ‘Unspecified’. Start and end date of study were also recorded where available. Before analysis all data were converted to kilometres and square kilometres using the following conversion table:

Original Units	Conversion Units
1 Square Metre	0.000001 square kilometres
1 Hectare	0.01 square kilometres
1 Acre	0.0041 square kilometres
1 Square Mile	2.59 square kilometres
1 Metre – Linear	0.001 kilometres
1 Mile – Linear	1.6093 kilometres

Table 2.1 Conversion units used in analyses.

Study area size - where reported for experimental studies with defined transect or study boundaries I recorded study area size.

Source quality descriptors – Source quality was recorded as primary (published in a peer-reviewed journal) or secondary (reported in a book or in the grey literature).

Method of estimating dispersal distance was recorded as: Capture-mark-recapture, Radio-telemetry, Trapping, Direct Observation or Unspecified.

Proportion of study population dispersing – where provided, the size of the study population and the proportion of individuals undertaking a dispersal movement were recorded.

Population density estimates – a separate table was created to hold population density estimates. Estimates had to be reported in the same study or directly quoted by the study author as pertaining to the same population being studied for dispersal distance. Density measure could be either a single measure or more commonly the lower and upper range of density throughout the study period. The units being reported were

recorded as Individuals or Family groups. Estimation methods were recorded as Direct counts, Indirect counts (e.g. based on tracks, scats etc), Mathematical functions based on mark-recapture counts (e.g. use of modelling programmes such as MARK or Density) or Unspecified. Study area size was also recorded.

Raw data – a separate table was created to store all individual dispersal distances from a study, where given. Data was also collected from histograms and graphs. Data aggregated in ‘bins’ was recorded as the mid-point of the bin interval and annotated accordingly.

Figure 2.1 Data entry form for dispersal database.

2.5 PanTheria trait database

Ecological and life history trait data was taken from the PanTHERIA database (Jones et al. 2009) which contains 100740 lines of biological data for extant and recently extinct mammalian species. In order to maximise the use of available dispersal data, this database was supplemented by collecting missing values for key variables using a targeted literature search based on the species name and the missing trait value. Data was collected from primary and secondary data sources and from grey literature.

Many of the missing values were originally excluded from PanthTHERIA as their taxonomic affiliation could not be unambiguously determined (Jones et al. 2009). For this study, the smaller size of the data set allowed the collection of more recent data which was taxonomically referenced. If such data could not be found the taxonomic rules were relaxed to allow data from the grey literature to be used. To ensure consistency between the newly collected data and the original PanTHERIA data, the supplementary data was added to the original unadjusted data set and median values were re-calculated using the method detailed in Jones et al. (2009). Supplementary data and references are listed in Appendix 1 (Supp. Table A1.1).

2.6 Description of data and data quality

The database comprises 615 records of mean, median and maximum dispersal distance for 202 species and 147 records for 58 species of the distribution of dispersal distances across a study population. Data availability was highest for records of natal dispersal and movement distance (i.e. unspecified one way movement; see Figure 2.2). Data was available for 16 taxonomic orders (Figure 2.3) and from all biogeographic realms bar Antarctica. The majority of data, however, came from studies conducted in the Palearctic (152 records) and Nearctic (358 records). The distributions of dispersal distances for all movement types were right skewed (Figure 2.4) and most dispersal and movement distances were less than 50km. Dispersal data and references are listed in Appendix 1 (Supp Table A1.2).

To ensure dispersal estimates were not confounded by study parameters or reporting methods, I implemented several measures to quantify and control for data quality. Firstly, where maximum dispersal distances were recorded as the edge of the study area, studies were marked and excluded from analyses. Secondly, I assigned data

quality scores to each record based on the ancillary data. This allows low quality data to be removed from analyses to check for an effect. A quality score was calculated for each study by coding study descriptors as follows: type of source (2, journal article; 1, secondary source; 0, unknown), estimation method (3, direct observation or radio telemetry; 2, trapping or capture-mark-recapture; 1, other; 0, unknown), and whether or not a measure of variation was calculated (1, yes; 0, no). I summed these scores to determine the quality score, which could range from 0 (lowest quality) to 6 (highest quality) for each study. Studies with a score from 0 to 3 were considered poor quality, and those with scores from 4 to 6 were considered high quality. A high proportion of the data was scored as high quality (Figure 2.2).

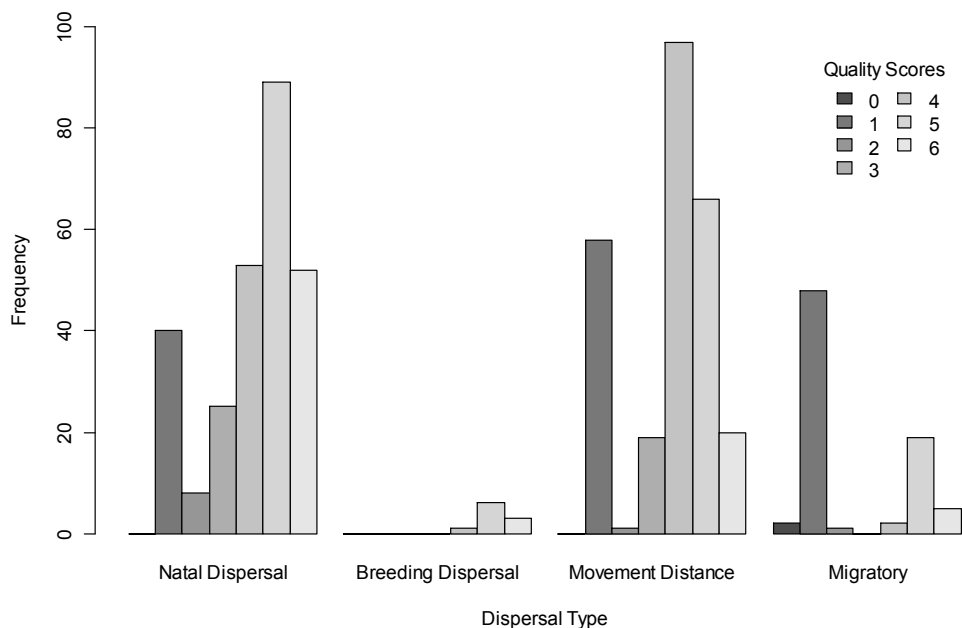


Figure 2.2 Quality scores and data availability for dispersal distance data. Scores 0 - 3 are considered low quality and 4-6 are considered high quality.

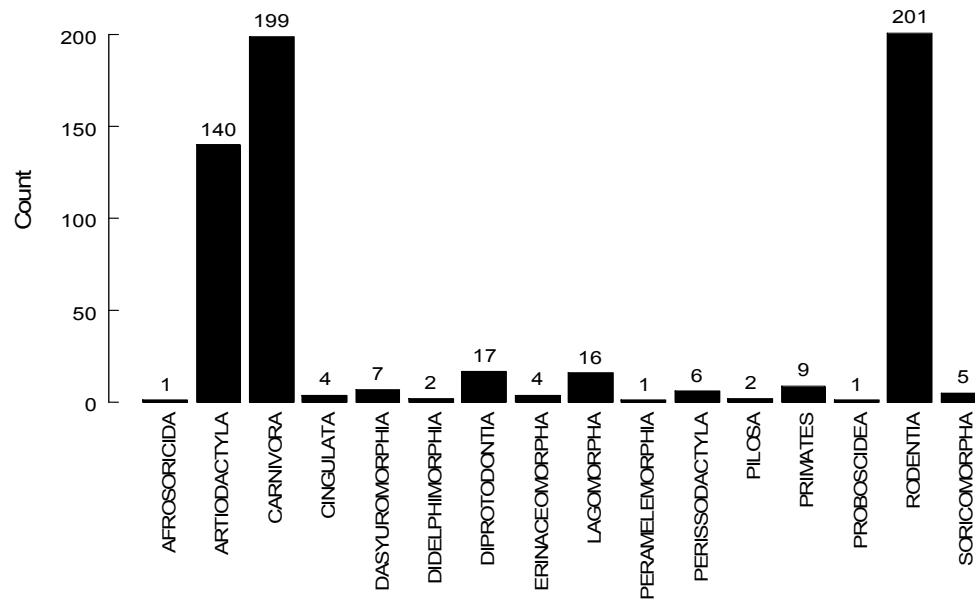


Figure 2.3 Distribution of taxonomic orders within the database

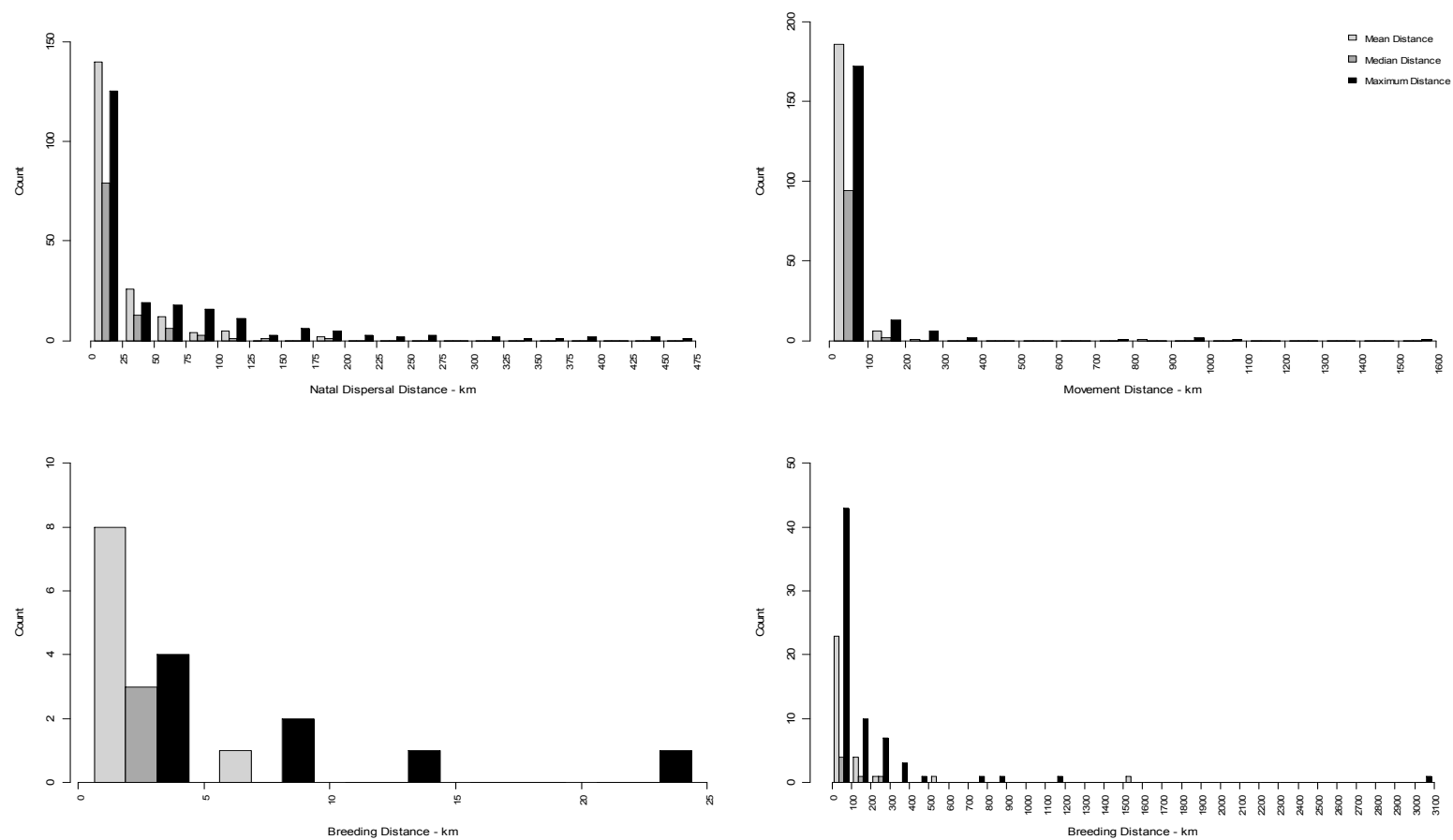


Figure 2.4 Distribution of mean, median and maximum natal dispersal distances in kilometres.

2.8 Dispersal kernel data

I used data from studies that describe the distribution of dispersal distances for a population or subset of populations, to examine whether there was a consistent trend in the shape of dispersal distance distribution by testing the fit of the data against three probability density functions (exponential, Weibull and half-Cauchy) using the method described in Paradis et al (2002) and R code provided by Emmanuel Paradis. This method uses a maximum likelihood approach to estimate the parameters for each density function and calculates the AIC for each function, allowing the fit of different functions to be compared. The model with the lowest AIC is identified as arising from the function which best describes the data.

The exponential distribution can be interpreted as the probability of long distance dispersal declining at a constant rate (λ) with increasing distance from the source and is equivalent to a linear rate of spread, consistent with a pattern of local diffusion (Turchin 1998). The Weibull distribution is a two parameter model, allowing it to have more flexibility through optimisation of shape (β) and scale parameters, and therefore possibly provide a better approximation for a variety of observed dispersal kernels and thus account for both short- and long-distance dispersal (Brøseth et al. 2005; Trakhtenbrot et al. 2005). The half-Cauchy distribution is centred at a fixed location (x_0) of zero with an optimised scale (σ). It has a ‘fat-tail’, with observed dispersal distances declining less rapidly in contrast to an exponential function and they are potentially a good model for species which undertake long distance dispersal (Nathan et al. 2003).

I combined data for male and females and removed data sets with less than 14 data points, as they could not be modelled accurately with all density functions. This left 27 dispersal distributions from 23 species available for analysis. I treated

dispersal distances as precise known values ('exact': Paradis et al. 2002). Where data was reported in intervals I took the mid-point of the interval as the exact measure.

Analyses were run in R (version 2.12.0; R Development Core Team 2010).

Species Name	n	Exponential	Weibull	Half-Cauchy
<i>Dipodomys spectabilis</i>	49	-189.68	-190.65	-187.20
<i>Dipodomys stephensi</i>	333	-1271.62	-1442.97	-1192.80
<i>Ammospermophilus leucurus</i>	117	-262.76	-313.06	-229.30
<i>Castor canadensis</i>	18	135.27	135.94	133.04
<i>Dipodomys merriami</i>	168	-396.95	-458.56	-354.07
<i>Dipodomys microps</i>	243	-745.87	-799.12	-697.78
<i>Lepus timidus</i>	99	713.70	688.93	658.40
<i>Lynx rufus</i>	34	210.28	211.59	213.01
<i>Perognathus longimembris</i>	73	-241.70	-246.06	-233.96
<i>Procyon lotor</i>	16	137.70	139.45	138.80
<i>Rattus fuscipes</i>	35	-121.05	-122.90	-117.12
<i>Spermophilus beecheyi</i>	81	40.48	-2.30	61.85
<i>Sylvilagus floridanus</i>	103	-432.55	-441.59	-415.40
<i>Canis latrans</i>	20	227.16	224.33	230.55
<i>Dipodomys spectabilis</i> - pop 2	54	-192.62	-190.89	-195.98
<i>Dipodomys stephensi</i> - pop 2	75	-315.29	-344.50	-300.81
<i>Dipodomys stephensi</i> pop 3	27	-95.21	-101.83	-89.56
<i>Equus caballus</i>	102	172.35	117.20	202.46
<i>Mustela erminea</i>	23	68.81	70.79	70.25
<i>Odocoileus hemionus</i>	137	792.45	764.99	733.80
<i>Panthera leo</i>	14	100.27	88.99	104.49
<i>Peromyscus maniculatus</i>	90	-75.69	-78.60	-65.53
<i>Spermophilus richardsonii</i>	87	-258.06	-257.14	-257.04
<i>Canis lupus</i>	34	405.43	406.46	407.18
<i>Lepus californicus</i>	208	71.93	-4.20	-144.84
<i>Vulpes vulpes</i>	295	1092.37	1092.51	1099.95

Table 2.1 Model AIC results and sample size for dispersal kernels from 23 species of mammal.

Models with the smallest AIC denoted in grey and bold.

I found that the Weibull probability density function was the functional form most likely to give the lowest AIC and thus the best fit to the data provided (Table 2.1). This contrasts with the findings of Paradis et al (2002) who found that the half-Cauchy model best described distributions of dispersal distances in blue tit (*Parus caeruleus*) and great tit (*Parus major*) records from the UK and Ireland. Similarly to the Paradis study, however, differences between AICs for one sample were often small (Paradis et al. 2002). Interestingly, AICs for Weibull models did not seem to be unduly penalised by estimating two parameters (shape and scale) compared to the exponential and half-Cauchy which only estimate one parameter each (rate and scale respectively). In this analysis, the flexibility provided by estimation of two parameters often produces a better model fit than alternative models. Better AIC values for Weibull models may also arise from an increased success of describing the left hand side of the dispersal kernel compared to exponential and half-Cauchy models. Exponential and half-Cauchy models have their location set at 0, while the mode of a Weibull model can be offset from 0 (Figure 2.5). Therefore the exclusion of non-dispersing individuals from the model (or from the original study) may lead to a better fit by the Weibull functional form for short dispersal distances.

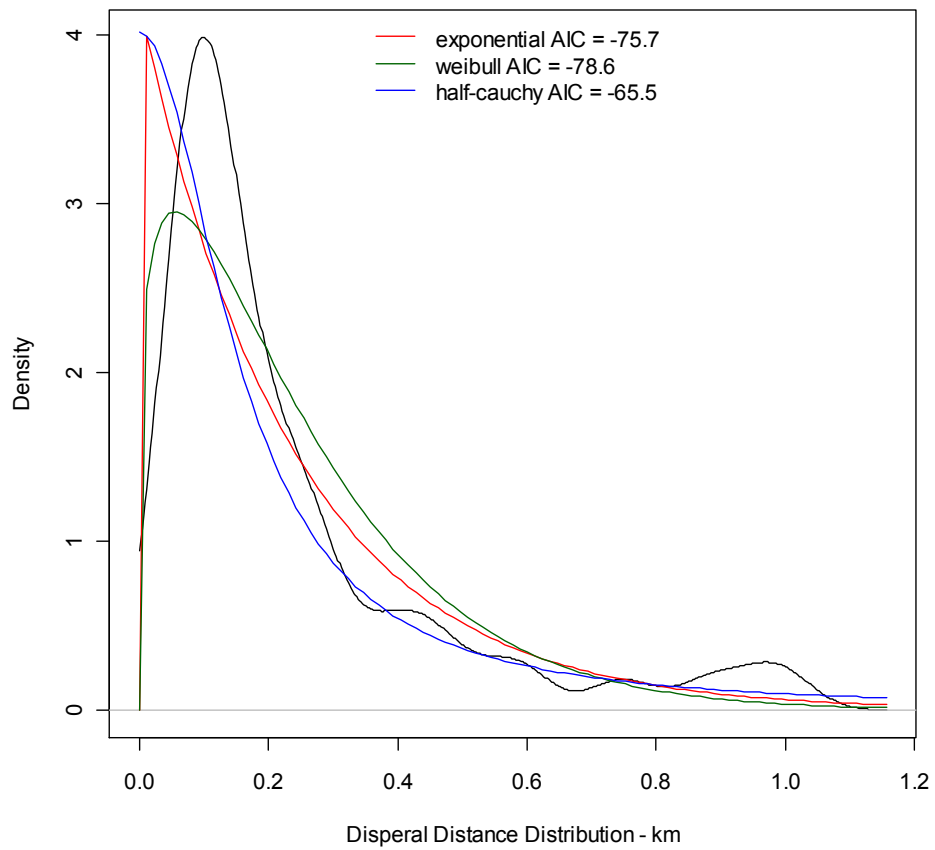


Figure 2.5 Dispersal kernel for the deer mouse (*Peromyscus maniculatus*) – actual data given in black, estimates of best fit from three functional forms, exponential Weibull and half-Cauchy given in red, green and black respectively. Data taken from (Dice and Howard 1951).

Chapter 3. Predicting dispersal distance in mammals: A trait based approach¹

3.1 Abstract

While dispersal is one of the principal mechanisms influencing ecological and evolutionary processes, quantitative empirical data are unfortunately scarce. As dispersal is likely to influence population responses to climate change, whether by adaptation or migration, there is an urgent need to obtain estimates. Cross-species correlative approaches identifying predictors of dispersal distance can provide much needed insights into this data-scarce area. Here I describe the compilation of a new data set of natal dispersal distances and use it to test life history predictors of dispersal distance in mammals and examine the strength of the phylogenetic signal in dispersal distance. I find that both maximum and median dispersal distances have strong phylogenetic signals. No single model performs best in describing either maximum or median dispersal distances when phylogeny is taken into account but many models show high explanatory power, suggesting that dispersal distance per generation can be estimated for mammals with comparatively little data availability. Home range size, geographic range size and body mass are identified as the most important terms across models. Cross-validation of models supports the ability of these variables to successfully predict dispersal, suggesting that models may be extended to species where dispersal distance is unknown.

¹ A version of chapter is in submission at the Journal of Animal Ecology as: Whitmee, S.L. and Orme, C.D.L. Predicting dispersal distance in mammals: A trait based approach.

3.2 Introduction

Natal dispersal, the movement an animal, plant or propagule undertakes from its point of origin to the place where it reproduces, is a demographic parameter which is almost ubiquitous in its importance to ecology and evolution (Howard 1960; Greenwood 1980; Vellend and Orrock 2010). Its effects are seen at all spatial scales, from the distribution of genes and individuals within populations to community composition and the position and extent of species geographic ranges (Slatkin 1987; Johnson and Gaines 1990; Stenseth and Lidicker 1992; Gaston 2003; Dytham 2009). For this reason there is a growing recognition of the value of including quantitative descriptions of dispersal in spatially explicit population models and species distribution modelling (SDM) techniques (Araújo and Guisan 2006; Hawkes 2009).

Despite its importance however, dispersal distance is often poorly parameterised within models. Few models currently account for long distance dispersal (LDD) events and accurate descriptions of dispersal distances are lacking from most models (Macdonald and Johnson 2001; but see Fagan & Lutscher 2006). For example, SDMs predicting the impact of climate change on species distributions frequently contrast scenarios of unconstrained and no dispersal with the caveat that, in reality, most species will show a range of dispersal distances which falls between these two assumptions (Araújo and Rahbek 2006; Broennimann et al. 2006; Botkin et al. 2007). There are a number of reasons for this shortfall, including inconsistencies in measurements and definitions of dispersal, difficulties in collecting empirical data due to the 'once in a life time' nature of dispersal events in many species and the inability of most studies to capture long-distance dispersal events (Koenig et al. 1996; Bowman et al. 2002). Difficulties also arise because the process itself takes many

forms, from a gradual range shift to an adjacent home range, to a one-way movement over a great distance.

There are also few studies of how dispersal scales with species' life history. To date, most research has focused on single or dual traits hypothesised to correlate with dispersal ability (Paradis et al. 1998; Van Vuren 1998; Sutherland et al. 2000; Bowman et al. 2002; Bowman 2003) which have been of limited scope and have failed to account for the effects of shared evolutionary history (Felsenstein 1985; Pagel 1999, but see Belliure et al. 2000; Dawideit et al. 2009). In addition, while complex theoretical models describing the dispersal process have been developed, there is little evidence to suggest they have been incorporated into applied conservation management models or, to any large degree, to forecasting climate change impacts on biodiversity (Travis et al. 2010). This may be partly attributed to the focus of many studies on the evolution of dispersal within populations of a single species rather than comparative studies across species (Murrell et al. 2002; Phillips et al. 2008; Burton et al. 2010). Further work is now needed to enable robust predictions of species dispersal distance to be made, and hence parameterise models when data are scarce.

I compiled a database of dispersal distance in mammals, spanning a broad taxonomic and geographic range to explore these questions. I used mammals as data availability across the group is relatively high, including the mammal supertree, a recent species-level phylogeny of 5020 extant mammals (Bininda-Emonds et al. 2007; Fritz et al. 2009) and a database of mammalian life history traits (Jones et al. 2009). Mammals are also ecologically diverse and show a range of sizes and variability across axes of life history that allow robust comparisons to be made across the group. Here, I use this dispersal database to test scaling of dispersal distance across median

and maximum measures and use a multi-predictor framework to test a number of traits that are thought to predict mammalian dispersal distance. I present the first test of phylogenetic signal in dispersal for any taxonomic group. I also examine the predictive power of models and make recommendations for those wishing to predict dispersal distance where empirical evidence is lacking.

3.3 Methods

Data collection

Dispersal distance data came from experimental and observational studies and from reports of individual movement distances. I excluded distances derived from genetic information. While empirical data may underestimate long distance dispersal (LDD; Kot et al. 1996), there is relatively good data availability and measurements reflecting actual dispersal distances across a variety of known locations and timescales. I gathered data from systematic searches of relevant peer-reviewed journals including all issues of *Mammalian Species* (1969 – 2009), all issues of the *Journal of Zoology* from 1998 to 2009 and all issues of the *Journal of Mammalogy* from 2000 onwards. In addition, I queried electronic search engines from ISI Web of Knowledge, JSTOR and Google Scholar using the terms; “dispersal”, “natal dispersal” and “dispersal distance”. Natal dispersal was defined as “the movement of a propagule between its birthplace or natal group and its first breeding site or group” and demarcated this from breeding dispersal which was defined as “the movement between consecutive breeding sites or groups of adult breeders” (Greenwood et al. 1979; Shields 1982) as data availability for natal dispersal was higher. In addition to empirical studies and observational data, I used papers reporting previous meta-analyses of dispersal data (Van Vuren 1998; Sutherland et al. 2000; Harris et al. 2009).

I combined maximum and median natal dispersal distances for juveniles, sub-adults and adults undertaking a permanent movement away from the natal home range. Maximum dispersal values ($D_{\max}$) were defined as the maximum recorded distance travelled by a species across all studies, and excluded any values where the maximum distance coincided with the limit of the study area as this underestimates maximum dispersal distances. Median dispersal distances (D_{med}) were calculated as the median of all reported distances for a species across all studies (i.e. the median of average dispersal distances). The proportion of variance in dispersal distance attributed to the sex of the dispersing individual was small ($D_{\max} = 0.34\%$, $D_{\text{med}} = 2.15\%$) compared to variation between species ($D_{\max} = 81.16\%$, $D_{\text{med}} = 87.72\%$) and therefore I combined data for both sexes (Appendix 1: Supp. Table A1.1).

From these datasets, I obtained maximum natal dispersal distances ($D_{\max}$) and matching trait data for 82 species (based on 210 dispersal records) and median natal dispersal distances (D_{med}) plus traits for 77 species (based on 203 dispersal records). Sixty one species had data for both maximum and median dispersal distance. Data spans 9 mammalian orders and 33 different families. Maximum dispersal distances range between 0.087km and 467km and median dispersal distances range between 0.0159km and 86.65 km. Although the dispersal data are predominantly from the Nearctic and Palearctic, the data set covers all terrestrial biogeographic realms except Oceania (Olson and Dinerstein 1998).

Predictor variables

I chose body mass (grams), home range size (km^2), trophic level (carnivore/herbivore/omnivore), population density (number of individuals per km^2) and geographic range size (km^2) based on extent of occurrence, to use as explanatory variables in my model (Van Vuren 1998; Sutherland et al. 2000; Bowman et al. 2002;

Gaston 2003; Lester et al. 2007). Following Bielby et al (2007), I also chose gestation length and weaning age to represent two axes of the ‘fast-slow’ life history continuum, respectively representing the timing of reproductive bouts and the trade-off between offspring size and offspring number independently of body size (Smith and Fretwell 1974; Bielby et al. 2007). Of the traits explored by Bielby et al (2007), these variables both describe the axes well and are available for the species in my sample. I specifically chose a broad interpretation of the definition of species traits which included ecological ‘traits’ (Freckleton et al. 2002) in the belief that traits which already reflect how species perceive and interact with their environment may correlate with dispersal distance and thus help predict dispersal for species where data is unavailable.

Explanatory variables were chosen specifically based on *a priori* assumptions about their relationship with dispersal ability. Body mass is thought to be a key correlate of dispersal distance in terrestrial vertebrates (Van Vuren 1998; Sutherland et al. 2000; Bowman et al. 2002; Bowman 2003; Jenkins et al. 2007): locomotion becomes energetically cheaper as body size increases, allowing larger daily movements thereby giving rise to larger overall dispersal distances (Schmidt-Nielsen 1984; Biewener 1989; Jetz et al. 2004). Home range size captures aspects of a species’ habitat use and energy requirements, as well as broadly reflecting other traits such as dietary requirement (Bowman et al. 2002; Bowman 2003). Trophic level can give an indication of the distribution of resources and distances required to maintain populations, as carnivores tend to range over wider areas than herbivores and omnivores (Carbone et al. 2005). Empirical work has also demonstrated that competition plays a role in dispersal decisions, therefore, after controlling for body size, average population density may be a predictor of dispersal distance (Johnson and

Gaines 1990). Both positive and negative density-dependent interactions have been observed to affect intra-specific dispersal patterns but it is unknown if species which live at comparatively higher densities also tend to disperse over longer distances (Lambin et al. 2001; Enfjäll and Leimar 2009). As colonisation ability is not only determined by dispersal but includes other measures of competitive ability such as speed of life history, measures of fecundity or timing of reproduction may also be related to dispersal. Trade-offs between competitive ability and dispersal are well established in both modelling and empirical literature for within species studies but it remains to be established if this holds across species (Hughes et al. 2003). Finally, dispersal ability has been shown to correlate with geographic range size in a number of taxa (for example Böhning-Gaese et al. 2006; but see Lester et al. 2007) therefore this trait is included as a predictor even though the direction of causality may run counter to that for other predictor variables (Gaston 2003). Dispersal can provide opportunities for rapid access to newly available and climatically suitable habitats, for example, after periods of environmental change (Böhning-Gaese et al. 2006). Additionally, species with low dispersal ability often exhibit reduced levels of gene flow between populations which can lead to a higher probability of speciation through either peripheral isolation or vicariance which means such species may inherit a smaller starting range from which to expand (Bellare et al. 2000; Jablonski and Roy 2003; Phillimore et al. 2007).

I obtained data for explanatory variables from the PanTHERIA database (Jones et al. 2009) and supplemented this data with a targeted collection in the primary and grey literature for missing data values (Appendix 1: Supp. Table A1.2). I checked variance inflation factors (VIFs) to discount the influence of multi-collinearity between predictor variables on the results: all VIFs were less than 10 and

therefore I included all predictors in the analyses (Appendix 2: Supp. Table A2.1). I combined trophic levels for herbivores and omnivores to enable comparison with a previous study by Sutherland et al (2000). I used a generalized additive model to identify model terms which had a significantly non-linear relationship with dispersal (Wood 2006). Gestation length and weaning age showed non-linear relationships with both median and maximum dispersal distance. The maximal model therefore included log body mass (grams), log home range (km²), trophic level, log population density (individuals/km²), log geographic range size (km²), log gestation length (days), log weaning age (days) and quadratic terms for weaning age and gestation length. All continuous predictor variables and dispersal distances were log transformed for the analyses.

Relationship between median and maximum dispersal distance

I explored the relationship between maximum and median dispersal distance within the subset of 61 species where both measures were available using standardised major axis (SMA) regression, which is desirable when the aim is to summarise the relationship between two variables rather than identify a predictive relationship (Warton et al. 2006). In order to assess the effects of clade structure and phylogeny in shaping this relationship I calculated the SMA slope using a generalised linear mixed model within a Bayesian framework using Markov chain Monte Carlo (MCMC) methods using MCMCglmm (Hadfield and Nakagawa 2010). The null model was fitted just with a bivariate response ($D_{\max}$ and D_{med}) and the SMA slope was estimated from the posterior distribution of residual covariances. I then added random effects describing the effects of taxonomic order, phylogeny and the combination of both phylogeny and order. The inclusion of taxonomic order over and above the inclusion of phylogeny was to rule out possible clade effects arising from taxonomic bias in

data availability. I used the deviance information criterion (DIC) to compare model complexity and fit (Spiegelhalter et al. 2002). I specified the error structure for all models as Gaussian and used flat priors. I ran all models for 250000 iterations with a burn-in of 3000 iterations and a thinning interval of 10 iterations. Method of dispersal data collection and sample size may be dependent on the size and habits of the study species (e.g. use of mark-recapture techniques and larger sample sizes in smaller species which live at higher densities and use of radio telemetry for large bodied species which tend to roam widely). This methodological bias may introduce directionality in data quality between groups of species that may subsequently affect the slope of the relationship. I therefore used sample size as a model covariate to act as a proxy for study effort / method and to test for bias in the relationship.

Phylogenetic signal of dispersal distance

The shared ancestry of species means that there may be similarity in trait values between close relatives, leading to statistical non-independence between data points (Felsenstein 1985). Traits, such as body mass, which are thought to influence dispersal show a strong phylogenetic signal (Freckleton et al. 2002), therefore dispersal distance itself may show a signal. If there is limited or no evidence of dispersal distance evolving under Brownian motion (i.e. evolution occurring a random walk with constant trait variance over time Felsenstein 1985) then it may be, when looking across species, that population level drivers such as landscape structure or more labile behavioural traits are more important than species' traits in determining dispersal (Blomberg et al. 2003). I first measured the strength of the phylogenetic signal in the dispersal distance data set and continuous explanatory variables using Pagel's λ statistic (Pagel 1999; Freckleton et al. 2002), finding the maximum likelihood (ML) value of λ for the given phylogeny and trait distribution. A λ value

of 0 corresponds to no phylogenetic signal in the trait in question and $\lambda = 1$ shows that the trait distribution corresponds to the distribution expected under a model of Brownian evolution. Phylogenetic signal in trophic level was measured using D , a measure of phylogenetic signal strength in a binary trait, based on the sum of sister-clade differences in a given phylogeny - in this case presence or absence of carnivory (Fritz and Purvis 2010). The estimated D value is tested for significant departures from 1 (random trait distribution across the selected tree) and 0 (trait distribution is clumped as expected under a model of Brownian evolution). All phylogenetic analyses were conducted using the mammalian supertree (Bininda-Emonds et al. 2007; updated by Fritz et al. 2009) and the caper package (Orme et al. 2008) in R 2.12.0 (R Development Core Team 2010). Throughout, I used the taxonomy of Wilson and Reeder to define species (Wilson and Reeder 2005).

Multi-predictor models, model selection and averaging

Preliminary analyses indicated that many combinations of predictor variables are capable of producing highly explanatory models. Here, I am interested in exploring which combinations of variables are most useful in predicting dispersal. I therefore used multi-model inference to assess support for a set of candidate models, generate a confidence set of models based on the relative weight of evidence for each model and finally calculate a weighted average of parameter estimates (Burnham and Anderson 2004; Johnson and Omland 2004). I assessed the 287 possible simplifications of the maximal model described previously. This is a disproportionately large number of models to fit to relatively small data sets ($D_{\max}$: $n=82$; D_{med} : $n = 77$; (Burnham and Anderson 2002). However the prior selection of traits with existing biological relevance, lack of a priori knowledge of which specific combinations should be chosen and existing studies with competing findings meant that fitting all

combinations was the only way to test all possible correlates of dispersal distance. I fitted models using phylogenetic generalised linear models (PGLM; Freckleton et al. 2002), which incorporates the expected covariances between species, calculated using the ML value of λ into the error term of the model. Quadratic terms for gestation length and weaning age were only included in conjunction with their linear terms. I obtained AICc values (Akaike information criterion – corrected for small sample size) and used these to calculate Akaike weights for each model. The highest weighted models which summed to an Akaike weight greater than 0.95 (the 95% set; Burnham and Anderson 2002) were selected and used to calculate model-averaged parameter estimates and standard errors across all models using the MuMIn package in R (Barton 2010). Predictors were averaged only over the models in which they appeared. Finally, I wanted to test for the presence of particular combinations of variables consistently occurring together in highly weighted models and subsequently identify axes of explanatory power in the predictor traits. Therefore, I calculated variable weights across models for each explanatory term and from this I derived the relative variable importance for all pairwise combinations of explanatory traits (Burnham and Anderson 2002).

Cross-validation

To test the ability of my models to correctly predict dispersal distances beyond the set of species for which I have information, I re-ran the models using k-fold cross-validation to obtain comparisons between estimated and observed dispersal distances (Arlot and Celisse 2010). Each of the 287 possible simplifications of the maximal model was fitted 100 times using PGLM with a randomised three-fold partition which retained one third of data from the model building and averaging process to test predictions against. Lambda was constrained to the ML value derived from the same

model with the full data set fitted, as computing λ for each subset of the variance-covariance matrix was computationally intensive. To examine the predictive power of each model, and the ability of models to correctly predict dispersal distances for individual species, I calculated the residual variance of predictions from empirically observed dispersal distances. This residual variance was then averaged separately across models and species. Weighted means were calculated for species using the overall model Akaike weight. I used Kruskal Wallis tests on the deviation between observed values and weighted predictions across model to look for taxonomic differences at the order level in both the direction and variation (using absolute deviation) of species predictions.

3.4 Results

Phylogenetic signal of dispersal distance

Maximum and median dispersal distance show strong phylogenetic signal: ML values of λ for $D_{\max}$ = 0.74 (0.512 - 0.883 95% CI), and for D_{med} = 0.84 (0.663 - 0.937 95% CI). The phylogenetic signal in continuous explanatory variables was >0.81 for all traits except geographic range size which exhibits a low phylogenetic signal with wide confidence limits (Appendix 2: Supp. Table A2.2). Trophic level also showed high phylogenetic signal with distributions not significantly different from that expected under a model of Brownian trait evolution. Multi-predictor models showed extremely low phylogenetic signal across the 95% set with a mean lambda across models for $D_{\max}$ of 0.002 (0 - 0.006) and for D_{med} of 0.203 (0.171 - 0.235).

Relationship between median and maximum dispersal distance

Without accounting for the relatedness of species, the SMA slope of the relationship between maximum and median dispersal distance was found to be not significantly

different from 1. However, DIC values for more complex models describing the relationship indicate that the best model includes phylogeny fitted as a random effect (Figure 3.1). Once the effects of phylogenetic relatedness are accounted for the SMA slope is 1.432 (1.118 - 1.818 95% CI); given that both variables are log-transformed, maximum dispersal increases allometrically with median dispersal, rather than increasing as constant proportion of median dispersal. No significant effect of sample size was found.

Multi-predictor models, model selection and averaging

The best supported multi-predictor models for both maximum and median dispersal distance had low Akaike weight ($D_{\max} = 0.092$, $D_{\text{med}} = 0.127$, Appendix 2: Supp. Table A2.3), indicating no overwhelming support for any particular model (Johnson and Omland 2004). Furthermore, a large number of models are included in both 95% confidence sets of models: 78 for maximum dispersal distance and 74 for median dispersal distance. The explanatory power of all models in both 95% confidence sets was high. Models predicting maximum dispersal distance had a mean adjusted r^2 of 0.717 (95% CI: 0.712 – 0.721), while models predicting median dispersal distance had a mean adjusted r^2 of 0.818 (95% CI: 0.816 – 0.820). A list of all model coefficients for Akaike weights greater than 0.02 can be found in Appendix 2: Supp Table A2.3.

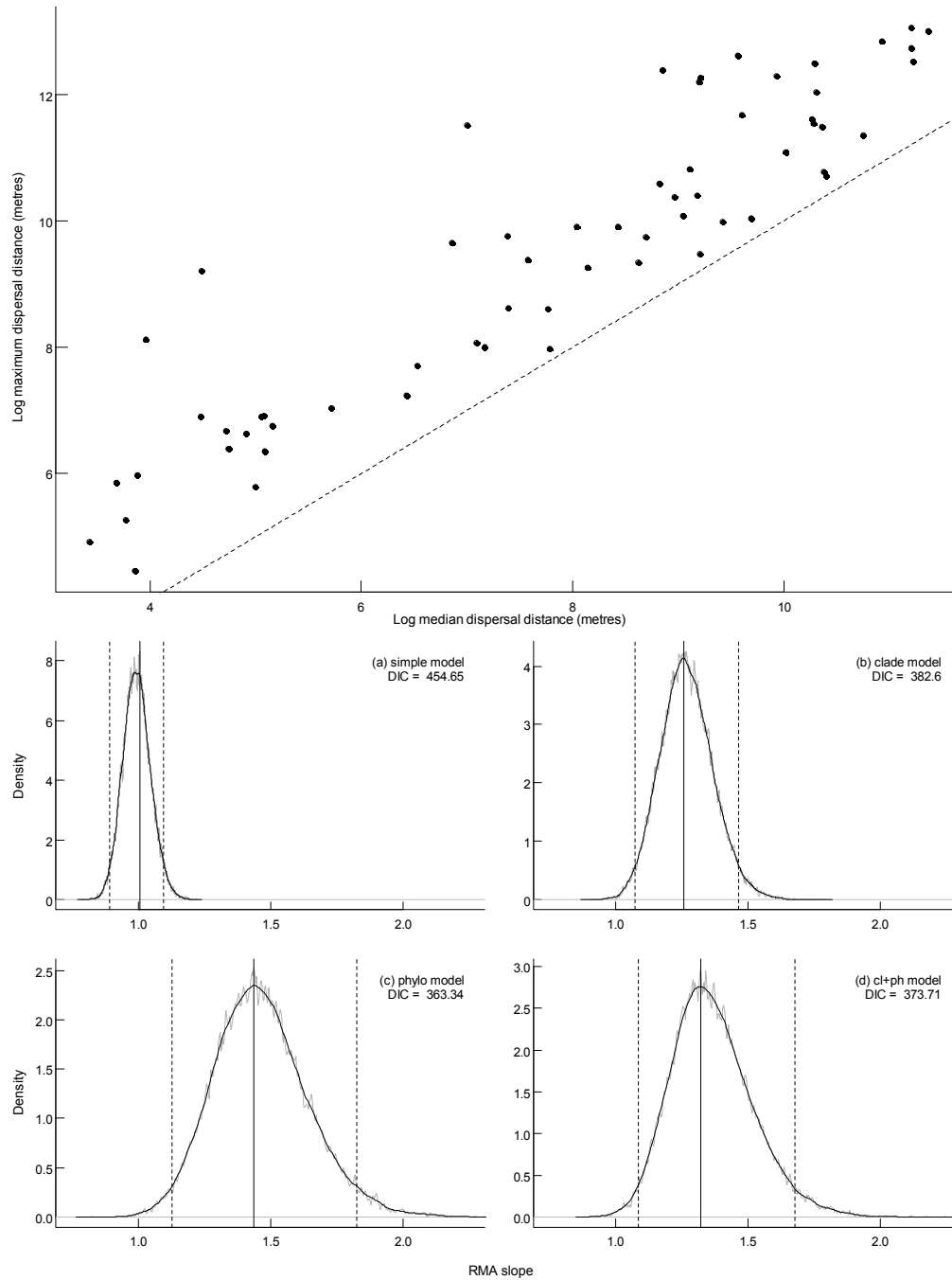


Figure 3.1 Main plot: Relationship between log median and maximum dispersal for 61 species, showing the 1:1 slope (dashed). Sub plots show the posterior distribution of slope estimates and DIC estimates for Markov chain Monte Carlo bivariate linear mixed models of maximum and median dispersal distance for a null model (a) and models with random effects of order (b), phylogeny (c) and both order and phylogeny (d). The posterior mode (solid line) and 95% confidence estimates (dashed lines) are shown.

For maximum dispersal, model averaged variable weights ($\sum Aw$, Table 3.1) support geographic range size, body mass and home range size as the three most important terms ($\sum Aw > 0.79$) and all three terms show significant positive slopes when averaged across the model set (Table 3.1). Weaning age, its quadratic term and population density also show relatively high variable weights ($\sum Aw > 0.45$, Table 3.1); however the slopes of their relationships are not estimated precisely, with wide confidence limits indicating variability around model predictions. For median dispersal, variable weights support home range as the most important variable ($\sum Aw > 0.90$), with body mass, population density, weaning age and its quadratic term also showing high weightings ($\sum Aw \geq 0.58$). Variable weights are low ($\sum Aw < 0.26$) for all other continuous terms and model averaged confidence limits of estimated slopes include zero for all variables apart from home range (Table 3.1). Trophic level shows low variable weight in both models ($\sum Aw < 0.26$) and there is no clear pattern between variables: carnivores appear to have higher maximum dispersal but lower median dispersal in comparison to herbivores and omnivores (Table 3.1). Differences in model averaged intercept values between trophic levels were not significant for models of maximum or median dispersal distance. There is no evidence of consistent aggregation between pairs of variables to form alternative model subsets (Figure 3.2, Appendix 2: Supp. Table A2.4): the mostly strongly supported variables form a single cluster with highest weights in all models in which they co-occur.

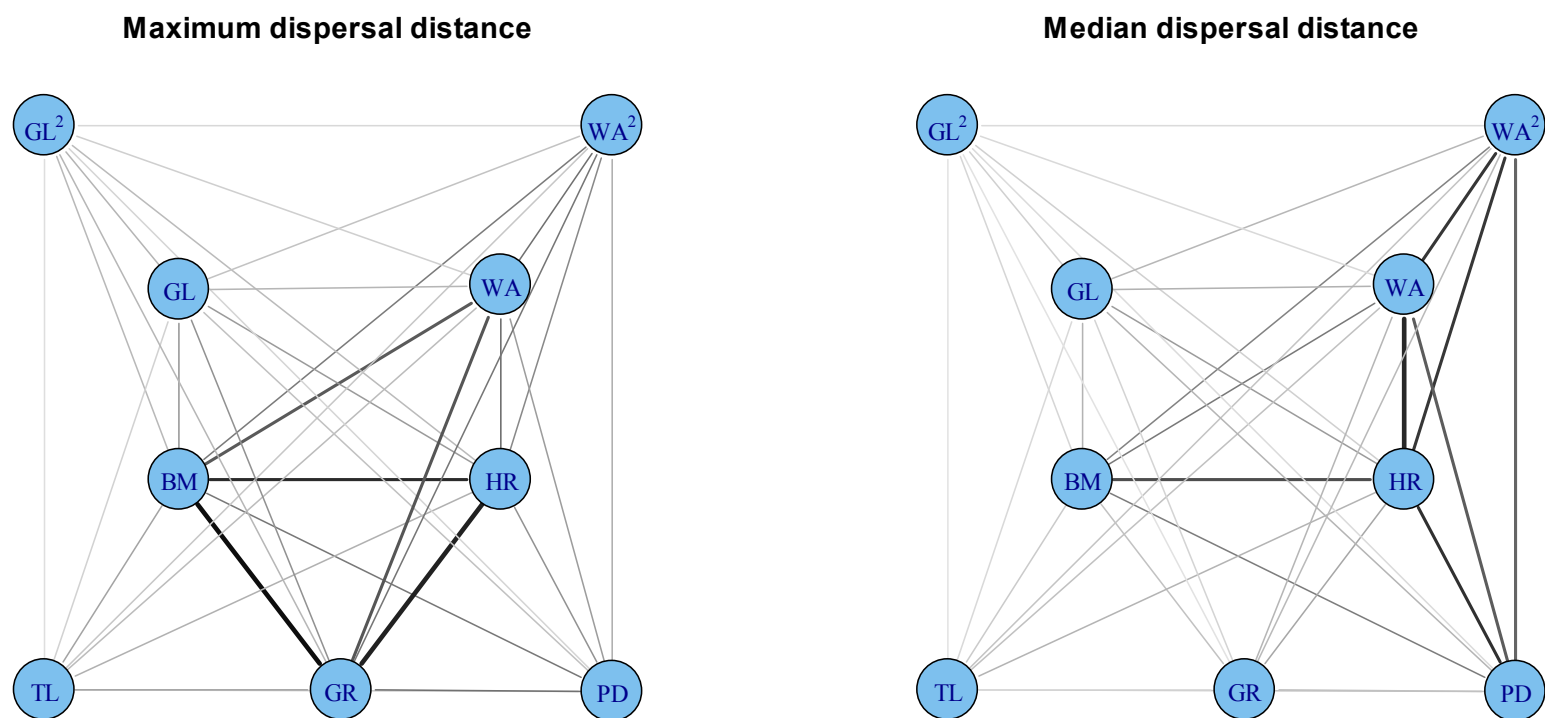


Figure 3.2. Summed akaike weights for all pairs of variables across the whole model set. Darker, heavier lines indicate higher weighting in models in which the terms occur together (Appendix 2: Supp. Table A2.4). BM - Body Mass, HR – Home Range Size, GR – Geographic Range Size, TL – Trophic Level, PD – Population Density, GL – Gestation Length, WA – Weaning Age.

	(a)	$\sum Aw$	Model averaged coefficient	(b)	$\sum Aw$	Model averaged coefficient
<i>(Intercept)</i>	-		-1.153 (-13.620 / 11.314)	-		1.100 (-9.282 / 11.481)
<i>Trophic level</i>	0.257	-		0.176	-	
Herbivore and omnivore	-		-0.895 (-11.990 / 10.199)	-		0.806 (-8.799 / 10.410)
Carnivore	-		-0.433 (-8.259 / 7.393)	-		0.734 (-4.777 / 6.244)
<i>Adult body mass (grams)</i>	0.873		0.315 (0.018 / 0.613)	0.585		0.178 (-0.069 / 0.425)
<i>Home range (km²)</i>	0.794		0.220 (0.009 / 0.431)	0.949		0.328 (0.117 / 0.538)
<i>Population density (individuals per km²)</i>	0.460		-0.137 (-0.337 / 0.064)	0.703		-0.153 (-0.340 / 0.034)
<i>Geographic range (km²)</i>	0.925		0.252 (0.029 / 0.474)	0.232		0.062 (-0.118 / 0.242)
<i>Gestation length (days)</i>	0.319	-		0.261	-	
without quadratic term	-		0.028 (-0.705 / 0.761)	-		-0.172 (-0.849 / 0.504)
with quadratic term	-		4.235 (-1.351 / 9.821)	-		2.655 (-3.474 / 8.784)
<i>Weaning age (days)</i>	0.576	-		0.723	-	
without quadratic term	-		-0.207 (-0.773 / 0.358)	-		-0.025 (-0.507 / 0.458)
with quadratic term	-		3.202 (-0.505 / 6.909)	-		3.716 (0.236 / 7.195)
<i>Gestation length² (days)</i>	0.183		-0.505 (-1.164 / 0.154)	0.076		-0.334 (-1.047 / 0.380)
<i>Weaning age² (days)</i>	0.453		-0.372 (-0.774 / 0.030)	0.686		-0.406 (-0.783 / -0.029)

Table 3.1: Summed akaike weight ($\sum Aw$) and weighted average coefficient for each model term across the 95% set for a) maximum dispersal distance models and b) median dispersal distance models. Confidence limits for coefficient estimates at 95% given in brackets. Average coefficients with consistently positive or negative slopes indicated by confidence limits are shown in bold.

Cross-validation

Variation in predictive ability was observed depending on both the model and the species for which the data were being estimated (Figures 3.3 and 3.4). Across species, both the accuracy and precision of estimated dispersal distance was related to the Akaike weight of the 287 models from the full data set. Highly weighted models had no systematic bias in dispersal estimates, with mean differences between observed and predicted values across species close to zero for ($D_{\max} = 0.00013 \log$

metres; $D_{\text{med}} = 0.00014$ log metres, Appendix 2: Supp Table A2.3). The standard error in mean differences between observed and predicted across species is also low ($D_{\text{max}} = 0.164$; $D_{\text{med}} = 0.153$; Figure 3.3, Supp Table A2.3). Therefore, models and terms identified in the main analysis as high weighted are the most likely to provide robust estimates of dispersal distance in cross-species analyses where data are lacking. Species varied widely in the average accuracy of predictions (Figure 3.4). For models of maximum dispersal distance, neither direction (D_{max} : $\chi^2 = 6.97$, d.f. = 8, $p = 0.54$) nor variation (D_{max} : $\chi^2 = 10.87$, d.f. = 8, $p = 0.21$) in departures from observed values were predicted by taxonomic order. For models of median dispersal distance, average variation in departure from empirical data was not predicted by taxonomic order (D_{med} : $\chi^2 = 8.18$, d.f. = 7, $p = 0.32$), however mean direction of departures (D_{med} : $\chi^2 = 14.71$, d.f. = 7, $p = 0.04$) showed weakly significant differences between orders, possibly caused by an under-prediction of dispersal distances for species of Diprotodontia.

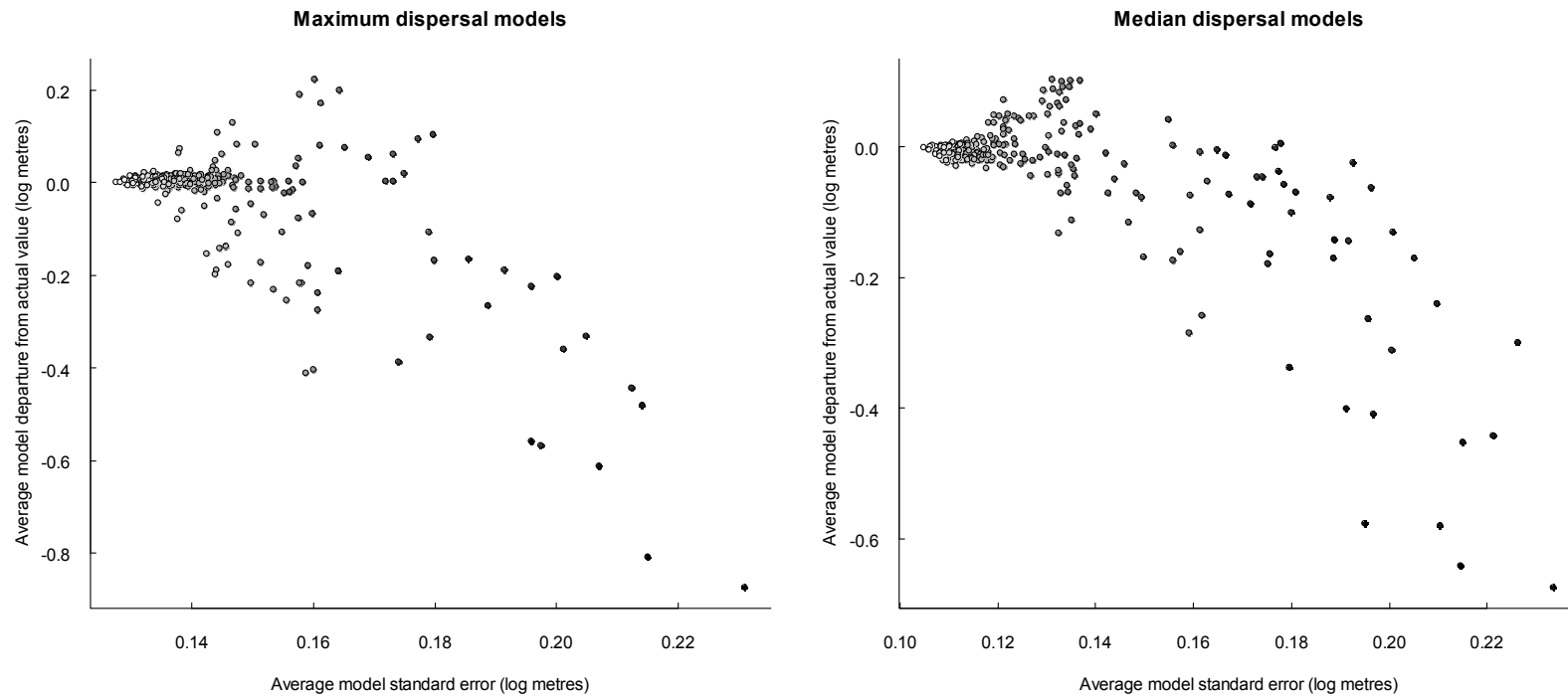


Figure 3.3 Average departure from empirically derived dispersal distance against the standard error in predictions across 100 runs - each point represents a single model. Colour shading of points denotes $\sum Aw$ scaled from 0 to 1 - lighter shading denotes higher $\sum Aw$.

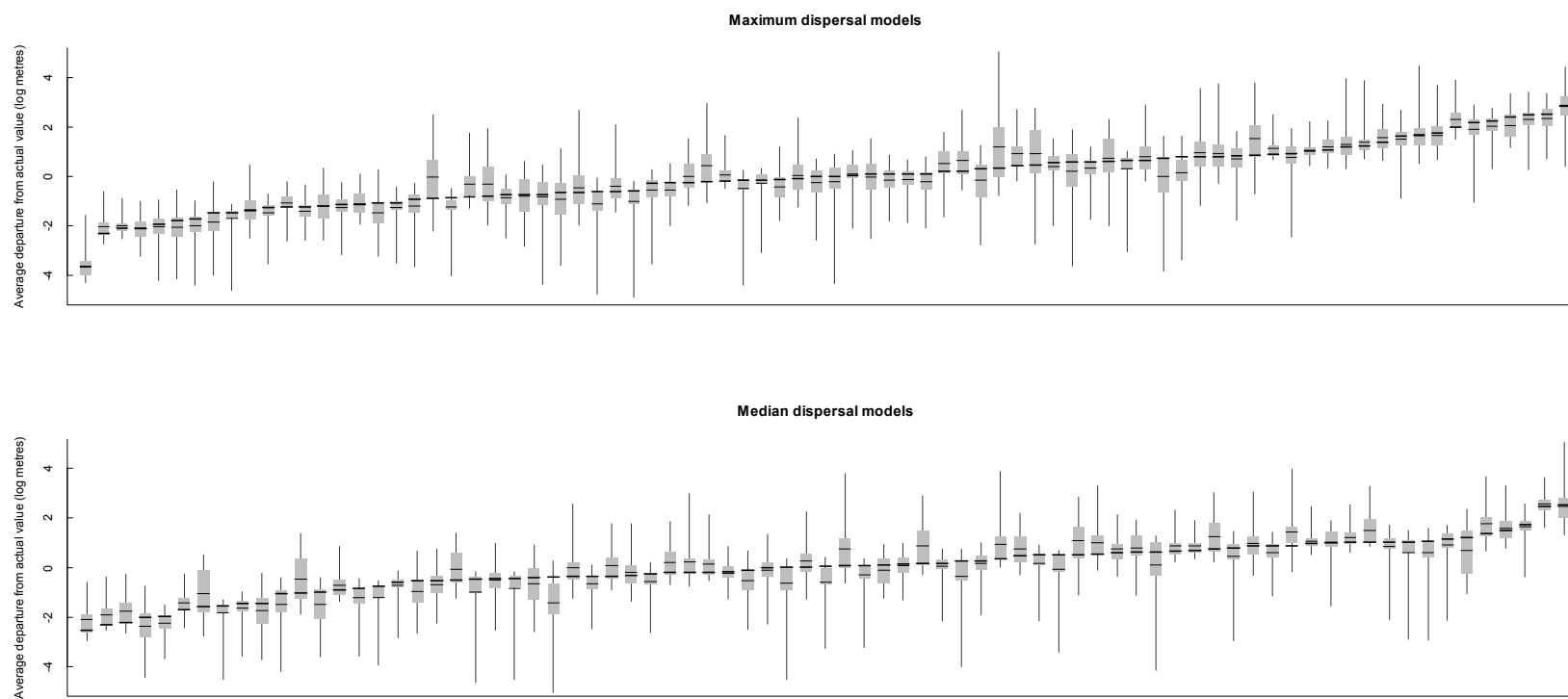


Figure 3.4 Within species variation in predictive accuracy. Each grey box represents the interquartile range of residuals from model predictions and the average residual value for one species. Bold horizontal lines are weighted residual means across all model predictions. Thin horizontal lines are unweighted residual means.

3.5 Discussion

I found that no single model performed best in describing either maximum or median dispersal distances. Support for a wide range of models across all predictor variables shows that a number of different aspects of a species life history and ecology can be used to robustly predict dispersal distances. This is an encouraging finding, suggesting that the number of species for which dispersal distance can be predicted is large. This support for many model combinations may reflect the complex nature of the evolution and expression of dispersal as one part of a co-evolving suite of interlinked behavioural, physiological and ecological traits (Ferriere et al. 2000). For example, if selection is to favour dispersal then individuals must possess the physical ability to disperse and to survive the dispersal process, but they must also be able to successfully reproduce upon arrival in a suitable environment (Johnson and Gaines 1990).

Supporting evidence for multiple correlates of dispersal has recently been demonstrated by Lyons et al (2010). Using data from the fossil record, they found significant relationships between several life history traits, such as gestation length and maximum lifespan and the distance moved by the range centroid of North American mammals during the glacial-interglacial cycles of the Late-Pleistocene epoch. Therefore the correlations between multiple life history parameters and dispersal distance found in this study are not unexpected, but the mechanisms behind the co-evolution of ‘dispersive traits’ are unclear and beyond the remit of this study. The traits used in my models vary in the way that they are hypothesised to interact with dispersal: traits such as large body size may aid the dispersal process by lowering the energetic cost of dispersal and decreasing predation risk, some traits such as population density are thought to be drivers of dispersal and some traits such as home

range, and age at sexual maturity may be a reflection of dispersal and colonisation ability. Thus, my study correlates traits to allow for prediction rather than identifying mechanisms for dispersal.

Although, no single model outperformed all others, body mass and home range consistently emerged as important predictors of dispersal ability in accordance with findings of previous studies (Van Vuren 1998; Sutherland et al. 2000; Bowman et al. 2002). I do not find a strong effect of trophic level (cf. Sutherland et al 2000). This is likely due to the inclusion of phylogeny in the models. As trophic level shows strong phylogenetic signal, studies which fail to account for the non-independence of species may confound results by introducing pseudoreplication into the analyses, e.g. species with smaller home ranges tend to be herbivores and also show lower dispersal distance (Purvis et al. 2005). I find that the simple models described in previous studies show lower explanatory power when applied to a broader range of species and when phylogenetic non-independence is taken into account. Body mass alone has relatively low predictive power for both median and maximum dispersal distance ($D_{\text{med}} r^2 = 0.307$, $D_{\text{max}} r^2 = 0.373$). Home range size was a better predictor of dispersal distance than body mass ($D_{\text{med}} r^2 = 0.798$, $D_{\text{max}} r^2 = 0.672$), however the amount of variance in maximum dispersal distance explained by home range size was still lower than found in a previous study by Bowman et al (2002). The high weighting of these terms may reflect the ability of species to cross landscapes, the spatial scale at which landscape is perceived and/or energetic constraints to dispersal distance imposed by size, as these are factors which are mediated by body mass and reflected in home range extent and as such make these variables useful in predicting dispersal distance (Holt 2003; Jetz et al. 2004; Lester et al. 2007).

Interestingly, geographic range size was found to be the term with highest model weighting across models of maximum dispersal distance but amongst the lowest weighted in models of median dispersal distance. This may be related to the capacity of species for long distance dispersal, a trait that can facilitate access to new habitats which subsequently leads to range expansion and subsequently range size (Kot et al. 1996; Gaston 2003; Petrovskii and Morozov 2009). The contrast in predictive power of geographic range between models of maximum and median dispersal distance indicates that different parts of the dispersal distance distribution may have evolved independently and under different selection pressures. For example, short distance dispersal undertaken by large proportions of the population may be selected for inbreeding avoidance whereas longer movement distances undertaken by relatively few individuals may be selected for based on the benefit of finding empty territories (Lambin et al. 2001; Higgins et al. 2003; Ronce 2007). The hypothesis that median and maximum dispersal distances may be under differing selection processes is given weight by the high variable weightings of population density and weaning age in models of maximum dispersal distance, a finding not echoed for models of median dispersal distance. Although the confidence intervals of the slopes for these relationships are broad they hint at some interesting underlying drivers of dispersal. In the case of weaning age this may be linked to the importance of competitive ability upon arrival in new habitats (Burton et al. 2010).

Both maximum and median dispersal distance show evidence of strong phylogenetic conservatism. Phylogeny may therefore be used to guide predictions of dispersal distances for species where data is lacking but where information for closely related species is available (Fisher and Owens 2004; Thomas 2008) and the inclusion of phylogeny in any future comparative models of dispersal ability is strongly

recommended. The strength of this phylogenetic signal is perhaps more than would be expected based on studies examining the evolution of dispersal kernels across populations of the same species (Murrell et al. 2002; Burton et al.; Travis et al. 2010) and therefore likely masks within species flexibility in response to the often diverse landscapes and locations within the range which impose differing dispersal costs. Comparative analyses of the shape of dispersal kernel might therefore reveal greater phylogenetically lability (Simmons and Thomas 2004). For example, evidence of changes in both dispersal kernel shape and frequency of ‘disperser’ morphs have been found in cane toads (Phillips et al. 2008) and wing-dimorphic bush crickets (Simmons and Thomas 2004). Without the inclusion of phylogeny, correlations of median and maximum dispersal distance may also be confounded by clade effects when, in fact, maximum dispersal distance scales faster with median dispersal than would be expected from a linear relationship.

Cross-validation of the predictive accuracy of models showed that highly weighted models could also successfully predict dispersal distances for species excluded from the data set for testing purposes. This leads us to conclude that, with knowledge of relatively few life history and ecological traits, predictions of dispersal distance can be made where empirical data is lacking, given the set of preferred models presented in this study. For example, home range size provides high explanatory power for models of median and maximum dispersal, when phylogeny is considered, and is relatively easy to obtain for many species in one measure or another. The clear relationship between median and maximum dispersal distance also provides the opportunity to predict longer distance movements from those more readily observed and available shorter dispersal distances. Such comparative predictions are useful at broad taxonomic levels across many groups, however, further

work must be undertaken to assess the quality and quantity of data necessary to make accurate predictions for specific species in a landscape context. The relationship of average dispersal distance to 'true' LDD is unknown as capturing the tail of the dispersal kernel is extremely difficult, especially from observational studies (Koenig et al. 1996). In the future, tests which combine indirect genetic data and data from direct or observational studies may help improve estimates of LDD but these are currently unavailable (Ferriere et al. 2000).

Broad findings about the dispersal capabilities of mammals may belie significant differences between sexes in specific cases. Due to the comparative nature of my analyses I discounted differences between sexes as the contribution of disperser sex to overall variance in dispersal distance was small. However, in mammals, it is not uncommon for one sex to disperse widely while another is almost wholly philopatric (Pusey 1987; Handley and Perrin 2007). Sexual dimorphism is also seen in home range size, due to constraints of mating system and resource defence (Mace et al. 1984). Therefore, when incorporating dispersal estimates into population level models, I recommend that information on variation in both response and predictor variables by males and females are taken into account. Predicting dispersal is also complicated by unwillingness of some species to cross unsuitable habitat types, making dispersal estimates contingent on environment. For example, Laurance (1991) finds good evidence that many rare Australian mammals, such as the lemuroid ringtail possum, will fail to disperse to suitable areas across narrow (< 50m wide) forest clearings or areas of secondary growth. More research is needed into the interplay between physical vagility (an organisms ability to perceive and cross potentially unsuitable habitat) and its observed behaviour, which can be shaped more by factors such as mating system and resource defence (Greenwood 1980; Prevedello

et al. 2010) or by landscape effects such as land transformation or habitat fragmentation (Selonen et al. 2010; Doerr et al. 2011). Additionally, the potential to generalise my findings to other taxonomic groups is not well supported by the literature. Similar studies using birds find much lower explanatory power or that (perhaps unsurprisingly) proxies of flight ability outweigh other variables (Paradis et al. 1998; Sutherland et al. 2000; Bowman 2003; Dawideit et al. 2009). Body mass does seem to have a broad applicability for active dispersers across groups (Jenkins et al. 2007) but in this study it was not outstanding as a single model predictor in terms of explanatory power.

One criticism levelled at direct measures of dispersal distance is that they frequently fail to capture rare long distance dispersal events (Koenig et al. 1996; Kot et al. 1996) and that using gene flow measures provides a more robust way of capturing the tail of the dispersal kernel. Indirect measures of gene flow, such as F_{ST} , which quantify variance in allele frequency between populations can be combined with measure of distance between sampled populations in pair-wise comparisons to create models of isolation by distance (IBD; Wright 1965; Slatkin 1987; Rousset 1997) from which dispersal rates can be inferred. However, such models are only effective at the spatial scale at which the samples are taken. Ascertaining estimates for long distance dispersal can be confounded when two populations separated by great distances both receive migrants from the same intervening populations (Lester et al. 2007). Although these distantly separated populations may exchange no individuals they show low genetic variance due to the homogenizing effect of migration from the same source, which can lead to an incorrect inference of high migration distances (Whitlock and McCauley 1999). Incomplete knowledge of barriers to dispersal between populations may also confound IBD estimates, as highly

impermeable habitats may produce estimates of low gene flow and subsequently low levels of dispersal, contrary to estimates taken from homogeneous environments (Raybould et al. 2002). These caveats are not insurmountable and gene flow measures have much to offer the study of dispersal, however these problems mean that amount of data available to create robust IBD models is limited and therefore the number of species which can be studies is relatively small.

Combining predictions of dispersal distance with generation time can give realistic estimates about how far and how quickly species can track changing climates and move between protected areas. Some small bodied species, however, may offset low dispersal distances with fast generation times which may enable them to keep pace with climate change or adapt to changing conditions. Cross-validation of models identified species that were consistently over or under predicted in their dispersal ability (Figure 3.4). This may be a true reflection of a mismatch between vagility and life history or may be due to the failure of empirical studies to capture the true maximum dispersal distance of the species or as a result of landscape effects modifying dispersal distances seen from empirical studies. Species which fail to disperse as far as would be expected given their life history warrant further field research to identify those who are truly limited in dispersal capability. Although there is no clear taxonomic pattern to which species are over-predicted, it can be inferred that these species may be at higher risk from the impacts of climate change, as they show lower vagility than organisms of similar size and life history speed. Finally, species range maps can be combined with information of speed of climate change in that area to identify species which are poor dispersers given their size, range and life history and also inhabit areas likely to experience high velocity of climate change (Loarie et al. 2009).

In conclusion, I identify a number of high weighted models capable of predicting dispersal distance. These high weighted models are also corroborated by cross-validation results. I conclude that, in conjunction with a phylogenetic tree, dispersal distance can be predicted for a large range of mammals. Several plant focussed SDMs have started to incorporate migration limits and dispersal estimates into models (Engler and Guisan 2009; Thuiller et al. 2009b). My study allows these techniques to be extended to mammals where a better understanding of how far species can disperse could help us to understand drivers of extinction risk and improve conservation planning, especially when predicting the impacts of climate change.

Chapter 4. Comparative estimates of range filling in mammals are related to dispersal and colonisation ability.²

4.1 Abstract

Aim

Identifying the determinants of species range limits is a major challenge for ecology. Recent work quantifying the proportion of suitable environmental space occupied by a species, termed “range filling”, has found that species may be absent from large areas of suitable habitat. If environmental conditions do not control range limits there are serious implications for our ability to correctly predict the impacts of environmental change on biodiversity. Low range filling is often attributed to dispersal limitation, but evidence to date is lacking and range filling remains poorly understood. Here, I aim to test of the role of dispersal ability in explaining variation in the extent of range filling in mammals. I also examine the role of model parameterisation on predictions of potential niche size and the effect of study area size on range filling estimates.

Location

Worldwide.

Methods

I examine the correlation between range filling, dispersal distance, colonisation ability and species evolutionary age in 74 mammal species. I also explore the effects of methodological effects on potential range size and range filling estimates by using alternative species distribution modelling techniques, three presence/absence decision thresholds and by varying study extent.

² A version of chapter is in submission at Diversity and Distributions as: Whitmee, S.L. and Orme, C.D.L. Comparative estimates of range filling in mammals are related to dispersal and colonisation ability.

Results

Many species do not completely fill their potential environmental niche space. However, estimates of the size of potential environmental niche space, and hence range filling, are highly sensitive to definitions of study extent and the particular modelling algorithm. Constraining geographic extent to the realm of species occurrence produces higher range filling estimates than allowing species potential niche space to occur unrestricted across the globe. Dispersal distance and age at sexual maturity are correlated with extent of range filling, but the strength of relationships varies depending on model specification.

Main conclusions

Understanding the determinants of range filling is important for correctly predicting species response to climate change. I found dispersal distance and colonisation ability correlate with range filling above and beyond their role in determining realised range size. Therefore, species who do not fill their potential range may be poor dispersers who are unable to track changing climates into the future. However, my study identified a number of methodological factors that may impact estimates of potential niche size and confound analysis.

Keywords

Dispersal limitation, geographic range limits, species distribution modelling, phylogenetic comparative analysis, potential distribution, life history.

4.2 Introduction

Species distribution modelling (SDM) techniques are increasingly being employed to investigate determinants of species' range limits (Gaston 2003; Araújo and Pearson 2005). If species' distributions are primarily determined by abiotic factors, then relating such distributions to the environmental conditions at sites of occurrence can tell us about the conditions under which the species can persist, and subsequently inform our understanding of what limits range expansion (Gaston and Fuller 2009). Species which fail to inhabit all environmentally suitable areas must, if we have correctly modelled their environmental requirements, be limited by something other than just environmental tolerances (Diamond 1970; Anderson et al. 2002; Guisan and Thuiller 2005). At the macro-scale, dispersal limitation and historical climate change, plus interactions between the two, may contribute to a species being absent from some areas that are environmentally suitable (the potential area of distribution), creating the observed distribution or realised niche (Hutchinson 1957; Soberón and Peterson 2005; Soberón 2007; Soberón and Nakamura 2009).

A recent approach to assess whether species are at equilibrium with environment has focused on quantifying the proportion of the potential niche which is actually occupied, termed 'range filling' (sensu Gaston 2003; Svenning and Skov 2004) and correlating range filling extent with life history and ecological traits. The rationale behind such studies is convincing: if a species fills its entire potential environmental niche then dispersal limitation or biotic interactions are likely to have a limited impact on the species current distribution and the species can be said to be at equilibrium with its environment (Root 1988; Graham et al. 2010; Jiménez-Valverde et al. 2011).

If range filling is determined by dispersal limitation then stronger dispersers should more completely fill their range. Studies on a variety of taxa and regions have attempted to correlate degree of range filling with dispersal ability measures, including Kipp's distance (a measure of wing tip length in birds), movement mode in mammals, and height and seed size or shape in plants (Svenning and Skov 2004; Munguía et al. 2008; Paul et al. 2009; Graham et al. 2010; Levinsky et al. 2010). Recently, more complex measures such as extent of range change since the last glacial maximum, and process-based models requiring information on dispersal vector been employed (Schurr et al. 2007; Normand et al. 2011). Studies have largely found low levels of range filling, but direct evidence for the role of dispersal in driving range filling extent has been limited. This may be because the proxies of dispersal ability used are inadequate for the task (Gaston and Blackburn 2003).

SDMs operate under the assumption that the realised range provides an adequate description of the types of climate in which a species can persist. Any species which fail to fill their potential niche may therefore be poorly described by the range of environments in the realised niche, making predictions for such species unreliable (Araújo and Pearson 2005; Beale et al. 2008; Angert et al. 2011). Identifying species, or groups of species, which are not at equilibrium with their environment permits the identification of common causes of low range filling, which has implications for forecasting species distributions into the future under climate change (Pearson and Dawson 2003; Araújo and Pearson 2005). Species which fail to fill potential climatic niche space may be poor dispersers, limited by biotic interactions or by the nature of the environment surrounding the range edge (Gaston 2009; McInnes et al. 2009). These species may be less likely to track their optimum environment in the future and therefore will be at increased risk of range loss due to

climate change, especially in areas of high exposure to climate change (Araújo and Guisan 2006).

In several studies, realised range size has been shown to be highly correlated with potential range size (Munguía et al. 2008), range filling extent (Levinsky et al. 2010) or both (Skov and Svenning 2004; Svenning et al. 2006). As wider ranging species are thought to often possess broader environmental tolerances, a positive relationship between realised and potential range size is, perhaps, inevitable (Brown 1995). However, if range filling is to tell us more about what limits species ranges than range size itself then relationships between life history traits and range filling must hold beyond those driving realised range sizes.

Estimates of range filling may also be sensitive to the species distribution modelling process used. In addition to variation in model performance caused by differences in species life history and ecology (McPherson and Jetz 2007), factors such as prevalence (Liu et al. 2005; Jiménez-Valverde and Lobo 2007), sample size (Mateo et al. 2010), selection of pseudo-absence data (Lobo et al. 2007) and relative area of occurrence (ROA; Barve et al. 2011) have all been shown to influence model performance and evaluation and therefore possibly affect the projected extent of potential niche space. Crucially, many studies to date have restricted potential range projections to a single study area and used endemic species to allow comparisons across an ‘even playing field’. These restrictions have a number of implications for range filling estimates and their potential correlates. Choosing to solely model the range filling capability of endemic species allows the key environmental limits of the species to be confidently captured (Peterson et al. 2009), but may have the unfortunate consequence that the most dispersal limited species from a clade are selected for analyses. Likewise, imposing artificial study limits affects the range filling estimates

of species with comparatively large geographic ranges: these species will appear to fill a high proportion of their potential niche, but altered study limits may make give a different answer. For example, Svenning and Skov (2004) estimated the extent of range filling for European tree species restricting the domain to the Western Palearctic (median range filling estimate = 28%). They found a bimodal distribution of range filling values (lower peak 10-20%, upper peak 70-80%), suggesting that species may have been limited by the upper boundary imposed by artificial study limits on potential niche projections (Svenning et al. 2006; Welk and Bruehlheide 2006).

Here, I test for a relationship between range filling and dispersal ability in a diverse group of terrestrial mammals using a newly compiled database of dispersal distances in mammals. I also investigate the effects of life history speed because, having reached a new region, species with faster life cycles are more likely to establish (Schurr et al. 2007). Some models of speciation predict that species may initially occupy only a limited range (Mayr 1942; Chesson and Zink 1994) and so the extent of range filling may depend on the time since speciation and therefore opportunity for range expansion (Webb and Gaston 2000; Paul et al. 2009). I therefore include the age of species as a measure of the time available for range expansion. I test whether these traits explain the proportion of range filling in order to identify relationships in dispersal and colonisation ability over and above those which may be important in determining realised range size. Finally, I test how the size of potential niche space varies dependent on the modelling method used, the presence threshold applied and the definitions on the limits of the study area.

4.3 Methods

Trait data

I obtained dispersal data from experimental and observational studies and from reports of individual movement distances (Appendix 1: Supp. Table A1.1). Values were defined as the maximum recorded distance travelled by an individual of a species. While acknowledging that empirical data may underestimate long distance dispersal (LDD; Kot et al. 1996), I used empirical data as there is good data availability for measurements across a variety of landscapes and known timescales. I combined dispersal distances for juveniles, sub-adults and adults undertaking a permanent movement away from the natal home range. Where the maximum dispersal distance of a species coincided with the limit of the study area, I excluded this data from the analysis to avoid underestimating the true maximum dispersal distance. As the proportion of variance in log transformed dispersal distance attributed to the sex of the dispersing individual was small (0.34%) compared to variation between species (81.16%), I combined data for both sexes. Data on age at sexual maturity was taken from PanTheria (Jones et al. 2009) and supplemented by a targeted search of primary and secondary literature sources (Appendix 1: Supp. Table A1.2). I calculated species age as time since divergence in millions of years (MY; Paul et al. 2009), using a recent species-level phylogeny of 5020 extant mammals (Bininda-Emonds et al. 2007; Fritz et al. 2009). Data for all three traits was available for 82 species from 10 orders and 33 families and covered all terrestrial biogeographic realms except Oceania (Olson and Dinerstein 1998). Throughout, I used the taxonomy of Wilson and Reeder (Wilson and Reeder 2005) to define species. All data were log 10 transformed prior to analyses.

Range and environmental data

I obtained mammal range maps from the Global Mammal Assessment (Schipper et al. 2008; IUCN 2010) and converted range polygons to a Behrmann equal area presence-absence grid at a resolution of 96.5 km in ArcGIS. I counted species as present in a cell if it overlapped any part of the species' range polygon. The realised niche of species occurring in less than fifty cells could not be confidently modelled with all methods and I therefore excluded those species from the analysis, leaving 73 species available for analysis. Environmental data was obtained from WorldClim (Hijmans et al. 2005). I chose six variables that represent total energy, water availability and the water-energy balance, and are therefore thought to be important for controlling vertebrate distributions (Hawkins et al. 2003; Whittaker et al. 2007). These were: annual mean temperature (BIO 1); mean temperature of the warmest (BIO 10) and coldest (BIO 11) quarters; annual rainfall (BIO 12); rainfall seasonality (BIO 15) and rainfall in the warmest quarter (BIO 18). I re-sampled data in ArcGIS to match the Behrmann range occurrence grid. No variables showed strong collinearity (all pairwise Kendall correlation coefficients < 0.85 ; Appendix 3: Supp. Table A3.1), therefore I included all variables in the analyses.

Species distribution modelling

I examined the effects on range filling estimates of four commonly used SDM methods. Three methods (Generalised Additive Models, GAM; Generalised Boosted Model, GBM; and Maxent) were chosen for their ability to fit complex interaction terms and their generally high performance in tests of species distribution modelling ability (Hijmans and Graham 2006; Elith et al. 2011). GAMs in particular have been demonstrated as capable of modelling vagile organisms and have shown good predictive ability in previous studies modelling mammal ranges (Guisan et al. 2002;

Araújo et al. 2005; Thuiller et al. 2006). I generated GAMs with cubic-smooth splines bounded by a degree of smoothness of four for each climatic predictor. GBMs were fitted with an interaction depth of 4, a learning rate of 0.001, and a maximum of 5000 trees fitted to the data. Maxent was used with default regularization settings; however, only hinge features were allowed, allowing a step in the fitted response function and also a change in gradient of response. These settings create models similar to those produced by a GAM (Elith et al. 2011). The final method, Surface Range Envelope (SRE), is a simple method that describes the climatic envelope of a species as a rectilinear volume, similar to the BIOCLIM method used in many early modelling studies (Thuiller et al. 2009a). This method assumes that a species can tolerate locations where values of all climatic parameters fit within the extreme values of its climate envelope (Beaumont et al. 2009). I used the SRE method to enable the results from this study to be compared with earlier studies of range filling which used simple rectilinear envelope methods and also to enable me to test the performance of a simpler model against the other more complex ones (e.g. Svenning and Skov 2004).

As data on species absences are unavailable when using range maps, I supplied GAM and GBM models with pseudo-absences, while Maxent and SRE methods are designed to work with presence-only data. Pseudo-absence locations were selected only from areas outside the SRE of potentially suitable climate for each species. The drawing of pseudo-absences was limited to occupied realms and those realms adjacent to species presences. This allows absences to be drawn from environments which, although unlike those encountered by the species, are in potentially accessible areas, and thus generate more biologically realistic pseudo-absences (Engler et al. 2004; Chefaoui and Lobo 2008; Lobo et al. 2010) but see Wisz and Guisan (2009). Although absence data is unnecessary for Maxent models, extent

of background data can affect model evaluation statistics and variable importance within the model building process. Casting background or pseudo-absence extent too widely can lead to increasingly simple models and overly coarse predictions of potential niche space, therefore I used background data taken from both occupied and adjacent realms (VanDerWal et al. 2009). Sampling prevalence for all species was held at 0.5 in all models apart from SRE method.

To initially quantify model performance, I split the data into calibration and testing sets, where a third of the occurrence data for each species was retained from the model building process and subsequently used to test the predictive power of the model (Guisan and Zimmermann 2000; Pearson 2007). However, the final model used to predict the potential niche for each species was built using 100% of the data to provide as much information about the potential niche as possible. I assessed model performance for test data using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC; Swets 1988; Fielding and Bell 1997), and model sensitivity; the proportion of correctly predicted presences (Pearson 2007). AUC can be thought of as the probability that a model will correctly distinguish between a presence record and an absence record, if each record is selected randomly from the set of presences and absences. A value of 0.5 can be interpreted as being no better than a random guess (Franklin 2009). However, with presence only models, the AUC can only test the probability that a randomly chosen presence site is ranked above a random background or pseudo-absence site and, as such the maximum AUC can only be less than 1 (Phillips et al. 2006). Similarly, with presence-absence data, sensitivity can be balanced against specificity, which is a measure of correctly predicted absences. Without a measure of specificity, it is possible to misinterpret high sensitivity scores arising simply from over-predicting the extent of suitable area.

Hence, with presence only data, sensitivity scores must be tested for statistical significance against a null model accounting for the proportion of available area predicted as suitable. I used an exact one-tailed binomial test to examine whether the accuracy of presence predictions is better than expected by chance given the area predicted as suitable.

I projected models using two extents to examine the effect of restricted study limits on range filling predictions. Projections of the potential distribution were firstly limited to the realm or realms spanned by the realised distribution (occupied realm projection extent) and secondly allowed to occur anywhere in the world (whole world projection extent). The threshold measure used to convert presence probabilities to binary presence/absence data will also have a significant impact on the extent of the potential distribution, especially when true absence data is lacking (Liu et al. 2005; Jiménez-Valverde and Lobo 2007). Therefore, I applied three threshold measures to assess their impact on the extent of potential distribution to be assessed. Firstly, lowest presence threshold (LPT), which selects all cells at least as suitable as those where a species' presence has been recorded, was chosen to give the broadest prediction of potential available suitable climate (Pearson et al. 2007). Secondly, a defined specificity measure which allows the model to miss no more than 10 percent of cells containing observations (90% sensitivity, Pearson et al. 2004) was chosen as an intermediate predictor of potential niche space. Lastly, a threshold maximising sensitivity and specificity (MaxSS) was chosen to produce predictions which balance correctly predicted presences against false absences (or in this case pseudo-absences), providing a conservative estimate of potential niche space (Manel et al. 2001).

SRE model predictions are binary and therefore do not permit thresholds. However, it is liable to be unduly influenced by the extremes of the data (i.e. climates

at range margins). I therefore tested the influence of extreme values on predictions by running models with the most extreme 5% of values removed for the calibration process (5% quantile) in addition to using all values (0% quantile). GAM, GBM and SRE methods were implemented in BIOMOD (Thuiller 2003; Thuiller et al. 2009b), Maxent models were implemented using a command line interface from R (R Development Core Team 2010) to the Java program Maxent, version 3.3.3e (Phillips et al. 2006; Phillips and Dudík 2008). AUC and threshold values were calculated in R using the 'PresenceAbsence' package (Freeman 2009). A diagram illustrating the modelling process can be found in Appendix 3: Supp Figure A3.1.

Realised and potential range size across models

The realised range size (R) was the sum of all occupied cells, potential niche sizes (P) were calculated as the number of cells predicted as a presence dependent on projection extent, model type and threshold level and the range filling ratio was calculated as R / P .

Correlations between modelling methods in predicting potential range size

I used $\log(P)$ across species to calculate Euclidean distances between each combination of projection extent, model type and presence/absence threshold (Nenzén 2010). I used hierarchical cluster analysis on this distance matrix, using the single linkage method, to identify which models are most similar in the potential range estimates produced and which modelling decisions produce the biggest differences in P. In addition, I used analysis of variance to test the statistical significance of modelling decisions on potential niche estimates.

Calculating consensus models

I looked at the degree of overlap in predictions between modelling methods for both occupied realms and whole world projections at each threshold value. For each species, every cell at the relevant projection extent and threshold, I summed the number of models agreeing in prediction of presence. Finally, I calculated a consensus prediction across SDM model types, counting a species as present in any cell in which three or more modelling methods predicted presence given the extent type and threshold. I then used the consensus predictions to calculate range filling estimates.

Phylogenetic signal of range filling

I tested the phylogenetic signal of range filling (R/P) for each model using a phylogenetic generalised linear squares method (PGLM; Freckleton et al. 2002) which calculates the maximum likelihood value of the λ transformation given the data available (Pagel, 1999). I used the mammalian supertree (Bininda-Emonds et al. 2007; updated by Fritz et al. 2009) and the caper package (Orme et al. 2011) in R for all phylogenetic analyses.

Correlates of range filling

I used a generalised linear model with quasi-binomial error structure and a logit link function to test the predictive power of dispersal ability, age at sexual maturity and species evolutionary age to explain the proportion of range filling for my study species. Range filling data derived from occupied realm projections included an extra term to account for the differing sizes of realms and therefore differing extent of area available for the potential niche to occupy. Data limitations precluded the use of interaction terms between predictor variables. Variance inflation factors were calculated and found to be below 2.7 for all predictor variables within the linear

models (Appendix 3: Supp. Table A3.2). All analyses were conducted in R version 2.12.0 (R Development Core Team 2010)

4.4 Results

Model performance

Model performance assessed by AUC score (Swets 1988) was generally good ($0.8 \geq \text{AUC} < 0.9$) or excellent ($0.9 \geq \text{AUC} < 1$; Appendix 3: Supp. Table A3.3), with 3 Maxent models having only fair performance ($0.7 \geq \text{AUC} < 0.8$). Sensitivity of models was also generally high: median sensitivity by threshold type was 0.80, 0.90, 0.94 and 0.99 for SRE, 90% ST, MaxSS and LPT respectively. All predictions across species and model type were more accurate than by chance given the size of the area predicted to be suitable (all $p < 0.001$, exact one-tailed binomial test).

Range filling estimates

Range filling estimates tended to be low (Table 4.1), however maximum R/P values of greater than 1 indicate that some species appeared to possess realised range sizes which are larger than modelled potential. This is likely caused by the application of more conservative model thresholds to species with large realised range sizes and was not found for the broader projections using the LPT threshold. Range filling values were significantly higher for occupied realm models than for whole world models ($t = -53.39$, $df = 813$, $P < 0.001$, paired one-tailed t-test). Across occupied and whole world models a clear pattern of increased range filling with increasing range size emerged (Figure 4.1). Estimates varied depending on the species in question (Figure 4.1) and model specification (modelling method, projection extent and threshold applied). Hierarchical cluster analysis and analysis of variance both demonstrate that model

similarity was primarily driven by projection extent and secondarily by the threshold applied (Figure 4.2, Table 4.2).

	a) Occupied realm			b) Whole world		
	Min	Med	Max	Min	Med	Max
<i>Consensus Model - 90% ST</i>	0.131	0.842	1.079	0.05	0.295	1.038
<i>Consensus Model - LPT</i>	0.088	0.482	0.843	0.02	0.137	0.61
<i>Consensus Model - MaxSS</i>	0.184	0.783	1.07	0.043	0.263	1.042
<i>GAM - 90% ST</i>	0.112	0.787	1.079	0.017	0.219	1.014
<i>GAM - LPT</i>	0.087	0.414	0.835	0.013	0.105	0.485
<i>GAM - MaxSS</i>	0.099	0.768	1.059	0.016	0.194	1.029
<i>GBM - 90% ST</i>	0.177	0.91	1.084	0.032	0.304	0.993
<i>GBM - LPT</i>	0.092	0.517	0.847	0.02	0.126	0.611
<i>GBM - MaxSS</i>	0.201	0.772	1.08	0.032	0.278	1.073
<i>Maxent - 90% ST</i>	0.117	0.812	1.08	0.04	0.275	1.023
<i>Maxent - LPT</i>	0.076	0.382	0.837	0.018	0.122	0.548
<i>Maxent - MaxSS</i>	0.162	0.802	1.113	0.033	0.255	0.999
<i>SRE - 0% QT</i>	0.07	0.462	0.842	0.027	0.163	0.493
<i>SRE - 5% QT</i>	0.092	0.833	1.187	0.039	0.354	1.057

Table 4.1 Ratio of realised range size / potential range size for (a) occupied realm and (b) whole world extents. Minimum, median and maximum values across all species are given by model specification.

	Estimate	Std. error	t-value
<i>(Intercept)</i>	3.021	0.041	73.274 ***
<i>Projection: Whole World</i>	0.521	0.010	54.739 ***
<i>Model: GBM</i>	-0.084	0.012	-7.194 ***
<i>Model: Maxent</i>	-0.063	0.012	-5.379 ***
<i>Threshold: LPT</i>	0.298	0.012	25.576 ***
<i>Threshold: MaxSS</i>	0.046	0.012	3.907 ***

Table 4.2. Linear mixed effect model of projection extent, model type and threshold on size of potential niche (1253 d.f.). Species identify is included as a random effect. The significance of terms is shown as * $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.**

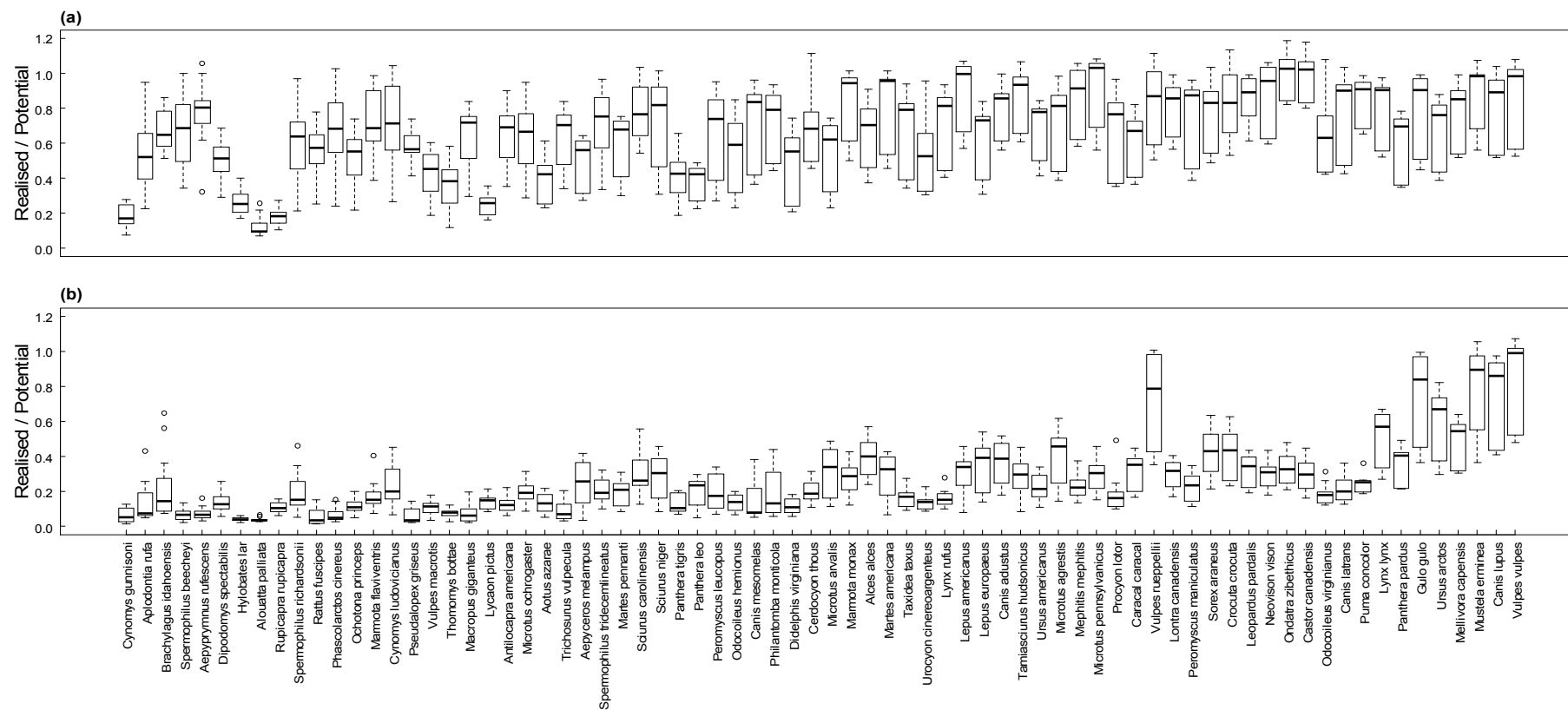


Figure 4.1. Range filling estimates by species for a) occupied realm projections and b) whole world projections. Species are sorted by realised range size

from left (smallest range size) to right (largest range size), each box shows data from 11 model combinations.

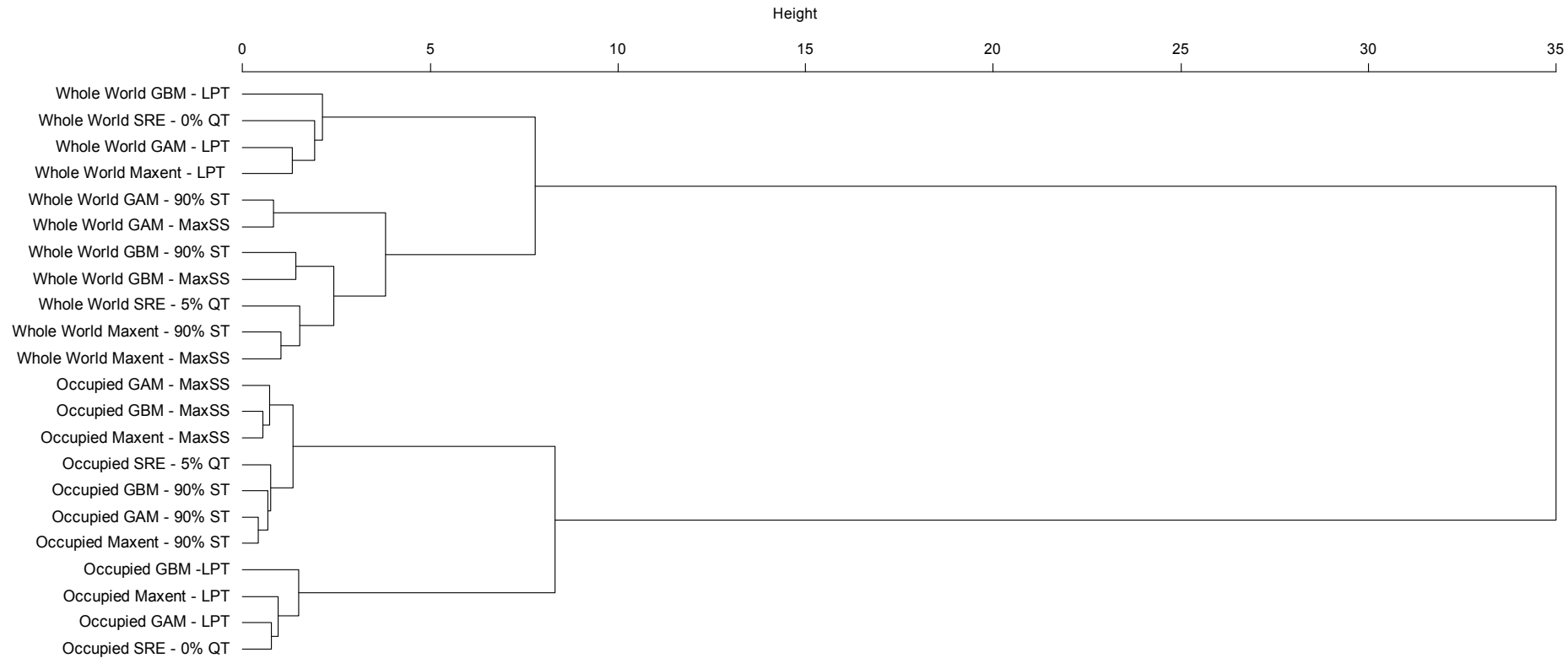


Figure 4.2. Hierarchical cluster analysis measuring model similarity across all model types, projections and thresholds.

Model concurrence

The degree of overlap between modelling methods, calculated as the mean number of models predicting presence in a cell, was highest using the LPT method at the occupied realm projection extent and lowest for the LPT method at the whole world projection extent (Figure 4.3). Models conditioned with thresholds using maximum sensitivity plus specificity and 90% sensitivity were less sensitive to projection extent showing a peak of 2.5 cells agreeing in their prediction at the cell level, regardless of projection extent.

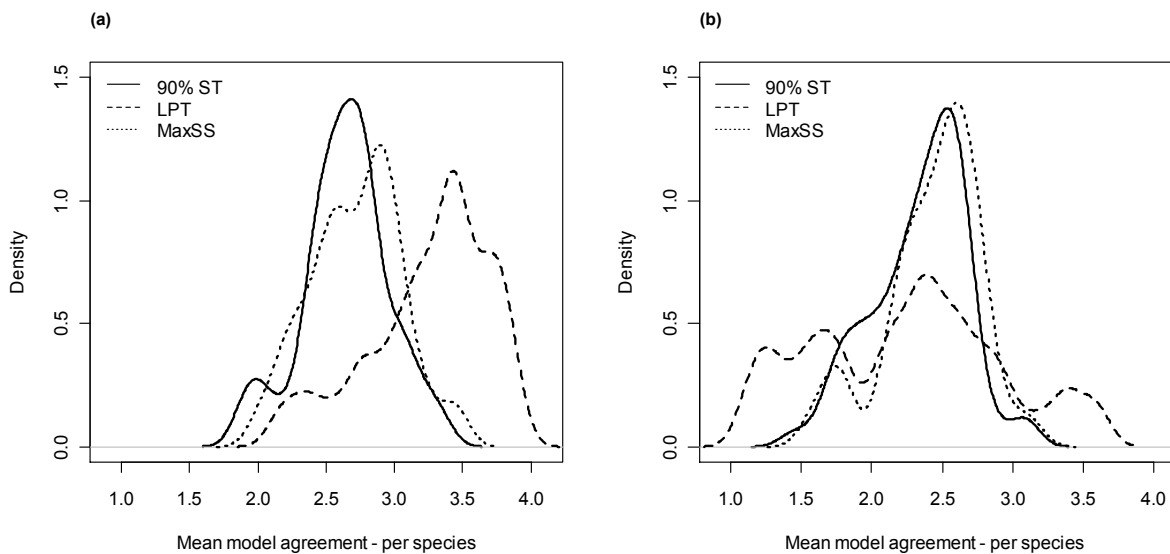


Figure 4.3. Mean model agreement per species by threshold type as the number of models (Maxent, GAM, GBM, SRE) predicting presence per cell for (a) occupied realm and (b) whole world projections.

Correlates of range filling and phylogenetic signal of range filling

Maximum likelihood λ estimates of the phylogenetic signal of range filling ratio were low and were often not significantly different from zero (Table 4.3). The explanatory power and significance of terms for predictors of estimated range filling were consistent between consensus models and individual SDM models (Table 4.4).

Minimum adequate models for both occupied realm and whole world projection extents included all terms except species' age which was not a significant term in any model. Results varied between SDM models, but maximum dispersal distance and age at sexual maturity were frequently significant terms (Table 4.4). Positive slopes for dispersal distance indicate that species that disperse comparatively longer distances fill a higher proportion of their range regardless of realised range size. Negative slopes for age at sexual maturity were observed for all models bar one, indicating that proportion of range filled decreased as speed of life history increased. Those models projected solely into occupied realm space also included a term to control for the total area available for potential niche space (realm area). Model simplification across different SDM types did not consistently exclude this term; therefore it was retained for the minimum adequate model. Although rarely significant, models consistently indicate reduced range filling with increasing realm area.

	a) Occupied realm		b) Whole world	
	λ	95% CI	λ	95% CI
<i>Consensus Model - 90% ST</i>	0.358	(NA-0.709)	0.085	(NA-0.371)
<i>Consensus Model - LPT</i>	0	(NA-0.542)	0.143	(NA-0.443)
<i>Consensus Model - MaxSS</i>	0	(NA-0.419)	0.123	(NA-0.382)
<i>GAM - 90% ST</i>	0.328	(NA-0.709)	0.122	(NA-0.392)
<i>GAM - LPT</i>	0	(NA-0.297)	0.179	(0.01-452)
<i>GAM - MaxSS</i>	0	(NA-0.386)	0.124	(NA-0.379)
<i>GBM - 90% ST</i>	0.37	(NA-0.718)	0.076	(NA-0.362)
<i>GBM - LPT</i>	0.309	(NA-0.802)	0.118	(NA-0.408)
<i>GBM - MaxSS</i>	0	(NA-0.448)	0.142	(NA-0.402)
<i>Maxent - 90% ST</i>	0.367	(NA-0.722)	0.106	(NA-0.383)
<i>Maxent - LPT</i>	0	(NA-0.632)	0.204	(0.019-0.497)
<i>Maxent - MaxSS</i>	0.171	(NA-0.562)	0.145	(NA-0.408)
<i>SRE - 0% QT</i>	0	(NA-0.565)	0.189	(NA-0.54)
<i>SRE - 5% QT</i>	0	(NA-0.659)	0.103	(NA-0.417)

Table 4.3. Phylogenetic signal of potential niche estimates for a) occupied realm and b) whole world extents. Maximum likelihood lambda values and 95% confidence intervals are given. NA indicates a confidence interval truncated by the zero lower bound on lambda

	a) Occupied realm					b) Whole world		
	I	MDD	ASM	RS		I	MDD	ASM
<i>Consensus Model - 90% ST</i>	3.19	0.48*	-1.768**	0.64	<i>Consensus Model - 90% ST</i>	1.03	0.45**	-0.87*
<i>Consensus Model - LPT</i>	1.24	0.16	-0.385	-0.15	<i>Consensus Model - LPT</i>	-0.66	0.42***	-0.59
<i>Consensus Model - MaxSS</i>	5.91 .	0.76***	-1.996***	-0.07	<i>Consensus Model - MaxSS</i>	1.45	0.59***	-1.13**
<i>GAM - 90% ST</i>	5.52	0.44	-1.26*	-0.39	<i>GAM - 90% ST</i>	-1.12	0.41*	-0.19
<i>GAM -LPT</i>	3.12	0.22	-0.02	-0.96*	<i>GAM -LPT</i>	-2.07*	0.36*	-0.07
<i>GAM - MaxSS</i>	7.51*	0.73**	-1.70**	-0.73	<i>GAM - MaxSS</i>	-0.69	0.50**	-0.44
<i>GBM - 90% ST</i>	6.96	0.52	-1.51*	-0.49	<i>GBM - 90% ST</i>	-0.94	0.26	-0.06
<i>GBM -LPT</i>	2.91	0.09	0.1	-0.88	<i>GBM -LPT</i>	-1.96*	0.35*	-0.1
<i>GBM - MaxSS</i>	7.58*	0.74**	-1.29*	-0.98	<i>GBM - MaxSS</i>	-0.33	0.40*	-0.36
<i>Maxent - 90% ST</i>	5.18	0.55*	-1.49*	-0.12	<i>Maxent - 90% ST</i>	-0.11	0.33*	-0.34
<i>Maxent -LPT</i>	3.07	0.30 .	-0.25	-0.82	<i>Maxent -LPT</i>	-1.59*	0.35**	-0.18
<i>Maxent - MaxSS</i>	8.39*	0.71**	-1.57**	-1	<i>Maxent - MaxSS</i>	0.11	0.44**	-0.53
<i>SRE - 0% QT</i>	4.12*	0.24	-0.28	-1.03*	<i>SRE - 0% QT</i>	-1.24	0.24 .	-0.17
<i>SRE - 5% QT</i>	3.75	0.34	-1.12 .	0.04	<i>SRE - 5% QT</i>	0.58	0.35*	-0.57

Table 4.4 Coefficient estimates from generalised linear models for a) occupied realm and b) whole world extent. Variables are: I – intercept; MDD – log 10 maximum dispersal distance (km); ASM – log 10 age at sexual maturity (days); and RS – occupied realm size (cell count). The significance of terms is shown as * p < 0.001; ** p < 0.01; * p < 0.05; . p 0.05 - 0.06.**

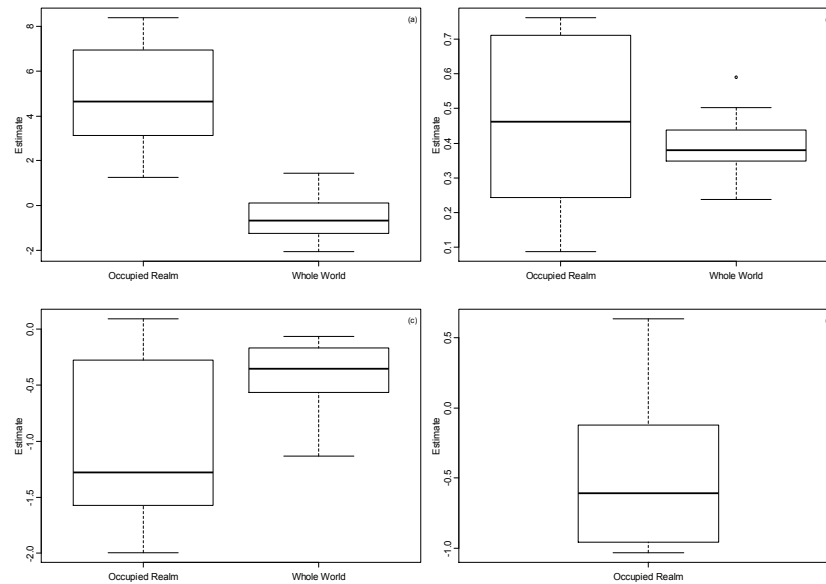


Figure 4.4 Coefficient estimates across SDM model types from generalised linear models with quasi-binomial response of realised range size and unoccupied potential range size (measured by cell count). (a) Intercept estimates; (b) $\log_{10}$ (dispersal distance – km^2) estimates; (c) $\log_{10}$ (age at sexual maturity – days) estimates; (d) $\log_{10}$ (realm size – cell count) estimates.

4.5 Discussion

In accordance with previous studies, my analyses shows that, at the global scale, many species do not fill their potential environmental niche (Svenning and Skov 2004; Schurr et al. 2007; Munguía et al. 2008; Paul et al. 2009; Graham et al. 2010; Levinsky et al. 2010; Normand et al. 2011). In addition to any role in determining realised range size, dispersal distance and age at sexual maturity are identified as significant predictors of range filling for most model specifications. Interestingly, previous studies found little evidence to relate range filling with mobility and colonisation traits (Svenning and Skov 2004; Schurr et al. 2007; Munguía et al. 2008; Levinsky et al. 2010). These earlier analyses primarily used methods aimed at creating the widest possible projections of potential niche space and projected only to a limited study extent. I also find that models using thresholds and methods which

predict broader potential niches, or which were projected solely in the occupied realm of occurrence, were less likely to show a relationship with dispersal and age at sexual maturity than alternative thresholds or models projected at wider extent. Possibly by casting the net too widely within a limited area, these models are failing to accurately capture the true potential niche and therefore the signal is eroded.

There is little evidence for a relationship between species evolutionary age and range filling (Schurr et al. 2007; Paul et al. 2009). However a signal of evolutionary age may not be observed if young species expand to large range size quickly, if some species maintain small ranges through time or if general age/range patterns are driven primarily by selective extinction (Pigot et al. 2011). Phylogenetic signal of range filling was low and often not significantly different from zero. Maximum likelihood estimates of λ were lower than those previously found for geographic range size in primate and carnivores (Jones et al. 2005) and Australian marsupials (Freckleton et al. 2002), but similar to the previous lower estimate bounds in Jones et al (2005) for whole world projections in Tables 3 and 4.

I examined the impact of modelling algorithm, projection extent and binary threshold choice on predictions of potential environmental niche space. Model specification has a profound effect on these estimates, which in turn has consequences for range filling estimates. I show that higher range filling estimates are produced from models restricted to projecting in the occupied realm, when compared to models projected across the world without restriction. Limiting study extent to occupied realms therefore affects the ability of range filling estimates to be truly comparative. I recognise that allowing potential niche space to be entirely dictated by the environmental limits, with no regard for hard boundaries such as continent edges is biologically unrealistic and therefore open to criticism. One way forward may be to

model potential niche space with reference to the accessible area for the species and subsequently control for varying size in study extent (Hortal et al. 2005; Barve et al. 2011).

It should be borne in mind that model performance has been shown to vary systematically with range size (McPherson et al. 2004; Segurado and Araújo 2004; Hernandez et al. 2006; McPherson and Jetz 2007; Chefaoui and Lobo 2008; Jiménez-Valverde et al. 2008), which may mean that my response variable could have non-independent errors associated with its estimation. Local adaptation of subpopulations in wide ranging species that encounter a variety of environmental conditions would lead to overestimation of the climatic tolerances of a species as a whole (Stockwell and Peterson 2002; McPherson and Jetz 2007). Conversely, small range species are vulnerable to over-fitting, especially when effects size is small or a disproportionately large number of environmental variables are used in the model fitting process (Franklin 2009). Estimates of potential niche space are highly influenced by the modelling methods used. As it is impossible to test which model parameters come closest to accurately describing the true potential distribution I recommend that care is taken in selecting appropriate parameters, and that a range of measures are tested. Bearing in mind the aim of accurately estimating the potential niche, a consensus approach may be the best way forward if model estimates differ (Pearson et al. 2004; Hernandez et al. 2006; Pearson 2007).

Dispersal and colonisation factors show evidence of a relationship with range filling. There is great scope to further explore these relationships by incorporating more spatially explicit measures such as connectivity of habitats, landscape permeability, and habitat quality. (Hortal et al. 2005; Nathan 2005; Trakhtenbrot et al. 2005; Araújo and Luoto 2007; Mcrae et al. 2008; McInnes et al. 2009; Crooks et al.

2011). Better quantification of dispersal and colonisation costs is needed, especially for mammals which may, as trophic consumers, be co-limited by habitat and climate (Grayson 2000; Pearson et al. 2004; Thuiller et al. 2006). Whatever factors are attributed to lack of equilibrium, robust techniques for modelling species, which enable comparative methods to be used will be needed.

Chapter 5. Unravelling the shared effects of space and phylogeny on range filling: what can different methods tell us?

5.1 Abstract

The ability of species to track changing environmental conditions is thought to be crucial in mediating against the effects of extinction risk from climate change. It is therefore important that when identifying species at risk of climate change we understand their dispersal capabilities. Availability of data on dispersal is, unfortunately, low. Therefore proxy measures of dispersal ability are needed to inform conservation measures. Disparities in the relative extent of species realised range size and the extent of area of environmental suitability (the potential range), are thought to be partially controlled by species specific differences in dispersal ability. Therefore ‘range filling’ may be able to tell us something about relative differences in species dispersal ability. In reality, however, this ‘range filling’ ability is likely to be the result of heritable traits, such as body size, dispersal ability or breadth of environmental tolerance, and spatially related factors, such as the topography of the landscape and variation in environmental conditions. Here, I undertake a comparative study, in a biogeographical context to make robust inferences about the relative importance of geographic location and shared evolutionary history in determining why species succeed or fail to fill suitable environmental space. I model ratio of realised range size to potential range size (R/P), at a global extent, in 676 species of mammal and treat R/P as a species-level trait. I then test two models, with constraining evolutionary assumptions about the roles of location and species relatedness in driving the observed patterns in R/P . I find that variation in R/P values across species is primarily correlated with species location. At the global scale, evidence for the role of species relatedness in determining patterns of R/P is limited.

This suggests that our ability to infer dispersal ability from comparisons of realised and potential range sizes needs to account for the location of the species in question.

5.2 Introduction

Dispersal limitation is thought to affect a species' ability to fill its potential range, that is, the area of space where conditions are suitable for survival and reproduction (sensu Gaston 2003; Svenning and Skov 2004; Munguía et al. 2008). Measuring the amount of potential range space actually occupied by a species (the realised range) may therefore be helpful for identifying dispersal limited species. This is especially important under climate change, as dispersal limited species may be unable to successfully move to keep pace with changing environmental conditions (Engler and Guisan 2009; Thomas et al. 2010). So far, however, evidence for the role of dispersal ability in controlling this 'range filling' has been limited (Svenning and Skov 2004; Munguía et al. 2008; Gove et al. 2009; Paul et al. 2009; Graham et al. 2010; Levinsky et al. 2010) but see Chapter 4.

Range filling is calculated from the relative sizes of the realised and potential range. The potential range is a measure of available habitat within species-specific tolerance limits and in the absence of dispersal limitations and biotic interactions (Svenning and Skov 2004; Soberón 2007; Soberón and Nakamura 2009). Realised range size has, to date, shown varying degrees of heritability depending on the taxa, the model used to test heritability and the spatial scale of the study (Freckleton et al. 2002; Jones et al. 2005; Waldron 2007). Potential range size is likely to be jointly influenced by phylogenetically conserved traits such as dispersal, niche breadth, and physiological tolerance and spatially mediated factors such as climatic regime, and biome extent (Böhning-Gaese et al. 2006; Cooper et al. 2011; Olalla-Tárraga et al. 2011). Recent developments allowing the effects of space and phylogeny to be jointly estimated, indicate that both range size and environmental tolerances (inferred from the species' realised range limits) may be more affected by spatial factors than

constraints imposed by shared common ancestors (Freckleton and Jetz 2009; Cooper et al. 2011; Machac et al. 2011; McInnes 2011). It is currently unclear, however, if patterns in range filling are primarily driven by phylogenetically constrained traits, such as dispersal, reproduction rate and environmental tolerances, or by spatially mediated factors such as topography or climate heterogeneity (Harvey and Purvis 1991; Sutherland et al. 2000; Freckleton et al. 2002; McInnes et al. 2009; Öckinger et al. 2010). It is likely that a combination of factors will come into play: for example, highly heterogeneous landscapes or patchy habitats could impose costs on phylogenetically conserved dispersal distances in a spatially non-random way (Thomas 2000).

The problem is further complicated by the role of dispersal in controlling where closely related species may be found in space (Cooper et al. 2011). In groups with lower dispersal ability, related species may be found in close proximity through a failure to expand following speciation (Hubbell 2001; Graham et al. 2010). These species will share environmental conditions, but similarities in range filling extent may be driven primarily by phylogenetic non-independence, causing them to possess traits that are not conducive to dispersal and colonisation. For example, if body mass and life history speed are phylogenetically conserved, these traits may impede a species ability to reach new habitats. Such species therefore share environmental conditions as a by-product of their shared evolutionary history. Additionally, post-glacial recolonisation by species with good dispersal ability in high Northern latitudes ($>40/50^{\circ}\text{N}$) may mean that species at this latitude show high range filling due to phylogenetically controlled factors such as thermal tolerance, body size and dispersal ability rather than environmental conditions (Price et al. 1997; Böhning-Gaese et al. 2006). Indeed, latitudinal patterns in range filling have been reported and linked to

past climatic regimes (Svenning and Skov 2004; Munguía et al. 2008). However, recent evidence for both realised range size and range filling indicates that geographic constraints may be a more likely proximate cause of observed patterns in both, with phylogenetic similarity arising through speciation of a geographically constrained group (Gove et al. 2009; Machac et al. 2011).

Therefore, before inferences about dispersal ability can be made from range filling extent, it is important that the relative roles of phylogeny and geography in driving observed patterns are considered. Here, I use two methods which employ different models of trait evolution to jointly estimate spatial and phylogenetic signals in range filling at the global extent for more than 650 species of mammal. I hypothesise that range filling extent will be phylogenetically labile, with signal driven primarily by spatial factors or evenly between space and phylogenetic factors. At the global scale of analyses, species will tend to covary due to location alone rather than phylogeny. I also compare my findings on range filling to those for body mass in the same group of species. Body mass is commonly found to be highly phylogenetically conserved (Gittleman and Purvis 1998), and provides a contrast within our analyses for more labile measures, which may be the case with some dispersal enabling traits (Blomberg et al. 2003). I hypothesise that body mass will show a high phylogenetic signal and low spatial signal and that species will covary primarily due to shared ancestry rather than space. By comparing model performance from two methods which make differing underlying assumptions about the evolutionary mechanisms that generate observed patterns in range filling I aim to disentangle the factors limiting species' ranges.

5.3 Method

Distribution maps and environmental data

I obtained distribution data from the Global Mammal Assessment (GMA; IUCN et al. 2008; Schipper et al. 2008). Although the GMA provides range maps for all mammal species, I calculate range filling extent only for those species where body mass data were also available. Species distribution modelling requires point or cell based presence data; therefore I converted distribution shapefiles to a Behrmann equal area projection in ArcGIS and overlaid an equal area grid (96.5 x 96.5 km cells) to extract grid cell occurrences for each species. Species were counted as present in a cell if any part of its range overlapped with that cell. I excluded primarily marine (Cetacea, Sirenia) and volant (Chiroptera) orders from the analyses along with species occurring in less than five cells. This left 676 species available for analysis.

I used environmental data obtained from WorldClim (Hijmans et al. 2005), re-sampled in ArcGIS to match the Behrmann species occurrence grid described above. The environmental variables used were: annual mean temperature; mean temperature of the warmest and coldest quarters; annual rainfall; rainfall seasonality and rainfall in the warmest quarter. I chose these variables to represent total energy, water availability and the water-energy balance, which are thought to be key in determining vertebrate distributions (Hawkins et al. 2003; Whittaker et al. 2007).

Species distribution modelling (SDM)

In order to check the consistency of results, regardless of modelling method, I used four SDM methods to predict potential range size. I used Generalised Additive Models (GAM), Generalised Boosted Models (GBM), Maxent (a machine learning method based on maximum entropy) and Surface Range Envelopes (SRE), a simple rectilinear envelope method, to relate species occurrence data to the environmental

predictor variables (Guisan and Zimmermann 2000; Araújo et al. 2005; Hijmans and Graham 2006; Thuiller et al. 2009a). I used default regularization settings in Maxent, but limited the selection of features to hinge parameters, which enable non-linear responses to be confidently modelled (Phillips and Dudík 2008). I parameterised GAMs with cubic-smooth splines and I bounded the response to each climatic predictor by a degree of smoothness of four (Thuiller et al. 2009b). I fitted GBMs with a learning rate of 0.001, an interaction depth of 4 and a limit of 5000 trees fitted to the data (Thuiller et al. 2009b). I fitted SRE models with all observed environmental variables (no restricted quantiles), a method which includes all extreme values in predictions to cast potential range sizes as broadly as possible. I restricted species with occurrence in less than fifty cells to predictions with Maxent, as this method has been proven to successfully model small range species (Hernandez et al. 2006; Pearson et al. 2007). Therefore I modelled 518 species with GAM, GBM and SRE methods and 676 species with Maxent.

Pseudo-absence data are required by GAM and GBM methods when true absence data are unavailable (Thuiller et al. 2009a). When projecting suitable habitats for potential range estimates, it is recommended that environments similar to those found within the realised distribution are excluded from consideration as absences. Such absences may be caused by dispersal barriers or biotic factors rather than unsuitable environment (Lobo et al. 2010; Barve et al. 2011). Including such absences in the model would therefore cause an underestimation of the potential range. To train models, I therefore selected pseudo-absences from environments unlike those found within the realised range by initially applying an SRE to identify dissimilar environments (Thuiller et al. 2009a). To control for the effect of range size on species prevalence (i.e. ratio of presence to absence data) I selected as many

pseudo-absence points as there are presence points for each species and therefore hold the prevalence ratio constant at 0.5 (McPherson and Jetz 2007; VanDerWal et al. 2009). I took pseudo-absences and background data for Maxent from occupied realms and, for wide ranging species, also took pseudo-absences from adjacent realms that may be accessible for species with high mobility (Engler et al. 2004; Chefaoui and Lobo 2008; Lobo et al. 2010).

I evaluated model performance by testing the statistical significance of model sensitivity (the proportion of correctly predicted presences; Pearson 2007) and from calculation of the Area Under the Curve of the Receiver Operating Characteristic (AUC; Manel et al. 2001). I calculated the statistical significance of model sensitivity using an exact one-tailed binomial test, which eliminates models with high sensitivity resulting purely from broad scale over-prediction of species' presences. I calculated AUCs using training and testing data, with a third of the data held back from model training and used to test the accuracy of predictions (true and false presences and absences). It should be noted that, with presence only data, AUC estimates can range between 0.5 (model is no better than random) and 1 (no misclassification of test points; Fielding and Bell 1997; Pearson 2007; Phillips and Dudík 2008). While AUC does not assess a model's ability to correctly predict the potential range, which is unknown, it does give quantify the model's general performance.

Following assessment of model performance, I used all occurrence data to build the final model and I allowed potential ranges to occur without restriction across the whole world. While this method does overestimate the accessible area available to species, it also allows comparable measurements of range filling across my test species and permits the examination of the strength of spatial location on range filling estimates. I use a global extent for practical reasons, as more realistic constraints on

the accessibility of potential range extent would require consideration on a species by species basis. In addition, as there is little evidence for a relationship between species age and range filling extent, the possibility of unlimited dispersal given time may be a more appropriate test, particularly given the wide ranging nature of some of the species analysed in this study (Schurr et al. 2007; Paul et al. 2009).

I use two threshold measures, lowest presence threshold (LPT) and maximum sensitivity and specificity (MaxSS) to convert presence probabilities to binary presence/absence data. The lowest presence threshold selects cells with presence probabilities equal to or higher than the lowest probability from the species' observed range. This method generally gives broad predictions of potential range extent (Pearson et al. 2007). The threshold maximising sensitivity and specificity balances correctly predicted presences against false absences, which gives a conservative estimate of potential range size compared to the LPT method (Manel et al. 2001). I ran GAM, GBM and SRE using the BIOMOD package in R (Thuiller 2003; Thuiller et al. 2009b; R Development Core Team 2011). I ran Maxent models using a command line interface from R to the Java program Maxent 3.3.3e (Phillips et al. 2006; Phillips and Dudík 2008). I calculated presence-absence threshold values in R using the 'PresenceAbsence' package (Freeman 2009).

I calculated realised range size (R) for each species as the count of all cells occupied by that species and potential range size (P) as the number of cells predicted as a presence after application of the relevant binary threshold. I therefore calculated range filling ratios as R / P . I treated R/P values as proportion data and therefore arcsine square-root transformed prior to analysis (Crawley 2007). For wide ranging species, the application of conservative thresholds may lead to ratio values greater than 1 (i.e. the species realised range extent is greater than the predicted potential

range extent). Arcsine data transformation is only possible between -1 and 1; therefore I rounded down ratio values greater than 1. I obtained median body mass data (grams) from the PanTHERIA database (Jones et al. 2009) and log transformed data prior to analysis. I used the a supertree of mammals (Bininda-Emonds et al. 2007; Fritz et al. 2009) to describe the shared evolutionary history between species, using the maximum likelihood estimates of node divergence dates.

Estimating spatial / phylogenetic signal

I estimated spatial and phylogenetic signals in range filling extent using two methods, with R code provided by R. P. Freckleton and N. Cooper. In both methods, a phylogeny is used to capture shared evolutionary history, but they differ in the method used to capture similarity between species due to shared location. The first method, ‘distance2’ (Freckleton and Jetz 2009), scales the branch lengths of the phylogeny using the geodesic distances. This method partitions the overall phylogenetic signal in a trait (λ) into a proportion that is attributable to space (ϕ), and a remaining proportion attributable solely to phylogeny having accounted for space ($\lambda' = (1 - \phi) \lambda$). Residual variance (γ) is calculated as $(1 - \phi) (1 - \lambda)$. The second method, ‘brutal’ (Freckleton Unpublished) uses instead a full spatial matrix of pairwise geodesic distances between species alongside a phylogenetic covariance matrix between species. Maximum likelihood is then used to optimise a transformation of each matrix to independently capture the degree of spatial (ϕ) and phylogenetic (λ) similarity between species. The ‘distance2’ method therefore treats location as a character that can evolve in a Brownian fashion within evolutionary constraints, whereas ‘brutal’ dissociates spatial from phylogenetic similarity.

The ‘distance2’ method is implemented using phylogenetically independent contrasts and requires a phylogenetic tree with no polytomies. Since the mammal

supertree is only partially resolved, I randomly resolved polytomies into a series of dichotomies with branch lengths of zero using the *ape* package in R (Paradis and Strimmer 2004). Even deep nodes may not be fully resolved, especially for poorly known clades and therefore there may be bias in the number and distribution of polytomies throughout the tree (Cooper et al. 2011). Forcing these nodes to become dichotomous may artificially separate closely related species that also live in close geographic proximity, creating artificial separation between spatial and phylogenetic signals. I therefore randomly resolved the tree 100 times and took mean estimates of model AIC, spatial and phylogenetic signals plus a measure of the standard deviation in each estimate. If some resolutions of the tree have a disproportionate impact on λ , ϕ or model AIC estimates, then this should be apparent from the 100 tree resolutions. I used range centroids as a descriptor of species location; centroids were calculated in ArcGIS as the absolute mid-point of the species range across all fragments. Spatial distances between species were then calculated as the geodesic distance between geographical range centroids.

Fitting models with differing evolutionary interpretations allows us to compare model AICs and infer more about the relative roles of space and phylogeny than from using one method alone. If the AIC using ‘brutal’ is lower then the spatial similarity in the data is underlain by factors that vary across space independently of phylogeny: species are similar simply because of where they live. However, if the AIC of the ‘distance2’ model indicates better fit then the spatial effects evolve with the phylogeny: species covary because of location in which the clade has diversified. All analyses were conducted in R, version 2.13.0 (R Development Core Team 2011)

5.4 Results

Potential range size (P) estimates varied by nearly three orders of magnitude, between 17 cells (Milne-Edward's sportive lemur, *Lepilemur edwardsi* - Maxent + LPT combination) and 16712 cells (Red fox, *Vulpes vulpes* – GBM+ LPT combination). Mean R/P (range filling) ratio values were low (Figure 5.1), regardless of the SDM modelling method or presence/absence threshold used. The inclusion of small range species (realised range between five and fifty cells) in Maxent models did not have an obvious effect on average range filling estimates since average R/P ratios were in line with those from the reduced datasets where small range species had been excluded (Figure 5.2). Estimates of potential range size were significantly lower when the MaxSS threshold was applied in contrast to the LPT threshold (paired t-tests: GAM models $t=27.45$, $df=517$, $P<0.001$; GBM models $t=23.82$, $df=517$, $P<0.001$; Maxent models $t=26.795$, $df=675$, $P<0.001$). As expected, the narrower MaxSS threshold therefore produces higher R/P ratio values compared to potential range estimates using the LPT. Mean SRE estimates of potential range were intermediate between LPT and MaxSS estimates (Figure 5.1).

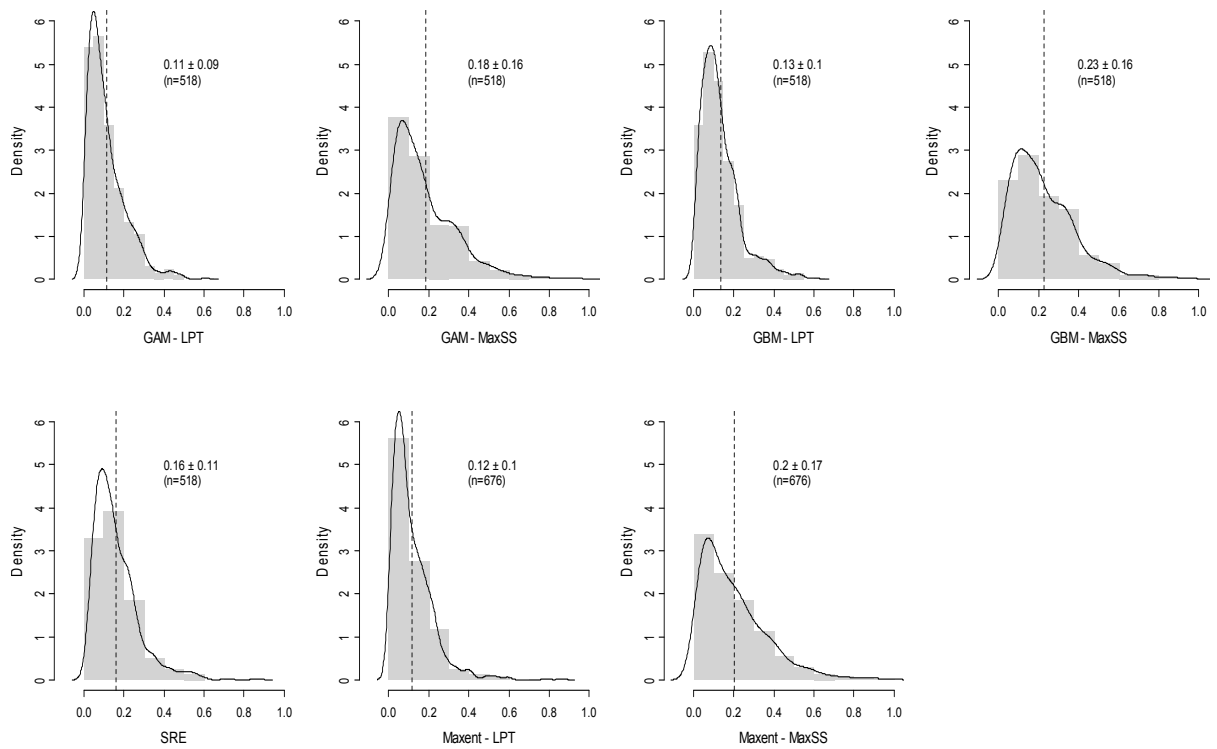


Figure 5.1 Range filling (R/P) estimates by modelling method and threshold type. Dashed line is the mean range filling per model with mean values ± 1 s.d and sample given for each model.

SDM model performance

AUC scores for Maxent, GAM and GBM models computed using 30% of data retained for testing during the cross-validation procedure were high, ranging between 0.75 and 0.99. All GAM and GBM models had AUCs considered “good” or “excellent” ($0.8 \geq \text{AUC} < 1$; Appendix 4: Supp. Figure A4.1). 56 Maxent models had only fair performance $0.7 \geq \text{AUC} < 0.8$, while the rest were “good” or “excellent” (Supp. Figure 1; Swets 1988). Model sensitivity (number of correctly predicted presences) was generally high (Appendix 4: Supp Figure A4.2). Testing the statistical significance of model sensitivity demonstrated that the accuracy of predictions is

greater than expected by chance when accounting for the size of area predicted for the potential range (all $p < 0.001$, exact one-tailed binomial test).

Spatial and phylogenetic signals of range filling

Model AICs were consistently much lower for the ‘brutal’ models compared to the ‘distance2’ models for range filling (R/P): species covary in their range filling extent due to shared location rather than by a dual process of location driven by shared ancestry (Table 5.1a+b). Both methods showed more evidence for the effects of space on range filling as compared with the effects of phylogeny. Conversely, both ‘brutal’ and ‘distance2’ models estimate that variation in body mass is primarily driven by shared evolutionary history, rather than space. However, the difference in AICs between the two methods for body mass was as small (between 3 and 10 AIC units; Table 5.1c). Figure 5.2 suggests that some of the spatial variation in range filling extents may be due to a latitudinal effect of proportionally lower available area or available environmental space (bounded by the Arctic) at higher latitudes (Gaston et al. 1998).

(a)	AIC brutal	Mean AIC (± 1 s.d.) distance2	λ brutal	λ' (± 1 s.d.) distance2	ϕ brutal	ϕ (± 1 s.d.) distance2
<i>GAM Least Presence Threshold</i>	-982.773	-684.425 (± 2.21)	0.107	0.005 ($\pm 2.67\text{E-}04$)	0.926	0.478 ($\pm 2.67\text{E-}02$)
<i>GAM Maximum Sensitivity Specificity</i>	-727.876	-400.711 (± 3.28)	0.215	0.003 ($\pm 2.73\text{E-}04$)	0.944	0.658 ($\pm 2.73\text{E-}02$)
<i>GBM Least Presence Threshold</i>	-945.586	-708.689 (± 1.44)	0.052	0.007 ($\pm 1.84\text{E-}04$)	0.896	0.299 ($\pm 1.84\text{E-}02$)
<i>GBM Maximum Sensitivity Specificity</i>	-758.269	-420.792 (± 2.56)	0.129	0.005 ($\pm 2.76\text{E-}04$)	0.948	0.481 ($\pm 2.76\text{E-}02$)
<i>SRE</i>	-922.999	-670.341 (± 1.77)	0.089	0.008 ($\pm 1.42\text{E-}04$)	0.951	0.214 ($\pm 1.42\text{E-}02$)

(b)	AIC brutal	Mean AIC (± 1 s.d.) distance2	λ brutal	λ' (± 1 s.d.) distance2	ϕ brutal	Φ (± 1 s.d.) distance2
<i>Maxent Least Presence Threshold</i>	-1146.214	-826.810 (± 1.51)	0.091	0.007 ($\pm 1.37\text{E-}04$)	0.957	0.285 ($\pm 1.37\text{E-}02$)
<i>Maxent Maximum Sensitivity Specificity</i>	-909.303	-515.002 (± 3.24)	0.327	0.004 ($\pm 2.50\text{E-}04$)	0.969	0.601 ($\pm 2.50\text{E-}02$)

(c)	AIC brutal	Mean AIC (± 1 s.d.) distance2	λ brutal	λ' (± 1 s.d.) distance2	ϕ brutal	ϕ (± 1 s.d.) distance2
<i>Body Mass (n=518)</i>	614.070	617.322 (± 0.75)	0.997	0.96 ($\pm 5.32\text{E-}03$)	0.001	0.03 ($\pm 5.38\text{E-}03$)
<i>Body Mass (n=676)</i>	693.543	704.227 (± 1.12)	1.000	0.95 ($\pm 5.62\text{E-}03$)	0.011	0.04 ($\pm 5.67\text{E-}03$)

Table 5.1 (a) models of arcsine square-root transformed R/P with n=518. (b) models of arcsine square-root transformed R/P with n= 676. (c) models of log transformed body mass (grams) for a. n=518 and b. n=676. Note for contrast models that as ϕ , λ' and γ sum to 1 there is no need to present the γ values.

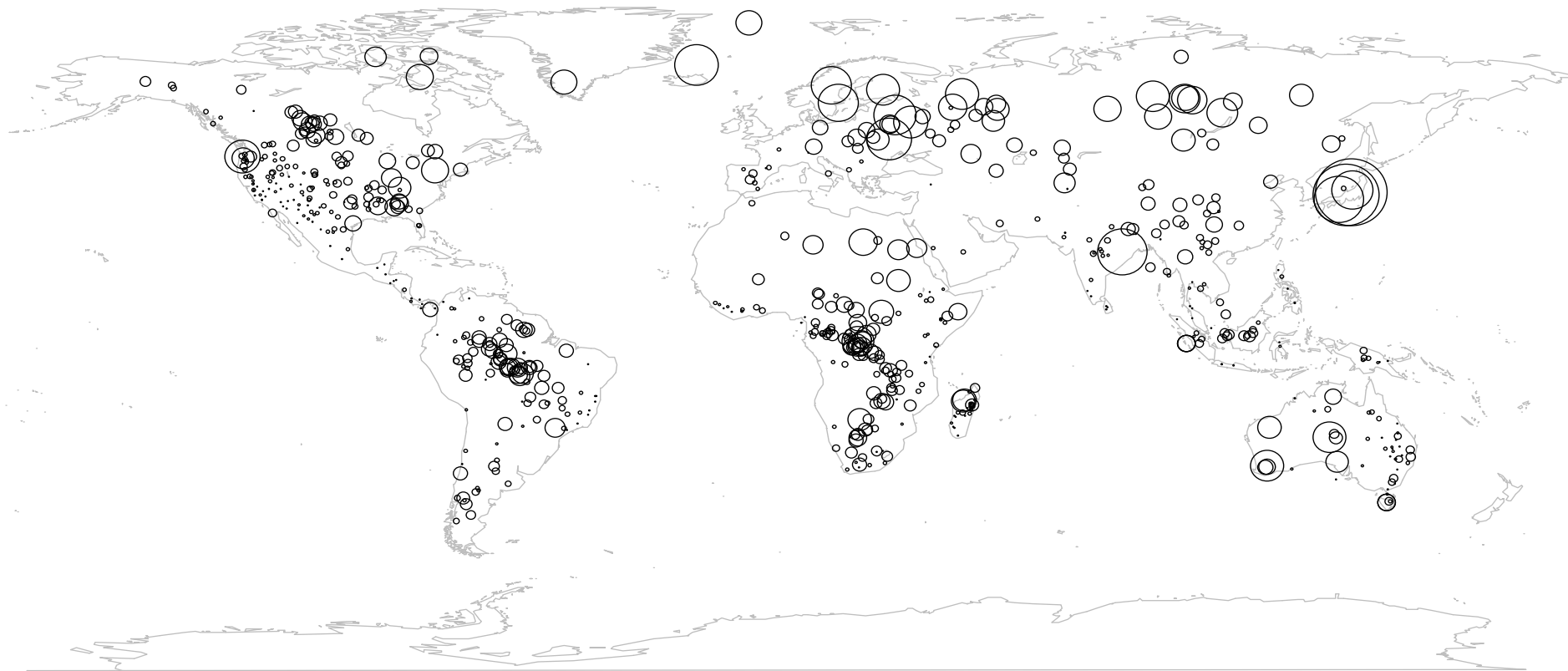


Figure 5.2 Range filling extent plotted by range centroid. Larger circles denote higher levels of range filling.

5.5 Discussion

I find that the extent of range filling in mammals is better predicted by a statistical model accounting independently for space and phylogeny than by one in which the distribution of species reflects their evolutionary history. This model also indicates that spatial factors are the main driving force behind the patterns of range filling seen in mammals. These results were consistent across different methods of modelling potential range size and across different thresholds for defining species presence. In contrast, analyses of body mass for the same species indicates that shared evolutionary history is the main driver of variation in this trait when compared to the relative effects of location. Again, the model including independent spatial effects proved a better fit to the body mass data than a model in which location evolves under a model of Brownian evolution. Difference in model performance between the two methods, measured using AIC were, however, very small for body mass (Table 5.1 c).

Either method may be affected by phylogenetic biases in the species sampled, as the sampling strategy was driven by trait data availability (Cooper et al. 2011). However, the sensitivity of the methods to incomplete sampling, particularly with respect to the resulting differences in AIC, could be retested by randomly sampling from within the data used here, or by identifying clades with complete trait data and a fully resolved phylogeny. For the model fitted using contrasts, random resolution of the phylogenetic tree seemed to have little impact on estimates of the spatial and phylogenetic signal in range filling as standard deviation in estimates of λ' and ϕ were small for both range filling and body mass (Table 5.1).

The high spatial signal seen in range filling estimates may be driven by large differences in the location of subclades due, for example to separate radiations of mammals in North America and Europe. Spatial and phylogenetic signals in range

filling should therefore be retested at the realm or continent level to see if results are comparable after controlling for continent-scale differences in location (McInnes 2011). Regardless, the role of broad scale geographic constraints should be considered in range filling studies, an element that, to date, has been lacking from such studies.

I therefore conclude that if dispersal ability is to be inferred from range filling then this must happen with reference to the spatial context of the species realised and potential ranges. If I have correctly modelled the potential range, then I can infer that many species fail to inhabit suitable environmental space. This is a worrying finding given current predictions of the rate and scale of climatic change (Loarie et al. 2009). Geographic or environmental constraints imposed by a species' location play a bigger part in determining how well a species fills its potential range than may have been posited given the heritability of traits thought to influence range filling (Freckleton et al. 2002; Olalla-Tárraga et al. 2011) and chapter 3 of this thesis. The role of dispersal ability may, however, come into play at smaller spatial scales of study and this may prove an interesting avenue for further work (Machac et al. 2011). For global scale studies on the impact of climate change, and the role of dispersal ability in mediating its effects, a focus on landscape barriers to movement in areas of rapid climate change (exposure) is recommended (Dawson et al. 2011). The present study also highlights the utility of developing models that can separate spatial and phylogenetic signals and the use of model performance to inform our understanding of broad scale patterns in biogeography.

Chapter 6. Conclusion

6.1 Summary of results

In this thesis I have explored ways in which dispersal distances and dispersal ability can be predicted for mammals. In chapter 2, I used a phenomenological approach to identify similarities in the shapes of mammalian dispersal kernels and found that the Weibull probability density function, which is a ‘fat-tailed’ kernel, often provided the best description of the observed data. To my knowledge, this type of cross species analysis of dispersal kernels has never been carried out for mammals. In chapter 3, I identify a number of life history and ecological traits which correlate with average and maximum mammalian dispersal distances. Although no one set of traits proved outstanding in terms of explanatory power, the amount of variation explained by models was high. This bodes well for our ability to extrapolate dispersal distance estimates from life history traits when actual distances are unknown. Combining results from chapters 2 and 3 means that both rate and distance of dispersal may now be predicted for mammals and used to parameterise species distribution models. Indeed, the applications may go beyond species distribution modelling. For example, models of habitat connectivity, gene flow or community assemblage may also benefit from improved dispersal estimates.

Chapters 4 and 5 examine the role of dispersal in determining broad biogeographical patterns of mammalian potential range filling, that is, the ability of mammals to fill all the environmental space which is available within their tolerance limits. Chapter 4 identifies correlations between potential range filling and dispersal distance and age at sexual maturity. This demonstrates that the ability to reach and colonise new habitats plays a role in determining which species’ are at equilibrium with their environment. Chapter 5 expands this analysis to examine what drives

patterns in species' potential range filling at the global scale. I find that where a species lives is a much better predictor of potential range filling than their shared ancestry. There is also a pattern of higher filling of potential ranges with increasing latitudinal gradient. This may be due to landscape and environmental conditions at higher latitudes, or may be driven by species with good dispersal ability reaching and exploiting post-glaciation habitats. If patterns are driven by dispersal ability there is little evidence for strong phylogenetic associations between the species in question. Taken together chapters 4 and 5 show that inferences about comparative dispersal ability in mammals can be made from estimates of potential range filling, but the complex landscapes that species' inhabit also play a large part in driving these patterns.

6.2 Directions for future work

Modelling mammalian dispersal kernels

The phenomenological models of dispersal distance in mammals, used in chapter 2, prove that generalities in the shape of these kernels can be identified. Only three simple kernels were analysed in this thesis. Ability to accurately describe kernel shape may improve with analysis of further probability density functions which have increased numbers of parameters fitted to the observed data. For example, Clark's 2Dt is another 'fat-tailed' kernel which is thought to provide a good fit to seed dispersal data (Clark et al. 1999). Alternatively, a kernel with two components, one for shorter dispersal distances and one for long distance dispersal, may prove informative (for example Higgins and Richardson 1999). However, with low data availability we must be cautious about fitting highly parameterised models with limited understanding of the mechanisms driving the observed distributions (Paradis et al. 2002). It may also prove fruitful to compare predictions from the tail of the

observed dispersal kernel with predictions from isolation by distance (IBD) regressions, calculated from genetic data, in order to test their ability of modelled kernels to predict long distance dispersal, ‘the tail of the tail’ (Palumbi 2003; Lester et al. 2007; Jenkins et al. 2010).

Predicting dispersal distances

Chapter 3 demonstrates that a number of life history traits correlate with dispersal ability in mammals. Cross validation of correlation coefficients shows that estimates are within an order of magnitude of actual distances. Therefore, using available life history trait data, dispersal distances could now be predicted for many mammals beyond those for which empirical dispersal estimates are available. Further tests of the robustness of the estimates may prove interesting, for example, the ability of correlation coefficients trained on data from Palearctic species to predict dispersal distances for species in the Nearctic, and vice-versa. A further useful addition would be to have a complementary database to hold information on the mating system, resource defence and group dynamics of the species in question (Greenwood 1980; Pusey 1987). These species specific features play a significant role in determining whether a species will disperse, and also the sex of the dispersing individuals which would be useful information for many modelling studies.

Correlates of potential range filling in mammals

In chapter 4 I found significant correlations between range filling and dispersal ability and age at sexual maturity; the first time such a relationship has been proved (Svenning and Skov 2004; Munguía et al. 2008). I used generalised linear models with quasi-binomial error structure to test potential range filling for different model types. In this study the phylogenetic signal in range filling was very low and often not

significantly different from zero. Therefore I did not account for the effects of species relatedness in assessing the relationship between potential range filling and dispersal, colonisation ability (measured as age at sexual maturity) and species age. Methods now exist which enable bivariate data to be tested within a phylogenetic framework and results could be retested to ensure robustness (Hadfield and Nakagawa 2010). Additionally, accurately modelling species environmental limits in order to infer the extent of the potential range is difficult. Estimates are affected by the decisions made in the modelling process, especially the extent of area which the potential range is allowed to occupy. Artificial limits to the extent of the potential range can make comparisons across species uninformative. Ideally projections of the potential niche space would be driven by the species accessible area (Barve et al. 2011) and determined by something other than dispersal ability. Connectivity of habitats using methods such as electrical circuit theory or landscape resistance to movement (impermeability) may prove a useful extension to the analyses described here (Hortal et al. 2005; McInnes 2007; Mcrae et al. 2008; Doerr et al. 2010; Koen et al. 2010).

Chapter 5 shows that the environment shared by species is more important in determining potential range filling than shared evolutionary history or coevolution given shared environments. I believe this makes it all the more important to look at range filling taking into account the landscape inhabited by the species. My analyses were conducted at the global scale. It would be wise, however, to repeat analyses at the realm scale to see if relationships hold. Methods to jointly analyse spatial and phylogenetic signals in potential range filling using a binomial response variable do not yet exist, but may be possible to develop them, with the aim of keeping analyses consistent with those in chapter 4. Similarly, it is possible to alter 'distance2' models

to take a matrix of phylogenetic distances, which would mean that random resolutions of polytomies within the phylogenetic tree are no longer necessary. Our repeated random resolutions of the mammal phylogeny do not appear to cause changes in AIC estimates. However, using a matrix would reduce another potential source of error. This may be important, especially for use in analysing signals in traits which may have a flat joint likelihood surface of space and phylogeny and thus be greatly affected by biases in the resolution of the phylogenetic tree. Finally, a new technique exists to further quantify the similarity of unoccupied potential range space to that within the realised range. Multivariate environmental similarity surfaces (MESS), a new feature of Maxent, report the closeness of selected points to the distribution of reference points, in this instance the realised range (Elith et al. 2010). Negative values are given for dissimilar points and the sum of these could be calculated for each species unfilled potential range and compared to range filling extent. This would indicate if there are species specific biases in prediction accuracy of the potential range (through poor characterisation of the species realised environmental niche) and thus whether modelling methods need to be amended.

6.3 Concluding remarks

I have identified a number of ways to successfully parameterise species distribution models with information on the dispersal rate and distance for mammals. I have also identified potential range filling as a way forward to gain estimates of relative dispersal ability for mammals. Although predicting dispersal distance is not simple, it is achievable and therefore greater effort should be taken to incorporate dispersal estimates into assessments of species based vulnerability to climate change.

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Appendix 1. Supporting information for chapter 2.

Table A1.1 - Dispersal database.

All mean, median, minimum and maximum dispersal data collected plus data type, sex of dispersers and method of estimation. Only mean, median, and maximum dispersal distances were used in chapter 3. Original units presented here, data was transformed into kilometres prior to analyses using the conversion metrics detailed in chapter 2.

Species Name	Sex	Data Type	Mean Value	Median Value	Lower Value	Upper Value	Units	Estimation Method	Ref
<i>Vulpes vulpes</i>	Male	Movement Distance	122.59	122.59	0.17	245	Miles - Linear	Other	1
<i>Connochaetes taurinus</i>	Unspecified	Migratory	NA	NA	NA	200	km - Linear	Unspecified	2
<i>Myocastor coypus</i>	Male	Migratory	61.25	62.5	40	80	km - Linear	Trapping	3
<i>Vulpes vulpes</i>	Male	Natal Dispersal	35	19.67	0	153	km - Linear	Capture-Mark-Recapture	4
<i>Vulpes vulpes</i>	Female	Natal Dispersal	25.33	5.67	0	302	km - Linear	Capture-Mark-Recapture	4
<i>Ammospermophilus leucurus</i>	Male	Movement Distance	0.12	0.11	0.03	0.52	km - Linear	Capture-Mark-Recapture	5
<i>Ammospermophilus leucurus</i>	Female	Movement Distance	0.12	0.11	0.03	0.32	km - Linear	Capture-Mark-Recapture	5
<i>Dipodomys merriami</i>	Male	Movement Distance	0.1	0.08	0.031	1.127	km - Linear	Capture-Mark-Recapture	5
<i>Dipodomys merriami</i>	Female	Movement Distance	0.09	0.08	0.031	2.93	km - Linear	Capture-Mark-Recapture	5
<i>Dipodomys microps</i>	Male	Movement Distance	0.08	0.05	0.031	0.412	km - Linear	Capture-Mark-Recapture	5

Dipodomys microps	Female	Movement Distance	0.069	0.05	0.031	0.43	km - Linear	Capture-Mark-Recapture	5
Onychomys torridus	Male	Movement Distance	0.17	NA	0.031	0.33	km - Linear	Capture-Mark-Recapture	5
Onychomys torridus	Female	Movement Distance	0.1	NA	0.031	0.33	km - Linear	Capture-Mark-Recapture	5
Peromyscus maniculatus	Male	Movement Distance	0.16	NA	0.031	0.33	km - Linear	Capture-Mark-Recapture	5
Peromyscus maniculatus	Female	Movement Distance	0.1	NA	0.031	0.12	km - Linear	Capture-Mark-Recapture	5
Chaetodipus formosus	Male	Movement Distance	0.06	NA	0.031	0.195	km - Linear	Capture-Mark-Recapture	5
Chaetodipus formosus	Female	Movement Distance	0.047	NA	0.031	0.09	km - Linear	Capture-Mark-Recapture	5
Perognathus longimembris	Male	Movement Distance	0.071	0.031	0.031	0.23	km - Linear	Capture-Mark-Recapture	5
Perognathus longimembris	Female	Movement Distance	0.054	0.031	0.031	0.24	km - Linear	Capture-Mark-Recapture	5
Canis latrans	Female	Movement Distance	NA	NA	NA	11	km - Linear	Radio Telemetry	6
Peromyscus maniculatus	Unspecified	Movement Distance	49.9	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Peromyscus maniculatus	Unspecified	Movement Distance	33.7	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Dipodomys ordii	Unspecified	Movement Distance	76.1	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Dipodomys ordii	Unspecified	Movement Distance	15.5	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Microtus montanus	Unspecified	Movement Distance	20.2	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Microtus montanus	Unspecified	Movement Distance	11.3	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Microtus montanus	Unspecified	Movement Distance	21.9	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	7
Odocoileus hemionus	Female	Natal Dispersal	NA	NA	NA	180	km - Linear	Unspecified	8
Odocoileus hemionus	Unspecified	Migratory	15.4	NA	1.6	241	km - Linear	Unspecified	8
Lepus timidus	Unspecified	Movement Distance	13.39	2	0	200	km - Linear	Trapping	9

<i>Aplodontia rufa</i>	Male	Natal Dispersal	142.7	NA	NA	NA	Metres - Linear	Radio Telemetry	10
<i>Aplodontia rufa</i>	Both	Natal Dispersal	152.5	130.5	23	326	Metres - Linear	Radio Telemetry	10
<i>Marmota flaviventris</i>	Male	Natal Dispersal	NA	1.5	NA	15.5	km - Linear	Unspecified	11
<i>Marmota flaviventris</i>	Female	Natal Dispersal	NA	0.4	NA	6.4	km - Linear	Unspecified	11
<i>Martes pennanti</i>	Male	Natal Dispersal	17.3	17.7	10.9	23	km - Linear	Radio Telemetry	12
<i>Martes pennanti</i>	Female	Natal Dispersal	14.92	15.1	7.5	22.6	km - Linear	Radio Telemetry	12
<i>Vulpes velox</i>	Male	Natal Dispersal	11	NA	NA	NA	km-Linear	Radio Telemetry	13
<i>Vulpes velox</i>	Female	Natal Dispersal	9.8	NA	NA	NA	km-Linear	Radio Telemetry	13
<i>Canis lupus</i>	Female	Movement Distance	115	99	32	256	km - Linear	Radio Telemetry	14
<i>Canis lupus</i>	Male	Movement Distance	148.67	96	22	732	km - Linear	Radio Telemetry	14
<i>Castor canadensis</i>	Both	Natal Dispersal	11.29	4.75	0	31	Miles - Linear	Capture-Mark-Recapture	15
<i>Mellivora capensis</i>	Female	Natal Dispersal	NA	NA	NA	53	km - Linear	Radio Telemetry	16
<i>Puma concolor</i>	Male	Natal Dispersal	63.25	69	19	77	km - Linear	Radio Telemetry	17
<i>Puma concolor</i>	Female	Natal Dispersal	NA	NA	NA	48	km - Linear	Radio Telemetry	17
<i>Saiga tatarica</i>	Unspecified	Migratory	NA	NA	200	1200	km - Linear	Direct Observation	18
<i>Canis lupus</i>	Female	Natal Dispersal	58	58	37	79	km - Linear	Radio Telemetry	19
<i>Canis lupus</i>	Male	Natal Dispersal	183.4	146	46	432	km - Linear	Radio Telemetry	19
<i>Rangifer tarandus</i>	Female	Migratory	NA	NA	NA	3066	km - Linear	Radio Telemetry	20
<i>Rangifer tarandus</i>	Female	Migratory	NA	NA	NA	767	km - Linear	Radio Telemetry	20
<i>Tamiasciurus hudsonicus</i>	Both	Natal Dispersal	96	60	NA	NA	Metres - Linear	Capture-Mark-Recapture	21

Tamias ruficaudus	Male	Movement Distance	115.2	NA	NA	450	Metres - Linear	Capture-Mark-Recapture	22
Tamias ruficaudus	Female	Movement Distance	79.8	NA	NA	255	Metres - Linear	Capture-Mark-Recapture	22
Tamias ruficaudus	Both	Movement Distance	69.6	NA	NA	285	Metres - Linear	Capture-Mark-Recapture	22
Ammospermophilus nelsoni	Male	Movement Distance	NA	NA	NA	1260	Metres - Linear	Capture-Mark-Recapture	23
Ammospermophilus nelsoni	Female	Movement Distance	NA	NA	NA	900	Metres - Linear	Capture-Mark-Recapture	23
Dicrostonyx groenlandicus	Both	Movement Distance	NA	NA	1.9	102.7	Metres - Linear	Radio Telemetry	24
Canis lupus	Male	Natal Dispersal	31.5	31	14	50	km - Linear	Radio Telemetry	25
Canis lupus	Female	Natal Dispersal	32.5	36	13	45	km - Linear	Radio Telemetry	25
Proteles cristata	Unspecified	Movement Distance	16.1	9.7	3.2	35.4	km - Linear	Capture-Mark-Recapture	26
Canis mesomelas	Unspecified	Movement Distance	1.8	1.6	0	4.8	km - Linear	Capture-Mark-Recapture	26
Canis mesomelas	Unspecified	Natal Dispersal	55.5	55.5	8	103	km - Linear	Capture-Mark-Recapture	26
Canis mesomelas	Unspecified	Adult Dispersal	13	NA	1.6	57.9	km - Linear	Capture-Mark-Recapture	26
Canis latrans	Female	Movement Distance	40.7	42.2	7.1	94.1	km - Linear	Radio Telemetry	27
Canis latrans	Male	Movement Distance	18.67	16.6	3.4	64	km - Linear	Radio Telemetry	27
Ovis dalli	Unspecified	Migratory	NA	NA	8	48	km - Linear	Unspecified	28
Microtus arvalis	Female	Breeding Dispersal	NA	49	16	537	Metres - Linear	Radio Telemetry	29
Microtus arvalis	Female	Natal Dispersal	NA	NA	20.7	101.6	Metres - Linear	Radio Telemetry	29
Canis lupus	Both	Natal Dispersal	96.3	NA	15.6	254.9	km - Linear	Radio Telemetry	30
Crocota crocuta	Male	Natal Dispersal	6.8	NA	NA	40	km - Linear	Radio Telemetry	31
Lagostomus maximus	Male	Breeding Dispersal	242	NA	NA	NA	Metres - Linear	Direct Observation	32

Lagostomus maximus	Male	Breeding Dispersal	154	NA	NA	NA	Metres - Linear	Direct Observation	32
Lagostomus maximus	Female	Adult Dispersal	150	NA	NA	NA	Metres - Linear	Direct Observation	32
Heterocephalus glaber	Male	Movement Distance	410.91	180	20	2250	Metres - Linear	Capture-Mark-Recapture	33
Heterocephalus glaber	Female	Movement Distance	388.5	190	5	2400	Metres - Linear	Capture-Mark-Recapture	33
Neotoma micropus	Male	Natal Dispersal	61.4	NA	NA	NA	Metres - Linear	Unspecified	34
Neotoma micropus	Female	Natal Dispersal	61.2	NA	NA	NA	Metres - Linear	Unspecified	34
Lepus europaeus	Both	Natal Dispersal	NA	1615	742	17353	Metres - Linear	Radio Telemetry	35
Cervus elaphus	Unspecified	Movement Distance	13.42	14	2.5	20	Miles - Linear	Direct Observation	36
Hylobates lar	Male	Natal Dispersal	620	500	300	1000	Metres - Linear	Direct Observation	37
Hylobates lar	Female	Natal Dispersal	NA	NA	NA	1400	Metres - Linear	Direct Observation	37
Dipodomys spectabilis	Both	Adult Dispersal	NA	20	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Dipodomys ordii	Both	Adult Dispersal	NA	25	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Dipodomys merriami	Both	Adult Dispersal	NA	26	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Chaetodipus penicillatus	Both	Adult Dispersal	NA	30	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Perognathus flavus	Both	Adult Dispersal	NA	40	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Reithrodontomys megalotis	Both	Adult Dispersal	NA	95	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Peromyscus maniculatus	Both	Adult Dispersal	NA	75	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Peromyscus eremicus	Both	Adult Dispersal	NA	110	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Onychomys leucogaster	Both	Adult Dispersal	NA	72	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
Onychomys torridus	Both	Adult Dispersal	NA	73	NA	NA	Metres - Linear	Capture-Mark-Recapture	38

<i>Neotoma albigula</i>	Both	Adult Dispersal	NA	23	NA	NA	Metres - Linear	Capture-Mark-Recapture	38
<i>Martes americana</i>	Both	Movement Distance	33.3	NA	28	43.2	km - Linear	Radio Telemetry	39
<i>Martes americana</i>	Both	Movement Distance	8.1	NA	6	9.6	km - Linear	Radio Telemetry	39
<i>Odocoileus hemionus</i>	Male	Adult Dispersal	15.2	NA	NA	32	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Female	Adult Dispersal	12.2	NA	NA	30	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Male	Movement Distance	3.5	NA	NA	NA	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Female	Movement Distance	2.4	NA	NA	NA	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Male	Movement Distance	3.3	NA	NA	NA	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Female	Movement Distance	2.5	NA	NA	NA	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Male	Movement Distance	1.8	NA	NA	NA	km - Linear	Capture-Mark-Recapture	40
<i>Odocoileus hemionus</i>	Female	Movement Distance	1.7	NA	NA	NA	km - Linear	Capture-Mark-Recapture	40
<i>Mustela erminea</i>	Male	Movement Distance	NA	NA	NA	22	Miles - Linear	Trapping	41
<i>Ondatra zibethicus</i>	Male	Natal Dispersal	64.5	NA	NA	NA	Metres - Linear	Trapping	42
<i>Ondatra zibethicus</i>	Female	Natal Dispersal	40.8	NA	NA	NA	Metres - Linear	Trapping	42
<i>Rupicapra rupicapra</i>	Unspecified	Movement Distance	5.4	NA	NA	NA	Miles - Linear	Unspecified	43
<i>Hemitragus jemlahicus</i>	Unspecified	Movement Distance	1.1	NA	NA	NA	Miles - Linear	Unspecified	43
<i>Cervus elaphus</i>	Unspecified	Movement Distance	1	NA	NA	NA	Miles - Linear	Unspecified	43
<i>Cervus elaphus</i>	Unspecified	Movement Distance	1	NA	NA	NA	Miles - Linear	Unspecified	43
<i>Cervus nippon</i>	Unspecified	Movement Distance	1	NA	NA	NA	Miles - Linear	Unspecified	43
<i>Dama dama</i>	Unspecified	Movement Distance	0.5	NA	NA	NA	Miles - Linear	Unspecified	43

<i>Odocoileus virginianus</i>	Unspecified	Movement Distance	0.6	NA	NA	NA	Miles - Linear	Unspecified	44
<i>Rusa timorensis</i>	Unspecified	Movement Distance	0.5	NA	NA	NA	Miles - Linear	Unspecified	44
<i>Rusa unicolor</i>	Unspecified	Movement Distance	0.4	NA	NA	NA	Miles - Linear	Unspecified	44
<i>Cervus elaphus</i>	Unspecified	Movement Distance	0.4	NA	NA	NA	Miles - Linear	Unspecified	44
<i>Sylvilagus floridanus</i>	Male	Movement Distance	0.054	NA	0.0043	0.222	km - Linear	Capture-Mark-Recapture	45
<i>Sylvilagus floridanus</i>	Male	Movement Distance	0.0444	NA	0.0079	0.086	km - Linear	Capture-Mark-Recapture	45
<i>Sylvilagus floridanus</i>	Female	Movement Distance	0.0424	NA	0	0.106	km - Linear	Capture-Mark-Recapture	45
<i>Sylvilagus floridanus</i>	Female	Movement Distance	0.0398	NA	0.013	0.165	km - Linear	Capture-Mark-Recapture	45
<i>Meles meles</i>	Male	Movement Distance	4.53	NA	2.6	8.3	km - Linear	Capture-Mark-Recapture	46
<i>Meles meles</i>	Female	Movement Distance	3.45	NA	3.2	3.7	km - Linear	Capture-Mark-Recapture	46
<i>Meles meles</i>	Male	Movement Distance	3.92	NA	2.6	5.3	km - Linear	Capture-Mark-Recapture	46
<i>Meles meles</i>	Female	Movement Distance	5.35	NA	2.9	7.8	km - Linear	Capture-Mark-Recapture	46
<i>Chlorocebus aethiops</i>	Male	Natal Dispersal	NA	NA	NA	0.5	km-Linear	Direct Observation	47
<i>Cynomys leucurus</i>	Unspecified	Movement Distance	NA	NA	NA	2.7	km - Linear	Unspecified	48
<i>Trichosurus vulpecula</i>	Male	Movement Distance	6	4.5	3.5	10	km - Linear	Trapping	49
<i>Trichosurus vulpecula</i>	Male	Movement Distance	3.72	3.5	2	9	km - Linear	Trapping	49
<i>Trichosurus vulpecula</i>	Female	Movement Distance	NA	NA	NA	5	km - Linear	Trapping	49
<i>Ursus americanus</i>	Male	Natal Dispersal	38	NA	22	62	km-Linear	Radio Telemetry	50
<i>Ursus americanus</i>	Female	Natal Dispersal	3	NA	0	5	km-Linear	Radio Telemetry	50
<i>Trichosurus vulpecula</i>	Both	Natal Dispersal	5.54	4.5	3	11.5	km - Linear	Radio Telemetry	51

<i>Odocoileus hemionus</i>	Both	Migratory	8.3	NA	3.2	13.2	km - Linear	Radio Telemetry	55
<i>Thomomys bottae</i>	Both	Natal Dispersal	NA	NA	40	300	Metres - Linear	Trapping	52
<i>Capreolus pygargus</i>	Unspecified	Migratory	NA	NA	NA	500	km - Linear	Unspecified	53
<i>Ovis canadensis</i>	Male	Movement Distance	19.05	19.05	18.9	19.2	km - Linear	Radio Telemetry	54
<i>Ovis canadensis</i>	Male	Movement Distance	NA	NA	NA	32.9	km - Linear	Radio Telemetry	54
<i>Ovis canadensis</i>	Male	Movement Distance	20.15	20.15	9.4	30.9	km - Linear	Radio Telemetry	54
<i>Ovis canadensis</i>	Female	Movement Distance	7.4	NA	NA	NA	km - Linear	Radio Telemetry	54
<i>Ovis canadensis</i>	Female	Movement Distance	9.8	NA	NA	NA	km - Linear	Radio Telemetry	54
<i>Ovis canadensis</i>	Female	Movement Distance	3.7	NA	NA	NA	km - Linear	Radio Telemetry	54
<i>Castor canadensis</i>	Both	Natal Dispersal	3.5	NA	0.1	8	km - Linear	Radio Telemetry	56
<i>Peromyscus maniculatus</i>	Female	Natal Dispersal	132.87	776.2	0	1005.84	Metres - Linear	Capture-Mark-Recapture	57
<i>Peromyscus maniculatus</i>	Male	Natal Dispersal	188.6	137.16	0	883.92	Metres - Linear	Capture-Mark-Recapture	57
<i>Apodemus sylvaticus</i>	Both	Movement Distance	273.82	250.5	150	450.5	Metres - Linear	Capture-Mark-Recapture	58
<i>Myodes glareolus</i>	Both	Movement Distance	250.3	250.5	150	450.5	Metres - Linear	Capture-Mark-Recapture	58
<i>Apodemus sylvaticus</i>	Both	Movement Distance	0.25	0.25	0.15	0.45	km-Linear	Capture-Mark-Recapture	58
<i>Myodes glareolus</i>	Both	Movement Distance	0.15	0.15	0.15	0.15	km-Linear	Capture-Mark-Recapture	58
<i>Apodemus sylvaticus</i>	Both	Movement Distance	0.2	0.15	0.15	0.35	km-Linear	Capture-Mark-Recapture	58
<i>Myodes glareolus</i>	Both	Movement Distance	0.2	0.2	0.15	0.25	km-Linear	Capture-Mark-Recapture	58
<i>Phascolarctos cinereus</i>	Male	Natal Dispersal	3.5	2	1.1	9.7	km-Linear	Radio Telemetry	59
<i>Phascolarctos cinereus</i>	Female	Natal Dispersal	3.4	1.7	0.3	10.6	km-Linear	Radio Telemetry	59

<i>Spermophilus beecheyi</i>	Male	Natal Dispersal	179.25	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	60
<i>Spermophilus beecheyi</i>	Female	Natal Dispersal	87.47	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	60
<i>Erinaceus europaeus</i>	Both	Movement Distance	NA	NA	NA	3.78	km-Linear	Radio Telemetry	61
<i>Gazella gazella</i>	Male	Breeding Dispersal	4	NA	1.3	7.3	km-Linear	Radio Telemetry	62
<i>Gazella gazella</i>	Female	Breeding Dispersal	2.8	NA	0.3	8.3	km-Linear	Radio Telemetry	62
<i>Mustela erminea</i>	Male	Natal Dispersal	2.73	1.81	0.35	5.51	km - Linear	Capture-Mark-Recapture	63
<i>Mustela erminea</i>	Female	Natal Dispersal	0.51	0.49	0.22	1.01	km - Linear	Capture-Mark-Recapture	63
<i>Brachylagus idahoensis</i>	Male	Natal Dispersal	NA	1	0	6.5	km-Linear	Radio Telemetry	64
<i>Brachylagus idahoensis</i>	Female	Natal Dispersal	NA	2.9	0	11.9	km-Linear	Radio Telemetry	64
<i>Spermophilus beecheyi</i>	Male	Natal Dispersal	0.48	0.41	0.21	1.14	km - Linear	Capture-Mark-Recapture	65
<i>Spermophilus beecheyi</i>	Female	Natal Dispersal	0.43	0.41	0.21	1.14	km - Linear	Capture-Mark-Recapture	65
<i>Ovis ammon</i>	Unspecified	Migratory	NA	NA	NA	15	km - Linear	Unspecified	66
<i>Capra sibirica</i>	Unspecified	Migratory	NA	NA	20	30	km - Linear	Unspecified	67
<i>Capra sibirica</i>	Unspecified	Migratory	NA	NA	40	50	km - Linear	Unspecified	67
<i>Capra sibirica</i>	Unspecified	Migratory	NA	NA	50	100	km - Linear	Unspecified	67
<i>Rangifer tarandus</i>	Male	Migratory	14.9	NA	NA	NA	km - Linear	Radio Telemetry	68
<i>Rangifer tarandus</i>	Female	Migratory	15.7	NA	NA	NA	km - Linear	Radio Telemetry	68
<i>Aotus azarae</i>	Male	Natal Dispersal	790.44	656	185	2243	Metres - Linear	Radio Telemetry	69
<i>Aotus azarae</i>	Female	Natal Dispersal	587.71	593	262	962	Metres - Linear	Radio Telemetry	69
<i>Antechinus stuartii</i>	Male	Natal Dispersal	NA	NA	0	1230	Metres - Linear	Capture-Mark-Recapture	70

<i>Antechinus stuartii</i>	Female	Natal Dispersal	NA	NA	110	270	Metres - Linear	Capture-Mark-Recapture	70
<i>Lepus californicus</i>	Both	Movement Distance	0.27	0.13	0	28	Miles - Linear	Trapping	71
<i>Canis lupus</i>	Both	Movement Distance	29	NA	5	70	km - Linear	Radio Telemetry	72
<i>Panthera leo</i>	Male	Natal Dispersal	12.3	13.85	3.4	21.9	km - Linear	Direct Observation	73
<i>Gulo gulo</i>	Male	Natal Dispersal	NA	NA	NA	378	km - Linear	Unspecified	74
<i>Cynomys ludovicianus</i>	Male	Natal Dispersal	3.05	3.55	0.5	5.5	km - Linear	Radio Telemetry	75
<i>Cynomys ludovicianus</i>	Female	Natal Dispersal	1.66	1.3	0.5	3.9	km - Linear	Radio Telemetry	75
<i>Procyon lotor</i>	Male	Natal Dispersal	9.7	NA	2.25	33	km - Linear	Radio Telemetry	76
<i>Procyon lotor</i>	Female	Movement Distance	0.6	NA	0.11	1.38	km - Linear	Radio Telemetry	76
<i>Sigmodon hispidus</i>	Unspecified	Movement Distance	7	NA	NA	NA	Miles - Linear	Trapping	77
<i>Neovison vison</i>	Male	Natal Dispersal	33	33	21	45	km - Linear	Radio Telemetry	78
<i>Canis lupus</i>	Both	Natal Dispersal	77	35	8	354	km - Linear	Radio Telemetry	79
<i>Scapanus townsendii</i>	Female	Natal Dispersal	0.181	NA	0.0131	0.856	km-Linear	Capture-Mark-Recapture	80
<i>Scapanus townsendii</i>	Male	Natal Dispersal	0.166	NA	0.013	0.722	km-Linear	Capture-Mark-Recapture	80
<i>Procyon lotor</i>	Male	Movement Distance	19.8	10	3	75	Miles - Linear	Capture-Mark-Recapture	81
<i>Procyon lotor</i>	Female	Movement Distance	9.33	8.5	2	16	Miles - Linear	Capture-Mark-Recapture	81
<i>Hippocamelus bisulcus</i>	Female	Movement Distance	NA	NA	NA	8	km - Linear	Radio Telemetry	82
<i>Hippocamelus bisulcus</i>	Both	Migratory	552	NA	44	1219	Metres - Linear	Radio Telemetry	82
<i>Lepus americanus</i>	Female	Natal Dispersal	3.1	0.275	0.025	16.5	km - Linear	Radio Telemetry	83
<i>Lepus americanus</i>	Male	Natal Dispersal	1.63	1.1	0.125	6.75	km - Linear	Radio Telemetry	83

<i>Alouatta palliata</i>	Female	Natal Dispersal	1300	NA	NA	3000	Metres - Linear	Direct Observation	84
<i>Ursus arctos</i>	Male	Movement Distance	31.5	NA	5	98	km - Linear	Capture-Mark-Recapture	85
<i>Ursus arctos</i>	Male	Movement Distance	48.5	NA	6	134	km - Linear	Capture-Mark-Recapture	85
<i>Ursus arctos</i>	Female	Movement Distance	21.8	NA	2	82	km - Linear	Capture-Mark-Recapture	85
<i>Ursus arctos</i>	Female	Movement Distance	16.6	NA	2	81	km - Linear	Capture-Mark-Recapture	85
<i>Ammotragus lervia</i>	Unspecified	Movement Distance	NA	NA	NA	32.3	km - Linear	Unspecified	86
<i>Ammotragus lervia</i>	Unspecified	Migratory	NA	NA	NA	23.4	km - Linear	Unspecified	86
<i>Equus burchellii</i>	Unspecified	Migratory	NA	NA	100	150	km - Linear	Unspecified	87
<i>Dasyurus maculatus</i>	Male	Movement Distance	NA	NA	NA	11	Miles - Linear	Capture-Mark-Recapture	88
<i>Syncerus caffer</i>	Female	Movement Distance	100.2	120	49	133	km-Linear	Radio Telemetry	89
<i>Pteromys volans</i>	Male	Natal Dispersal	1130	NA	0	5940	Metres - Linear	Radio Telemetry	90
<i>Pteromys volans</i>	Female	Natal Dispersal	2400	NA	0	8720	Metres - Linear	Radio Telemetry	90
<i>Alcelaphus buselaphus</i>	Both	Migratory	NA	NA	NA	200	km - Linear	Unspecified	91
<i>Antidorcas marsupialis</i>	Both	Migratory	NA	NA	0	12.5	km - Linear	Unspecified	91
<i>Connochaetes taurinus</i>	Unspecified	Migratory	NA	NA	NA	300	km - Linear	Radio Telemetry	91
<i>Connochaetes taurinus</i>	Unspecified	Migratory	NA	NA	NA	100	km - Linear	Unspecified	91
<i>Equus burchellii</i>	Unspecified	Migratory	NA	NA	NA	100	km - Linear	Unspecified	91
<i>Eudorcas thomsonii</i>	Unspecified	Migratory	NA	NA	NA	100	km - Linear	Unspecified	91
<i>Kobus kob</i>	Unspecified	Migratory	NA	NA	150	200	km - Linear	Unspecified	91
<i>Taurotragus oryx</i>	Unspecified	Migratory	NA	NA	NA	200	km - Linear	Unspecified	91

<i>Antilocapra americana</i>	Unspecified	Migratory	64	NA	NA	NA	km - Linear	Unspecified	91
<i>Antilocapra americana</i>	Unspecified	Migratory	110	NA	NA	NA	km - Linear	Unspecified	91
<i>Antilocapra americana</i>	Unspecified	Migratory	15	NA	NA	NA	km - Linear	Unspecified	91
<i>Antilocapra americana</i>	Unspecified	Migratory	15	NA	NA	NA	km - Linear	Unspecified	91
<i>Bison bison</i>	Unspecified	Migratory	NA	NA	NA	80	km - Linear	Unspecified	91
<i>Bison bison</i>	Unspecified	Migratory	NA	NA	NA	40	km - Linear	Unspecified	91
<i>Cervus elaphus</i>	Both	Migratory	NA	NA	NA	36.5	km - Linear	Unspecified	91
<i>Cervus elaphus</i>	Both	Migratory	NA	NA	NA	30	km - Linear	Unspecified	91
<i>Cervus elaphus</i>	Both	Migratory	NA	NA	NA	100	km - Linear	Unspecified	91
<i>Rangifer tarandus</i>	Both	Migratory	1515.5	NA	NA	NA	km - Linear	Unspecified	91
<i>Pantholops hodgsonii</i>	Unspecified	Migratory	NA	NA	250	300	km - Linear	Unspecified	91
<i>Vulpes vulpes</i>	Male	Movement Distance	0.28	0.3	0.2	0.4	km - Linear	Capture-Mark-Recapture	92
<i>Vulpes vulpes</i>	Male	Natal Dispersal	2.42	2.3	1.3	3.4	km - Linear	Capture-Mark-Recapture	92
<i>Vulpes vulpes</i>	Female	Movement Distance	0.27	0.3	0.2	0.3	km - Linear	Capture-Mark-Recapture	92
<i>Vulpes vulpes</i>	Female	Natal Dispersal	1.73	1.7	1.4	2.2	km - Linear	Capture-Mark-Recapture	92
<i>Canis latrans</i>	Male	Natal Dispersal	112.89	90	40	308	km - Linear	Radio Telemetry	93
<i>Canis latrans</i>	Female	Natal Dispersal	93.82	61	51	342	km - Linear	Radio Telemetry	93
<i>Odocoileus hemionus</i>	Male	Natal Dispersal	41.25	37.5	20	70	Miles - Linear	Capture-Mark-Recapture	94
<i>Puma concolor</i>	Male	Natal Dispersal	NA	NA	NA	118	km - Linear	Capture-Mark-Recapture	95
<i>Puma concolor</i>	Female	Natal Dispersal	NA	NA	NA	120	km - Linear	Capture-Mark-Recapture	95

<i>Castor canadensis</i>	Both	Movement Distance	9.26	6	0.5	67	Miles - Linear	Capture-Mark-Recapture	96
<i>Spermophilus beldingi</i>	Male	Natal Dispersal	239	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Female	Natal Dispersal	230	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Male	Natal Dispersal	328	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Female	Natal Dispersal	406	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Male	Movement Distance	8	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Female	Movement Distance	6	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Male	Movement Distance	10	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Spermophilus beldingi</i>	Female	Movement Distance	8	NA	NA	NA	Metres - Linear	Radio Telemetry	97
<i>Cynomys gunnisoni</i>	Female	Natal Dispersal	126	NA	38	221	Metres - Linear	Capture-Mark-Recapture	98
<i>Cynomys gunnisoni</i>	Male	Natal Dispersal	198	NA	34	575	Metres - Linear	Capture-Mark-Recapture	98
<i>Cynomys gunnisoni</i>	Female	Breeding Dispersal	125	NA	59	214	Metres - Linear	Capture-Mark-Recapture	98
<i>Cynomys gunnisoni</i>	Male	Breeding Dispersal	163	NA	34	529	Metres - Linear	Capture-Mark-Recapture	98
<i>Antilocapra americana</i>	Both	Migratory	47.1	NA	4.8	64.8	km - Linear	Radio Telemetry	99
<i>Antilocapra americana</i>	Both	Migratory	53.6	NA	11.5	97.7	km - Linear	Radio Telemetry	99
<i>Antilocapra americana</i>	Both	Migratory	32.9	NA	6.8	62	km - Linear	Radio Telemetry	99
<i>Myodes rufocanus</i>	Male	Natal Dispersal	35	NA	NA	NA	Metres - Linear	Radio Telemetry	100
<i>Myodes rufocanus</i>	Female	Natal Dispersal	31	NA	NA	NA	Metres - Linear	Radio Telemetry	100
<i>Procapra gutturosa</i>	Female	Migratory	223.55	223.55	161.7	285.4	km - Linear	Radio Telemetry	101
<i>Procapra gutturosa</i>	Female	Migratory	165.25	165.25	129.7	200.8	km - Linear	Radio Telemetry	101

<i>Antilocapra americana</i>	Female	Natal Dispersal	28.25	28.4	15	41.2	km - Linear	Radio Telemetry	102
<i>Antilocapra americana</i>	Male	Natal Dispersal	101.67	26.2	11.8	267.3	km - Linear	Radio Telemetry	102
<i>Antilocapra americana</i>	Female	Natal Dispersal	25.08	15.6	9.7	75.8	km - Linear	Radio Telemetry	102
<i>Antilocapra americana</i>	Male	Natal Dispersal	30.48	10.5	6.2	132.6	km - Linear	Radio Telemetry	102
<i>Peromyscus leucopus</i>	Male	Natal Dispersal	NA	85	5	183	Metres - Linear	Capture-Mark-Recapture	103
<i>Peromyscus leucopus</i>	Female	Natal Dispersal	NA	25	1	129	Metres - Linear	Capture-Mark-Recapture	103
<i>Vulpes vulpes</i>	Male	Natal Dispersal	NA	NA	NA	110	km - Linear	Capture-Mark-Recapture	104
<i>Vulpes vulpes</i>	Female	Natal Dispersal	NA	NA	NA	140	km - Linear	Capture-Mark-Recapture	104
<i>Aepyprymnus rufescens</i>	Female	Natal Dispersal	NA	NA	0	600	Metres - Linear	Capture-Mark-Recapture	105
<i>Bettongia tropica</i>	Both	Natal Dispersal	NA	NA	900	1300	Metres - Linear	Other	105
<i>Setonix brachyurus</i>	Both	Natal Dispersal	750	NA	NA	NA	Metres - Linear	Unspecified	106
<i>Macropus rufogriseus</i>	Male	Natal Dispersal	670	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	106
<i>Lasiorchinus krefftii</i>	Female	Breeding Dispersal	1.41	1.23	0.3	3.37	km - Linear	Radio Telemetry	107
<i>Lasiorchinus krefftii</i>	Male	Movement Distance	NA	NA	NA	0.38	km - Linear	Radio Telemetry	107
<i>Lontra canadensis</i>	Male	Movement Distance	16.84	8.7	5.6	66.2	km - Linear	Radio Telemetry	108
<i>Lontra canadensis</i>	Female	Movement Distance	6.5	4.5	3.3	12	km - Linear	Radio Telemetry	108
<i>Dipodomys spectabilis</i>	Male	Natal Dispersal	29	17	NA	NA	Metres - Linear	Capture-Mark-Recapture	109
<i>Dipodomys spectabilis</i>	Female	Natal Dispersal	66	30	NA	NA	Metres - Linear	Capture-Mark-Recapture	109
<i>Dipodomys spectabilis</i>	Male	Adult Dispersal	15	0	NA	NA	Metres - Linear	Capture-Mark-Recapture	109
<i>Dipodomys spectabilis</i>	Female	Adult Dispersal	21	0	NA	NA	Metres - Linear	Capture-Mark-Recapture	109

Dipodomys spectabilis	Both	Natal Dispersal	NA	NA	0	87	Metres - Linear	Trapping	110
Dipodomys spectabilis	Both	Natal Dispersal	NA	NA	0	16	Metres - Linear	Trapping	110
Equus burchellii	Both	Migratory	NA	NA	NA	55	km - Linear	Direct Observation	111
Lynx rufus	Both	Natal Dispersal	71.3	84	45	85	km - Linear	Radio Telemetry	112
Peromyscus leucopus	Male	Natal Dispersal	109	NA	20	201	Metres - Linear	Capture-Mark-Recapture	113
Peromyscus leucopus	Female	Natal Dispersal	88	NA	20	282	Metres - Linear	Capture-Mark-Recapture	113
Lynx rufus	Female	Natal Dispersal	22.1	NA	0	56	km - Linear	Radio Telemetry	114
Lynx rufus	Male	Movement Distance	NA	NA	NA	182	km - Linear	Capture-Mark-Recapture	115
Canis lupus	Male	Natal Dispersal	NA	109	35	445	km - Linear	Radio Telemetry	116
Canis lupus	Female	Natal Dispersal	NA	99	60	390	km - Linear	Radio Telemetry	116
Vulpes macrotis	Both	Natal Dispersal	7.8	NA	1.8	32.3	km - Linear	Radio Telemetry	117
Sciurus carolinensis	Unspecified	Natal Dispersal	NA	NA	NA	100	km - Linear	Unspecified	118
Sciurus niger	Unspecified	Natal Dispersal	NA	NA	NA	64.4	km - Linear	Unspecified	119
Sciurus carolinensis	Male	Natal Dispersal	1.1	NA	0.38	3.23	km - Linear	Capture-Mark-Recapture	120
Sciurus carolinensis	Female	Natal Dispersal	NA	NA	NA	0.32	km - Linear	Capture-Mark-Recapture	120
Oryctolagus cuniculus	Male	Natal Dispersal	NA	67.3	NA	NA	Metres - Linear	Direct Observation	121
Oryctolagus cuniculus	Female	Natal Dispersal	NA	44	NA	NA	Metres - Linear	Direct Observation	121
Alces alces	Both	Natal Dispersal	14.8	5.7	NA	NA	km - Linear	Radio Telemetry	122
Peromyscus leucopus	Unspecified	Natal Dispersal	100	NA	NA	1000	Metres - Linear	Unspecified	123
Microtus townsendii	Male	Natal Dispersal	19.4	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	124

<i>Microtus townsendii</i>	Female	Natal Dispersal	12.4	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	124
<i>Vulpes rueppellii</i>	Unspecified	Adult Dispersal	14	NA	5	48	km - Linear	Unspecified	125
<i>Vulpes rueppellii</i>	Unspecified	Natal Dispersal	32	NA	14	48	km - Linear	Unspecified	125
<i>Tamiasciurus hudsonicus</i>	Both	Movement Distance	88.6	NA	0	323	Metres - Linear	Radio Telemetry	126
<i>Cynictis penicillata</i>	Both	Natal Dispersal	2.5	NA	NA	NA	km - Linear	Direct Observation	127
<i>Ursus americanus</i>	Male	Movement Distance	13.55	6.15	0.9	80	km - Linear	Radio Telemetry	128
<i>Ursus americanus</i>	Female	Movement Distance	2.9	1.7	0.2	13.9	km - Linear	Radio Telemetry	128
<i>Castor canadensis</i>	Both	Natal Dispersal	5.6	NA	1	11	Miles - Linear	Capture-Mark-Recapture	129
<i>Pantholops hodgsonii</i>	Female	Migratory	NA	NA	NA	400	km - Linear	Unspecified	130
<i>Castor canadensis</i>	Male	Movement Distance	NA	NA	NA	200	Miles - Linear	Trapping	131
<i>Puma concolor</i>	Male	Natal Dispersal	123	NA	39	241	km - Linear	Radio Telemetry	132
<i>Puma concolor</i>	Female	Natal Dispersal	56.5	56.5	47	66	km - Linear	Radio Telemetry	132
<i>Taxidea taxus</i>	Male	Movement Distance	NA	NA	NA	0.8	km - Linear	Radio Telemetry	133
<i>Taxidea taxus</i>	Female	Movement Distance	NA	NA	NA	2.1	km - Linear	Radio Telemetry	133
<i>Equus caballus</i>	Female	Natal Dispersal	0.848	0.745	0	1.99	km-Linear	Direct Observation	134
<i>Puma concolor</i>	Male	Natal Dispersal	175.67	193	60	274	km - Linear	Capture-Mark-Recapture	135
<i>Puma concolor</i>	Female	Natal Dispersal	11.5	11.5	9	14	km - Linear	Capture-Mark-Recapture	135
<i>Rupicapra rupicapra</i>	Female	Breeding Dispersal	5.8	4	3.5	10.7	km - Linear	Direct Observation	136
<i>Rupicapra rupicapra</i>	Male	Natal Dispersal	5.95	4.1	3.4	17	km - Linear	Direct Observation	136
<i>Rupicapra pyrenaica</i>	Female	Movement Distance	825	7	5	14	km - Linear	Direct Observation	136

<i>Rupicapra pyrenaica</i>	Male	Natal Dispersal	10.6	6	5	32	km - Linear	Direct Observation	136
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	NA	NA	NA	212.6	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	36	NA	NA	NA	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	38	NA	NA	161	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	19	NA	NA	NA	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	18.5	NA	NA	NA	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	10	NA	NA	56	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	8	NA	NA	40.6	km - Linear	Radio Telemetry	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	8.5	NA	NA	35.8	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	7	NA	NA	31.5	km - Linear	Radio Telemetry	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	6.4	NA	NA	22	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	3	NA	NA	7.1	km - Linear	Unspecified	137
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	4.4	NA	NA	NA	km - Linear	Unspecified	137
<i>Dasypus novemcinctus</i>	Male	Movement Distance	231.4	NA	2.3	612.4	Metres - Linear	Capture-Mark-Recapture	138
<i>Dasypus novemcinctus</i>	Female	Movement Distance	210.1	NA	21.8	342.8	Metres - Linear	Capture-Mark-Recapture	138
<i>Dasypus novemcinctus</i>	Male	Movement Distance	202.1	NA	143.7	318.3	Metres - Linear	Capture-Mark-Recapture	138
<i>Dasypus novemcinctus</i>	Female	Movement Distance	299.9	NA	159.9	690.1	Metres - Linear	Capture-Mark-Recapture	138
<i>Canis mesomelas</i>	Both	Natal Dispersal	2.8	NA	NA	NA	km - Linear	Radio Telemetry	139
<i>Canis adustus</i>	Both	Natal Dispersal	4.6	NA	NA	NA	km - Linear	Radio Telemetry	139
<i>Procyon lotor</i>	Male	Movement Distance	NA	NA	NA	165	Miles - Linear	Capture-Mark-Recapture	140

<i>Cerdocyon thous</i>	Both	Natal Dispersal	2370	NA	1900	2900	Metres - Linear	Unspecified	141
<i>Acinonyx jubatus</i>	Male	Natal Dispersal	20	NA	NA	NA	km-Linear	Unspecified	142
<i>Meles meles</i>	Male	Movement Distance	604	400	NA	NA	Metres - Linear	Capture-Mark-Recapture	143
<i>Meles meles</i>	Female	Movement Distance	470	414	NA	NA	Metres - Linear	Capture-Mark-Recapture	143
<i>Aplodontia rufa</i>	Both	Movement Distance	85.73	0	0	563.88	Metres - Linear	Radio Telemetry	144
<i>Spermophilus tridecemlineatus</i>	Male	Natal Dispersal	266.7	NA	152.4	670.56	Metres - Linear	Capture-Mark-Recapture	145
<i>Spermophilus tridecemlineatus</i>	Female	Natal Dispersal	190.5	NA	30.48	762	Metres - Linear	Capture-Mark-Recapture	145
<i>Odocoileus hemionus</i>	Male	Natal Dispersal	4.25	NA	1.9	7.3	km - Linear	Radio Telemetry	146
<i>Odocoileus hemionus</i>	Male	Natal Dispersal	7.86	NA	2.1	14.9	km - Linear	Radio Telemetry	146
<i>Microtus ochrogaster</i>	Male	Natal Dispersal	33	23	4	136	Metres - Linear	Trapping	147
<i>Microtus ochrogaster</i>	Female	Natal Dispersal	28.7	18	2	127	Metres - Linear	Trapping	147
<i>Lycaon pictus</i>	Male	Natal Dispersal	NA	40.7	7.2	169	km-Linear	Radio Telemetry	148
<i>Lycaon pictus</i>	Female	Natal Dispersal	NA	19	3.9	65.3	km-Linear	Radio Telemetry	148
<i>Naemorhedus goral</i>	Unspecified	Migratory	NA	NA	NA	2	km-Linear	Unspecified	149
<i>Bison bison</i>	Unspecified	Migratory	NA	NA	14	40	km - Linear	Unspecified	150
<i>Canis lupus</i>	Unspecified	Movement Distance	NA	NA	NA	206	km - Linear	Unspecified	151
<i>Canis lupus</i>	Unspecified	Migratory	NA	NA	NA	360	km - Linear	Unspecified	151
<i>Lynx canadensis</i>	Female	Movement Distance	NA	NA	NA	79.8	km - Linear	Capture-Mark-Recapture	152
<i>Macaca sylvanus</i>	Male	Natal Dispersal	NA	NA	NA	7.1	km-Linear	Other	153
<i>Lontra canadensis</i>	Male	Natal Dispersal	NA	NA	NA	32	km - Linear	Radio Telemetry	154

<i>Lontra canadensis</i>	Female	Natal Dispersal	NA	NA	NA	192	km - Linear	Radio Telemetry	154
<i>Taxidea taxus</i>	Male	Natal Dispersal	34.1	15	3.75	110	km - Linear	Radio Telemetry	155
<i>Taxidea taxus</i>	Female	Natal Dispersal	23.42	12.5	5.75	52	km - Linear	Radio Telemetry	155
<i>Spermophilus richardsonii</i>	Male	Natal Dispersal	108.33	50	0	975	Metres - Linear	Trapping	156
<i>Spermophilus richardsonii</i>	Female	Natal Dispersal	69.75	50	10	525	Metres - Linear	Trapping	156
<i>Spermophilus richardsonii</i>	Male	Natal Dispersal	NA	NA	3	10	km - Linear	Unspecified	157
<i>Lutra lutra</i>	Unspecified	Movement Distance	NA	NA	15	30	km - Linear	Unspecified	158
<i>Ovis aries</i>	Unspecified	Movement Distance	20	NA	5	70	km - Linear	Unspecified	158
<i>Carcal caracal</i>	Unspecified	Movement Distance	20	NA	NA	NA	km - Linear	Unspecified	158
<i>Carcal caracal</i>	Unspecified	Movement Distance	20	NA	NA	NA	km - Linear	Unspecified	158
<i>Mellivora capensis</i>	Unspecified	Movement Distance	18	NA	10	22	km - Linear	Unspecified	158
<i>Vormela peregusna</i>	Unspecified	Movement Distance	NA	NA	1	2	km - Linear	Unspecified	158
<i>Spermophilopsis leptodactylus</i>	Unspecified	Movement Distance	0.4	NA	NA	0.5	km - Linear	Unspecified	158
<i>Mustela eversmanii</i>	Unspecified	Movement Distance	NA	NA	1	3	km - Linear	Unspecified	158
<i>Allactaga severtzovi</i>	Unspecified	Movement Distance	0.05	NA	NA	0.5	km - Linear	Unspecified	158
<i>Allactaga severtzovi</i>	Unspecified	Movement Distance	300	NA	NA	NA	km - Linear	Unspecified	158
<i>Lynx lynx</i>	Unspecified	Movement Distance	20	NA	10	40	km - Linear	Unspecified	158
<i>Mustela eversmanii</i>	Unspecified	Movement Distance	5	NA	1	10	km - Linear	Unspecified	158
<i>Spermophilopsis leptodactylus</i>	Unspecified	Movement Distance	1	NA	NA	2	km - Linear	Unspecified	158
<i>Ovis ammon</i>	Unspecified	Movement Distance	NA	NA	5	10	km - Linear	Unspecified	158

<i>Spermophilopsis leptodactylus</i>	Unspecified	Movement Distance	0.6	NA	NA	1	km - Linear	Unspecified	158
<i>Paraechinus hypomelas</i>	Unspecified	Movement Distance	0.01	NA	NA	NA	km - Linear	Unspecified	158
<i>Paraechinus hypomelas</i>	Unspecified	Movement Distance	0.02	NA	NA	NA	km - Linear	Unspecified	158
<i>Paraechinus hypomelas</i>	Unspecified	Movement Distance	0.02	NA	NA	0.03	km - Linear	Unspecified	158
<i>Marmota menzbieri</i>	Unspecified	Movement Distance	150	NA	100	300	km - Linear	Unspecified	158
<i>Lynx lynx</i>	Unspecified	Movement Distance	NA	NA	15	20	km - Linear	Unspecified	158
<i>Hystrix indica</i>	Unspecified	Movement Distance	NA	NA	1	5	km - Linear	Unspecified	158
<i>Cervus elaphus</i>	Unspecified	Movement Distance	30	NA	10	90	km - Linear	Unspecified	158
<i>Marmota menzbieri</i>	Unspecified	Natal Dispersal	NA	NA	NA	3.4	km - Linear	Unspecified	158
<i>Marmota menzbieri</i>	Unspecified	Natal Dispersal	NA	NA	NA	5	km - Linear	Unspecified	158
<i>Marmota menzbieri</i>	Unspecified	Natal Dispersal	NA	NA	1	4.5	km - Linear	Unspecified	158
<i>Panthera pardus</i>	Unspecified	Natal Dispersal	NA	NA	100	200	km - Linear	Unspecified	158
<i>Saiga tatarica</i>	Unspecified	Migratory	200	NA	NA	360	km - Linear	Unspecified	158
<i>Ovis aries</i>	Unspecified	Migratory	NA	NA	35	70	km - Linear	Unspecified	158
<i>Ovis ammon</i>	Unspecified	Movement Distance	NA	NA	5	10	km - Linear	Unspecified	158
<i>Desmana moschata</i>	Unspecified	Movement Distance	10	NA	6	22	km - Linear	Unspecified	158
<i>Ovis ammon</i>	Unspecified	Movement Distance	25	NA	10	100	km - Linear	Unspecified	158
<i>Gazella subgutturosa</i>	Unspecified	Movement Distance	100	NA	50	150	km - Linear	Unspecified	158
<i>Ovis ammon</i>	Unspecified	Movement Distance	NA	NA	30	200	km - Linear	Unspecified	158
<i>Ursus arctos</i>	Unspecified	Movement Distance	NA	NA	10	20	km - Linear	Unspecified	158

Gazella subgutturosa	Unspecified	Movement Distance	50	NA	30	70	km - Linear	Unspecified	158
Ovis ammon	Unspecified	Movement Distance	25	NA	10	100	km - Linear	Unspecified	158
Ursus arctos	Unspecified	Movement Distance	30	NA	20	50	km - Linear	Unspecified	158
Ursus arctos	Unspecified	Movement Distance	5	NA	NA	NA	km - Linear	Unspecified	158
Ovis ammon	Unspecified	Movement Distance	NA	NA	5	20	km - Linear	Unspecified	158
Ovis ammon	Unspecified	Movement Distance	100	NA	50	200	km - Linear	Unspecified	158
Capra falconeri	Unspecified	Migratory	60	NA	50	80	km - Linear	Unspecified	158
Ovis aries	Unspecified	Migratory	50	NA	25	100	km - Linear	Unspecified	158
Uncia uncia	Unspecified	Migratory	30	NA	80	NA	km - Linear	Unspecified	158
Equus hemionus	Unspecified	Migratory	NA	NA	50	200	km - Linear	Unspecified	158
Equus hemionus	Unspecified	Migratory	50	NA	30	100	km - Linear	Unspecified	158
Ovis aries	Unspecified	Migratory	NA	NA	10	15	km - Linear	Unspecified	158
Neovison vison	Male	Movement Distance	0.3	NA	0	3	Miles - Linear	Trapping	159
Neovison vison	Female	Movement Distance	0.1	NA	0	1.8	Miles - Linear	Trapping	159
Neovison vison	Male	Movement Distance	0.6	NA	0	2.7	Miles - Linear	Trapping	159
Neovison vison	Female	Movement Distance	0.1	NA	0	0.4	Miles - Linear	Trapping	159
Philantomba monticola	Female	Natal Dispersal	NA	NA	1.5	1.5	km-Linear	Radio Telemetry	160
Arvicola amphibius	Both	Adult Dispersal	452	336.5	186	949	Metres - Linear	Radio Telemetry	161
Leopardus pardalis	Male	Natal Dispersal	11	11	10	12	km - Linear	Unspecified	162
Leopardus pardalis	Male	Natal Dispersal	8.8	10	3.5	13	km - Linear	Unspecified	162

<i>Aepyceros melampus</i>	Male	Natal Dispersal	1.2	NA	0.4	3.2	km-Linear	Direct Observation	163
<i>Capreolus capreolus</i>	Male	Migratory	3.8	NA	2.5	7.1	km - Linear	Radio Telemetry	164
<i>Capreolus capreolus</i>	Female	Migratory	12.4	NA	0.7	45.7	km - Linear	Radio Telemetry	164
<i>Canis latrans</i>	Male	Movement Distance	13.5	NA	5.5	28.2	km - Linear	Capture-Mark-Recapture	165
<i>Canis latrans</i>	Female	Movement Distance	16.9	NA	6.6	31.5	km - Linear	Capture-Mark-Recapture	165
<i>Lynx canadensis</i>	Male	Movement Distance	NA	NA	NA	102	Miles - Linear	Capture-Mark-Recapture	166
<i>Odocoileus virginianus</i>	Male	Breeding Dispersal	3.4	NA	NA	22	km - Linear	Radio Telemetry	167
<i>Odocoileus virginianus</i>	Male	Natal Dispersal	12	NA	NA	NA	km - Linear	Radio Telemetry	167
<i>Odocoileus virginianus</i>	Female	Natal Dispersal	58.71	35.2	17.6	168	km - Linear	Radio Telemetry	168
<i>Odocoileus virginianus</i>	Female	Migratory	27.17	24.5	20	45	km - Linear	Radio Telemetry	169
<i>Peromyscus leucopus</i>	Male	Movement Distance	152.4	85.34	60.96	457.2	Metres - Linear	Capture-Mark-Recapture	170
<i>Peromyscus leucopus</i>	Female	Movement Distance	121.92	121.92	91.44	152.4	Metres - Linear	Capture-Mark-Recapture	170
<i>Peromyscus leucopus</i>	Male	Movement Distance	187.96	228.6	60.96	274.32	Metres - Linear	Capture-Mark-Recapture	170
<i>Peromyscus leucopus</i>	Female	Movement Distance	NA	NA	NA	167.64	Metres - Linear	Capture-Mark-Recapture	170
<i>Urocyon cinereoargenteus</i>	Male	Natal Dispersal	16.17	16	8.5	24	km - Linear	Radio Telemetry	171
<i>Urocyon cinereoargenteus</i>	Female	Natal Dispersal	0.75	0	0	3	km - Linear	Radio Telemetry	171
<i>Caracal caracal</i>	Male	Natal Dispersal	NA	NA	NA	90	km-Linear	Unspecified	172
<i>Lepus americanus</i>	Both	Natal Dispersal	3.38	0.4	0.21	12.5	Miles - Linear	Capture-Mark-Recapture	173
<i>Antilocapra americana</i>	Both	Migratory	NA	NA	NA	160	km - Linear	Unspecified	174
<i>Genetta genetta</i>	Male	Movement Distance	NA	NA	NA	22	km - Linear	Radio Telemetry	175

Bettongia lesueur	Male	Natal Dispersal	5200	NA	NA	NA	Metres - Linear	Radio Telemetry	176
Bettongia lesueur	Female	Natal Dispersal	1900	NA	NA	NA	Metres - Linear	Radio Telemetry	176
Gulo gulo	Male	Movement Distance	NA	NA	NA	64	km - Linear	Unspecified	177
Gulo gulo	Female	Movement Distance	NA	NA	NA	38	km - Linear	Unspecified	177
Gulo gulo	Female	Movement Distance	NA	NA	NA	300	km - Linear	Unspecified	177
Canis latrans	Both	Natal Dispersal	40	NA	NA	NA	km - Linear	Radio Telemetry	178
Canis latrans	Both	Natal Dispersal	53	NA	NA	NA	km - Linear	Radio Telemetry	178
Ochotona princeps	Unspecified	Natal Dispersal	91.25	NA	15	396	Metres - Linear	Trapping	179
Rattus fuscipes	Both	Movement Distance	35.32	NA	0	280	Metres - Linear	Capture-Mark-Recapture	180
Spermophilus elegans	Male	Natal Dispersal	90	NA	NA	NA	Metres - Linear	Direct Observation	181
Spermophilus elegans	Female	Natal Dispersal	77	NA	NA	NA	Metres - Linear	Direct Observation	181
Vulpes vulpes	Male	Natal Dispersal	18.4	10.1	0	101.2	Miles - Linear	Capture-Mark-Recapture	182
Vulpes vulpes	Female	Natal Dispersal	6.2	2.2	NA	52.1	Miles - Linear	Capture-Mark-Recapture	182
Lynx lynx	Both	Movement Distance	163	88	17	930	km - Linear	Radio Telemetry	183
Dipodomys stephensi	Female	Adult Dispersal	35.6	22.7	0	246.2	Metres - Linear	Capture-Mark-Recapture	184
Dipodomys stephensi	Male	Adult Dispersal	38	30	0	216.9	Metres - Linear	Capture-Mark-Recapture	184
Dipodomys stephensi	Female	Natal Dispersal	28.7	16.5	0	170.6	Metres - Linear	Capture-Mark-Recapture	184
Dipodomys stephensi	Male	Natal Dispersal	33.3	22.4	0	267.1	Metres - Linear	Capture-Mark-Recapture	184
Dipodomys stephensi	Female	Adult Dispersal	34.7	30	0	223	Metres - Linear	Capture-Mark-Recapture	184
Dipodomys stephensi	Male	Adult Dispersal	43	33.5	0	323.1	Metres - Linear	Capture-Mark-Recapture	184

Dipodomys stephensi	Female	Natal Dispersal	46.2	15	0	351.1	Metres - Linear	Capture-Mark-Recapture	184
Dipodomys stephensi	Male	Natal Dispersal	61.5	30	0	262.4	Metres - Linear	Capture-Mark-Recapture	184
Procyon lotor		Movement Distance	NA	NA	NA	165	Miles - Linear	Capture-Mark-Recapture	185
Calomys venustus	Male	Natal Dispersal	NA	NA	NA	28	Metres - Linear	Direct Observation	186
Calomys venustus	Female	Natal Dispersal	NA	NA	NA	28	Metres - Linear	Direct Observation	186
Microcebus murinus	Male	Natal Dispersal	NA	251	0	1000	Metres - Linear	Capture-Mark-Recapture	187
Microcebus murinus	Female	Natal Dispersal	NA	63	0	351	Metres - Linear	Capture-Mark-Recapture	187
Peromyscus maniculatus	Both	Movement Distance	306.3	NA	141	1320	Metres - Linear	Capture-Mark-Recapture	188
Peromyscus californicus	Male	Natal Dispersal	70	41	0	450	Metres - Linear	Capture-Mark-Recapture	189
Peromyscus californicus	Female	Natal Dispersal	155	97	12	791	Metres - Linear	Capture-Mark-Recapture	189
Oreamnos americanus	Unspecified	Migratory	NA	NA	NA	16	km - Linear	Unspecified	190
Oreamnos americanus	Unspecified	Migratory	NA	NA	1.7	11.1	km - Linear	Unspecified	190
Odocoileus hemionus	Male	Natal Dispersal	4.34	1.55	0.5	42	Miles - Linear	Capture-Mark-Recapture	191
Odocoileus hemionus	Female	Natal Dispersal	3.59	0.5	0.5	51	Miles - Linear	Capture-Mark-Recapture	191
Odocoileus hemionus	Male	Natal Dispersal	NA	NA	60	150	Miles - Linear	Capture-Mark-Recapture	191
Lynx rufus	Female	Movement Distance	3.33	2.75	0	7	Miles - Linear	Capture-Mark-Recapture	192
Lynx rufus	Male	Movement Distance	5.54	2.5	0	23	Miles - Linear	Capture-Mark-Recapture	192
Canis latrans	Female	Movement Distance	11.1	5	0	115	Miles - Linear	Capture-Mark-Recapture	192
Canis latrans	Female	Movement Distance	21.4	NA	NA	NA	Miles - Linear	Capture-Mark-Recapture	192
Canis latrans	Male	Movement Distance	7.9	2	NA	NA	Miles - Linear	Capture-Mark-Recapture	192

<i>Canis latrans</i>	Male	Movement Distance	28.5	NA	NA	NA	Miles - Linear	Capture-Mark-Recapture	192
<i>Lynx rufus</i>	Female	Movement Distance	4.52	1.5	0.13	19	Miles - Linear	Capture-Mark-Recapture	192
<i>Tamandua tetradactyla</i>	Female	Movement Distance	0.842	0.74	0.25	1.52	km - Linear	Radio Telemetry	193
<i>Tamandua tetradactyla</i>	Male	Movement Distance	1.213	1.13	0.34	2.17	km - Linear	Radio Telemetry	193
<i>Ursus americanus</i>	Male	Natal Dispersal	61	49	13	219	km - Linear	Radio Telemetry	194
<i>Ursus americanus</i>	Female	Natal Dispersal	0.71	0	0	11	km - Linear	Radio Telemetry	194
<i>Spermophilus tridecemlineatus</i>	Female	Natal Dispersal	53.1	NA	0	144	Metres - Linear	Capture-Mark-Recapture	195
<i>Spermophilus tridecemlineatus</i>	Male	Natal Dispersal	80.3	NA	0	239	Metres - Linear	Capture-Mark-Recapture	195
<i>Helogale parvula</i>	Male	Movement Distance	NA	0.5	NA	1.8	km - Linear	Direct Observation	196
<i>Helogale parvula</i>	Female	Movement Distance	NA	1	NA	5	km - Linear	Direct Observation	196
<i>Puma concolor</i>	Both	Natal Dispersal	86.8	NA	30	155	km - Linear	Radio Telemetry	197
<i>Antechinus minimus</i>	Male	Natal Dispersal	41.2	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	198
<i>Antechinus minimus</i>	Female	Natal Dispersal	40.9	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	198
<i>Microtus agrestis</i>	Male	Natal Dispersal	58.5	NA	7.8	159	Metres - Linear	Capture-Mark-Recapture	199
<i>Microtus agrestis</i>	Female	Natal Dispersal	28.6	NA	0	193.6	Metres - Linear	Capture-Mark-Recapture	199
<i>Microtus agrestis</i>	Male	Movement Distance	10.2	7.2	0	80.5	Metres - Linear	Trapping	200
<i>Microtus agrestis</i>	Female	Movement Distance	9	5.9	0	108	Metres - Linear	Trapping	200
<i>Lynx canadensis</i>	Female	Movement Distance	2.75	1.5	0	5.5	Miles - Linear	Capture-Mark-Recapture	201
<i>Lynx canadensis</i>	Male	Movement Distance	14.67	5	1.5	64	Miles - Linear	Capture-Mark-Recapture	201
<i>Odocoileus hemionus</i>	Both	Migratory	84.1	NA	20	158	km - Linear	Radio Telemetry	202

<i>Antilocapra americana</i>	Female	Migratory	177.2	NA	116	258	km - Linear	Radio Telemetry	202
<i>Perameles gunnii</i>	Male	Movement Distance	NA	NA	NA	2.3	km - Linear	Unspecified	203
<i>Ovis canadensis</i>	Unspecified	Migratory	NA	NA	NA	48	km - Linear	Unspecified	204
<i>Vulpes vulpes</i>	Male	Natal Dispersal	NA	NA	NA	17	Miles - Linear	Capture-Mark-Recapture	205
<i>Vulpes vulpes</i>	Male	Movement Distance	NA	NA	NA	11	Miles - Linear	Capture-Mark-Recapture	205
<i>Vulpes vulpes</i>	Female	Natal Dispersal	2.75	2.75	0.5	5	Miles - Linear	Capture-Mark-Recapture	205
<i>Vulpes vulpes</i>	Female	Movement Distance	1.75	1.75	1.5	2	Miles - Linear	Capture-Mark-Recapture	205
<i>Urocyon cinereoargenteus</i>	Female	Movement Distance	31.5	31.5	11	52	Miles - Linear	Capture-Mark-Recapture	205
<i>Elephas maximus</i>	Unspecified	Migratory	NA	NA	30	40	km - Linear	Unspecified	206
<i>Canis simensis</i>	Female	Natal Dispersal	NA	NA	NA	7.5	km-Linear	Unspecified	207
<i>Lycalopex griseus</i>	Unspecified	Natal Dispersal	NA	NA	8	65	km-Linear	Unspecified	208
<i>Canis adustus</i>	Unspecified	Natal Dispersal	NA	NA	NA	20	km-Linear	Unspecified	208
<i>Ochotona princeps</i>	Both	Natal Dispersal	0.00556	0	0	0.17	km-Linear	Direct Observation	209
<i>Panthera tigris</i>	Male	Natal Dispersal	33.01	25.8	9.5	65.7	km - Linear	Radio Telemetry	210
<i>Panthera tigris</i>	Female	Natal Dispersal	11.65	6.8	0	33	km - Linear	Radio Telemetry	210
<i>Odocoileus virginianus</i>	Unspecified	Migratory	NA	NA	15.6	23.2	km - Linear	Unspecified	211
<i>Tamias striatus</i>	Unspecified	Movement Distance	NA	NA	NA	857	Metres - Linear	Unspecified	212
<i>Phascogale tapoatafa</i>	Male	Natal Dispersal	5.03	NA	NA	NA	km - Linear	Radio Telemetry	213
<i>Phascogale tapoatafa</i>	Female	Natal Dispersal	0.66	NA	NA	NA	km - Linear	Radio Telemetry	213
<i>Saiga tatarica</i>	Unspecified	Migratory	NA	NA	80	120	km-Linear	Unspecified	214

Bison bison	Unspecified	Migratory	NA	NA	NA	150	Miles - Linear	Unspecified	215
Microtus oeconomus	Male	Movement Distance	1310	1000	850	2350	Metres - Linear	Radio Telemetry	216
Ursus arctos	Male	Natal Dispersal	118.9	NA	NA	467	km - Linear	Radio Telemetry	217
Ursus arctos	Female	Natal Dispersal	28	NA	NA	90	km - Linear	Radio Telemetry	217
Vulpes vulpes	Male	Natal Dispersal	31	22	0	210.18	km-Linear	Radio Telemetry	218
Vulpes vulpes	Female	Natal Dispersal	10.78	3.06	0	107.83	km-Linear	Radio Telemetry	218
Urocyon cinereoargenteus	Female	Movement Distance	1.75	0.5	0.25	4.5	Miles - Linear	Capture-Mark-Recapture	219
Tamiasciurus hudsonicus	Male	Natal Dispersal	115	100	0	260	Metres - Linear	Radio Telemetry	220
Tamiasciurus hudsonicus	Female	Natal Dispersal	242.5	185	0	600	Metres - Linear	Radio Telemetry	220
Panthera pardus	Male	Natal Dispersal	9.83	10	8.5	11	km - Linear	Radio Telemetry	221
Didelphis virginiana	Male	Natal Dispersal	NA	NA	NA	4.3	km-Linear	Unspecified	222
Didelphis virginiana	Female	Natal Dispersal	NA	NA	NA	5.152	km-Linear	Unspecified	222
Sorex araneus	Both	Natal Dispersal	NA	NA	NA	0.869	km-Linear	Trapping	222
Mephitis mephitis	Male	Natal Dispersal	NA	NA	NA	10.1	km-Linear	Unspecified	222
Mephitis mephitis	Female	Natal Dispersal	NA	NA	NA	21.7	km-Linear	Unspecified	222
Microtus pennsylvanicus	Both	Natal Dispersal	NA	NA	NA	0.245	km-Linear	Unspecified	222
Martes americana	Both	Natal Dispersal	NA	NA	NA	61	km-Linear	Unspecified	222
Ondatra zibethicus	Both	Natal Dispersal	NA	NA	NA	3.37	km-Linear	Unspecified	222
Alces alces	Both	Natal Dispersal	NA	NA	NA	118	km-Linear	Unspecified	222
Puma concolor	Male	Natal Dispersal	101.3	NA	47.1	192.5	km - Linear	Radio Telemetry	223

Puma concolor	Female	Natal Dispersal	28.3	NA	5.6	78.5	km - Linear	Radio Telemetry	223
Puma concolor	Female	Movement Distance	3.2	NA	0.7	9.9	km - Linear	Radio Telemetry	223
Alces alces	Both	Migratory	33.03	34.9	8	55.4	km - Linear	Radio Telemetry	224
Alces alces	Both	Migratory	34.65	36.2	5	53.3	km - Linear	Radio Telemetry	224
Marmota monax	Female	Natal Dispersal	NA	NA	NA	685	Metres - Linear	Capture-Mark-Recapture	225
Marmota monax	Male	Natal Dispersal	NA	NA	NA	768	Metres - Linear	Capture-Mark-Recapture	225
Peromyscus polionotus	Male	Natal Dispersal	175	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	226
Peromyscus polionotus	Female	Natal Dispersal	140.5	NA	NA	NA	Metres - Linear	Capture-Mark-Recapture	226
Microtus breweri	Both	Movement Distance	NA	30.5	30.5	750	Metres - Linear	Capture-Mark-Recapture	227
Rattus fuscipes	Female	Natal Dispersal	NA	NA	NA	213	Metres - Linear	Unspecified	228
Rattus fuscipes	Male	Natal Dispersal	NA	NA	NA	762	Metres - Linear	Unspecified	228
Rattus fuscipes	Both	Natal Dispersal	NA	NA	NA	365	Metres - Linear	Trapping	228
Rattus fuscipes	Unspecified	Natal Dispersal	NA	NA	NA	500	Metres - Linear	Other	228
Rattus fuscipes	Unspecified	Natal Dispersal	NA	NA	NA	550	Metres - Linear	Unspecified	228
Puma concolor	Male	Movement Distance	NA	NA	NA	1067	km - Linear	Radio Telemetry	229
Canis lupus	Both	Movement Distance	20.1	NA	1	184	km-Linear	Radio Telemetry	230
Vulpes vulpes	Male	Natal Dispersal	7.9	NA	1.6	13.7	km - Linear	Capture-Mark-Recapture	231
Vulpes vulpes	Female	Natal Dispersal	3.1	NA	1.6	5.2	km - Linear	Capture-Mark-Recapture	231
Vulpes vulpes	Male	Natal Dispersal	2.8	NA	NA	NA	km - Linear	Capture-Mark-Recapture	231
Vulpes vulpes	Male	Natal Dispersal	NA	NA	NA	19	km - Linear	Capture-Mark-Recapture	231

<i>Vulpes vulpes</i>	Male	Natal Dispersal	NA	NA	2.5	52	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	NA	NA	2.5	24	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Male	Natal Dispersal	NA	NA	NA	110	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	NA	NA	NA	140	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Male	Natal Dispersal	29.8	NA	8	64.9	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	38.6	NA	8	67.7	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Male	Natal Dispersal	NA	NA	NA	86	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	NA	NA	NA	4	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Male	Natal Dispersal	34.2	NA	8	61.4	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	28.6	NA	8	85.7	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Male	Natal Dispersal	17.4	NA	2.4	89.6	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	11.1	NA	2.4	60.8	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Male	Natal Dispersal	31.2	NA	3	122	km - Linear	Capture-Mark-Recapture	231
<i>Vulpes vulpes</i>	Female	Natal Dispersal	8.4	NA	3	50	km - Linear	Capture-Mark-Recapture	231
<i>Spermophilus saturatus</i>	Male	Natal Dispersal	181.8	NA	166.4	197.2	Metres - Linear	Capture-Mark-Recapture	232
<i>Spermophilus saturatus</i>	Female	Natal Dispersal	157.5	NA	44.6	270.5	Metres - Linear	Capture-Mark-Recapture	232
<i>Bison bison</i>	Both	Migratory	NA	NA	NA	25	km - Linear	Direct Observation	233
<i>Blarina brevicauda</i>	Unspecified	Movement Distance	NA	162	NA	NA	Metres - Linear	Unspecified	234
<i>Microtus pennsylvanicus</i>	Unspecified	Movement Distance	NA	66	NA	NA	Metres - Linear	Unspecified	234
<i>Tamias striatus</i>	Unspecified	Movement Distance	NA	116	NA	NA	Metres - Linear	Unspecified	234

<i>Vulpes macrotis</i>	Unspecified	Movement Distance	NA	5535	NA	NA	Metres - Linear	Unspecified	234
<i>Spermophilus columbianus</i>	Unspecified	Movement Distance	NA	345	NA	NA	Metres - Linear	Unspecified	234
<i>Mustela nigripes</i>	Unspecified	Movement Distance	NA	2473	NA	NA	Metres - Linear	Unspecified	234
<i>Marmota flaviventris</i>	Both	Movement Distance	NA	NA	NA	15.5	km - Linear	Radio Telemetry	235
<i>Gulo gulo</i>	Male	Natal Dispersal	51	NA	11	101	km - Linear	Radio Telemetry	236
<i>Gulo gulo</i>	Female	Natal Dispersal	60	NA	15	178	km - Linear	Radio Telemetry	236
<i>Thomomys bottae</i>	Male	Movement Distance	66.14	NA	38.1	109.73	Metres - Linear	Trapping	237
<i>Thomomys bottae</i>	Female	Movement Distance	31.39	NA	0	83.82	Metres - Linear	Trapping	237
<i>Thomomys bottae</i>	Male	Movement Distance	111.56	NA	30.5	274.32	Metres - Linear	Trapping	237
<i>Thomomys bottae</i>	Female	Movement Distance	137.16	NA	61	213.36	Metres - Linear	Trapping	237
<i>Thomomys talpoides</i>	Male	Movement Distance	377.95	NA	160	789.43	Metres - Linear	Trapping	237
<i>Thomomys talpoides</i>	Female	Movement Distance	158.5	NA	76.2	233.17	Metres - Linear	Trapping	237
<i>Thomomys talpoides</i>	Male	Movement Distance	190.5	NA	NA	NA	Metres - Linear	Trapping	237
<i>Thomomys talpoides</i>	Female	Movement Distance	248.41	NA	15.2	643.13	Metres - Linear	Trapping	237
<i>Lasiorninus latifrons</i>	Male	Movement Distance	660	NA	NA	1849	Metres - Linear	Other	238
<i>Lasiorninus latifrons</i>	Female	Movement Distance	449	NA	NA	1253	Metres - Linear	Other	238
<i>Canis lupus</i>	Both	Migratory	508	NA	NA	NA	km - Linear	Radio Telemetry	239
<i>Sciurus vulgaris</i>	Male	Movement Distance	NA	NA	NA	350	Metres - Linear	Radio Telemetry	240
<i>Sciurus vulgaris</i>	Female	Movement Distance	280	280	60	500	Metres - Linear	Radio Telemetry	240
<i>Sciurus vulgaris</i>	Male	Movement Distance	NA	NA	NA	1460	Metres - Linear	Radio Telemetry	240

<i>Sciurus vulgaris</i>	Male	Movement Distance	NA	NA	NA	710	Metres - Linear	Radio Telemetry	240
<i>Sciurus vulgaris</i>	Female	Movement Distance	547.5	547.5	125	970	Metres - Linear	Radio Telemetry	240
<i>Capra caucasica</i>	Unspecified	Migratory	NA	NA	NA	5	km - Linear	Unspecified	241
<i>Capra caucasica</i>	Unspecified	Migratory	NA	NA	NA	5	km - Linear	Unspecified	241
<i>Capra caucasica</i>	Unspecified	Migratory	NA	NA	NA	15	km - Linear	Unspecified	241
<i>Leopoldamys sabanus</i>	Both	Movement Distance	1443	NA	618	4742	Metres - Linear	Radio Telemetry	242
<i>Thomomys bottae</i>	Male	Movement Distance	112.5	NA	55	215	Metres - Linear	Trapping	243
<i>Thomomys bottae</i>	Female	Movement Distance	74.44	NA	45	120	Metres - Linear	Trapping	243
<i>Cratogeomys castanops</i>	Male	Movement Distance	391	NA	135	595	Metres - Linear	Trapping	243
<i>Cratogeomys castanops</i>	Female	Movement Distance	85	NA	60	100	Metres - Linear	Trapping	243
<i>Cratogeomys castanops</i>	Female	Movement Distance	185	NA	65	340	Metres - Linear	Trapping	243
<i>Microtus xanthognathus</i>	Female	Movement Distance	0.3	0.3	0.3	0.3	km - Linear	Trapping	244
<i>Microtus xanthognathus</i>	Female	Movement Distance	0.3	0.3	0.3	0.3	km - Linear	Trapping	244
<i>Microtus xanthognathus</i>	Male	Movement Distance	0.55	0.55	0.3	0.8	km - Linear	Trapping	244
<i>Microtus xanthognathus</i>	Male	Movement Distance	0.28	0.3	0.2	0.3	km - Linear	Trapping	244
<i>Vulpes lagopus</i>	Female	Migratory	NA	NA	NA	840	km - Linear	Trapping	245
<i>Vulpes lagopus</i>	Unspecified	Movement Distance	NA	NA	NA	1000	km - Linear	Radio Telemetry	245
<i>Vulpes lagopus</i>	Unspecified	Movement Distance	NA	NA	NA	1530	km - Linear	Trapping	245
<i>Odocoileus hemionus</i>	Both	Migratory	18.5	NA	0.25	80	Miles - Linear	Direct Observation	246
<i>Macropus giganteus</i>	Male	Natal Dispersal	NA	NA	NA	17	km-Linear	Unspecified	247

Vulpes vulpes	Both	Natal Dispersal	NA	NA	5	100	km - Linear	Radio Telemetry	248
Lynx lynx	Male	Natal Dispersal	27.68	26.6	4.5	56	km - Linear	Radio Telemetry	249
Lynx lynx	Female	Natal Dispersal	18.82	20.6	7.4	33.3	km - Linear	Radio Telemetry	249
Lynx lynx	Male	Natal Dispersal	51.18	31.4	19.1	97.3	km - Linear	Radio Telemetry	249
Lynx lynx	Female	Natal Dispersal	35.59	27.6	2.1	80.7	km - Linear	Radio Telemetry	249

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Supplementary Table A1.2 – Extra life history trait data from literature search.

Species Name	Trait	Original data	Original units	Measure	Ref
Sciurus niger	Body Mass	800	grams	Unspecified	5
Scapanus townsendii	Body Mass	141.7	grams	Mean	14
Neovison vison	Body Mass	1260	grams	Mean	26
Neovison vison	Body Mass	750	grams	Mean	26
Marmota menzbieri	Body Mass	2386.05	grams	Mean	43
Lycalopex griseus	Body Mass	4000	grams	Mean	54
Lycalopex griseus	Body Mass	3300	grams	Mean	54
Spermophilus saturatus	Body Mass	275	grams	Unspecified	60
Bettongia lesueur	Diet count	4	-	-	7
Macropus rufogriseus	Diet count	2	-	-	9
Calomys venustus	Diet count	2	-	-	15
Chlorocebus aethiops	Diet count	7	-	-	16
Antechinus minimus	Diet count	2	-	-	18
Bettongia tropica	Diet count	6	-	-	19
Rupicapra pyrenaica	Diet count	3	-	-	23
Sciurus niger	Diet count	5	-	-	30
Peromyscus polionotus	Diet count	4	-	-	35
Microtus agrestis	Diet count	3	-	-	37
Microtus arvalis	Diet count	5	-	-	39
Neovison vison	Diet count	2	-	-	40
Phascogale tapoatafa	Diet count	2	-	-	41
Vulpes macrotis	Diet count	2	-	-	44
Aepyprymnus rufescens	Diet count	7	-	-	45
Myodes rufocanus	Diet count	3	-	-	52
Lycalopex griseus	Diet count	2	-	-	54
Spermophilus beecheyi	Diet count	3	-	-	56
Scapanus townsendii	Diet count	2	-	-	58
Spermophilus saturatus	Diet count	6	-	-	60
Lepus europaeus	Diet count	3	-	-	62
Chlorocebus aethiops	Gestation Length	162	days	Unspecified	1
Lycalopex griseus	Gestation Length	56	days	Unspecified	2

Neovison vison	Gestation Length	42	days	Unspecified	3
Sciurus niger	Gestation Length	44	days	Unspecified	5
Spermophilus saturatus	Gestation Length	28	days	Unspecified	6
Dipodomys stephensi	Gestation Length	30	days	Unspecified	13
Scapanus townsendii	Gestation Length	35	days	Unspecified	14
Chlorocebus aethiops	Gestation Length	165	days	Unspecified	16
Rupicapra pyrenaica	Gestation Length	170	days	Unspecified	23
Vulpes rueppellii	Gestation Length	50	days	Unspecified	29
Calomys venustus	Gestation Length	22	days	Unspecified	48
Aotus azarae	Gestation Length	129.5	days	Unspecified	55
Vulpes macrotis	Gestation Length	52.5	days	Unspecified	63
Mellivora capensis	Home Range	541	km2	Mean	10
Mellivora capensis	Home Range	126	km2	Mean	10
Chlorocebus aethiops	Home Range	0.4	km2	Mean	17
Aotus azarae	Home Range	0.103	km2	Unspecified	21
Aepyprymnus rufescens	Home Range	51.5	hectares	Mean	22
Aepyprymnus rufescens	Home Range	90	hectares	Mean	22
Bettongia tropica	Home Range	51	hectares	Unspecified	22
Bettongia tropica	Home Range	74	hectares	Unspecified	22
Neovison vison	Home Range	3.3	km2	Median	25
Neovison vison	Home Range	2.2	km2	Median	25
Setonix brachyurus	Home Range	5.91	hectares	Mean	27
Setonix brachyurus	Home Range	6.92	hectares	Mean	27
Spermophilus beldingi	Home Range	500	m2	Median	28
Rattus fuscipes	Home Range	0.25	km2	Unspecified	33
Rupicapra pyrenaica	Home Range	125	hectares	Mean	36
Rupicapra pyrenaica	Home Range	400	hectares	Mean	36
Philantomba monticola	Home Range	5.86	km2	Mean	38
Phascogale tapoatafa	Home Range	40	hectares	Mean	41
Phascogale tapoatafa	Home Range	100	hectares	Unspecified	41
Calomys venustus	Home Range	98-710	m2	Mean	47
Calomys venustus	Home Range	98-588.7	m2	Mean	47
Antechinus minimus	Home Range	1.7	hectares	Mean	50
Antechinus minimus	Home Range	2.7	hectares	Mean	50

Scapanus townsendii	Home Range	0.17	hectares	Mean	51
Bettongia lesueur	Home Range	1	km2	Maximum	53
Lycalopex griseus	Home Range	2.45	km2	Mean	54
Caracal caracal	Population Density	0.35	Individuals/km2	Mean	8
Mellivora capensis	Population Density	0.1	Individuals/km2	Unspecified	11
Mellivora capensis	Population Density	0.03	Individuals/km2	Unspecified	11
Lepus europaeus	Population Density	47	Individuals/km2	Mean	12
Scapanus townsendii	Population Density	0.42-12.4	Individuals/ha	Unspecified	14
Pteromys volans	Population Density	0.04	Individuals/ha	Unspecified	24
Pteromys volans	Population Density	0.08	Individuals/ha	Unspecified	24
Vulpes rueppellii	Population Density	0.18-0.44	Individuals/km2	Unspecified	32
Equus caballus	Population Density	9.89	Individuals/km2	Mean	34
Rupicapra pyrenaica	Population Density	34	Individuals/km2	Minimum	36
Rupicapra rupicapra	Population Density	24	Individuals/km2	Minimum	36
Neovison vison	Population Density	9-22	Individuals/square mile	Unspecified	40
Ondatra zibethicus	Population Density	6-90	Individuals/ha	Unspecified	42
Calomys venustus	Population Density	66	Individuals/ha	Mean	49
Lycalopex griseus	Population Density	1	Individuals/km2	Unspecified	54
Cynictis penicillata	Population Density	6.0-7.1	Individuals/100ha	Unspecified	57
Spermophilus saturatus	Population Density	2-4.5	Individuals/ha	Unspecified	59
Marmota menzbieri	Population Density	30	Individuals/km2	Mean	61
Bettongia lesueur	Trophic Level	2	-	-	7
Macropus rufogriseus	Trophic Level	1	-	-	9
Calomys venustus	Trophic Level	2	-	-	15
Chlorocebus aethiops	Trophic Level	2	-	-	16
Antechinus minimus	Trophic Level	3	-	-	18
Bettongia tropica	Trophic Level	2	-	-	19
Rupicapra pyrenaica	Trophic Level	1	-	-	23
Sciurus niger	Trophic Level	2	-	-	30
Peromyscus polionotus	Trophic Level	2	-	-	35
Microtus agrestis	Trophic Level	1	-	-	37
Microtus arvalis	Trophic Level	2	-	-	39
Neovison vison	Trophic Level	3	-	-	40
Phascogale tapoatafa	Trophic Level	3	-	-	41

<i>Vulpes macrotis</i>	Trophic Level	3	-	-	44
<i>Aepyprymnus rufescens</i>	Trophic Level	2	-	-	45
<i>Myodes rufocanus</i>	Trophic Level	1	-	-	52
<i>Lycalopex griseus</i>	Trophic Level	3	-	-	54
<i>Spermophilus beecheyi</i>	Trophic Level	1	-	-	56
<i>Scapanus townsendii</i>	Trophic Level	2	-	-	58
<i>Spermophilus saturatus</i>	Trophic Level	2	-	-	60
<i>Lepus europaeus</i>	Trophic Level	1	-	-	62
<i>Neovison vison</i>	Weaning Age	49	days	Unspecified	3
<i>Pteromys volans</i>	Weaning Age	46	days	Unspecified	4
<i>Sciurus niger</i>	Weaning Age	84	days	Unspecified	5
<i>Spermophilus saturatus</i>	Weaning Age	43	days	Unspecified	6
<i>Brachylagus idahoensis</i>	Weaning Age	15.4	days	Mean	20
<i>Vulpes rueppellii</i>	Weaning Age	42-56	days	Unspecified	29
<i>Rupicapra pyrenaica</i>	Weaning Age	6	months	Unspecified	31
<i>Vulpes macrotis</i>	Weaning Age	8	weeks	Unspecified	44
<i>Calomys venustus</i>	Weaning Age	20	days	Unspecified	46
<i>Scapanus townsendii</i>	Weaning Age	30-36	days	Unspecified	51
<i>Lycalopex griseus</i>	Weaning Age	4-5	months	Unspecified	54
<i>Lepus europaeus</i>	Weaning Age	30	days	Mean	62

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Appendix 2. Supporting information for chapter 3.

Supplementary Table A2.1 - Variance inflation factors for maximal linear models of dispersal distance.

Main effects (log)	Maximum dispersal distance model	Median dispersal distance model
<i>Adult body mass (grams)</i>	5.122	5.408
<i>Home range (km²)</i>	7.691	8.869
<i>Trophic level</i>	2.337	2.520
<i>Population density (individuals per km²)</i>	4.753	6.722
<i>Geographic range (km²)</i>	1.405	1.736
<i>Gestation length (days)</i>	2.553	2.924
<i>Weaning age (days)</i>	1.728	1.797

Supplementary Table A2.2 - Phylogenetic signal of predictor variables in the data set.

Confidence limits are set at 95% for (a) maximum dispersal distance data set and (b) median dispersal distance data set. NOTE - D statistic for trophic level – maximum dispersal data set: 1 (probability of trait distribution resulting from no phylogenetic structure: 0 / probability of trait distribution resulting from Brownian phylogenetic structure: 1); D statistic for trophic level – median dispersal data set: -0.5167353 (probability of trait distribution resulting from no phylogenetic structure: 0 / probability of trait distribution resulting from Brownian phylogenetic structure: 0.981).

	(a) Lambda (95% CI)	(b) Lambda (95% CI)
<i>Body mass (grams)</i>	0.995 (0.964 – 1)	0.989 (0.948 – 1)
<i>Home range size (km²)</i>	0.869 (0.745 – 0.939)	0.817 (0.664 – 0.912)
<i>Population density (individuals per km²)</i>	0.814 (0.629 – 0.920)	0.869 (0.688 – 0.956)
<i>Geographic range (km²)</i>	0.456 (0.167 – 0.716)	0.641 (0.275 – 0.880)
<i>Gestation length (days)</i>	1 (0.994 – 1)	1 (0.993 – 1)
<i>Weaning age (days)</i>	0.928 (0.820 – 0.977)	0.961 (0.893 – 0.993)

Supplementary Table A2.3 - Model coefficients and akaike weights from main analyses and average predictive bias from the cross validation for all models where model Akaike weight (Aw) >0.02. Data from the model of (a) maximum natal dispersal distance; (b) median dispersal distance. Mean residual values are the average difference between predicted dispersal distance and actual dispersal distance for the 30% of species retained from the model for testing purposes. Coefficient codes: I = Intercept; BM = Body Mass; HRS = Home Range Size; TL-C = Trophic Level (Carnivores); PD = Population Density; GR = Geographic Range; GL = Gestation Length; WA = Weaning Age; WA² = Quadratic term for Weaning Age; GL² = Quadratic term for Gestation Length.

Models – Maximum Natal Dispersal Distance	Mean residual value	Aw	I	BM	HRS	TL-C	PD	GR	GL	WA	WA²	GL²
<i>LnBM + LnHRS + LnGR + LnWA + I(LnWA²)</i>	-0.001 (-0.133)	0.09	-3.15	0.29	0.24	-	-	0.25	-	3.25	-0.38	-
<i>LnBM + LnHRS + LnPD + LnGR + LnWA + I(LnWA²)</i>	0.005 (-0.134)	0.07	-2.50	0.28	0.16	-	-0.11	0.25	-	3.08	-0.36	-
<i>LnBM + LnHRS + LnGR</i>	0.001 (-0.132)	0.06	3.66	0.26	0.27	-	-	0.26	-	-	-	-
<i>LnBM + LnHRS + LnPD + LnGR</i>	0.008 (-0.137)	0.06	4.00	0.25	0.18	-	-0.13	0.25	-	-	-	-
<i>LnBM + LnHRS + LnGR + LnGL + I(LnGL²)</i>	-0.001 (-0.139)	0.05	-6.29	0.31	0.24	-	-	0.25	4.81	-	-	-0.58
<i>LnBM + LnHRS + TL + LnGR + LnWA + I(LnWA²)</i>	-0.001 (-0.138)	0.04	-3.16	0.33	0.19	-2.69	-	0.24	-	3.08	-0.36	-
<i>LnBM + LnPD + LnGR + LnWA + I(LnWA²)</i>	-0.002 (-0.134)	0.04	-4.78	0.38	-	-	-0.20	0.29	-	3.49	-0.40	-
<i>LnBM + LnHRS + TL + LnGR</i>	0.003 (-0.136)	0.03	3.18	0.31	0.21	3.75	-	0.25	-	-	-	-
<i>LnBM + LnHRS + LnGR + LnGL + LnWA + I(LnWA²) + I(LnGL²)</i>	-0.006 (-0.132)	0.03	-10.37	0.31	0.21	-	-	0.25	3.95	2.76	-0.32	-0.47
<i>LnBM + LnHRS + LnGR + LnWA</i>	0.004 (-0.144)	0.02	4.63	0.31	0.27	-	-	0.23	-	-0.22	-	-
<i>LnBM + LnHRS + LnPD + LnGR + LnWA</i>	0.013 (-0.150)	0.02	4.90	0.30	0.18	-	-0.12	0.23	-	-0.21	-	-
<i>LnBM + LnHRS + LnPD + LnGR + LnGL + I(LnGL²)</i>	0.010 (-0.142)	0.02	-4.78	0.30	0.18	-	-0.08	0.25	4.18	-	-	-0.51
<i>LnBM + LnPD + LnGR</i>	0.009 (-0.130)	0.02	2.42	0.38	-	-	-0.23	0.30	-	-	-	-
<i>LnBM + LnHRS + LnGR + LnGL + LnWA + I(LnWA²)</i>	-0.004 (-0.132)	0.02	-3.11	0.29	0.24	-	-	0.25	-0.01	3.24	-0.38	-
<i>LnBM + LnHRS + TL + LnPD + LnGR + LnWA + I(LnWA²)</i>	-0.007 (-0.130)	0.02	-2.61	0.31	0.14	-2.32	-0.09	0.24	-	3.00	-0.35	-
<i>LnBM + TL + LnPD + LnGR + LnWA + I(LnWA²)</i>	0.001 (-0.136)	0.02	-4.58	0.41	-	-4.07	-0.15	0.27	-	3.28	-0.38	-
<i>LnBM + LnHRS + TL + LnPD + LnGR</i>	0.002 (-0.138)	0.02	3.62	0.29	0.16	3.99	-0.10	0.25	-	-	-	-

Supplementary Table A2.3 – cont.

Models – Median Natal Dispersal Distance	Mean residual value	<i>Aw</i>	I	BM	HRS	TL-C	PD	GR	GL	WA	WA ²	GL ²
<i>LnBM + LnHRS + LnPD + LnWA + I(LnWA²)</i>	-0.001 (-0.105)	0.13	-0.53	0.15	0.27	-	-0.15	-	-	3.54	-0.39	-
<i>LnHRS + LnPD + LnWA + I(LnWA²)</i>	-0.005 (-0.106)	0.11	-0.21	-	0.32	-	-0.16	-	-	3.88	-0.42	-
<i>LnBM + LnHRS + LnPD</i>	-0.005 (-0.107)	0.05	7.11	0.16	0.29	-	-0.16	-	-	-	-	-
<i>LnBM + LnHRS + LnPD + LnGL + LnWA + I(LnWA²)</i>	-0.011 (-0.107)	0.04	0.01	0.19	0.28	-	-0.14	-	-0.21	3.53	-0.39	-
<i>LnBM + LnHRS + LnWA + I(LnWA²)</i>	-0.003 (-0.107)	0.04	-1.12	0.18	0.39	-	-	-	-	3.64	-0.41	-
<i>LnHRS + TL + LnPD + LnWA + I(LnWA²)</i>	0.001 (-0.107)	0.03	-0.16	-	0.33	-0.44	-0.17	-	-	3.94	-0.43	-
<i>LnHRS + LnPD + LnGR + LnWA + I(LnWA²)</i>	0.000 (-0.106)	0.03	-1.23	-	0.32	-	-0.14	0.05	-	3.92	-0.42	-
<i>LnBM + LnHRS + LnPD + LnGR + LnWA + I(LnWA²)</i>	-0.004 (-0.106)	0.03	-1.21	0.15	0.27	-	-0.13	0.04	-	3.59	-0.40	-
<i>LnHRS + LnPD</i>	-0.005 (-0.109)	0.03	8.47	-	0.36	-	-0.17	-	-	-	-	-
<i>LnBM + LnHRS + TL + LnPD + LnWA + I(LnWA²)</i>	0.001 (-0.107)	0.03	-0.53	0.15	0.27	-0.53	-0.15	-	-	3.54	-0.39	-
<i>LnHRS + LnPD + LnGL + LnWA + I(LnWA²)</i>	-0.006 (-0.108)	0.02	-0.26	-	0.32	-	-0.16	-	0.02	3.88	-0.42	-
<i>LnHRS + LnWA + I(LnWA²)</i>	-0.004 (-0.108)	0.02	-0.82	-	0.46	-	-	-	-	4.04	-0.44	-
<i>LnBM + LnHRS + LnGR + LnWA + I(LnWA²)</i>	-0.007 (-0.108)	0.02	-2.54	0.16	0.37	-	-	0.08	-	3.71	-0.41	-

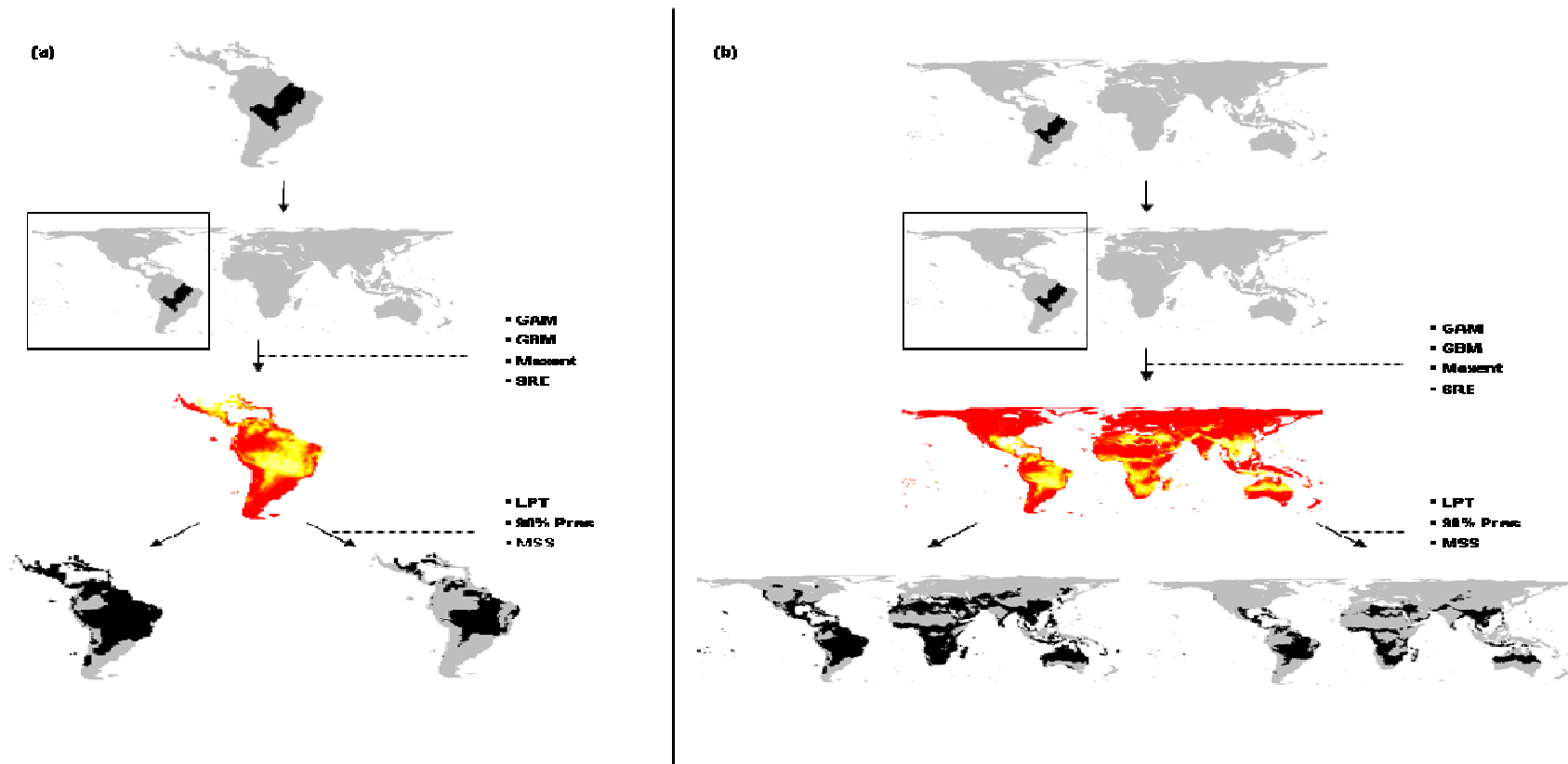
Supplementary Table A2.4 - Correlation coefficients between predictor**variables.** (a) maximum dispersal distance data set and (b) median dispersal data set.

(a)	<i>BM</i>	<i>HRS</i>	<i>TL</i>	<i>PD</i>	<i>GR</i>	<i>GL</i>	<i>WA</i>	$GL^{\wedge 2}$	$WA^{\wedge 2}$
<i>BM</i>	-	0.739	0.267	0.439	0.861	0.321	0.557	0.186	0.424
<i>HRS</i>	0.739	-	0.216	0.334	0.782	0.302	0.498	0.177	0.374
<i>TL</i>	0.267	0.216	-	0.123	0.268	0.088	0.173	0.040	0.131
<i>PD</i>	0.439	0.334	0.123	-	0.463	0.154	0.295	0.075	0.228
<i>GR</i>	0.861	0.782	0.268	0.463	-	0.339	0.573	0.192	0.447
<i>GL</i>	0.321	0.302	0.088	0.154	0.339	-	0.198	0.202	0.144
<i>WA</i>	0.557	0.498	0.173	0.295	0.573	0.198	-	0.098	0.469
$GL^{\wedge 2}$	0.186	0.177	0.040	0.075	0.192	0.202	0.098	-	0.065
$WA^{\wedge 2}$	0.424	0.374	0.131	0.228	0.447	0.144	0.469	0.065	-

(b)	<i>BM</i>	<i>HRS</i>	<i>TL</i>	<i>PD</i>	<i>GR</i>	<i>GL</i>	<i>WA</i>	$GL^{\wedge 2}$	$WA^{\wedge 2}$
<i>BM</i>	-	0.605	0.115	0.417	0.149	0.209	0.436	0.397	0.071
<i>HRS</i>	0.605	-	0.204	0.723	0.257	0.298	0.753	0.695	0.094
<i>TL</i>	0.115	0.204	-	0.149	0.052	0.060	0.155	0.143	0.020
<i>PD</i>	0.417	0.723	0.149	-	0.154	0.199	0.550	0.509	0.053
<i>GR</i>	0.149	0.257	0.052	0.154	-	0.078	0.196	0.182	0.023
<i>GL</i>	0.209	0.298	0.060	0.199	0.078	-	0.212	0.193	0.094
<i>WA</i>	0.436	0.753	0.155	0.550	0.196	0.212	-	0.696	0.058
$GL^{\wedge 2}$	0.397	0.695	0.143	0.509	0.182	0.193	0.696	-	0.051
$WA^{\wedge 2}$	0.071	0.094	0.020	0.053	0.023	0.094	0.058	0.051	-

Appendix 3. Supporting information for chapter 4.

Supplementary Figure A3.1 - Flow diagram of species distribution modelling



(a) 1. distribution data is sampled; 2 pseudo-absences are taken from the occupied realm and adjacent realms; 3 presence probability is projected at the extent of the occupied realm using 4 modelling methods; 4 presence/absence binary thresholds are applied. (b) is broadly similar except that for step 3 presence probability is projected to the whole world without restriction.

Supplementary Table A3.1 - Kendall pairwise correlation coefficients for environmental variables used in the species distribution modelling process.

	<i>BIO_1</i>	<i>BIO_10</i>	<i>BIO_11</i>	<i>BIO_12</i>	<i>BIO_15</i>	<i>BIO_18.</i>
<i>BIO_1</i>	-	0.740	0.848	0.246	0.220	0.103
<i>BIO_10</i>	0.740	-	0.590	0.084	0.257	-0.017
<i>BIO_11</i>	0.848	0.590	-	0.333	0.154	0.172
<i>BIO_12</i>	0.246	0.084	0.333	-	-0.167	0.680
<i>BIO_15</i>	0.220	0.257	0.154	-0.167	-	-0.133
<i>BIO_18</i>	0.103	-0.017	0.172	0.680	-0.133	-

Supplementary Table A3.2 – Variance inflation factors for maximal and maximal null linear models.

	log10 (Maximum dispersal distance - km)	log10(Age at sexual maturity – days)	log10 (Realm Size - cell count)	log10 (Species Age - m.y.)
<i>Models including realm size</i>	2.61	1.86	1.98	1.24
<i>Models excluding realm size</i>	2.56	1.86	-	1.19

Supplementary Table A3.3 - AUC scores calculated by cross-validation of data (30% of data retained by the model to test predictions of species presence and absence).

<i>Species Name</i>	<i>GAM</i>	<i>GBM</i>	<i>Maxent</i>
<i>Aepyceros melampus</i>	0.97	0.97	0.97
<i>Aepyprymnus rufescens</i>	0.99	0.99	0.99
<i>Alces alces</i>	0.98	0.99	0.95
<i>Alouatta palliate</i>	0.9	0.92	0.91
<i>Antilocapra americana</i>	0.98	0.98	0.96
<i>Aotus azarae</i>	0.93	0.96	0.92
<i>Aplodontia rufa</i>	0.99	0.96	0.99
<i>Brachylagus idahoensis</i>	1	0.99	0.99
<i>Canis adustus</i>	0.99	0.99	0.94
<i>Canis latrans</i>	0.95	0.96	0.81
<i>Canis lupus</i>	0.93	0.95	0.83
<i>Canis mesomelas</i>	0.95	0.96	0.96
<i>Caracal caracal</i>	0.98	0.98	0.91
<i>Castor canadensis</i>	0.99	0.99	0.86
<i>Cerdocyon thous</i>	0.9	0.93	0.9
<i>Crocuta crocuta</i>	1	1	0.93
<i>Cynomys gunnisoni</i>	0.97	0.98	0.97
<i>Cynomys ludovicianus</i>	0.99	0.99	0.98
<i>Didelphis virginiana</i>	0.96	0.97	0.91

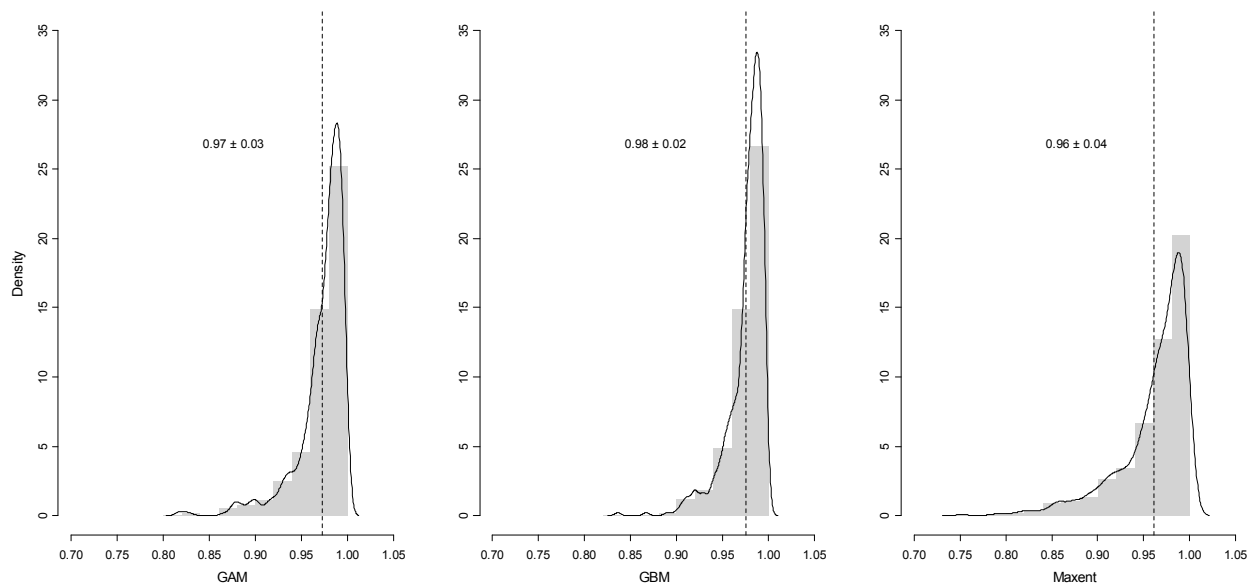
<i>Species Name</i>	<i>GAM</i>	<i>GBM</i>	<i>Maxent</i>
<i>Dipodomys spectabilis</i>	0.99	0.97	0.98
<i>Gulo gulo</i>	0.99	0.99	0.91
<i>Hylobates lar</i>	0.87	0.89	0.95
<i>Leopardus pardalis</i>	1	1	0.86
<i>Lepus americanus</i>	0.97	0.98	0.9
<i>Lepus europaeus</i>	0.97	0.98	0.93
<i>Lontra canadensis</i>	0.97	0.98	0.87
<i>Lycaon pictus</i>	0.97	0.98	0.95
<i>Lynx lynx</i>	0.99	0.99	0.89
<i>Lynx rufus</i>	0.97	0.98	0.89
<i>Macropus giganteus</i>	0.96	0.96	0.97
<i>Marmota flaviventris</i>	0.99	0.99	0.98
<i>Marmota monax</i>	0.98	0.98	0.92
<i>Martes americana</i>	0.98	0.98	0.91
<i>Martes pennanti</i>	0.97	0.98	0.95
<i>Mellivora capensis</i>	0.97	0.98	0.86
<i>Mephitis mephitis</i>	0.99	0.99	0.89
<i>Microtus agrestis</i>	0.99	0.99	0.94
<i>Microtus arvalis</i>	0.98	0.99	0.95

<i>Species Name</i>	<i>GAM</i>	<i>GBM</i>	<i>Maxent</i>
Microtus ochrogaster	0.99	0.99	0.96
Microtus pennsylvanicus	0.99	0.99	0.89
Mustela erminea	0.96	0.97	0.87
Neovison vison	0.99	0.99	0.86
Ochotona princeps	0.99	0.99	0.97
Odocoileus hemionus	0.97	0.98	0.92
Odocoileus virginianus	0.93	0.95	0.79
Ondatra zibethicus	1	0.99	0.86
Panthera leo	0.9	0.92	0.94
Panthera pardus	0.93	0.95	0.83
Panthera tigris	0.97	0.98	0.93
Peromyscus leucopus	0.99	0.98	0.93
Peromyscus maniculatus	0.96	0.98	0.86
Phascolarctos cinereus	0.99	0.99	0.98
Philantomba monticola	0.96	0.96	0.96
Procyon lotor	0.96	0.96	0.86
Pseudalopex griseus	0.99	0.99	0.96
Puma concolor	0.98	0.99	0.75

<i>Species Name</i>	<i>GAM</i>	<i>GBM</i>	<i>Maxent</i>
Rattus fuscipes	0.98	0.98	0.97
Rupicapra rupicapra	0.98	0.98	0.98
Sciurus carolinensis	1	0.99	0.96
Sciurus niger	1	0.99	0.96
Sorex araneus	0.99	0.99	0.93
Spermophilus beecheyi	1	0.99	0.99
Spermophilus richardsonii	0.98	0.99	0.98
Spermophilus tridecemlineatus	0.98	0.99	0.96
Tamiasciurus hudsonicus	0.97	0.97	0.89
Taxidea taxus	0.98	0.98	0.9
Thomomys bottae	0.98	0.98	0.96
Trichosurus vulpecula	0.94	0.96	0.96
Urocyon cinereoargenteus	0.95	0.96	0.86
Ursus americanus	0.96	0.98	0.87
Ursus arctos	0.97	0.98	0.9
Vulpes macrotis	0.98	0.98	0.96
Vulpes rueppellii	0.99	0.99	0.94
Vulpes vulpes	0.95	0.96	0.8

Appendix 4. Supporting information for chapter 5.

Supplementary Figure A4.1 - AUC scores on 30% test data from cross-validation procedure. GAM and GBM $n=518$, Maxent $n=676$. Dashed line is mean AUC score (mean value ± 1 s.d. given in legend).



Supplementary Figure A4.2 - Sensitivity scores.

Sensitivity scores proportion of correctly predicted presences) for all model types and thresholds baring SRE. (as with no limits on extreme values SRE will correctly classify all observed presences). Dashed lines represents mean sensitivity, true mean values given in legends ± 1 standard deviation.

