Connectivity conservation for large mammals in a human-dominated biodiversity hotspot

by

Aditya Gangadharan

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Department of Biological Sciences
University of Alberta

Abstract

The conservation of large mammals such as Asian elephant (*Elephas maximus*) and tiger (*Panthera tigris*) requires management of core reserves, as well as habitat and connectivity across multiple-use areas. These charismatic species may also help catalyze conservation investments that may benefit other species. Yet, it remains challenging to prioritize multiple-use areas in terms of their importance for habitat use and connectivity; assess whether flagship species also perform umbrella functions; achieve a balance between the complexities of single-species management and the use of surrogate species; and, manage carnivore presence in human-dominated connective areas. For conservation applications, these questions may need to be answered under constraints of time, finances and local capacity. Such challenges are especially urgent in biodiversity hotspots, and are typified in the Western Ghats of India, where the Shencottah Gap separates two major tiger reserves.

Using surveys for animal signs (collected between 2008 and 2010), I identified habitat with the highest potential for density of use, inter-reserve dispersal and movement across the major linear barrier in the region for elephant and gaur (*Bos gaurus*). I then developed models of elephant and tiger habitat use with camera-trap data (collected between 2011 and 2013), and evaluated the congruence between these models and the detection rates or presence of 22 other mammals. Combining sign and camera-trap surveys, I then classified 14 mammals into functional types reflecting their common niche characteristics. Finally, I used camera-trap data to evaluate whether tiger presence was best explained by spatial habitat attributes, temporal segregation with humans, individual variation or temporary infirmity.

Areas of high use by large herbivores had low overlap with connective areas, suggesting that prioritizing one function may come at the cost of the other. Detections of elephants and tigers were strongly correlated with each other and with gaur, but correlations with other species were more ambiguous. This suggests only mixed umbrella species functionality for elephants and tigers. Niche characteristics were used to divide mammals into four functional types, which ranged from those associated with closed forest to more human-associated species; threatened species were distributed across all groups. This suggests that multiple-use areas may be able to sustain a range of threatened species. Tiger presence at the population level was positively correlated to gaur use and negatively to distance from human infrastructure. However, individual tiger identity influenced the use of areas close to human infrastructure, and temporary infirmity was associated with avoidance of gaur habitat. Overall, these results suggest that both the opportunities and challenges of conservation in multiple-use areas must be identified before the implementation of participatory conservation programs.

Preface

This thesis is an original work by Aditya Gangadharan. The data used for this thesis were collected in collaboration with Srinivas Vaidyanathan, Foundation for Ecological Research, Advocacy and Learning.

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Chapter 1

1 General introduction

1.1 Protected areas in biodiversity conservation

Human demands on natural systems have caused habitat loss, habitat fragmentation and overhunting; they have also spread invasive species, increased pollution and led to climate change (Soule, 1991). The resulting impacts on wildlife populations, including large mammals, have been severe (Ceballos *et al.,* 2005; Pimm *et al.,* 2014), causing species extinctions (reviewed by Burney & Flannery, 2005), range contractions (Laliberte & Ripple, 2004) and simplifying ecosystems (Terborgh *et al.,* 2001). The biodiversity-rich tropical and sub-tropical regions of the world are especially threatened by these human impacts at the current time (Laurance *et al.,* 2012), because these regions often contain dense human populations (Cincotta *et al.,* 2000) and growing economic activity (Geist & Lambin, 2002). Consequently, the conservation of wildlife in these parts of the world is a challenging task for conservation biologists (Janzen 1986; Chazdon *et al.,* 2009a).

To address the above challenges, societies have traditionally set aside reserves for threatened species (reviewed by Naughton-Treves *et al.,* 2005). Historically, reserves were often set aside to manage resources for eventual human use, such war or game animals (Sukumar, 2003), timber (Bryant, 1996), or recreation (Callicott, 1990). In the latter part of the 20th Century, reserves were additionally set aside to conserve biodiversity for its own sake (Naughton-Treves *et al.,* 2005). As a result, protected areas now cover more than 12% of the world's terrestrial surface (Chape *et al.,* 2005).

Despite these successes in establishing protected areas, many mammals continue to be threatened with extinction (Schipper *et al.,* 2008), even within protected reserves (Woodroffe & Ginsberg, 1998). One reason for these threats is that reserves are not always situated in areas of the highest species diversity, endemism or vulnerability (Rodrigues *et al.,* 2004); instead, they may be placed in economically unproductive areas (Scott *et al.,* 2001). Consequently, many species may occur in unprotected or multiple-use land outside reserves (Brooks *et al.,* 2004). A second reason may be that protected areas are often small and isolated (Chape *et al.,* 2005), due to which they may contain only small populations. These populations may be vulnerable to demographic and environmental stochasticity (Lande, 1993), as well as inbreeding (Frankham & Ralls, 1998). Consequently, small, isolated or opportunistically-placed reserves may be inadequate to preserve biodiversity over the long term (Noss 1983; Wilcox & Murphy, 1985; Margules & Pressey, 2000).

1.2 The landscape approach to conservation

The problems of poor reserve placement and small size may be addressed through better targeting of reserves (*e.g.*, in biodiversity hotspots; Myers *et al.,* 2000), or by establishing 'mega-reserves' (Mittermeier *et al.,* 2003). But both of these approaches remain limited by political unwillingness to set aside large areas from development (Schwartz, 1999; Naughton-Treves *et al.,* 2005). An alternative paradigm to conservation – hereafter, the landscape approach (Noss, 1983; Franklin, 1993; Redford *et al.,* 2003; Chazdon *et al.,* 2009a) – is therefore increasingly popular in tropical areas. The landscape approach to conservation emphasizes the expansion of biodiversity conservation into working landscapes, to foster connectivity between reserves (Bennett, 2003), conserve species in multiple-use areas (Daily *et al.,* 2003), protect key habitats at the local scale (Eken *et al.,* 2004) while also managing conflict with potentially dangerous species (Carroll & Miquelle, 2006). Many applications of this paradigm also involve the integration of human development, because economic and social factors in surrounding land may hold the key to the biodiversity conservation in tropical reserves (DeFries *et al.,* 2005; Laurance *et al.,* 2009).

1.2.1 Connectivity through corridors and the matrix

A key component of the landscape approach is the enhancement of landscape connectivity (*sensu* Taylor *et al.,* 1993) between reserves (Beier & Noss, 1998; Bennett, 2003). Movement between reserves may enable animals to meet their ecological needs such as forage and water, mates or natal dispersal (reviewed by Chetkiewicz *et al.,* 2006; Hilty *et al.,* 2006). These movements may help 'rescue' (*sensu* Brown & Kodric-Brown, 1977) populations that are in danger of extinction (Hanski, 1998) and also foster genetic exchange (Aars & Ims, 1999). Further only a few individuals may be required to move between populations for demographic rescue (Stacey & Taper, 1992) or gene flow (Mills & Allendorf, 1996). Individuals may move using linear corridors, stepping stones suspended within the matrix, or the matrix itself (Merriam *et al.,* 1989; Forman, 1995; Gustafson & Gardner, 1996; Ricketts, 2001). All of these elements of habitat and connectivity may also need to be identified and conserved at several scales, ranging from large reserve networks (*e.g.*, Noss *et al.,* 2012) to linear barriers (*e.g.*, highways (Clevenger *et al.,* 2001).

1.2.2 Role of flagship species in matrix conservation

The role of the matrix in enhancing movement and connectivity relates to a second feature of the landscape approach: species conservation in multiple-use areas. A higher area of occupancy (*i.e.*, beyond reserve boundaries) may decrease extinction risk (Purvis *et al.,* 2000), and the spatial proximity of relatively suitable habitat may also enhance connectivity (Hodgson *et al.,* 2009). However, because matrix conservation involves opportunity costs (Rao & Geisler, 2008), conservation interventions may be built around the marketability of charismatic flagship species (*sensu* Caro, 2010; Verissimo *et al.,* 2011). The use of flagship species sometimes transforms into an implicit assumption that they also perform 'umbrella' functions (Andelman & Fagan, 2000; Roberge & Angelstam, 2004). However, different species occupy different niches (Hutchinson, 1957), and these niches may not correspond to that occupied by the flagship species (Simberloff, 1998). The empirical evidence for the utility of flagship species as umbrella species is mixed (reviewed by Caro, 2010); therefore, it is important to evaluate their umbrella capacity, particularly in regions where their presence may strongly influence conservation initiatives.

1.2.3 Variation among species in matrix use

Flagship species may serve as essential catalysts for conservation in matrix zones; however, different processes may threaten different species that occur within these areas (Caro *et al.,* 2005; Mace *et al.,* 2008). Despite the resulting need for diverse management activities, it may not be practical to tailor management interventions to each species (Wiens *et al.,* 1998), especially in biodiversity-rich regions facing resource limitations (*e.g.,* Bruner *et al.,* 2004). An alternative approach is to cluster species into functional types (*sensu* Lavorel *et al.*, 1997) defined by their common habitat requirements or restrictions (Lambeck, 1997; Wiens *et al.,* 1998). Functional types are often defined based on meta-analysis, literature review or expert knowledge (Lambeck, 1997; McKinney, 2002; Manne & Williams, 2003). In conservation applications at small scales, species may also be clustered with respect to their niche characteristics (*e.g.,* Hirzel *et al.,* 2002). In doing so, it may also be possible to identify the habitat attributes that enhance occupancy, and those that limit connectivity (Dolgener *et al.,* 2014). Thus, clustering species into functional types may enhance multi-species management in matrix areas.

1.2.4 Variation among individuals in matrix use

Different species and functional types may vary in their habitat associations; but individuals within a species may also exhibit a wide range of habitat preferences (*e.g.,* Ross *et al.,* 1997). The behavior of these individuals may determine connectivity (reviewed by Clobert *et al.,* 2001) as well as conflict (Hoare, 1999). Managers may be especially challenged to connect populations of large carnivores across multiple-use areas (reviewed by Treves & Karanth, 2003). Many carnivores may only rarely enter degraded, multiple-use habitat (Crooks, 2002), and those that do may often be illegally targeted by humans (Naughton-Treves *et al.,* 2003). But some individuals may survive in human-dominated areas without conflict (Athreya *et al.,* 2013), while others may enter into conflict with people (*e.g.,* Packer *et al.,* 2011). To balance the opportunities and challenges of carnivore conservation in multiple-use matrix, it may be crucial to identify the spatial (Karanth *et al.,* 2011), temporal (Boitani, 1982) and behavioral (Estes *et al.,* 2003; Yeakel *et al.,* 2012) correlates of their presence in multiple-use areas.

1.3 Description of the study area

1.3.1 The Western Ghats: a human-dominated biodiversity hotspot

The four challenges of the landscape approach described above (modelling connectivity through corridors and the matrix at multiple scales; evaluating whether flagship species also serve as umbrella species; grouping species based on how they use the matrix; and, quantifying variation within individual animals in matrix use) are applicable across the world, but may be especially urgent in the biodiversity hotspots of the world (Myers *et al.,* 2000). These regions contain high rates of endemism, making them irreplaceable, but are also highly threatened by human activity, making them vulnerable (*sensu* Margules & Pressey, 2000). In the tropical hotspots, reserves are increasingly isolated (DeFries *et al.,* 2005), fragmented by human infrastructure (Laurance *et al.,* 2009) and dependent on surrounding landscapes for their integrity (Laurance *et al.,* 2012). Consequently, biodiversity conservation may depend on the appropriate management of core reserves as well as their surrounding landscapes (Chazdon *et al.,* 2009b).

These challenges of biodiversity conservation in the hotspots are typified in the Western Ghats of India. This region consists of a rugged chain of mountains running down the west of peninsular India, and is particularly rich in endemic plants, amphibians and reptiles (Myers *et al.,* 2000). However, the Western Ghats also hold globally-significant populations of Asian elephants (*Elephas maximus*; hereafter, elephant), tigers (*Panthera tigris*), dholes (*Cuon alpinus*), lion-tailed macaques (*Macaca silenus*) and gaur (*Bos gaurus*). The conservation of these species is challenged by high human densities; 50 million people live within the 164,000 km^2 extent of this hotspot (Kasturirangan *et al.,* 2013). The designation of reserves has been the key to biodiversity conservation in the Western Ghats (Das *et al.,* 2004). However, the degradation of the Western Ghats has also increased over the past few decades (Jha *et al.,* 2000), and only 37% of the region is now thought to retain its native vegetation (Kasturirangan *et al.,* 2013).

As a result of these growing human needs, the conflict between conservation and development is now intense. This conflict has recently been fueled by two major governmental reports that recommended stringent – and unpopular – rules for zonation of land uses (Gadgil *et al.,* 2011; Kasturirangan *et al.,* 2013). The vigorous political debates that followed these reports (and continue to this day) suggest that both habitat and connectivity will need to be conserved beyond the boundaries of small reserves; conservation interventions will often rely on charismatic flagship species; management activities need to be condensed into a few core foci; and, carnivore connectivity will need to be managed across densely-populated areas.

1.3.2 The origin of my research

All of the problems described above apply to the Shencottah Gap, which is a multiple-use region situated between two tiger reserves in the southern end of the Western Ghats. I have been involved in both research and conservation activities here since 2008. My work in the Shencottah Gap was conducted in collaboration with the Foundation for Ecological Research, Advocacy and Learning, a non-governmental organization that is involved in applied research and conservation advocacy. My work formed part of a larger initiative by this organization that included evaluation of carbon stocks, development of systems to pay communities for the ecosystem services provided by their land, and develop methods for the certification of cash crops grown in private plantations.

1.3.3 Description of the Shencottah Gap

The Shencottah Gap is the southern-most of three major breaks in the Western Ghats (Robin *et al.,* 2010), and is located along the border between Kerala and Tamil Nadu States. To the north of the Shencottah Gap, the Periyar Tiger Reserve and adjoining Srivilliputhur Wildlife Sanctuary comprise approximately 1257 km^2 of protected habitat. To the south of the gap, Kalakkad-Mundanthurai Tiger Reserves anchors a 1247 km^2 complex of protected areas which includes the Shendurney, Neyyar and Peppara Wildlife Sanctuaries, together referred to as the Agastyamalai region. For the purposes of large mammal conservation, the Shencottah Gap may be defined as the approximately 850 km^2 region separating Periyar Tiger Reserve and Shendurney Wildlife Sanctuary.

The Shencottah Gap receives two monsoons: the south-west from June to September, and the north-east from October to December. Consequently, the windward (western) slopes were historically covered in evergreen or moist deciduous forests, and the eastern slopes (which are predominantly in Tamil Nadu) included dry deciduous and semi-evergreen forest (Champion & Seth, 1968). Human impacts have been relatively low in the northern part of the gap, due to its remoteness. The area of the highest conservation concern covers approximately 302 km^2, and is bounded by the Achenkovil River to the north and Shendurney Wildlife Sanctuary to the south. Approximately 17% of this area consists of government-owned monoculture plantations of timber – mainly teak (*Tectona grandis*), Acacia (*Acacia* spp.) and Eucalyptus (*Eucalyptus* spp.). Privately-owned plantations (10%) consist mainly of rubber (*Hevea brasiliensis*) and tea (*Camellia sinensis*), and settlements with associated agriculture cover 4% of this region. The remaining areas comprise forests that were logged into the latter half of the 20th Century, and are currently subject to extractive pressure at small scales, including the collection of firewood, spices, reed (*Ochlandra* spp.) and cane (*Calamus* spp.).

Two major roads pass through the Shencottah Gap: a small state highway towards the north and a busy national highway (NH-204) to the south. The latter is thought to be a major barrier to large mammal connectivity, because of heavy traffic congestion, steep embankments and the proliferation of settlements along the sides (Johnsingh *et al.,* 1991). A narrow-gauge train track lies along the national highway, and is currently being widened to enable higher traffic flow. These transportation routes form arterial economic links between Kerala and Tamil Nadu.

1.4 Thesis objectives and methodology

The overall goal of my thesis was to evaluate the four aspects of connectivity conservation in multiple-use areas described above. In doing so, I aimed to generate specific conservation insights for the Shencottah Gap as well as more generalizable outputs.

In Chapter 2, I examined the correspondence between areas that are important for habitat use, and areas that are potentially important for movement, of elephants and gaur. In doing so, I developed a model of connectivity that covers two scales, and examined differences in corridor inference between these scales. In Chapter 3, I evaluated whether habitat use models developed for elephants and tigers were correlated to the frequency of detection or the presence of other mammals. In particular, I asked whether globally-threatened species would be covered if the habitat used by these two conservation flagships was protected. In Chapter 4, I used a niche-based approach to evaluate how different mammals may be grouped by the position as well as the variance of their niches with respect to habitat characteristics. I also grouped them by their habitat associations to identify functional types of species with similar habitat requirements and restrictions. In Chapter 5, I examined how spatial habitat, temporal segregation, individual variation and infirmity may influence tiger presence in multiple-use areas. Hence, I evaluated the potential for tiger connectivity across the Shencottah Gap.

My methodology was prompted by the need to generate data on a diversity of species, in a manner that was non-invasive, cost-effective and replicable. Therefore, I used a combination of data types in my thesis. The two broad types were: surveys carried out on foot for animal signs (scats, tracks, and scent marks), and surveys carried out using camera traps. Sign surveys were predominantly carried out between 2008 and 2011, and were intended to maximize spatial coverage with minimal cost. The surveys laid the groundwork for subsequent camera-trap surveys, which were conducted between 2011 and 2013. The need to involve local communities in monitoring biodiversity was an important consideration in all surveys. I analyzed these data using regression as well as multivariate methods, as appropriate to the research question. In my thesis, I aim to demonstrate how these relatively simple field methods and analytical techniques can be combined for conservation inferences in densely-populated, multiple-use areas.

Chapter 2

2 Planning connectivity at multiple scales for large mammals in a human-dominated biodiversity hotspot[*]

2.1 Introduction

Island-like protected areas may be inadequate to prevent large mammal extinctions (Woodroffe & Ginsberg, 1998) due to the deleterious effects of small population size and isolation (Hanski, 1998), which may be mitigated by providing connectivity between reserves (reviewed in Hilty *et al.,* 2006). However, these inter-reserve regions may be subject to multiple human uses that vary in their scale and intensity of impact. Diffuse human impacts over large areas (*e.g.,* selective logging) may create variegated habitat mosaics that vary in quality, but can support residents at a low density (Dobson *et al.,* 1999) and, coincidentally, also provide connectivity for dispersers (Hodgson *et al.,* 2011). In the more fragmented parts of these landscape mosaics (*e.g.,* riparian habitat within agro-forestry zones), dispersal corridors that contrast strongly with their surroundings may support habitat use by dispersers as well as some residents (Bennett *et al.,* 1994). At even smaller spatial extents (*e.g.,* across a highway), animal use may be restricted to rare, rapid movement using specific routes across otherwise relict habitat (Hudgens & Haddad, 2003). At the spatial scale of reserve networks for large mammals, all three of variegated, fragmented and relict habitat (*sensu* McIntyre & Hobbs, 1999) may occur together in a spatial hierarchy (Bennett, 2003), providing a continuum of habitat and connectivity functions (Soule & Terborgh, 1999).

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[*] Authors of an associated manuscript in preparation: Aditya Gangadharan, Srinivas Vaidyanathan & Colleen Cassady St. Clair.

Conservation organizations often seek to conserve both of these functions within a framework of wise land-use management (*e.g.,* 'biodiversity conservation corridors' of Conservation International; Sanderson *et al.,* 2006). Such plans require identification of landscape linkages that may support residence and movement; dispersal corridors that may support movement and limited habitat use; and, movement paths that enable animals to cross short stretches of impermeable habitat (Bennett, 2003). To conserve land that supports such dual habitat-movement functions, animal habitat selection must be quantified at multiple spatial extents and resolutions of management relevance.

Such conservation applications are best conducted using local field data because habitat selection may vary between regions (Chetkiewicz & Boyce, 2009). Such data often involve difficult logistics, expensive equipment and are time-consuming to obtain for rare and elusive species. However, the species-rich parts of the world contain high human densities (Cincotta *et al.,* 2000), which offers a pool of local residents who are skilled in natural history and field observation. By combining this expertise of local communities with intensive sampling effort, it may be possible to collect data on rare and elusive species using methods that are rapid, reliable and inexpensive to implement in working landscapes (*e.g.,* Jhala *et al.,* 2011).

The conservation problems described above are relevant across the globe, and are exemplified by the Shencottah Gap, a multiple-use region separating two tiger reserves (Periyar and Kalakkad-Mundanthurai) in the southern end of the Western Ghats biodiversity hotspot of south India. Over the past century, large areas of the gap have been converted to forestry plantations *(e.g.,* teak *Tectona grandis*) managed by the government, intensive cash crop plantations (*e.g.,* rubber *Hevea brasiliensis*) managed by private companies, as well as settlements and associated small-scale agriculture; the remaining natural habitat is also increasingly degraded. However, several large mammal species, including Asian elephants (*Elephas maximus*) and gaur (*Bos gaurus*) continue to occur at low densities (KFD 2010). An arterial transportation route consisting of a highway, railway and associated human settlements appears to be a major barrier to movement between the two reserves, and elephant densities are thought to progressively decrease closer to this transportation route (Johnsingh *et al.,* 1991). Attempts to restore large mammal connectivity by some governmental agencies are challenged by concurrent plans to expand infrastructure by others (MOEF 2011). Such conflicts between development and conservation throughout the Western Ghats recently led to a coarse-scale delineation of allowed land uses across the entire biodiversity hotspot (Kasturirangan *et al.,* 2013). However, the local implementation of this plan will likely rely on identification of important wildlife habitat.

To support land-use planning for wildlife conservation in the southern Western Ghats, we carried out intensive surveys for animal sign, and modeled landscape linkages and dispersal corridors for elephant and gaur, while also evaluating the influence of analysis resolution on the locations of predicted corridors. We then modeled potential movement paths across the transportation route, and evaluated the potential for these paths to be restored. Finally, we combined model results for elephant and gaur in a visually explicit map of connectivity for policymakers.

2.2 Methods

2.2.1 Study area

Surveys covered a 621 km^2 subset of the Shencottah Gap in Kerala and Tamil Nadu states (Fig. 2.1), abutting Kalakkad-Mundanthurai Tiger Reserve in the south and ending 10 km short of Periyar Tiger Reserve (due to logistical limitations) in the north. Approximately 25% of the study area consists of anthropogenic land use types (15% forestry, 5% commercial plantations, 5% settlements). The remaining area consists of a few pristine patches of wet evergreen forest, interspersed with larger areas in various stages of degradation (Ramesh *et al.,* 1997).

2.2.2 *Field methods*

We undertook surveys for animal sign in the dryer part of the year (December 2008 – May 2009 and December 2009 – June 2010), using a 1.5 km grid that approximates standard resolutions for tiger (*Panthera tigris*) surveys (2 km; Jhala *et al.,* 2011), and is also used for studying co-occurring herbivore species (*e.g.*, Ramesh *et al.* 2012). We systematically walked in an 'S' pattern through each cell (Gopalaswamy *et al.,* 2012), ensuring that we passed through nine systematic points, each separated by 500 m, to achieve high spatial coverage and up to 4 km of effort per cell. Field teams included experienced trackers trained in operating GPS units and recording standardized data. Animal signs were recorded every 0.1 km, while taking care to avoid over-replication around the corners of the 'S' by using the tracking function of the GPS units. Only records of tracks and dung were used in subsequent analyses. We also collected ground-based covariates expected to influence species presence and our ability to detect the signs left by them (Appendix 2.1).

2.2.3 *Analytical methods*

Using the above data, we identified three complementary elements of landscape connectivity: landscape linkages, dispersal corridors and movement paths. Landscape linkages consisted of areas of high habitat selection, which may also support connectivity as a consequence of animal presence (Hodgson *et al.,* 2011). Dispersal corridors consisted of areas that may be used for movement, without necessarily providing high-quality resident habitat (*e.g.,* Haddad & Tewksbury, 2005). Movement paths consisted of specific routes across the major transportation route, where the main conservation priority is to enhance movement rather than habitat use (*sensu* Hudgens & Haddad, 2003).

Landscape linkage models

To identify landscape linkages for elephant and gaur, we used resource selection functions (RSF; Manly *et al.,* 2002) to quantify relative probability of habitat selection over the extent of the study area. Because animal presence is a consequence of habitat selection at multiple spatial scales (Meyer & Thuiller 2006), we followed Johnson *et al.,* (2004) to develop RSF models that were integrated across two resolutions of management relevance. We first used negative binomial regression to model the count of signs in a 1.5 km cell (henceforth, macro resolution). We then modeled animal presence at the 0.1 km resolution (henceforth, micro resolution) with the exponential form of the resource selection function under the 'use vs. available' framework (Manly *et al.,* 2002), constraining used and available locations to sampled paths. Only cells with a minimum effort of 0.5 km (macro resolution) and 0.05 km (micro resolution) were included for analysis. We then weighted the relative probability of selection for each micro cell by the area-weighted mean of RSF model predictions for the macro cells within a 1.5 km circular buffer, to derive scale-integrated probabilities of selection at the micro scale. Thus, the relative probability of selection of a cell at the micro-scale is a weighted function of both local habitat characteristics at that scale, as well as habitat characteristics at the macro-scale.

We considered a range of ground-based and remotely-sensed candidate explanatory variables representing land use, vegetation, human impacts, and terrain characteristics, as well as covariates affecting detection probability and survey effort (Appendix 2.1). Similar covariates have been found to influence habitat selection or use by elephants (*e.g.*, Fernando *et al.,* 2005; Gaucherel *et al.,* 2010) and gaur (Choudhury, 2002; Steinmetz *et al.,* 2010). After removing highly correlated variables ($|r>0.6|$), we followed a forward selection procedure based on the Akaike Information Criterion (AIC) for model selection, testing for quadratic fits and two-way interactions. We evaluated remnant overdispersion ($\hat{c}$) and residual spatial autocorrelation (semivariogram plots) in macro-resolution models, and predictive power of micro-resolution models (five-fold cross validation; Boyce *et al.,* 2002), using the statistical software R (version 3.0.1) for all analyses. Finally, we combined elephant and gaur landscape linkages derived from scale-integrated RSF models in Program

Zonation 3.1.10 (Moilanen *et al.,* 2005) using the basic ‘core-area zonation’ function to enhance reproducibility. This function first prioritizes and then combines the highest quality habitat for each species (Moilanen *et al.,* 2005).

Dispersal corridor models

To model elephant and gaur dispersal between the two reserves, we used circuit theoretical models (McRae *et al.,* 2008), which simulate random walks between source locations as a function of landscape conductance, producing an index of the number of random walkers passing through each cell (‘current flow’). We set the source regions to be a 1.5 km strip along the northern edge of the study area and all areas within Shendurney at the southern end, adding a 1.5 km buffer on the western edge to mitigate edge effects (Koen *et al.,* 2010). We used predicted values from scale-integrated RSF models as input into dispersal corridor models (Chetkiewicz & Boyce, 2009). To investigate the influence of analysis resolution and scale-integration on corridor locations, we also modeled corridors derived from macro resolution and micro resolution RSF models. We modeled dispersal corridors in Program Circuitscape (McRae & Shah, 2011).

To classify the continuous current-flow surface output from Circuitscape into binary corridor/ non-corridor we used a practical standard of plausibility. We assumed that the dense settlements along the transportation route (~332 houses/ km^2) were absolute barriers to elephants and gaur, leaving only two vegetated stretches as biologically plausible crossing zones (settlement boundaries were physically mapped; Appendix 2.1). We then ranked the predicted current-flow value for each cell from the scale-integrated models, and selected the cut-off as the percentile above which the only contiguous cells (four-neighbors) across the transportation route passed through one or both of these vegetated stretches. We then removed cells that were completely isolated, and categorized the remainder as potential dispersal corridors.

Movement path models

In multiple-use areas, corridor functionality may depend on particular atypical individual animals (Belisle, 2005) that are not well predicted by 'average' habitat selection models. Therefore, we anchored evaluation of animal movement across the transportation route on actual animal detections instead of modeled habitat quality. We first identified the nearest pairs of elephant and gaur locations on either side of the transportation route and assumed that an animal intending to cross this area would achieve the highest probability of success if it followed the least-cost path (Noss & Daly, 2006). We therefore modeled least-cost paths between these pairs, considering all micro-resolution cells contained by a 2-km buffer centered on each detection of a pair (Beier *et al.,* 2008), and setting any cell with more that 25% settlement area as an absolute barrier. As for dispersal corridors, we used predicted habitat suitability values from scale-integrated RSF model predictions as an estimate of cost of movement through a cell. We used the Linkage Mapper extension (McRae & Kavanagh, 2011) for ArcMap (ESRI, Redlands, USA) for this analysis. To evaluate the viability of the resultant movement path models, we computed the proportion of all animal detections that occurred in cells that were lower in habitat quality than the lowest, median and highest-quality cell of each movement path. We also compared modeled movement paths with random routes in the same landscape. We first generated 200 random paths that followed the same distribution of step lengths and turning angles as each modeled movement path. We then computed the proportion of random routes that had their lowest, median and highest-quality cells ranked lower than the corresponding cell of each modeled movement path.

2.3 Results

We conducted 840 km of sign surveys in 235 macro herbivore cells. At the micro resolution, we sampled 7731 cells of which 1618 and 839 cells were used by elephants and gaur respectively.

2.3.1 Landscape linkage models

At both macro and micro resolutions, elephant and gaur avoided land use types that were dominated by humans, and selected for areas that were further away from settlements (Table 2.1). Elephant and gaur avoidance of such habitats was exacerbated by high house density, but mitigated by the presence of natural habitat for elephant, and protected areas for gaur. Both elephant and gaur selected for areas with high leaf litter. Both herbivores selected against slope at the micro scale. Model fit and predictive power was adequate for all models (Appendix 2.2).

2.3.2 Dispersal corridor models

Macro-resolution dispersal corridor models showed relatively higher current flow in the east for both elephant and gaur (Fig. 2.2). In contrast, micro-resolution models showed high current flow both in the east and west. Corridors based on scale-integrated RSF models showed similar patterns of current flow to models based on micro-resolution RSF models, but were more compact, especially for gaur. Correlation between current flow and habitat quality was low for all models (Kendall's rank correlation, $0.19 \leq \tau_b \leq 0.27$; Appendix 2.3). Vegetated stretches along the transportation route were 970 m wide on the west and 150 m wide on the east, and we chose the top 4% and 5% quantile of elephant and gaur current flow respectively to define western and eastern corridors for these species (Fig. 2.3a)

2.3.3 Movement path models

The distance between the nearest elephant locations across the transportation route were similar in the eastern and western corridors (Fig. 2.3b & 2.3c), but gaur detections were found closer to the transportation route on the eastern side (Table 2.2). No detections were made adjacent to the transportation route for either species. Very few signs were detected in cells that were ranked lower in habitat quality than the lowest-quality cell of modeled movement paths across the transportation route (Table 2.2). The highest-ranked cells of the movement routes also remained in the lower half of the proportion of detections made in poorer habitat for all cases except for the western gaur corridor. Compared to randomly-generated paths, modeled movement paths were in the lower 50% in terms of the lowest, median and highest quality cells, in all cases except for the western gaur corridor.

2.3.4 Regional herbivore connectivity

The upper 50% quantile of the combined herbivore landscape linkage covered 284 km^2. This overlapped only 28% of the herbivore dispersal corridor area and 5% of the herbivore movement path length (Fig. 2.3a).

2.4 Discussion

Regional connectivity plans must often identify areas that can support habitat use and movement by multiple species, at extents and resolutions relevant to management. These goals must often be achieved under constraints of time, resources and technical capacity. We supported these goals in the Shencottah Gap by modeling connectivity between the Periyar and Kalakkad-Mundanthurai tiger reserves for two large mammals of high conservation concern. We modeled landscape linkages for elephant and gaur by identifying and combining high-quality habitat for each species. The locations of predicted dispersal corridors were sensitive to analysis resolution and scale integration. However, neither of the dispersal corridors appeared to be functional; the least costly movement paths across the transportation route incorporated habitat that was much lower in quality than the rest of the study area. Each of the three connectivity components that we modeled – landscape linkages, dispersal corridors and movement paths – identified areas that are important to different types of connectivity, and painted a more comprehensive picture of connectivity together than each of them in isolation.

Landscape linkages for elephant and gaur were determined to a large extent by covariates related to human activity and land use. Both species avoided areas of high human use, but this avoidance was mediated by the presence of natural habitat or legal protection (Table 2.1), potentially indicating a functional response in habitat selection (Mysterud & Ims, 1998). Circuit-theoretical models of dispersal corridors prioritized different areas depending on analysis resolution: the eastern part at the 1.5-km resolution, and both western and eastern parts at the 0.1-km resolution (Fig. 2.2). This apparent contradiction may reflect the fundamental dependence of spatial prioritization techniques on analysis resolution (Arponen *et al.,* 2012), and edge effects caused by the artificial truncation of the study area (Koen *et al.,* 2010), both of which are likely to hold in realistic applications of connectivity modeling. One way to incorporate these uncertainties may be to model habitat quality at multiple resolutions, and weight predictions at the smaller resolution by the habitat quality of its surroundings (scale-integrated resource selection functions; Johnson *et al.,* 2004). This protocol acknowledges that animals may select for high-quality habitat patches embedded in otherwise poor habitat or *vice versa* (*e.g.,* Mortelliti & Boitani, 2008). In our study, such scale-integrated models were more flexible than models based on large-resolution habitat quality, and more compact than models based on small-resolution habitat quality (Fig. 2.2). Therefore, we caution against the identification of potential corridors based on a single analysis resolution.

Corridor models based on graph-theoretical methods always result in corridors, but these corridors may not reflect whether animals can actually move between source areas or not (Beier *et al.,* 2008). In circuit theoretical models, high current flow in a cell may be caused by high habitat quality, spatial configuration of habitat types, or even artificial edges of the study area (Rudnick *et al.,* 2012), and correlation between habitat quality and current flow may be low (Appendix 2.4; Carroll *et al.,* 2012). Hence, corridors may pass through habitats that real animals are unlikely to use (*e.g.,* settlements that are very poor habitat, but which have high current flow; Table 2.1). One way to account for this is to simply exclude all settlements from the analysis, but we did not do so because we wanted to evaluate how well corridor models reflected animal habitat selection. Instead, we modified this tendency of corridor models in two ways. First, we imposed a realistic cut-off for identifying corridors, based on the assumption that elephants and gaur are unlikely to move through dense settlements along the transportation route. By doing so, we were able to identify the cells that had high current flow but excluded areas that were unrealistic.

Secondly, we considered the actual animal locations on either side of the transportation route, which is the most important barrier to movement across the gap. The nearest locations of animals on either side represent known true positives; our intensive sampling reduced the likelihood of having missed animal signs in between. By modeling least-cost paths across the intervening area, and comparing the habitat quality of the cells within movement paths to the habitat quality of cells where animals were detected, we were able to obtain a relative estimate of the potential for corridor functionality. Because only few animal detections were made in poorer habitat than the worst cell in the movement paths, a result supported by comparison of movement paths with similar random paths (Table 2.2), we conclude that the corridors do not currently appear functional. However, potential movement paths are well within the movement capability of both elephants and gaur, and a few elephant detections were made in worse habitat. Relatively rare instances such as these may be adequate for gene flow (Mills & Allendorf, 1996). Therefore, it may be possible to bridge the Shencottah Gap with appropriate management intervention. We note that the detection of these rare instances was because of our intensive sampling of areas that are not known to be good elephant habitat (*e.g.,* rubber plantations).

No single component of our connectivity analysis, by itself, identified all areas of potential importance for connectivity (Fig. 2.3); in fact, a focus on any one component to the exclusion of others would have ignored important conservation areas. This is because connectivity may depend on incremental movement of resident animals through suitable habitat (Hodgson *et al.,* 2009) or direct dispersal through low-quality corridors (Haddad & Tewksbury, 2005). Both may require barriers to be crossed, which may depend on the quality of habitat around the routes that are followed (*e.g.,* Vergara 2011). In applied situations, where connectivity is often modeled assuming that the rest of the landscape will be put to other uses (Beier *et al.,* 2008), conservation outcomes must not be limited by a singular focus on animal dispersal. Therefore, we recommend that connectivity designs between reserves incorporate both movement potential and habitat use (Moilanen, 2011). Such studies can be undertaken under the conceptual umbrella of regional connectivity, which offers opportunities to expand wildlife conservation beyond protected areas in a politically-feasible manner (Sanderson *et al.,* 2006).

Our study suggests that connectivity at the regional scale is best evaluated when it considers the potential for movement as well as other kinds of habitat use, both by dispersers and resident animals. The logistical and financial challenges imposed by such requirements may be overcome by leveraging the considerable *in situ* natural history expertise available even in very remote areas (*e.g.,* Jhala *et al.,* 2011; Karanth *et al.,* 2011; Sunarto *et al.,* 2012). However, this broad view of connectivity also necessarily requires consideration of the social, economic and political contexts of the landscape (Sanderson *et al.,* 2006). A holistic approach to regional connectivity may help in negotiating the hard trade-offs between conservation and development (McShane *et al.,* 2011) in working landscapes with multiple claimants for land.

2.5 Tables

Table 2.1 Standardized beta coefficients (SE)[a] of selected covariates from top resource selection function models at the macro resolution (1.5 km) and at the micro resolution (0.1 km) for elephant and gaur in the Shencottah Gap, India from 2008 to 2010.

Habitat covariate	Macro model coefficients		Micro model coefficients	
	Elephant	Gaur	Elephant	Gaur
Land use				
Human dominated[b]	-0.68 (0.11)***	-1.09 (0.19)***		-2.98 (0.71)***
Natural	0.36 (0.08)***			
Grassland[c]		0.41 (0.09)***		0.56 (0.08)***
Commercial plantation			-0.64 (0.58)	
Settlement/farm			-2.59 (0.72)***	
Habitat				
Leaf litter depth	0.19 (0.06)**	0.32 (0.09)***	0.24 (0.04)***	
House density	-0.31 (0.1)**	-0.91 (0.17)***		
Distance to nearest human dominated area[d]			0.59 (0.05)***	0.86 (0.07)***
Distance to nearest human dominated area^2			-0.31 (0.04)***	-0.94 (0.10)***
Protected				0.25 (0.12)*
Terrain				
Slope		-0.34 (0.08)***	-0.16 (0.03)***	-0.42 (0.04)***
Slope^2			-0.11 (0.03)***	-0.13 (0.05)**

Interactions				
Human dominated[b] x house density	-0.52 (0.16)***	-1.19 (0.37)**		
Human dominated x natural	0.34 (0.11)**			
Distance to human dominated [d] x commercial plantation			2.81 (0.78)***	
Distance to human dominated x protected area				-1.05 (0.21)***

[a] Statistical significance of coefficients (Wald's test): * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[b] For macro elephant cells, proportion of 3x3 cell neighborhood consisting of human dominated area; for macro gaur cells, proportion of each cell consisting of human dominated area; for micro gaur cells, land-use at center of cell.

[c] For macro cells, proportion of each cell consisting of grassland; for micro cells, land-use at center of cell.

[d] Distance to nearest settlement/farm.

Table 2.2 Comparison of western and eastern movement paths across the transportation route for elephant and gaur in terms of their distance, proportion of animal detections found in lower-quality habitat than cells included in the respective movement paths, and proportion of randomly-generated paths that included cells lower in habitat quality than the respective modeled movement paths.

	Elephant		Gaur	
	West	East	West	East
Distance between nearest detections across transportation route (km)				
Euclidean path	3.91	3.62	5.02	2.84
Least-cost path	4.04	5.40	10.96	5.18
Proportion of detections in lower-quality habitat than				
Lowest-ranked cell	0.01	0.01	0.00	0.00
Median-ranked cell	0.08	0.07	0.12	0.01
Highest-ranked cell	0.47	0.48	0.75	0.21
Proportion of random movement paths containing cells ranked lower than				
Lowest-ranked cell	0.35	0.29	0.53	0.41
Median-ranked cell	0.16	0.25	0.36	0.18
Highest-ranked cell	0.31	0.45	0.39	0.15

2.6 Figures

Figure 2.1 (a) Location of the Shencottah Gap within India, and (b) detailed map of study area showing protected areas (Periyar Tiger Reserve PTR, Shendurney Wildlife Sanctuary SWLS and Kalakkad-Mundanthurai Tiger Reserve KMTR) and intervening multiple-use habitat.

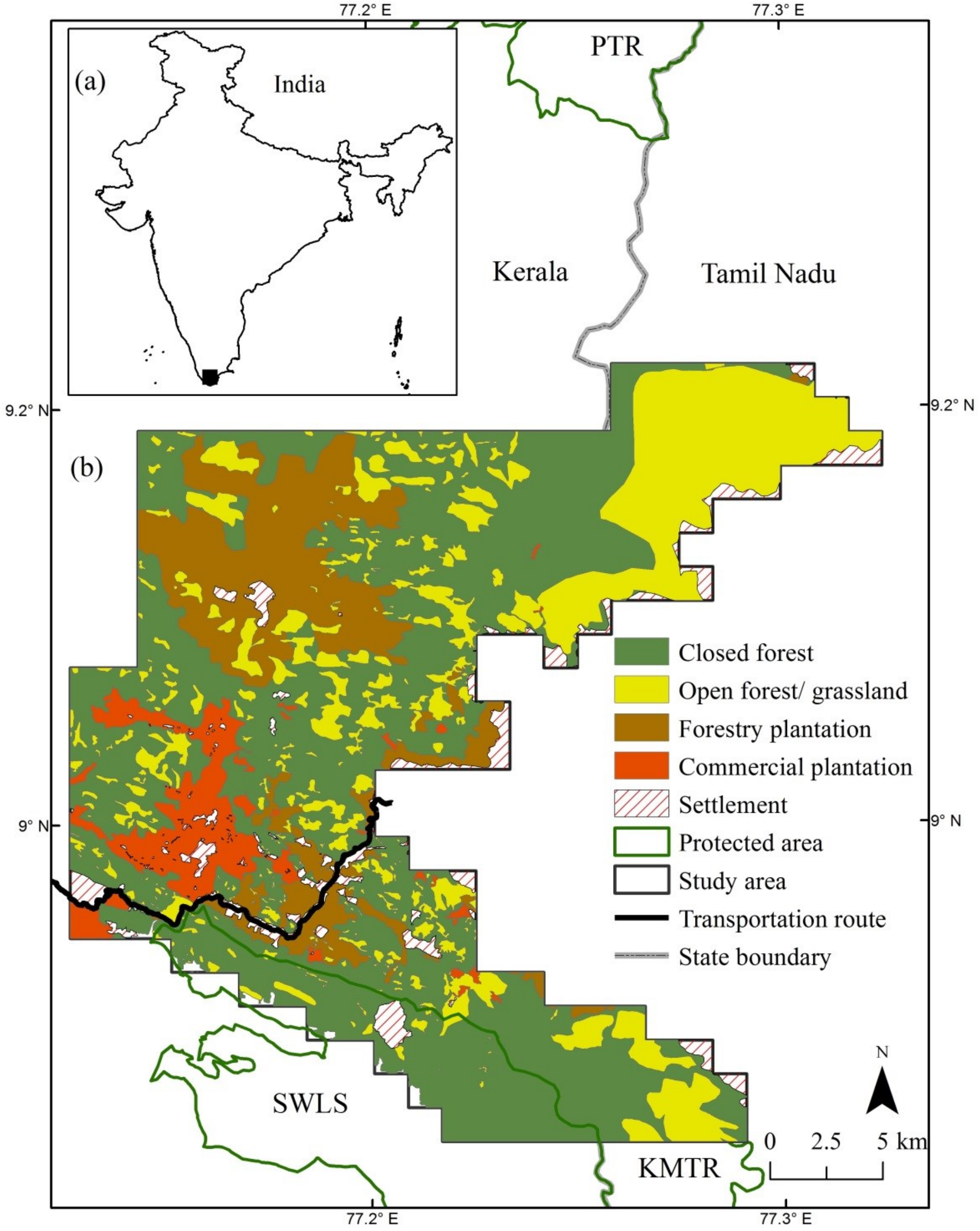


Figure 2.2 Effects of analysis resolution and scale-integration on the location and compactness of corridors, demonstrated with the highest 10% quantile of current-flow values from circuit theoretical corridor models for (a) elephant, and (b) gaur in the Shencottah Gap, India.

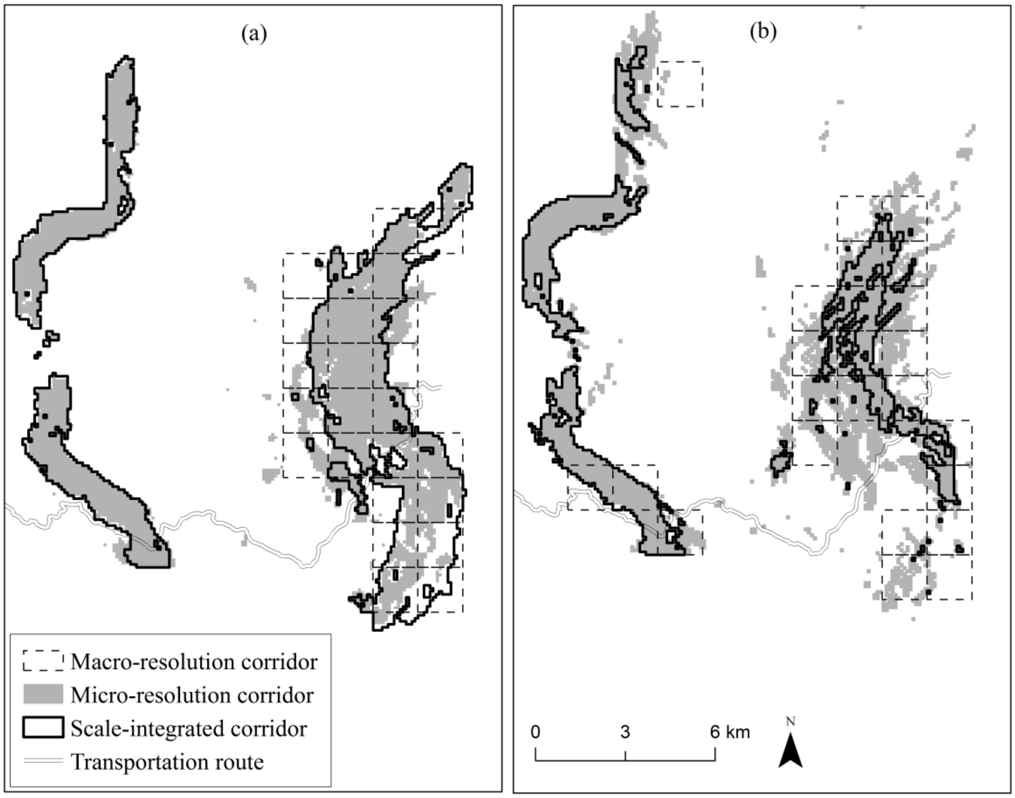
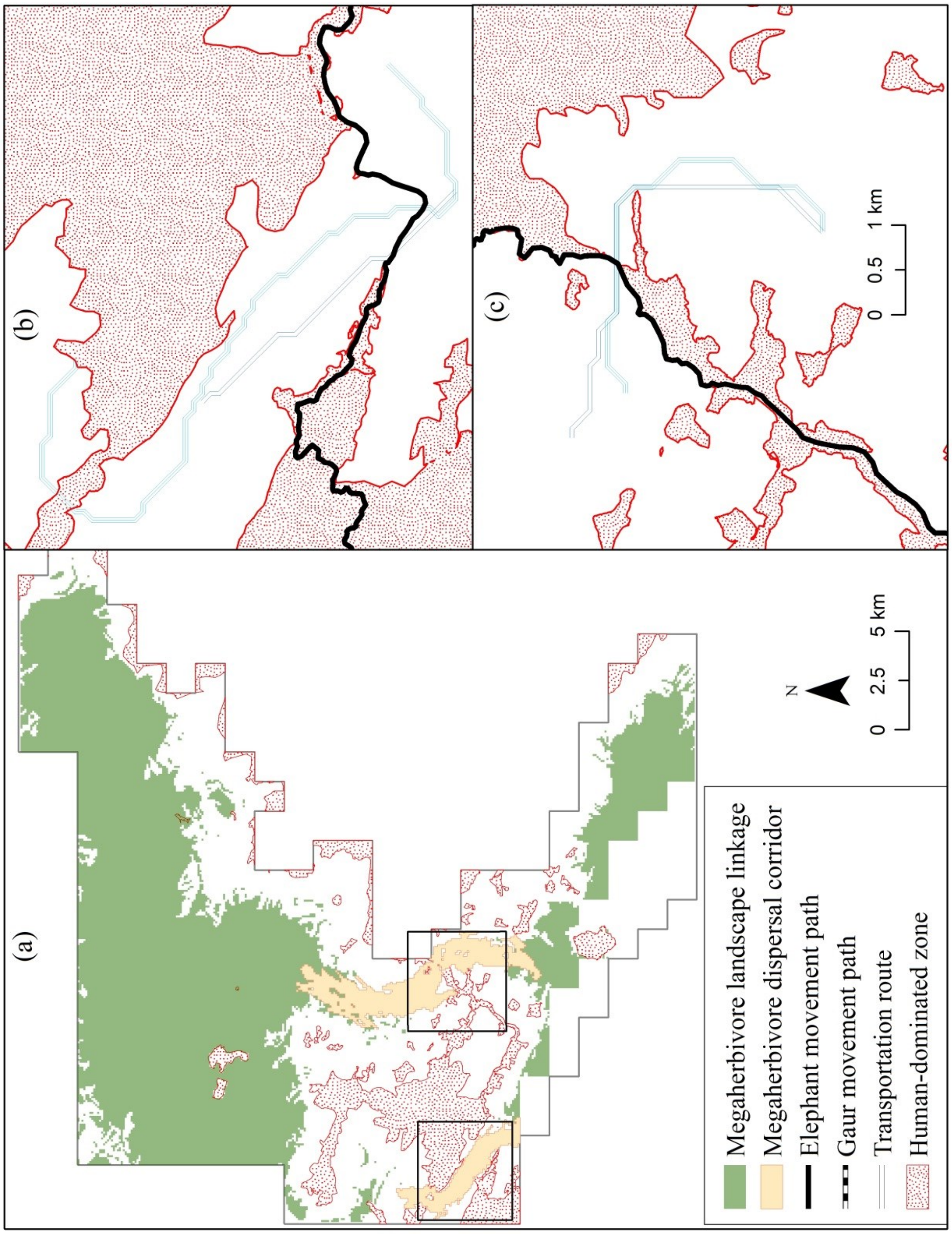


Figure 2.3 Combined regional connectivity map for elephant and gaur in the Shencottah Gap (a), and potential movement paths across the transportation route in the western dispersal corridor (b) and eastern dispersal corridor (c).



Chapter 3

3 Mixed evidence for the umbrella capacity of iconic flagship species[†]

3.1 Introduction

The concept of umbrella species – those species whose protection would also protect numerous other 'background species' (Caro, 2010) has been prevalent in conservation theory and application for several decades (reviewed by Favreau *et al.,* 2006). Much recent research in this field has been directed towards *a priori* identification of the characteristics of good umbrella species (*e.g.,* Fleishman *et al.,* 2000; Betrus *et al.,* 2005). Yet, in a world with accelerating extinction rates (Pimm *et al.,* 2014) and unprecedented transformations of land use in the most species-rich regions (reviewed by Laurance *et al.,* 2014), conservation planning and investment may not often be informed by such systematic assessments. Instead, conservation investments may target the most threatened species (Fleishman *et al.,* 2001). Among these, charismatic flagship species (often large mammals or birds; Simberloff, 1998; Clucas *et al.,* 2006) that humans can relate to (Lorimer *et al.,* 2007) may receive the most attention (Smith *et al.,* 2012).

Flagship species are capable of eliciting support from a wide range of stakeholders for conservation action (Verissimo *et al.,* 2011). For example, the Global Tiger Initiative is hosted by a developmental agency (the World Bank), and uses the recovery of tigers (*Panthera tigris*) as the symbol for halting biodiversity loss, enhancing ecosystem services and even promoting food security across 13 countries (Global Tiger Initiative, 2011). Large herbivores and carnivores may also be aggregated into 'flagship fleets' (Barua *et al.,* 2011); for example, African elephants (*Loxodonta* spp.) and lions (*Panthera*

[†] Authors of an associated manuscript in preparation: Aditya Gangadharan, Srinivas Vaidyanathan & Colleen Cassady St. Clair.

leo) as part of the 'Big 5' in Africa (Caro & Riggio, 2013), or tapirs (*Tapirus* spp.) and jaguars (*Panthera onca*) in Central and South America (Sanderson *et al.,* 2002; Caro *et al.,* 2004). Yet, such initiatives also assume that flagship species serve umbrella functions for background species (Lambeck, 1997; Leader-Williams & Dublin, 2000), *i.e.,* that they are 'flagship-umbrella' species (Caro, 2010). This assumption is a crucial part of conservation policy and implementation on the ground (Caro *et al.,* 2005; Roberge & Angelstam 2004), but is not often tested (Caro, 2010). The empirical evidence for the umbrella capacity of flagship species is mixed; some studies support their role (*e.g.,* Launer & Murphy, 1994; Sergio *et al.,* 2006) while others do not (*e.g.,* Berger, 1997; Andelman & Fagan 2000). The scale of inference may be an important determinant of the results of such evaluations (Favreau *et al.,* 2006).

In tropical regions that are rich in biodiversity but fragmented by multiple types of land use (reviewed by Laurance *et al.,* 2014), flagship-umbrella species may play an important role in determining the conservation status of land at both large (Lewis, 2005) and small scales (Caro *et al.,* 2004). This core role of flagship-umbrella species in conservation planning makes it important to test their umbrella capacity. However, many tropical areas do not possess the large amounts of multi-species data required to test these assumptions (Favreau *et al.,* 2006). Such databases are now being built by deploying inexpensive camera traps (reviewed by O'Connell *et al.,* 2010) as well as leveraging the knowledge and field skills of local residents (Silvertown, 2009; Hazzah *et al.,* 2014).

We used a series of surveys carried out over five years to evaluate whether habitat use by two iconic flagship species (Asian elephant *Elephas maximus* and tiger) in a densely-populated, multiple-use region was correlated to detection rates or presence of 22 other co-occurring mammals (Table 3.1). Among these species, we were particularly interested in the correlation of flagship habitat use with endangered or vulnerable species (IUCN, 2010; hereafter, threatened species), as well as the diversity of these species. Our study was carried out in the Western Ghats of India, where current governmental policy calls for the permanent delineation of conservation zones at small scales to balance development and biodiversity concerns (Kasturirangan *et al.,* 2013). This zonation of permitted land-uses will likely be greatly influenced by the presence of elephants and tigers (particularly tigers; Lewis, 2005), making the question of their umbrella capacity at small scales a crucial one to test.

3.2 Methods

3.2.1 Study area

The study area covered 302 km^2 of the Shencottah Gap, a multiple-use region separating the Periyar and Kalakkad-Mundanthurai Tiger Reserves in the southern end of the Western Ghats (Fig. 3.1). The study area comprised semi-evergreen and evergreen forest (Ramesh *et al.,* 1997) historically, but is now degraded in several areas, and has also been transformed into monoculture forestry plantations (teak, acacia and eucalyptus, 17% of study area), privately owned cash crop plantations (tea and rubber, 10%), settlements and associated agriculture (4%) and 56 km of inter-state transportation routes that are being expanded, including a national highway, a state highway and a railway line.

3.2.2 Field methods

We used two major types of data collected between 2008 and 2013 in this study: direct observation of animals and their signs on walking transects (hereafter, sign surveys), and surveys using camera traps. We first overlaid a grid of 1.5-km cells over the study area to allocate sampling effort, and then surveyed using both the above methods. Surveys for animal sign (scat, markings, tracks, sightings and calls) comprised three subsets: those conducted away from trails for multiple species, those conducted on trails for multiple species and those conducted on trails for carnivores. Off-trail surveys primarily targeted herbivores and arboreal mammals, while the first set of on-trail surveys targeted herbivores, carnivores and arboreal mammals. Both of the above were carried out from December 2008 to May 2009 and from December

2009 to June 2010 across all land use types described above. Additional surveys for large carnivores (tigers, leopards *Panthera pardus* and dhole *Cuon alpinus*) were carried out on trails from September 2012 to January 2013 in the publicly-owned areas, which are known locally as ‘reserved forests’. For all the above sign surveys, detections (presence or absence) were recorded once every 100m..

Camera trap surveys for terrestrial mammals were carried out between September 2011 and April 2013 in publicly-owned areas, and involved placing a single camera (Scoutguard SG 565V and Scoutguard SG 560V, HCO Outdoor Products, GA, USA; recovery time 8-14 s) on trails close to randomly-generated sampling locations. The spatial intensity of sampling within each 1.5 km cell was proportional to anticipated corridor importance (Chapter 1). Cameras were intended to sample every location for three months, but were sometimes active for shorter or longer periods depending on logistical limitations. In this study, we included only cameras that were active for at least three weeks. Camera trapping was conducted across all seasons, and cameras were active throughout the day and night. We defined a detection event as a photograph of a species that was separated from another of the same species by one hour (Tobler *et al.,* 2008). Intermittent photographs to a period of eight hours that were likely of the same animal group (*e.g.,* a group of animals grazing at night) were also defined as single events.

3.2.3 Modelling approach

Our approach conceptually follows that of Caro *et al.,* (2004): we wanted to mimic a real-world situation where the detection of iconic flagship species in fragmented lands outside reserves leads to increased protection of those areas at a relatively small scale. Therefore, we quantified habitat use for tigers and elephants using the camera trap data, by modelling the rate of their detection events against several covariates (below). We validated these models using the independent sign survey data, and applied these models to predict elephant and tiger habitat use at all sampled locations (via camera and sign).

We then evaluated whether the detection rate or presence of 22 other species could be predicted by flagship species habitat use, in two ways. We first used elephant or tiger habitat use as predictors for the detection rates or presence of other species; we also evaluated correlations at a coarser level between flagship habitat use quintiles and detection rates or presence of other species.

We modelled elephant and tiger habitat quality at a resolution of 100m, while incorporating covariates at varying extents around these small cells. Our approach accommodates the fact that the presence of an animal at a particular location can be indicative of habitat selection at a variety of scales (Johnson, 1980). This may be modelled using a fully-conditional approach (DeCesare *et al.,* 2012), or by using covariates at multiple extents around the predicted resolution (Meyer & Thuiller, 2006). We followed the latter method because our data consisted of animal locations without further information on home ranges or population ranges.

3.2.4 Covariates

For both elephant and tiger habitat use models, we used four types of covariates: land use and vegetation characteristics, human impact variables, physical habitat attributes and sampling covariates. Similar covariates have previously been found to influence habitat use by elephants (*e.g.,* Fernando *et al.,* 2005; Gaucherel *et al.,* 2010) and tigers (*e.g.,* Karanth *et al.,* 2011; Sunarto *et al.,* 2012). Each covariate was computed for every camera trap location, but incorporated larger spatial buffers that maximized explanatory power (below). Vegetation type was quantified using the eco-climatic distance, a multivariate index measuring the deviation from a reference category of wet evergreen forest (Krishnaswamy *et al.,* 2009; Appendix 2.1). Land use consisted of five categories (closed forest, open forest and grassland, forestry plantation, commercial plantation and settlement). To quantify human impact for each camera location, we measured the distance to the nearest human settlement, commercial plantation and major road, corrected for undulating terrain. We also calculated the density of buildings within circular buffers.

To ensure that the above covariates were applied at the scales where they had the greatest effect, we quantified mean eco-climatic distance and proportion of land use class at progressively larger buffer sizes (300 m, 600 m, 1200 m and 2400 m) around each camera location. We computed building density using circular neighbourhoods of 300 m, 600 m and 1200 m. These upper limits were set by data availability. For these multi-scale covariates, we used for analysis the scale that maximized explanatory power for observed counts.

To describe the physical habitat of each camera location, we measured several variables including slope, local curvature, mean slope to nearest settlement and mean slope to nearest commercial plantation. Finally, we also measured the number of trails that intersected at each camera location, as well as mean trail width because we expected them to influence the probability of detecting the study species (*e.g.,* Sunquist 1981).

For tigers, we additionally included a class of covariates related to prey use, quantified by daily detection rates at cameras of their major prey (number of events per trap-day). These species included gaur (*Bos gaurus*); sambar (*Rusa unicolor*); wild pig (*Sus scrofa*); northern red muntjac (*Muntiacus vaginalis*) and bonnet macaque (*Macaca radiata*; Karanth & Sunquist, 1995), as well as Indian crested porcupine (*Hystrix indica*). We also combined all of the above species for an overall index of prey use, as well as another index that combined all prey species smaller than gaur.

3.2.5 Flagship species model selection and validation

For both elephant and tiger, we modeled the number of events per trap-day as the response variable using mixed-effects negative binomial regression models with a log link. Because the density of camera traps varied within each 1.5-km cell (above), we set each cell as a random intercept to account for non-independence. We followed a forward selection process using the Akaike Information Criterion (AIC), whereby we sequentially added covariates until these no longer led to a decrease in AIC score greater than 2 per parameter

(Arnold, 2010); we also used likelihood ratio tests for nested models. We scaled all covariates and screened them for collinearity ($|r_s| > 0.6$), and included quadratic fits and biologically-meaningful two-way interaction terms.

We validated the elephant and tiger habitat models built with camera trap data using the independently-collected sign survey data. For each of these species, we predicted habitat use at the 100-m cells that were sampled using sign surveys and were within the covariate range of the above regression models. We then computed the proportion of elephant and tiger detections that occurred within each of ten deciles and quintiles respectively of predicted habitat use, reasoning that a good model should give a positive correlation between predicted quantile and the proportion of detections. This principle is inherent in approaches such as k-fold cross-validation (Boyce *et al.,* 2002). Because our top tiger model included gaur detection rate as a predictor (below), we separately built a model for gaur habitat use following the same procedures as above. We validated this model as described above; we then predicted gaur use at locations sampled for animal sign, and hence predicted tiger habitat use at these locations.

3.2.6 Umbrella capacity for other species

Using the above models of habitat use for elephant and tiger, we first predicted habitat use at each sampled camera or sign survey location (for cells of 100-m), setting sampling-level covariates and effort at a standardized level. We then assessed umbrella capacity in two ways: using regression models and correlations. For the 21 terrestrial and semi-terrestrial species that were detected on camera traps (all species except the arboreal lion-tailed macaque *Macaca silenus*, Nilgiri langur *Trachypithecus johnii* and Indian giant squirrel *Ratufa indica*; hereafter, giant squirrel), we modeled the events per trap-day as a function of predicted tiger or elephant habitat use. We followed the same model formulations and procedures described above. To control for the effects of sampling design, we additionally included sampling covariates (as described above) in these models. For the ten species that were detected at <100 camera locations (Table 3.1), we repeated the above analysis using logistic regression models that compared locations where they were detected to those where they were not.

For the 13 species that could be evaluated using sign survey data, we modeled their presence or absence in a cell using mixed-effects logistic regression. We included the effort (distance walked) in each cell as a covariate, because we expected this to influence the probability of sign detection and wanted to control for it.

The second way we evaluated umbrella capacity was by examining correlations between detection rates and flagship species habitat use quintiles. We used this coarse approach in addition to the above regressions because (a) we believe this is more likely to reflect the way surrogate species are used in conservation applications and (b) because the data for many of our species was sparse for regressions (Table 3.1). For the 21 camera-trapped species, we computed the mean number of detections per 100 trap-days in each of these quintiles, and hence estimated the correlation (r_S) between this rate and the flagship habitat quintile. For sign survey data, we computed the proportion of detections (corrected for effort) that occurred in each quintile, and estimated the correlation between this proportion and flagship habitat quintile.

3.2.7 *Umbrella capacity for species diversity*

To test whether flagship species habitat use was correlated to species diversity, we computed two heterogeneity indices (Magurran, 2003) for camera locations occurring in each tiger and elephant quintile: Shannon-Weaver index ($H' = -\sum_{i}^{S} p_i \log_e p_i$) and the Simpson index ($D' = 1 - \sum_{i}^{S} p_i^2$), where p_i is the proportional abundance of events of each species at a camera location (*i.e.,* the number of events of a given species / total number of events) and S is the total number of species. We used only the camera trap data for this to maximize the number of species included in the analysis, and did not use species richness because virtually all species were detected at least once in each quintile. We computed the above indices separately for seven threatened and 14 non-threatened species. Because sambar comprised 70% of the threatened species detections, we repeated the above analysis for threatened species other than sambar as well. All of the above statistical analyses were carried out in program R version 3.1.1 (R Foundation for Statistical Computing, Vienna, Austria).

3.3 Results

3.3.1 Elephant and tiger habitat models

Camera trap surveys were conducted at 445 locations for a total of 36,855 trap-days, giving 1142 detections of elephant at 231 locations and 73 detections of tigers at 50 locations (Table 3.1). Sambar was the most commonly detected species on camera (6570 events) and ruddy mongoose (*Herpestes smithii*) was the rarest (14 events). The amount of sign survey data that was used in this study varied from 436 to 630 km of effort, based on the covariate range of each flagship species habitat model and on whether the target species were herbivores, arboreal mammals or carnivores. Detections of species on sign surveys ranged from a low of 11 tiger detections to a high of 2325 sambar detections.

Elephant and tiger habitat use models both incorporated a positive response to distance from major road and a negative response to the proportion of commercial plantation (Table 3.2). Elephant use was also negatively correlated to building density and slope, as well as with eco-climatic distance (*i.e.,* areas that were less evergreen). Tiger use was positively correlated to distance from settlement, particularly when distance from major roads was also high. The frequency of independently-collected elephant sign data was highly correlated to predicted elephant habitat decile ($r_s = 0.96$, $P < 0.001$). For tigers, the 11 independent detections showed an upward trend with predicted habitat quintile ($r_s = 0.90$, $P = 0.08$).

3.3.2 Umbrella capacity for other species

Three broad groups of species emerged from regression and correlation analyses of the study species with elephant or tiger habitat use (Table 3.3). The first group exhibited positive correlations with elephant or tiger habitat use (or with both). In this group, elephants and tigers were strongly correlated with each other, and gaur were positively correlated to both of them (Fig. 3.2a-b & Fig. 3.3a-b). Stripe-necked mongoose (*Herpestes vitticollis*) also exhibited a positive trend with both flagship species (Fig. 3.2c), but Nilgiri langurs were positively correlated only to tiger habitat use (Fig. 3.3c). Brown palm civets (*Paradoxurus jerdoni*) exhibited a variable, but statistically significant positive relationship with elephants, although their relationship with tigers appeared more hump-shaped (Fig. 3.2d)

A second group of species were negatively correlated to one or both flagship species, among which sambar exhibited the most consistent negative trend (Fig. 3.2d & 3.3d). Wild pigs, muntjac and Indian chevrotain (*Moschiola indica*) also exhibited negative trends against at least one of the flagship species (Table 3.3). Dhole events on camera were negatively correlated to tiger habitat use (Fig. 3.2e), but their signs were not (Fig. 3.3e).

The third group of 12 species exhibited patterns that were inconsistent or ambiguous. Sloth bear (*Melursus ursinus*) detections appeared to increase and then flatten out or decrease with elephant and tiger habitat quality (Fig. 3.2f & Fig. 3.3g). Mean sloth bear detections on camera traps was 97% higher in the fourth tiger quintile when compared to the second (Wilcoxon rank-sum test; $W = 4450$, $P = 0.03$). Similarly, 31% of sloth bear signs were detected in the third elephant use quintile, compared to 11% and 9% in the first and fifth quintiles respectively. Indian pangolins (*Manis crassicaudata*) appeared to exhibit a similar tendency, particularly with respect to tiger habitat quintile (4.8 times higher in the third than the first tiger quintile; $W = 4411$, $P = 0.02$, Fig. 3.2h). Giant squirrel detections were positively correlated to tiger habitat use but negatively to elephant habitat use (Table 3.3). The sparse detections of

Indian brown mongoose (*Herpestes fuscus*) tended towards a hump-shaped correlation with elephants, while lion-tailed macaques did not exhibit any clear trend with either flagship species.

3.3.3 Umbrella capacity for species diversity

The diversity of seven threatened species as measured by Simpson's index steadily increased with elephant and tiger habitat use quintile (Fig. 3.4 a); results were qualitatively similar for the Shannon-Weaver index (Appendix 3.2). However, when sambar was not included in the threatened species group, Simpson's index decreased with elephant habitat use, and did not show a trend with tiger habitat use (Fig. 3.4b). In contrast, the Shannon-Weaver index did increase at higher quintiles for tiger and elephant, but this trend was no longer linear (Fig. 3.4c). Simpson's index did not show a clear trend with flagship species habitat use for non-threatened species (Fig. 3.4d), and the Shannon-Weaver index showed similar results (Appendix 3.2).

3.4 Discussion

Charismatic flagship species play an important role in eliciting public support for conservation initiatives (Verissimo *et al.,* 2011), but they are also often assumed to be umbrella species, whose protection confers protection on other co-occurring species (Leader-Williams & Dublin 2000). It is important to test this assumption in multiple-use areas outside reserves, because it is in these highly-contested areas that the presence of threatened flagship species can most strongly influence decisions on land use (Caro *et al.,* 2004). We asked two questions: how well do the detections of 22 other mammals correlate with elephant and tiger habitat use (and how well do these two flagship species correlate with each other)? And, how does the diversity of threatened and non-threatened species change with increasing elephant and tiger habitat use? We found that elephant and tiger detections were strongly correlated. However, only one other threatened species – gaur – was strongly correlated to both of them, and one more – Nilgiri langur – was strongly correlated to tiger but not elephant habitat use. Some threatened species (sambar, and dhole photographs) exhibited negative correlations; some others showed variable tendencies to peak at the mid-ranges of flagship species habitat quality (sloth bears, pangolins and brown mongoose); and the lion-tailed macaque did not show any correlation. The diversity of threatened species increased with flagship habitat quality when sambar was included; but when this species was excluded, diversity no longer increased linearly, and even decreased for elephant habitat quintile. Our results show only mixed evidence for the umbrella potential of elephants and tigers at small scales.

Among the threatened species, elephants, tigers and gaur were strongly correlated with each other. All three species are large-bodied habitat generalists that are mainly limited by human activity (Choudhury 2002; Fernando *et al.,* 2006; Karanth *et al.,* 2011). Such shared ecological requirements promote umbrella capacity (Swengel & Swengel, 1999). However, the correlation between elephants and tigers was not perfect; tigers occupy a much narrower niche in this landscape than elephants do (Chapter 4), possibly due to stronger avoidance of human infrastructure than elephants (Table 3.2). This greater avoidance of humans may explain why Nilgiri langur (which are often subject to poaching) were positively correlated to tigers but did not show a clear trend with elephants, although their preference for more rugged terrain may also be a factor (Kumara & Singh, 2004). The correlation of gaur with tigers reflects their role as preferred tiger prey (Karanth & Sunquist, 1995); more generally, top carnivores are often expected to be effective surrogates for their prey (Sergio *et al.,* 2006). However, both of the other large ungulates that tigers consume regularly across their range (sambar and wild pig; *e.g.,* Ngoprasert *et al.,* 2012) were negatively correlated to tigers in our study. Sambar and wild pig adapt well to anthropogenic habitat (Caley 1997; Meijaard & Sheill, 2008), and hence their density of use may not reflect the habitat requirements of a top carnivore that is often persecuted by humans. This implies that top carnivores may not necessarily be effective surrogates for their prey in multiple-use areas (see also Dalerum *et al.,* 2008 for similar arguments for carnivores in southern Africa).

Because anthropogenic activity is often the ultimate cause of species endangerment (Pimm *et al.,* 2014), threatened species may be expected to correlate positively to threatened umbrella species (Launer & Murphy, 1994), particularly in multiple-use areas. However, we did not find strong evidence of this once the threatened but abundant sambar was removed from the analysis. The Shannon-Weaver and Simpson indices did vary in their direction (with the Shannon-Weaver index suggesting that diversity increases at higher flagship species habitat quintiles); however, both indices previously agreed in their trends when sambar were included (Fig. 3.4a; Appendix 3.2), which suggests ambiguity in supporting species diversity, at the least. Threatened species may be threatened due to different reasons (Possingham *et al.,* 2002), and hence they may not necessarily correlate with each other at small scales (Caro, 2010). For example, lion-tailed macaques may persist in rainforest fragments within tea plantations if they are not poached (Singh *et al.,* 2002), while large carnivores may not (Terborgh *et al.,* 2001).

Our study was conducted within a small spatial extent and resolution, and mimicked a typical flagship-based conservation prioritization approach outside reserves (Caro *et al.,* 2004). However, assessments of umbrella capacity are scale-dependent (reviewed by Favreau *et al.,* 2006), and different taxa may perform surrogate functions at different scales (Buhning-Gaese 1997; although Carrascal *et al.,* 2012 did not find evidence for scale dependence in the umbrella capacity of birds). Our study site covers a small extent compared to the potential home ranges of our flagship species; yet, large mammals are often selected as umbrella species precisely because their home ranges should encompass the habitat requirements of many other species (*e.g.,* Noss *et al.,* 1996; Simberloff 1998; Carroll *et al.,* 2001). However, there are limits to the amount of land that is now available to protect for biodiversity (reviewed by Naughton-Treves *et al.,* 2005), particularly in the densely-populated Western Ghats (Cincotta *et al.,* 2000); the mean size of a protected area in India is approximately 240 km^2 (ENVIS 2014). It is due to this intense competition for land that current governmental policy aims to permanently delineate conservation areas and redirect other areas for development (Kasturirangan *et al.,* 2013). Further, even though our model predictions were made at a resolution of 100 m, they incorporated the influence of covariates up to a radius of 2.4 km (Meyer & Thuiller, 2006); each cell is therefore influenced by a neighborhood of approximately 17 km^2. As the resolution of analysis increases, we expect greater correspondence between the flagship species and other biodiversity (*e.g.,* Wolters *et al.,* 2006).

The need to evaluate flagship species for their umbrella function rather than assume this to be true raises the need for large-scale monitoring of biodiversity and ecosystem processes, which may be ironic because the use of umbrella species is considered a shortcut to conservation prioritization (Fleishman *et al.,* 2000). Nevertheless, the implicit use of flagship species as umbrella species may be inevitable due to their ability to raise public support for conservation (Caro, 2010). Automated technologies such as camera traps can greatly simplify such assessments (*e.g.,* O'Connell *et al.,* 2011), particularly when they are combined with local capacity (*e.g.,* citizen science programs; Silvertown 2009). Apart from the ability to collect multi-species data, the use of multiple survey methods gives scientists the ability to validate statistical models with independent data (as we did for our tiger and elephant models), a task that is not often undertaken when modeling species distributions (Araujo & Guisan, 2006).

In conclusion, we found only mixed evidence of the umbrella capacity of two iconic flagship species in a multiple-use region. While this finding does not in any way diminish the importance of their conservation or their ability to inspire conservation action, it does raise the need to evaluate rather than assume umbrella function. The use of flagship species as marketing tools for public support and raising funds (Verissimo *et al.,* 2011) should be accompanied by an empirical evaluation of their potential limitations, and species that do not benefit from the protection of flagship species must be protected through additional means.

3.5 Tables

Table 3.1 Detections of 24 threatened and non-threatened species between 208 and 2013 in the Shencottah Gap, India using camera trap surveys and sign surveys (giving the number of sign detections that were usable for comparison with elephant and tiger habitat use models, based on the covariate range of those models, Table 3.2). Red list status is taken from IUCN (2010).

Species	Red list status	Camera detections		Sign detections	
		Locations where present	Number of events	For elephant model	For tiger model
Asian elephant (*Elephas maximus*)	EN	231	1142	909	964
Dhole (*Cuon alpinus*)	EN	147	335	62	66
Tiger (*Panthera tigris*)	EN	50	73	11	11
Indian pangolin (*Manis crassicaudata*)	EN	47	65	NA	NA
Lion-tailed macaque (*Macaca silenus*)	EN	NA	NA	14	15
Sambar (*Rusa unicolor*)	VU	382	6570	2134	2325
Gaur (*Bos gaurus*)	VU	200	1122	484	507
Sloth bear (*Melursus ursinus*)	VU	61	106	64	69
Indian brown mongoose (*Herpestes fuscus*)	VU	20	47	NA	NA
Nilgiri langur (*Trachypithecus johnii*)	VU	NA	NA	87	96
Leopard (*Panthera pardus*)	NT	244	893	116	121
Wild pig (*Sus scrofa*)	LC	352	2386	442	489
Indian crested porcupine (*Hystrix indica*)	LC	347	2880	NA	NA

Northern red muntjac (*Muntiacus vaginalis*)	LC	299	1799	473	488
Indian chevrotain (*Moschiola indica*)	LC	229	1108	62	69
Bonnet macaque (*Macaca radiata*)	LC	140	337	32	33
Small Indian civet (*Viverricula indica*)	LC	116	375	NA	NA
Brown palm civet (*Paradoxurus jerdoni*)	LC	89	291	NA	NA
Stripe-necked mongoose(*Herpestes vitticollis*)	LC	82	174	NA	NA
Common palm civet (*Paradoxurus hermaphroditus*)	LC	29	77	NA	NA
Jungle cat (*Felis chaus*)	LC	20	32	NA	NA
Leopard cat (*Prionailurus bengalensis*)	LC	16	20	NA	NA
Ruddy mongoose (*Herpestes smithii*)	LC	11	14	NA	NA
Indian giant squirrel (*Ratufa indica*)	LC	NA	NA	141	147

Table 3.2 Coefficients and standard errors from the best habitat use models (based on ΔAIC) for elephant and tiger in the Shencottah Gap, India, obtained through regression of camera counts per trap-day (from 2011 to 2013) against habitat attributes using mixed-effects negative binomial regression models.

	Elephant			Tiger		
Fixed effects	Coefficient (SE)	*t*	*P*	Coefficient (SE)	*t*	*P*
Intercept	-4.1 (0.13)	-32.76	<0.001	-7.85 (0.39)	-20.35	<0.001
Building density	-0.97 (0.23)	-4.31	<0.001			
Distance to major road	0.47 (0.12)	3.95	<0.001	0.07 (0.29)	0.25	0.8
Distance to settlement				1.33 (0.38)	3.49	<0.001
Distance to settlement^2				-0.85 (0.31)	-2.76	0.006
Proportion of commercial plantation	-0.48 (0.11)	-4.49	<0.001	-0.47 (0.28)	-1.67	0.09
Eco-climatic distance	-0.53 (0.19)	-2.79	0.005			
Slope	-0.25 (0.08)	-3.04	0.002			
Gaur use				0.21 (0.06)	3.72	<0.001
Building density X eco-climatic distance	-1.69 (0.19)	-2.79	0.005			
Distance to settlement X distance to major road				0.48 (0.24)	2	0.05
Number of intersecting trails	0.14 (0.08)	1.89	0.06	0.35 (0.13)	2.65	0.008
Random effects						
Variance of sampling grid cell	0.44					

[a] 300-m buffer

[b] 600-m buffer for elephant, 300-m buffer for tiger

[c] 2400-m buffer

Table 3.3 Beta coefficients from regression models of camera data (detections per trap-day) or sign data (presence or absence of sign) modeled against predicted elephant or tiger habitat use in the Shencottah Gap, India, and Spearman rank coefficients from correlation of camera data (mean detection rate per trap-day) or sign data (proportion of signs corrected for effort) with predicted elephant or tiger habitat use quintiles for 24 species. The top part of the table comprises threatened and the bottom non-threatened species (each set sorted by positive, negative and ambiguous correlations). Bolded coefficients indicate statistical significance at α = 0.05 and terms in italics indicate significance at α = 0.1.

Species	Camera count regression		Sign presence regression		Camera count correlation		Sign proportion correlation	
	Elephant	Tiger	Elephant	Tiger	Elephant	Tiger	Elephant	Tiger
Elephant	NA	**1.4 (0.3)** **-1.6 (0.4)**[c]	NA	**0.4 (0.1)**[d]	NA	**1.0**	NA	**1.0**
Tiger	**0.9 (0.3)** **-0.4 (0.2)**[c]	NA	*2.4 (1.3)*	NA	**1.0**	NA	*0.9*	NA
Gaur	**1.0 (0.2)** **-0.4 (0.2)**[c]	**2.0 (0.4)** **-1.6 (0.4)**[c]	**0.6 (0.1)**[d]	**0.6 (0.1)**[d]	**1.0**	**1.0**	*0.9*	*0.9*
Nilgiri langur	NA	NA	-0.3 (0.2)	**0.7 (0.2)** *-0.2 (0.1)*[c]	NA	NA	-0.3	**1.0**
Sambar	**-0.6 (0.1)** **0.2 (0.1)**[c]	**-0.8 (0.3)** **0.7 (0.2)**[c]	**-0.5 (0.1)** **1.0 (0.3)**[c]	**-0.2 (0.1)**	**-1.0**	*-0.9*	**-1.0**	**-1.0**
Dhole	-0.0 (0.1)	**-1.8 (0.5)**	0.2 (0.2)	-0.2 (0.2)	0.4	*-0.9*	0.5	-0.2
Sloth bear	*0.3 (0.2)*	0.0 (0.2)	0.2 (0.2)	*0.5 (0.3)* **-7.4 (3.6)**[c]	0.7	0.6	-0.1	0.5
Pangolin	0.0 (0.3)	-1.2 (0.9)	NA	NA	-0.1	-0.3	NA	NA
Brown mongoose	0.1 (0.5) **-2.5 (1.3)**[*c]	-0.9 (0.7)	NA	NA	0.3	-0.7	NA	NA
Lion-tailed macaque	NA	NA	-0.8 (0.6)	0.1 (0.5)	NA	NA	0.7	0.1
Stripe-necked mongoose	**0.3 (0.2)**	-0.0 (0.2)	NA	NA	**1.0**	*0.9*	NA	NA
Brown palm civet	**0.4 (0.2)**	-0.9 (0.7)	NA	NA	0.4	0.3	NA	NA

Wild pig	**-0.4 (0.1)** *0.2 (0.1)*[c]	**-1.2 (0.2)** **1.1 (0.2)**[c]	**-0.5 (0.1)**	**-0.1 (0.1)**[d]	*-0.9*	*-0.9*	-0.7	-0.7
Bonnet macaque	**-0.4 (0.1)**	-0.9 (0.7)	-0.4 (0.2)	0.1 (0.2)	-0.4	*-0.9*	**-1.0**	-0.1
Muntjac	**-0.3 (0.1)**	-0.3 (0.2)	0.0 (0.0)	0.0 (0.0)	*-0.9*	*-0.9*	-0.1	0.2
Chevrotain	-0.1 (0.1)	**-0.9 (0.4)**	**-0.5 (0.3)**	0.1 (0.1)	-0.3	-0.1	-0.6	0.6
Giant squirrel	NA	NA	*-0.4 (0.2)*	**0.3 (0.1)**[d]	NA	NA	-0.8	0.5
Common palm civet	**-1.8 (0.6)**	*-8.2 (4.8)*	NA	NA	**-1.0**	**-1.0**	NA	NA
Small Indian civet	0.1 (0.2)	**-2.2 (0.7)**	NA	NA	0.3	-0.1	NA	NA
Jungle cat	NA	NA	NA	NA	-0.2	*-0.9*	NA	NA
Leopard	0.00 (0.1)	0.00 (0.1)	0.1 (0.1)	-0.2 (0.2)	0.4	0	0.2	0.5
Porcupine	-0.1 (0.1)	-0.1 (0.1)	NA	NA	-0.1	-0.5	NA	NA
Leopard cat	NA	NA	NA	NA	-0.3	-0.5	NA	NA
Ruddy mongoose	NA	NA	NA	NA	-0.5	-0.4	NA	NA

[a] Standardized beta coefficients

[b] Spearman rank correlation coefficients

[c] Quadratic term

[d] Log-transformed covariate

3.6 Figures

Figure 3.1 Map of Shencottah Gap, India, which lies between Periyar Tiger Reserve (PTR) and a complex including Kalakkad-Mundanthurai Tiger Reserve (KMTR) and Shendurney Wildlife Sanctuary (SWLS), along with major land-use types.

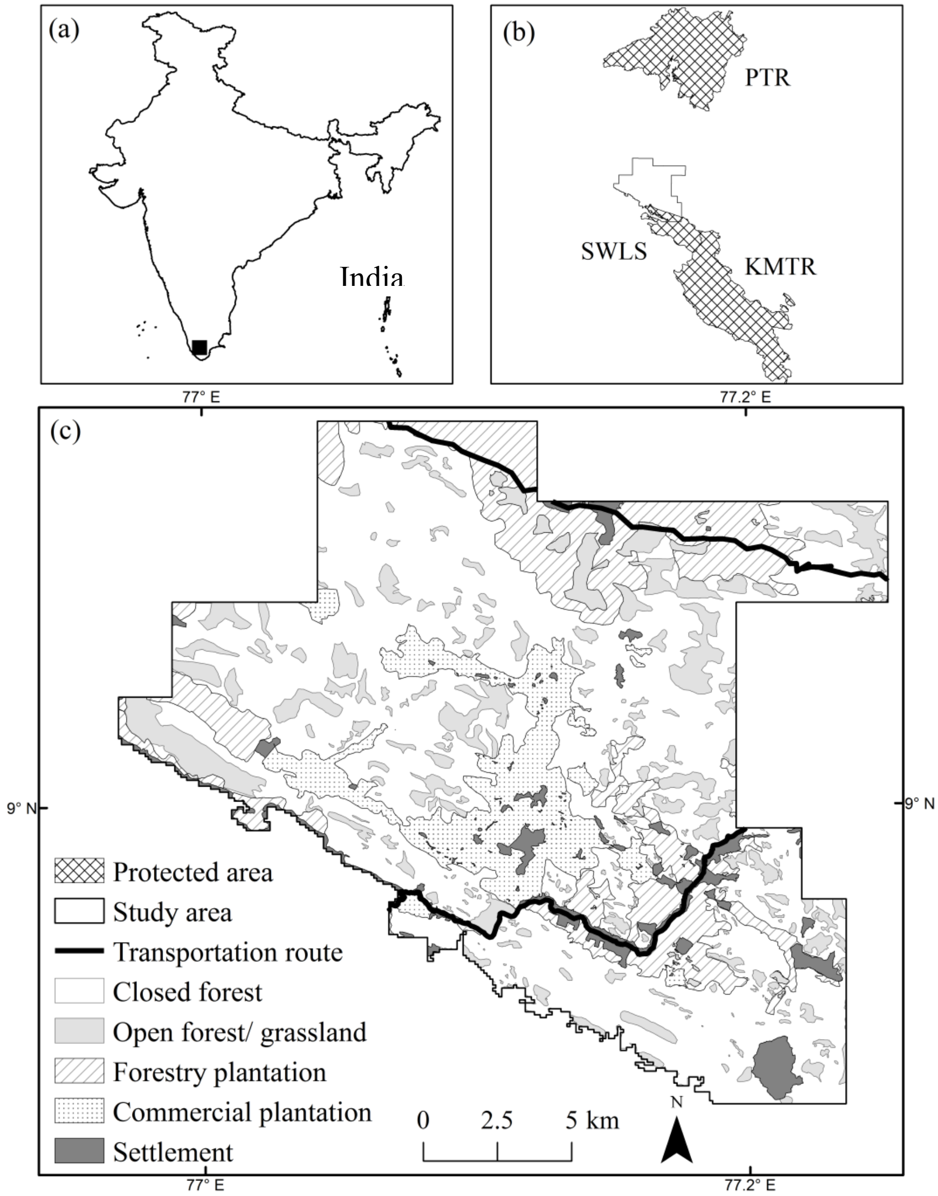


Figure 3.2 Detection rates (with standard errors) of selected species on camera traps between 2011 and 2013 in the Shencottah Gap, India, within each of five predicted elephant and tiger habitat use quintiles.

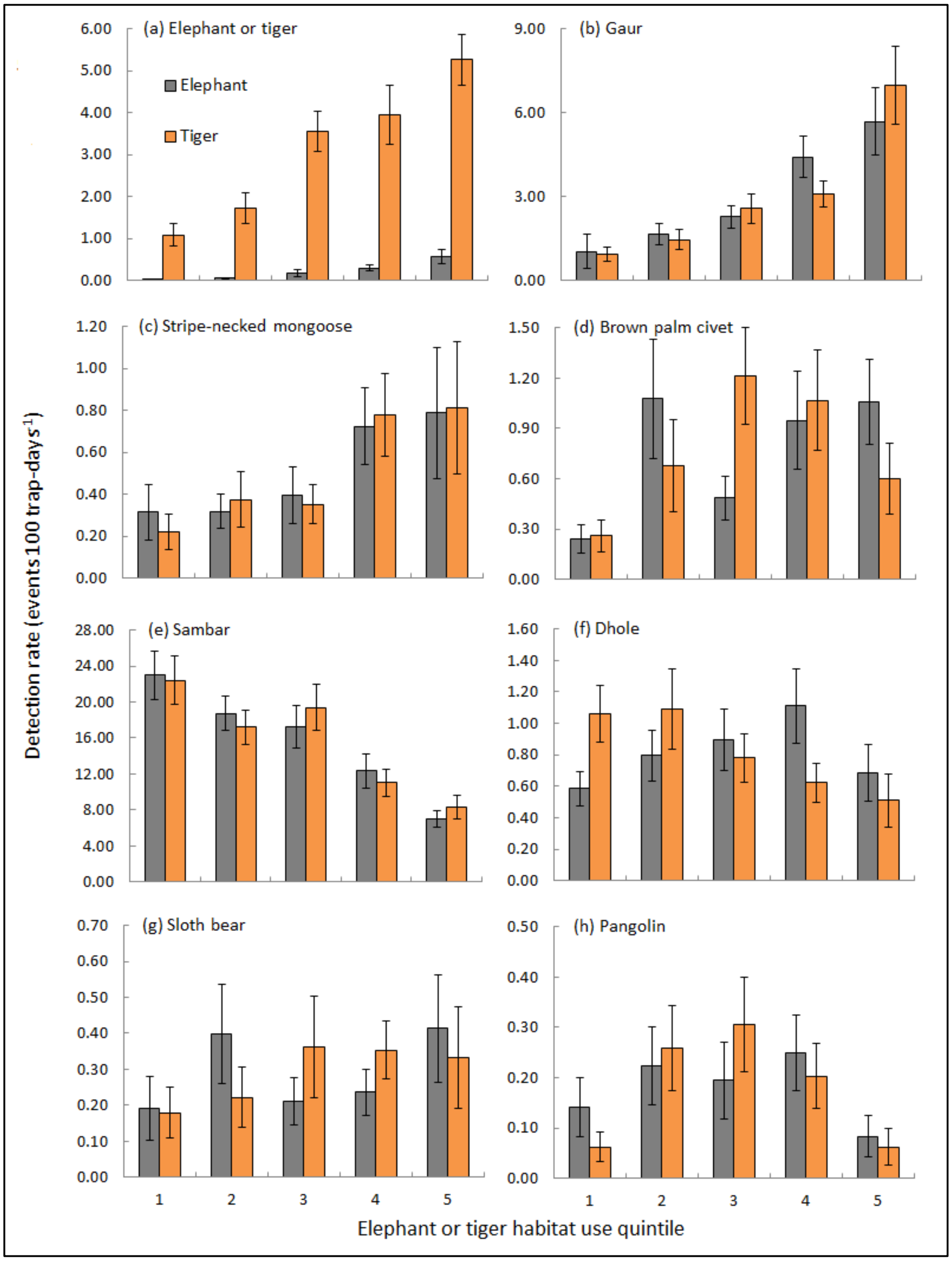


Figure 3.3 Proportion of sign detections (corrected for effort) between 2008 and 2011 of selected species that occurred within five predicted elephant and tiger habitat use quintiles in the Shencottah Gap, India.

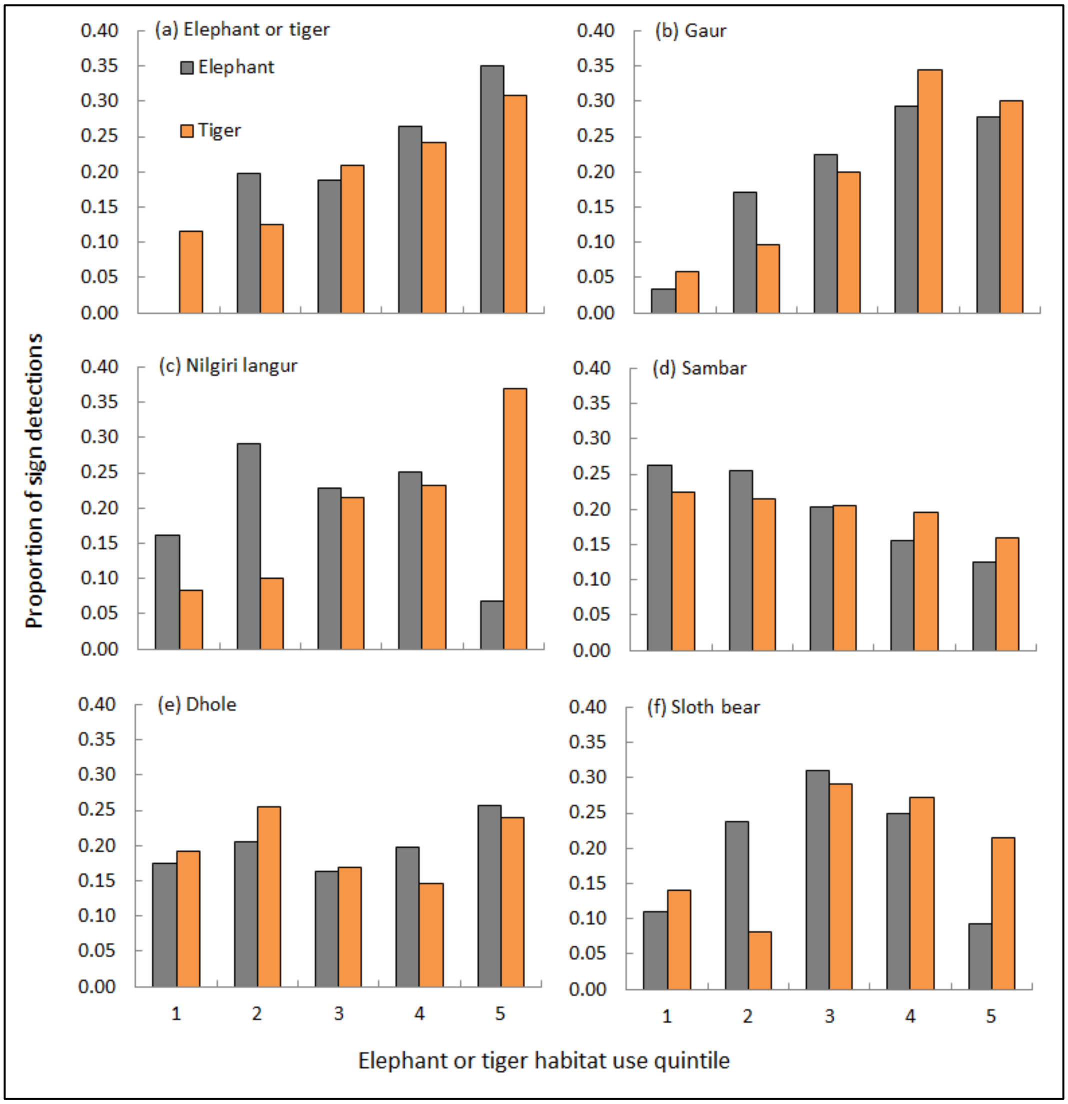
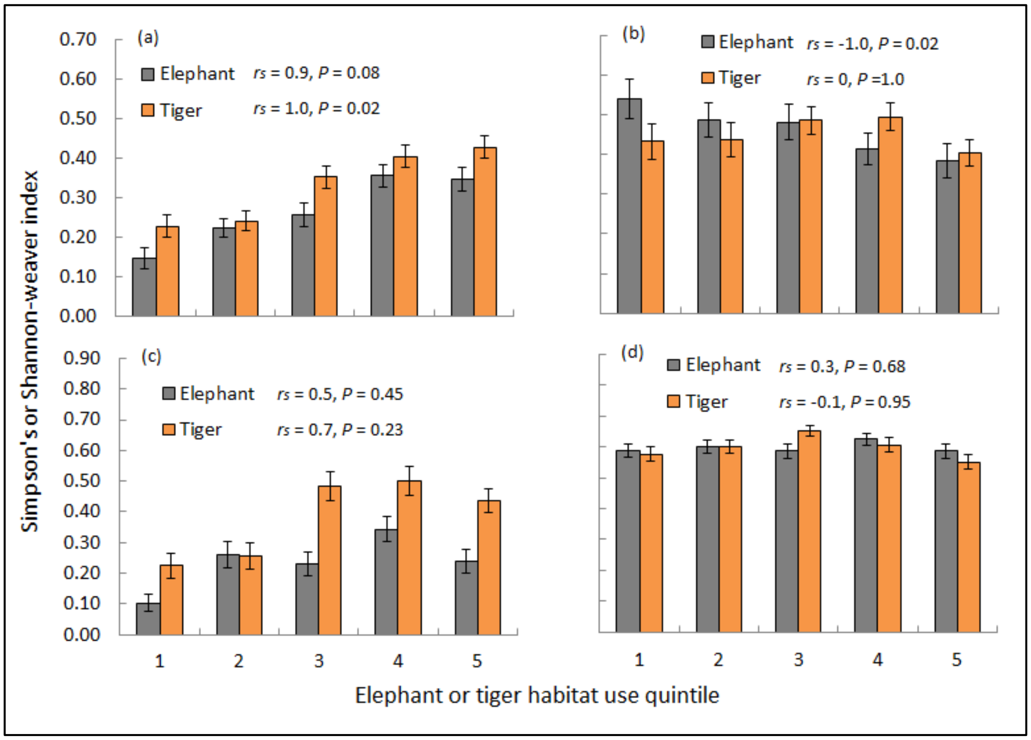


Figure 3.4 Trend in Simpson's index (panels a, b and d) and Shannon-Weaver index (panel c) for seven threatened species (panel a) and threatened species not including sambar (panels b and c), as well as non-threatened species (panel d) from camera trap data collected between 2011 and 2013 in the Shencottah Gap, India.



Chapter 4

4 Classifying mammalian niche characteristics helps clarify divergent conservation requirements[*]

4.1 Introduction

Conservationists often use large-scale planning tools to designate high-value regions (*e.g.,* biodiversity hotspots; Myers *et al.,* 2000), and subsequently prioritize conservation action at smaller scales within (Eken *et al.,* 2004). Because such priority sites are often constrained in their extent (reviewed by Schwartz, 1999), they strive to maximize the number of species or ecological traits protected within this limited space (reviewed by Fleishman *et al.,* 2006). However, species have different niches (Hutchinson, 1957) and respond to habitat characteristics dissimilarly (Franklin & Lindenmayer, 2009), even within taxonomic classes. Such discordance may be especially prevalent in biodiversity hotspots, which typically also encompass high habitat diversity, growing human activity, and physically-complex landscapes (Myers *et al.,* 2000; Cincotta *et al.,* 2000). This lack of uniform responses can limit identification of both anthropogenic problems and conservation solutions; for example, if critically endangered, endangered or vulnerable species (IUCN 2010; hereafter, threatened) have divergent habitat requirements (van Jaarsveld *et al.,* 1998).

To balance unique species requirements with management generalizability species may be aggregated into groups (‘functional types’; *sensu* Thompson *et al.,* 1996) that reflect their broad habitat requirements or restrictions. Such groupings have been applied to vegetation types (Lavorel *et*

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[*] Authors of an associated manuscript in preparation: Aditya Gangadharan, Srinivas Vaidyanathan & Colleen Cassady St. Clair.

al., 1997), ants (King *et al.,* 1998) and mammals (McKinney, 2002) to provide insights for their management. For example, by classifying mammals into 'urban avoiders', urban adaptors' and 'urban exploiters', McKinney (2002) provided a tractable framework for their management in the face of urban sprawl. Hence, identifying functional types could help balance the focus of single-species approaches (Simberloff, 1998) with the prioritization of habitat types (*e.g.,* Eken *et al.,* 2004), while also quantifying conservation potential in working landscapes (*e.g.,* Daily *et al.,* 2001). Yet, these classifications are typically based on *ad hoc* methods rather than quantitative criteria (Lavorel *et al.,* 1997), limiting their rigour.

Ecological Niche Factor Analysis (Hirzel *et al.,* 2002; Basille *et al.,* 2008; hereafter, ENFA) provides a promising approach to delineating functional types of species based on their realized niches. This multivariate tool compares habitat characteristics at locations where a species is present to locations that are available, hence producing two or more axes describing the realized niche. The first axis, termed marginality, maximizes the difference between the mean habitat characteristics of locations where a species is present, and the mean habitat characteristics of the study area. The subsequent axes, termed specialization, maximize the ratio between the variance of habitat characteristics of locations where a species is present, to the variance in habitat characteristics of the study area. The specialization axes are often combined and expressed as their inverse, termed tolerance, which describes niche breadth. These two metrics – marginality and tolerance – therefore describe how much the most frequently-used habitat differs from what is available, and how narrow the range of habitats used is relative to what is available (Hirzel *et al.,* 2002). Recent studies that applied ENFA to multi-species assessments (*e.g.,* Durant *et al.,* 2010; Botts *et al.,* 2013) suggest the potential for broader application of this method to identify priority conservation actions.

We assessed the potential of ENFA to aggregate 14 mammals into functional types, and hence provide insights into their conservation needs in a multiple-use landscape in India's Western Ghats biodiversity hotspot (Myers *et* *al.,* 2000). We reasoned that the distribution of species across the marginality-tolerance space could provide novel insights into how they are limited by anthropogenic activity, and the extent to which they may be able to persist in human-impacted areas. Based on existing studies, we predicted relative marginality and tolerance scores for each species, hence placing them in five hypothesized functional types (Table 4.1; naming conventions follow IUCN 2010). Our predicted schematic identified one group with high marginality and low tolerance (tigers *Panthera tigris* and lion-tailed macaques *Macaca silenus*). This contrasted diagonally with species of low marginality and high tolerance (leopard *Panthera pardus*, sambar *Rusa unicolor*, wild pig *Sus scrofa* [hereafter pig], Northern red muntjac *Muntiacus vaginalis* [hereafter, muntjac] and bonnet macaque *Macaca radiata*). We predicted that the other seven species would occupy the intermediate ranges.

4.2 Methods

4.2.1 Study area

We surveyed a 787 km^2 multiple-use region in Kerala and Tamil Nadu, separating Periyar Tiger Reserve in the north and Kalakkad-Mundanthurai Tiger Reserve in the south (Fig. 4.1). Approximately 25% of the region consists of anthropogenic habitat types, including government-owned monoculture timber plantations (14%), private cash crop plantations (6%) and settlements consisting of buildings interspersed with gardens (5%). The remaining area is owned by the government and consists of evergreen and semi-evergreen forest (Ramesh *et al.,* 1997) in varying states of degradation. A transportation route consisting of a highway and railway line, and another smaller highway, passes through the study area, forming barriers to connectivity.

4.2.2 Field methods

The study area was divided into 1.5-km cells to allocate effort and surveyed using five different methods between 2008 and 2013 to maximize detections of multiple species. These included: (1) surveys of sign (scat, markings, tracks, sightings and calls) that were carried out away from trails; (2) comparable sign surveys carried out on trails; (3) camera-trap surveys; (4) surveys of carnivore sign; and (5) opportunistic detections. We used only detection-non detection data in this study. Methodological details for each survey type are depicted on a map (Fig. 4.1) and summarized by effort (Table 4.2).

Off-trail and on-trail surveys covered all land-use types, and were conducted in the dry season (December 2008 to May 2009 and December 2009 to June 2010). Off-trail surveys followed a systematic sampling protocol (described in Chapter 2) targeting terrestrial herbivores and arboreal species (Gopalaswamy *et al.,* 2012), while also recording carnivores opportunistically. On-trail surveys were conducted along existing human and animal trails, and unpaved roads (hereafter trails). These targeted terrestrial herbivores, arboreal mammals and carnivores (the latter are often more detectable on trails; Sunquist, 1981, Karanth *et al.,* 2011). For both off-trail and on-trail surveys, we recorded detections of a given species once every 100m along survey routes.

Camera trap surveys for terrestrial and semi-terrestrial species were conducted in all seasons between September 2011 and April 2013. Single cameras (Scoutguard SG 565V and Scoutguard SG 560V, HCO Outdoor Products, GA, USA) were placed on the trail nearest to randomly-generated sampling locations. We placed more cameras in areas where previous work suggested greater importance for corridor use by large mammals (Chapter 2). We intended cameras to sample each location for three months, but logistical constraints sometimes caused them to be operational for more or less time. Ninety-six percent of camera traps were located in publicly-owned areas ('Reserved forests' and forestry plantations).

Surveys specific to large carnivore sign were conducted on trails in publicly-owned areas between September 2012 and January 2013. This effort targeted signs left by tiger, leopard and dhole (*Cuon alpinus*), and were again recorded at 100-m intervals.

Finally, we also used two types of opportunistic data. One consisted of detections made while field teams were travelling anywhere in the study area, but were not engaged in a specified survey activity. The second type consisted of detections of a given species that were made using methods that were not targeted at it (Table 4.2). For example, all carnivore detections made in off-trail surveys were considered to be opportunistic (above). Detections of arboreal lion-tailed macaques, Nilgiri langur (*Trachypithecus johnii*) and Indian giant squirrel (*Ratufa indica*; hereafter, giant squirrel) on camera traps were also classified as opportunistic, but those of the semi-terrestrial bonnet macaque were not.

4.2.3 Covariates

To carry out the ENFA, we used 10 environmental covariates that encompassed three broad types: land use and vegetation characteristics, human impact characteristics and physical habitat attributes. Similar covariates have previously been found to influence habitat use by our study species (Table 4.1). Each variable was estimated for all surveyed cells at 100-m resolution, but some incorporated larger spatial buffers that maximized explanatory power (see below). Our approach accommodates the fact that the presence of an animal at a particular location reflects habitat selection at a variety of scales (Johnson, 1980), which may be modelled using a fully-conditional approach (DeCesare *et al.,* 2012) or by using covariates at multiple extents around the predicted resolution (Meyer & Thuiller, 2006). We followed the latter as our data consisted of animal locations without further information on home ranges or population ranges.

Vegetation type was quantified using the eco-climatic distance, an index measuring the deviation from a reference category of wet evergreen forest (Krishnaswamy *et al.,* 2009; Appendix 2.1). Land use consisted of five categories (closed forest, open forest and grassland, forestry plantation, commercial plantation and settlement). To quantify human impact characteristics, we measured the distance to the nearest human settlement, commercial plantation and major road, correcting each for undulating terrain. We also calculated the density of buildings within circular buffers (see below). To describe the physical habitat of each survey location, we measured slope and local curvature (an index of ruggedness). As we expected steeper slopes to enable animals to come closer to anthropogenic habitat, we measured mean slope to nearest settlement and mean slope to nearest commercial plantation.

To ensure that covariates were applied at appropriate scales, we quantified mean eco-climatic distance and proportion of land use class at progressively larger buffer sizes (300 m, 600 m, 1200 m and 2400 m) around each cell centroid. We computed building density using circular neighbourhoods of 300 m, 600 m and 1200 m; all buffer maxima were based on data availability. For each covariate, we used the buffer size that maximized discrimination between locations where species were detected and where they were not (measured using Pearson's *r*).

4.2.4 Ecological niche factor analysis

ENFA is a multivariate method that compares habitat characteristics at species locations ('used') to habitat characteristics in the study area ('available'), hence extracting marginality and tolerance scores, and covariate correlations with each axis (Hirzel *et al.,* 2002; Basille *et al.,* 2008). When only presence locations are known, 'available' samples are taken at random locations within the study area; however, our 'available' locations were those that we sampled using at least one method, but where we did not detect the species (Hirzel *et al.,* 2002). Hence, our results are conditional on sampling, and 'available' cells were species-specific (Table 4.2).

We applied the square-root transformation to increase normality of eco-climatic distance, distance to commercial plantation, distance to settlement and distance to major road (Basille *et al.,* 2008). To evaluate covariate effects, we computed the correlation of each covariate with the marginality axis and the first specialization axis (akin to factor loadings for a Principal Components Analysis). For the marginality axis, a negative correlation with a covariate indicates preference for lower values than the mean value prevalent in the study area (Hirzel *et al.,* 2002). For the specialization axes, which are ratios of used locations to available locations, only the absolute value of the correlation coefficient can be interpreted; a higher absolute value indicates a higher contribution towards restricting the variance of species presence (Hirzel *et al.,* 2002).

To evaluate the extent to which our sampled locations were representative of the study area, we compared the cells that were sampled for each species (Table 4.2) with un-sampled cells in the study area (Botts *et al.,* 2013), using the same covariates and procedures as above. For tiger, leopard and dhole, marginality of sampled locations was negatively correlated to slope ($-0.78 < r_s < -0.77$), indicating that we sampled less in the steepest parts of the study area. For all other species, sampled locations were negatively correlated to slope ($-0.50 < r_s < -0.64$), distance to settlement ($-0.30 < r_s < -0.36$) and proportion of closed forest ($-0.41 < r_s < -0.46$), and positively to the proportion of forestry plantation ($0.37 < r_s < 0.55$). See Appendix 4.1 & 4.2 for details.

For all analyses, we evaluated the statistical significance of the marginality axis and the first specialization axis by comparing the distribution of presence locations to randomly-distributed locations using a Monte-Carlo procedure with 1000 permutations (Basille *et al.,* 2008). We conducted these analyses in R 3.0.3 statistical software (R Foundation for Statistical Computing, Vienna, Austria), using the adehabitatHS package (Calenge, 2006).

4.2.5 Functional type classification

Using results from the above analyses, we clustered species into functional types in two different ways: using marginality and tolerance scores, and using the coefficients (Pearson’s *r*) produced by correlating explanatory variables to the marginality axes. For both, we used a clustering algorithm that minimized the sum of dissimilarities within each group (Kaufman & Rousseeau, 2008; Hennig, 2014). We log-transformed, centred, and scaled the raw marginality and tolerance values before analysis. We evaluated the fit of each group using the average silhouette width (ASW), which may be interpreted as the ratio of within-group dissimilarity to between-group dissimilarity (Calinski & Harbasz, 1974); this statistic is scaled between -1 and one, and higher values indicate better fit. We did not perform a clustering analysis based on covariate correlations with the specialization axes because only the absolute values of these correlations are interpretable (Hirzel *et al.,* 2002). This would make it difficult to evaluate, for example, whether a high correlation with settlements indicates preference or avoidance of settlements. We performed cluster analysis using R package fpc (Hennig, 2014).

4.3 Results

We conducted 840 km of off-trail surveys over 536 km^2, 334 km of on-trail surveys over 430 km^2, 37476 trap-days of effort at 523 camera locations over 302 km^2 and 301 km of on-trail carnivore surveys over 141 km^2. Raw detection rates ranged from 0.003 detections cell^{-1} for lion-tailed macaque, to 0.393 cell^{-1} for sambar (Table 4.2). The percentage of opportunistic detections was highest for tiger and lion-tailed macaque (18%).

For all species, there were statistically significant departures from a random distribution for both the marginality axis and the first specialization axis ($P < 0.001$ in all cases), indicating that none used habitat in proportion to availability. When pooled across species, marginality and tolerance were moderately correlated with the raw detection rate ($r_s = -0.45$ and $r_s = 0.49$ respectively).

The 14 species exhibited a wide range of marginality and tolerance scores, with threatened species distributed throughout this space (Fig. 4.2a). Lion-tailed macaque exhibited the highest marginality and lowest tolerance, and was classified into a highly-specialized functional type by itself (ASW = 0, because single species). Tiger and Nilgiri langur showed similar but less extreme values for these metrics, forming the second functional type of relatively habitat-restricted species (ASW = 0.16). Asian elephant (*Elephas maximus*; hereafter elephant), muntjac, Indian chevrotain (*Moschiola indica*; hereafter chevrotain), sloth bear (*Melursus ursinus*; hereafter bear), giant squirrel and bonnet macaque exhibited intermediate values of marginality and tolerance, and were clustered as relative habitat generalists (ASW = 0.53). Sambar and pig exhibited the lowest marginality and the highest tolerance, and were clustered with leopard, dhole and gaur (*Bos gaurus*) as the fourth functional type of the most generalist species (ASW = 0.45).

In terms of habitat covariate associations with the marginality axis, species showed four broad patterns (Table 4.3 & Appendix 4.3). Elephant, tiger, lion-tailed macaque, Nilgiri langur and giant squirrel were positively correlated to closed forest, negatively correlated to anthropogenic land use types, and negatively correlated to anthropogenic features such as roads or settlements. The second cluster – gaur and bear – showed similar negative correlations as the first cluster; however, they were positively correlated with open forest and grassland instead of closed forest. The third cluster (leopard, muntjac, chevrotain and bonnet macaque) exhibited mixed responses to natural and anthropogenic habitat characteristics. For example, muntjac was positively correlated to closed forest, but also preferred areas closer to commercial plantations. The final cluster (dhole, sambar and pig) were positively associated with anthropogenic habitat types.

The above groupings are depicted in Figure 4.2b, which partitions the 14 species based on two principal component axes that together explained 73% of the variance (note: these axes are used only for the illustrative purpose of this figure; cluster analysis was undertaken directly on the coefficients in Table 4.3 and Appendix 4.3). The loadings of the axes in Figure 4.2b are provided in Appendix 4.4. The three strongest correlations with component 1 were: slope to nearest commercial plantation (-0.90), slope to nearest settlement (-0.81) and eco-climatic distance (0.84). The three strongest correlations with component 2 were: distance to nearest commercial plantation (-0.95), proportion of open forest (-0.84) and proportion of commercial plantation (0.82). The average silhouette widths of the four functional types (previous paragraph; Figure 4.2b) were 0.36, 0.45, 0.50 and 0.11 respectively.

In contrast to the covariates associated with the marginality axes, covariate effects associated with the specialization axes were strongly concentrated on a few variables with less variation among species (Table 4.4 & Appendix 4.5). Commercial plantations affected the variance of locations used by large herbivores – elephants, gaur and sambar – as well as bears and Nilgiri langur. Settlements had a strong effect on all three large carnivores and gaur. Building density was strongly correlated with the specialization axes of all threatened species except for elephant and gaur.

4.4 Discussion

Globally, conservationists are challenged to identify actions that support the persistence of multiple species with diverse responses to habitat characteristics. One way to meet this formidable challenge may be to aggregate them into functional types that reflect broadly similar habitat requirements and restrictions; we tested the utility of ecological niche factor analysis (ENFA) for this goal. Our predictions of the relative positions of threatened species were broadly supported, particularly for the species most sensitive to anthropogenic change (lion-tailed macaque, tiger and Nilgiri langur) and the least sensitive (leopard, sambar and pig), although threatened species were more widely distributed over the marginality-tolerance space than we expected. Using marginality and tolerance scores, we identified four functional types of species, each of which reflects a different approach that is required for management. The specific management practices that would support these approaches are provided by the second set of functional types, *i.e.,* by targeting habitat associations of each functional type. Synthesizing results from the eight clusters of functional types produced from the two clustering analyses, we identify below four principles that may generalize to other regions, species and conservation contexts.

Before addressing these generalizations, we first acknowledge potential limitations of our study. Each survey method sampled a different subset of the study area at a different time (Fig. 4.1 & Table 4.2). Hence, if animal habitat selection differed between these regions or time periods, our inferences may be biased towards the region and time period contributing the largest proportion of detections. A related issue concerns differential detectability of animal signs across space (*e.g.,* as a function of habitat type). Finally, rare species such as lion-tailed macaque and tiger, for which opportunistic data comprise nearly a fifth of detections, may be vulnerable to sampling bias (Durant *et al.,* 2010). We explicitly quantified the level of sampling bias in Appendices 4.1 & 4.2; we are also currently investigating how inferences may be modified when the definition of availability is varied (*e.g.,* in spatial subsets). This is well-known in models of species-habitat relationships (*e.g.,* Hirzel *et al.,* 2002; McLoughlin *et al.,* 2010). Regression models for tiger, elephant and gaur use built from camera-trap data were highly correlated to the density of sign data ($0.9 < r_s < 0.98$; Chapter 3); this suggests that our results are relatively robust. However, gaur habitat use within the camera-trapped subset was much more correlated to elephants and tigers than in this analysis (Chapter 3). Similar differences were observed by Durant *et al.,* (2010) in successive analyses on different subsets of a common area, suggesting that the factors influencing habitat use may change over space. Hence we caution against directly applying our results to other landscapes, particularly if the mixture of available habitat characteristics differs.

Our first generalizable principle is that securing core habitat free of human disturbance may be critical to conserving some functional types. The endemic lion-tailed macaque, which has slow demographic rates (Singh *et al.,* 2006) and relies on dwindling evergreen forest (Singh *et al.,* 2002), was an example of this. Rare tigers and endemic Nilgiri langurs are also negatively impacted by anthropogenic change (Karanth *et al.,* 2010; Karanth *et al.,* 2011); and despite being relatively dissimilar to each other, they were located closer in space to lion-tailed macaques than the other functional types (Fig. 4.2a).

Indeed, high trophic level, endemism, low density of occurrence and slow demographic rates strongly predict extinction risk in extant carnivores and primates (Purvis *et al.,* 2000). We suggest these three species may be best served by promoting their core habitat requirements (closed forest, evergreen habitat; Table 4.3). We note, however, that tigers exhibited some evidence of flexibility in habitat use; they avoided commercial plantations at small scales, but paradoxically, were negatively associated with distance from commercial plantations (Table 4.3). This may reflect exploitation of high prey-availability in moderately-disturbed habitats while avoiding direct human encounters, which is also seen in other large carnivores (*e.g.,* wolves *Canis lupus*; Theuerkauf, 2009).

A second generalizable finding is the apparent ability of some threatened species to tolerate small-scale human impacts within a largely-intact landscape. Generalist herbivores and omnivores (such as elephant, gaur and bear) may even benefit from degradation of evergreen forests into deciduous seral stages, particularly if this degradation occurs at small scales within an otherwise intact landscape (Choudhury, 2002; Gaucherel *et al.,* 2010; Yoganand *et al.,* 2006). However, this tolerance may reverse rapidly when habitat degradation turns into habitat loss at a larger scale. Further, the decisive factor governing their ability to persist in such areas may be poaching pressure; this may explain why so many forests in south-east Asia are lack large mammals despite favourable habitat conditions (Brodie *et al.,* 2014). Therefore, a low level of human use may be compatible with some species, if such use remains at small scales and poaching is controlled.

Thirdly, some threatened species show a high association with anthropogenic habitat, emphasizing the urgent need to extend conservation beyond reserves. Sambar and other large ungulates such as elk (*Cervus elaphus*) may benefit from human-mediated opportunities for forage or refuge (Meijaard & Sheill, 2008; Hebblewhite *et al.,* 2005). Dholes were more associated with anthropogenic habitat than we expected; and while their functional type classification was relatively poor (Fig. 4.2b), they nevertheless remained an outlier among other endangered species. This suggests that other unmeasured niche characteristics may be important to them (McLoughlin *et al.,* 2010), such as interspecific competition and prey selection. Tigers may displace dholes into disturbed habitat at low prey densities (Steinmetz *et al.,* 2013), and a similar competitive dynamic may explain the apparent breadth of habitat use by African painted dogs *Lycaon pictus* (Creel & Creel, 1996). Prey selectivity is also a potential explanation; dholes select for smaller prey than tigers (Karanth & Sunquist, 2000), and their use of anthropogenic habitat may track sambar and pig habitat use. Regardless, animal use of anthropogenic habitat may increase mortality and disease risk (Rasmussen & McDonald, 2012; Durbin *et al.,* 2008). But it may enhance fitness given adequate prey availability and human tolerance (Woodroffe *et al.,* 2007; Athreya *et al.,* 2013), which we consider a priority in this landscape.

Based on the results of our second clustering analysis, we suggest that single-species planning approaches (*e.g.,* flagship or umbrella species; Simberloff, 1998) may not adequately meet the habitat needs of all species, even within our small set of mammals. For example, protecting the evergreen forests favoured by lion-tailed macaques may not adequately protect the grassland-associating gaur and bear, or the more tolerant dhole. Instead, more robust conservation outputs could result from planning for a set of representatives from each empirically-derived functional type (reviewed by Manne & Williams, 2003). Methods such as ENFA make explicit both the similarities and differences between species, hence improving our ability to identify the potential and the limitations of single-species approaches.

A final implication from our study is that ENFA can be used to identify the habitat characteristics that promote high animal use (quantified using marginality), and those that restrict use (quantified using specialization or its inverse, tolerance) – *i.e.,* the characteristics of core and connective habitat. Hence, marginality is conceptually similar to the results of species distribution models (*e.g.,* Aarts *et al.,* 2012), while tolerance can identify habitats that diverge from optimal but may support occasional use (*e.g.,* Haddad &

Tewksbury, 2005). In an application of this principle, (Dolgener *et al.,* 2014) found that amphibian specialization was most influenced by water runoff, which connected core populations. In our study, commercial plantations, settlements, and building density influenced tolerance (Table 4.4) and hence, managing these attributes may be critical to restoring connectivity across the Shencottah Gap.

In conclusion, setting conservation priorities for multiple species in participatory, multi-stakeholder situations often involves making difficult compromises over land uses, human access and human activity (McShane *et al.,* 2012). To ensure that ensuing decisions support broad-based conservation benefits, we suggest that approaches such as ENFA are deserving of wider application.

4.5 Tables

Table 4.1 Predicted categorical values for marginality and tolerance for 14 mammals based on the literature (footnotes), which produce five combinations that are hypothesized to represent functional groups. Red list status is from IUCN (2010) and the final column provides the approximate fit with predictions of the functional groups provided by analyses of mammals detected in the Shencottah Gap, India.

Species	Red list status	Predictions		Supported
		Marginality	Tolerance	
Tiger[a] *Panthera tigris*	EN	High	Low	Yes
Lion-tailed macaque[b] *Macaca silenus*	EN	High	Low	Yes
Sloth bear[c] *Melursus ursinus*	VU	High	Medium	No
Gaur[e] *Bos gaurus*	VU	High	Medium	No
Nilgiri langur[f] *Trachypithecus johnii*	VU	High	Medium	Yes
Asian elephant[d] *Elephas maximus*	EN	Medium	Medium	Yes
Dhole[g] *Cuon alpinus*	EN	Medium	High	No
Indian chevrotain[h] *Moschiola indica*	LC	Medium	High	No
Indian giant squirrel[i] *Ratufa indica*	LC	Medium	High	No

Leopard[j] *Panthera pardus*	NT	Low	High	Yes
Sambar[k] *Rusa unicolor*	VU	Low	High	Yes
Wild pig[l] *Sus scrofa*	LC	Low	High	Yes
Northern red muntjac[m] *Muntiacus vaginalis*	LC	Low	High	No
Bonnet macaque[n] *Macaca radiata*	LC	Low	High	No

[a] Jhala *et al.,* 2011; Karanth *et al.,* 2011

[b] Singh *et al.,* 2002; Singh *et al.,* 2006; Karanth *et al.,* 2010

[c] Yoganand *et al.,* 2006; Karanth *et al.,* 2009

[d] Fernando *et al.,* 2005; Gaucherel *et al.,* 2010

[e] Choudhury, 2002; Steinmetz *et al.,* 2010

[f] Karanth *et al.,* 2010; Pillay *et al.,* 2011

[g] Karanth & Sunquist, 2000; Pillay *et al.,* 2011; Steinmetz *et al.,* 2013

[h] Pillay *et al.,* 2011

[i] Sushma & Singh, 2006; Pillay *et al.,* 2011

[j] Karanth *et al.,* 2009; Athreya *et al.,* 2013

[k] Meijaard & Sheill, 2008; Karanth *et al.,* 2009

[l] Karanth *et al.,* 2009; Pillay *et al.,* 2011

[m] Meijaard & Sheill, 2008; Pillay *et al.,* 2011

[n] Karanth *et al.,* 2010; Pillay *et al.,* 2011

Table 4.2 Total effort (number of 100-m cells sampled) using off-trail surveys (OFT), on-trail surveys (ONT), camera trap surveys (CT) and on-trail carnivore surveys (ONTC) in the Shencottah Gap, India from 2008 to 2013, which resulted in both targeted and opportunistic detections of 14 mammals.

Species	Targeted sampling methods	Cells sampled	Number of detections			Detection rate (cell^{-1})
			Targeted	Opportunistic	Total	
Tiger	ONT, CT, ONTC	5474	62	14	76	0.01
Leopard	ONT, CT, ONTC	5474	489	22	511	0.09
Dhole	ONT, CT, ONTC	5474	268	10	278	0.05
Bear	OFT, ONT, CT	11984	311	17	328	0.03
Elephant	OFT, ONT, CT	11984	2526	138	2664	0.22
Gaur	OFT, ONT, CT	11984	1317	53	1370	0.11
Sambar	OFT, ONT, CT	11984	4507	207	4714	0.39
Pig	OFT, ONT, CT	11984	1389	39	1428	0.12
Muntjac	OFT, ONT, CT	11984	994	26	1020	0.09
Chevrotain	OFT, ONT, CT	11984	350	3	353	0.03
Lion-tailed macaque	OFT, ONT	11642	32	7	39	0.00
Nilgiri langur	OFT, ONT	11642	293	13	306	0.03
Bonnet macaque	OFT, ONT, CT	11984	231	9	240	0.02
Giant squirrel	OFT, ONT	11642	258	12	270	0.02

Table 4.3 Correlation coefficients (Pearson's *r; |r|* > 0.3 depicted in bold lettering) of selected covariates with marginality axis of an Ecological Niche Factor Analysis, which compared cells where each of 8 threatened species was detected or not detected in the Shencottah Gap, India from 2008 to 2013. Footnotes indicate scale of covariate measurement. See Appendix 4.3 for all covariates for all species.

Covariate	Elephant	Tiger	Lion-tailed macaque	Nilgiri langur	Gaur	Bear	Sambar	Dhole
Closed forest	**0.44**[d]	**0.46**[c]	**0.49**[a]	**0.39**[d]	0.05[b]	-0.26[d]	**-0.49**[d]	-0.13[d]
Open forest/grassland	-0.05[d]	-0.20[d]	-0.22[a]	-0.08[a]	**0.36**[d]	**0.49**[d]	**0.30**[a]	0.30[b]
Forestry plantation	-0.08[b]	**-0.31**[b]	-0.28[c]	-0.21[d]	-0.05[a]	-0.04[a]	0.21[c]	-0.16[d]
Commercial plantation	**-0.30**[c]	-0.14[a]	-0.11[a]	-0.20[d]	**-0.36**[c]	**-0.32**[d]	-0.20[a]	-0.10[a]
Settlement	**-0.33**[c]	-0.28[c]	-0.19[d]	-0.21[c]	**-0.37**[b]	-0.18[b]	**0.34**[d]	-0.21[a]
Eco-climatic	**-0.40**[d]	-0.22[d]	**-0.50**[a]	**-0.36**[c]	-0.10[a]	0.24[d]	**0.48**[d]	0.24[a]

distance								
House density	**-0.32**[c]	-0.22[b]	-0.13[b]	-0.20[c]	**-0.39**[c]	-0.23[b]	-0.12[a]	-0.13[a]
Distance to settlement	**0.43**	0.19	0.06	**0.45**	**0.37**	0.18	**-0.39**	**-0.55**
Distance to commercial plantation	0.21	**-0.43**	-0.20	0.11	**0.36**	**0.50**	-0.04	**-0.32**
Distance to road	0.17	-0.05	0.11	0.27	0.18	**0.31**	-0.19	**-0.34**

[a] 300 m

[b] 600 m

[c] 1200 m

[d] 2400 m

Table 4.4 Correlation coefficients (Pearson's *r; |r|* > 0.3 depicted in bold lettering) of selected covariates with the first specialization axis of an Ecological Niche Factor Analysis, which compared cells where each of 8 threatened species was detected or not detected in the Shencottah Gap, India from 2008 to 2013. Only the absolute value of the correlation coefficient is meaningful. See Table 4.3 for scale of covariate measurement and Appendix 4.5 for all covariates for all species

Covariate	Elephant	Gaur	Sambar	Tiger	Dhole	Bear	Lion-tailed macaque	Nilgiri langur
Commercial plantation	**-0.81**	**-0.84**	**-0.82**	-0.06	0.00	**-0.56**	0.13	**-0.54**
Settlement	0.28	**0.40**	0.16	**-0.50**	**0.58**	-0.06	-0.19	-0.25
House density	0.23	0.26	**-0.43**	**0.85**	**-0.75**	**0.82**	**-0.90**	**0.80**

4.6 Figures

Figure 4.1 (a) Location of the Shencottah Gap in India, (b) in the context of Periyar Tiger Reserve (PTR), Kalakkad-Mundanthurai Tiger Reserve (KMTR) and Shendurney Wildlife Sanctuary (SWLS), and (c) distribution of sampling effort through five methods: off-trail, on-trail, camera trap and on-trail carnivore surveys.

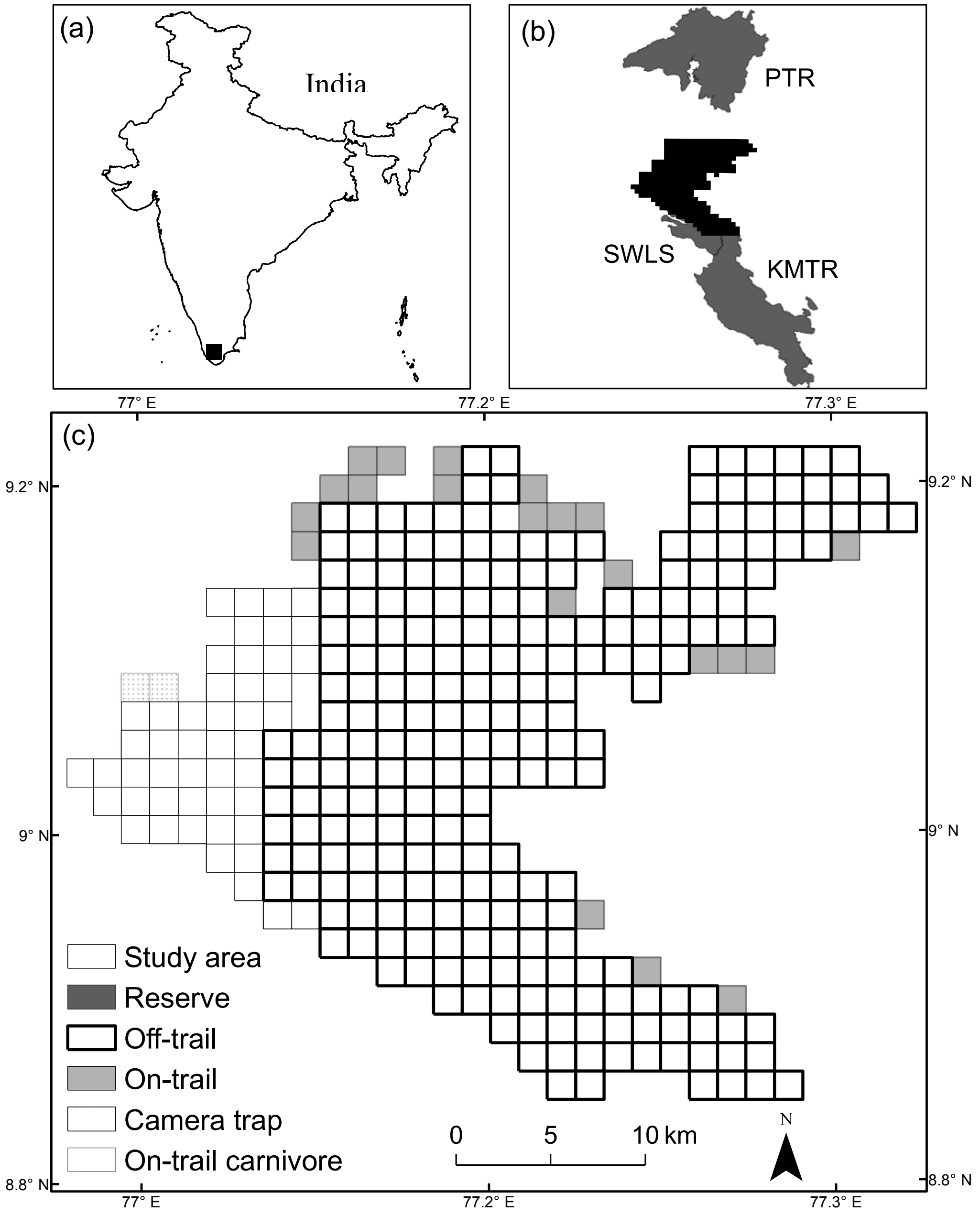
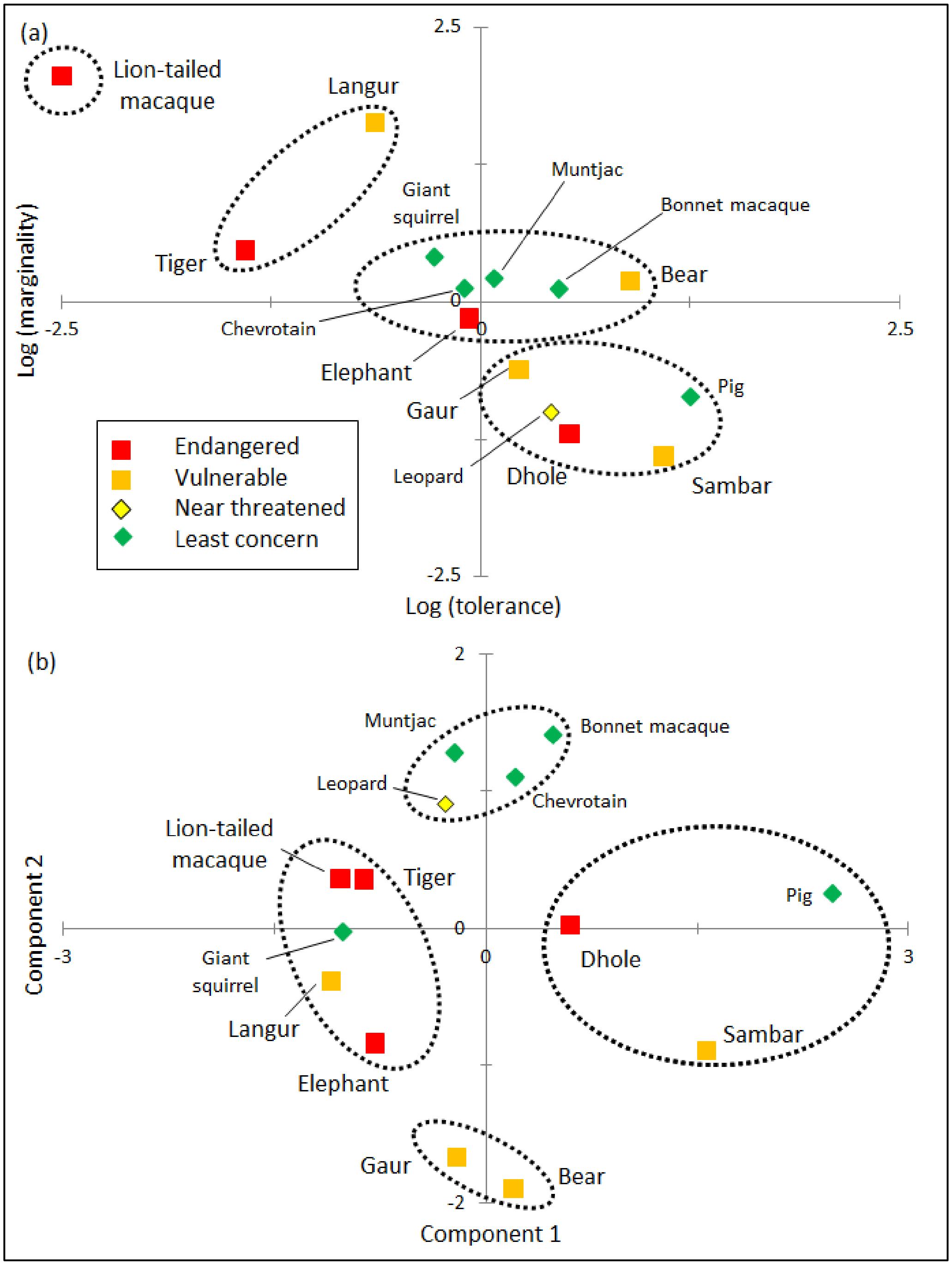


Figure 4.2 Classification of 14 mammalian species occurring in the Shencottah Gap, India into functional groups using two methods (a) marginality and tolerance scores, and (b) correlation coefficients of habitat variables with marginality axes.



Chapter 5

5 Carnivore infirmity may enhance connectivity potential across multiple-use landscapes[*]

5.1 Introduction

Carnivore populations are declining globally due to human impacts (reviewed by Ripple *et al.,* 2014) and the largest species among them, which typically occur at low population densities, range over wide areas and have a propensity for conflict with humans (Noss *et al.,* 1996; Purvis *et al.,* 2000; Crooks, 2002), are especially vulnerable. Therefore, well-protected reserves that separate animals from people form the foundation of large carnivore conservation, particularly for felids such as tigers (*Panthera tigris* Walston *et al.,* 2010), lions (*Panthera leo*; Packer *et al.,* 2013) and jaguars (*Panthera onca*; Sanderson *et al.,* 2002). But these reserves are often small and contain too few individuals to maintain long-term population viability (Woodroffe & Ginsberg, 1998). Therefore, effective carnivore conservation may also require connectivity among populations over large landscapes (Rabinowitz & Zeller, 2002; Wikramanayake *et al.,* 2011), which entails individual animals living or moving through the multiple-use areas that separate reserves.

This landscape-based approach to carnivore conservation poses two formidable management challenges. Large carnivores may only rarely enter connective habitat if it is poor in quality (Crooks, 2002), and those that do may not survive long (*e.g.,* Naughton-Treves *et al.,* 2003). Consequently, improving the quality and security of multiple-use connective habitat is often a management priority (Goodrich, 2010). But ironically, improved habitat

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[*] Authors of an associated manuscript in preparation: Aditya Gangadharan, Srinivas Vaidyanathan & Colleen Cassady St. Clair.

quality in multiple-use areas may also increase conflict with people (reviewed by Karanth & Gopal, 2005; Gurung *et al.,* 2008), leading managers to remove human-associated animals and once again reduce the potential for connectivity.

One way to balance these trade-offs may be to monitor carnivore use of multiple-use areas, and identify the spatial, temporal and behavioral attributes that are associated with the individuals that occur there (reviewed by Treves & Karanth, 2003; Goodrich, 2010). These attributes can then be modified to facilitate the minimal level of carnivore use necessary for connectivity, while inhibiting further increases in density and consequent conflict. However, our knowledge of the behavioral ecology of large carnivores outside reserves lags behind protected areas (Athreya *et al.,* 2013). This is unfortunate, because the individual carnivores that survive in human-impacted areas may exhibit behavioral adaptations that enable them to cope with high human impact (Theuerkauf *et al.,* 2003; Knopff *et al.,* 2014). These individuals may be only few in number (Walston *et al.,* 2010), but even low levels of migration between reserves may be adequate for demographic rescue (~ 5 migrants per generation; Stacey & Taper 1992) or gene flow (~1-10 effective migrants per generation; Mills & Allendorf, 1996; Wang, 2004). Ignoring these few but important individuals in favor of population averages may underestimate connectivity potential (reviewed by Clobert *et al.,* 2001); conversely, understanding their use of human-impacted habitat may provide crucial insights for carnivore conservation and connectivity in multiple-use areas (Caro, 1999).

Previous studies suggest several hypotheses on the correlates of carnivore presence in human-dominated areas, of which we consider four - the spatial habitat hypothesis, temporal segregation hypothesis, individual variation hypothesis and infirmity hypothesis (Table 5.1). The evidence for these four hypotheses (summarized in Table 5.1) spans several taxa, including tigers, lions, spotted hyena (*Crocuta crocuta*), cougars (*Puma concolor*), wolves (*Canis lupus*), coyotes (*Canis latrans*), sea otters (*Enhydra lutris*), black bears (*Ursus americanus*) and brown bears (*Ursus arctos*). The spatial habitat hypothesis suggests that carnivore presence is determined by high prey availability and low human impact (*e.g.,* Dickson & Beier, 2002). The temporal segregation hypothesis suggests that carnivores may displace their activity to periods when humans are not active (*e.g.,* Boitani, 1982), which may be viewed as a temporal partitioning of their niche due to interference competition with humans (*sensu* Carothers & Jaksic, 1984). The individual variation hypothesis suggests that carnivores may vary in the prey they select (Ross *et al.,* 1997) or the level of tolerance for human activity (Knopff *et al.,* 2014). Finally, the infirmity hypothesis (*sensu* Patterson *et al.,* 2003) holds physical infirmity as a cause of carnivore presence in human-dominated areas, which is often associated with conflict with people (*e.g.,* Das, 2012). These four hypotheses need not be mutually exclusive, particularly in mixed-use landscapes undergoing changes in land use (*e.g.,* Yeakel *et al.,* 2012).

While it is important to evaluate such hypotheses across the world (reviewed by Treves & Karanth, 2003), it is particularly urgent in the Western Ghats region of India. In this biodiversity hotspot (Myers *et al.,* 2000), a sixth of the world's remaining tigers (~500 individuals; Jhala *et al.,* 2011) co-occur with the highest human densities among the global hotspots (Cincotta *et al.,* 2000), often causing political friction between human and wildlife concerns (reviewed by Karanth & Gopal, 2005). The two southern-most tiger reserves of the Western Ghats (Periyar and Kalakkad-Mundanthurai) hold fewer than 50 tigers (Jhala *et al.,* 2011), whose their long-term viability may depend on connectivity through the intervening multiple-use Shencottah Gap (Ranganathan *et al.,* 2009). In turn, the persistence of tigers is crucial for preserving the irreplaceable (Das *et al.,* 2006) biodiversity of these two reserves, because tigers drive the political will and funding for conservation in India (Lewis 2005). Worryingly, a previous study (Gangadharan *et al.,* unpublished data) documented only 11 tiger signs (scats, tracks and sightings) within a 621 km^2 area, suggesting only rare tiger presence in the Shencottah Gap.

In this study, we report on the detection via camera traps of several tigers in the Shencottah Gap. Working from the above hypotheses, we examined how spatial habitat attributes, temporal covariates, individual variation and infirmity influence tiger presence, and hence the potential for connectivity between the two reserves. To support reliable inferences from our small sample sizes, we tested specific predictions derived from the literature, reasoning that effect sizes would provide evidence for or against these hypotheses (Oksanen, 2001). We tested the predictions that tiger use would be higher in prey-rich areas and lower in human-impacted areas; that tiger use of human-impacted areas would vary by diel cycle; that individual tigers would vary in their prey selection or human tolerance; and that infirmity would be associated with the use of human-impacted habitat (see Table 5.1 for details).

5.2 Methods

5.2.1 Study region

This study covered a 302 km^2 subset of the Shencottah Gap in the state of Kerala (Fig. 5.1). The southern edge of the study area overlaps Shendurney Wildlife Sanctuary, which is contiguous with Kalakkad-Mundanthurai Tiger Reserve. The study area historically consisted mainly of tropical semi-evergreen and evergreen forests (Ramesh *et al.,* 1997), but is now degraded in many areas and interspersed with government-owned monoculture plantations (mainly teak, acacia and eucalyptus, covering 17% of study area), privately owned cash crop plantations (mainly tea and rubber, 10%), settlements and associated agriculture (4%) and inter-state transportation routes (56 km, including a national highway, a state highway and a railway line). The national highway and associated railway line in the south of the study area are thought to be major barriers to large mammal connectivity (Johnsingh *et al.,* 1991), while the narrower state highway to the north may currently be less so. Subsistence use of forest areas includes extraction of minor forest produce such as spices, firewood and reed, as well as livestock grazing.

5.2.2 Field methods

Camera trap surveys were carried out between September 2011 and April 2013 in publicly-owned areas (‘Reserved forests’ and forestry plantations), and involved placing a single camera (Scoutguard SG 565V and Scoutguard SG 560V, HCO Outdoor Products, GA, USA; recovery time 8-14 s) on trails close to randomly-generated sampling locations. The spatial intensity of sampling within each 1.5 km cell (2-8 cameras per cell) was proportional to predicted corridor importance (Chapter 2). Cameras were intended to sample every location for three months, but were sometimes active for shorter or longer periods depending on logistical limitations. In this study, we included only cameras that were active for at least three weeks. This resulted in the inclusion of 445 locations, totaling 36,855 trap-days of effort. Camera trapping was conducted across all seasons, and cameras were active throughout the day and night. We defined a detection event as a photograph of a species that was separated from another of the same species by one hour (Tobler *et al.,* 2008). Intermittent photographs up to a period of eight hours that were likely of the same animal group (*e.g.,* a group of grazing animals) were also defined as single events.

5.2.3 Spatial habitat covariates

Two major categories of spatial covariates were of main interest to us: covariates that quantified prey use and those that quantified human impact. For major tiger prey (gaur *Bos gaurus*; sambar *Rusa unicolor*; wild pig *Sus scrofa*; northern red muntjac *Muntiacus vaginalis* and bonnet macaque *Macaca radiata*; Karanth & Sunquist, 1995), and also Indian crested porcupine (*Hystrix indica*), we calculated relative measures of use directly from camera trap data as mean daily detection rates. Apart from calculating use by each of these individual species, we also combined all of the above species for a combined index of prey use. Finally, we combined all prey smaller than gaur into a separate index of smaller prey use. Because a detection event of a species may include more than one animal, we also re-computed the above indices by weighting each event by the number of animals detected. These indices did not improve model fit in exploratory analyses (change in Akaike Information Criterion AIC > 2 in all cases), and therefore we dropped these from further analyses.

Using the same procedures as above, we also computed the mean daily detection rates of people on foot, of vehicles and of livestock, as well as a combined index of human impact that included all three of these human-related covariates. Other measures of human impact included linear distance to the nearest settlement, nearest commercial plantation and nearest major transportation route. Additionally, we computed the density of houses within circular buffers of 300 m, 600 m and 1200 m around each camera location.

Other spatial habitat variables included vegetation and land-use characteristics, terrain characteristics and sampling covariates. To quantify vegetation and land use characteristics, we measured the proportion of closed forest, open forest/ grassland, forestry plantation, commercial plantation and settlement within circular buffers of 300 m, 600 m, 1200 m and 2400 m around each camera location. At these same buffers, we computed the eco-climatic distance, an index of 'evergreenness' that measures departure from wet tropical evergreen forest (Krishnaswamy *et al.,* 2009; Appendix 2.1). To quantify terrain attributes, we used a digital elevation model (90-m LANDSAT data in 2008; United States Geological Survey, Sioux Falls, USA) to measure the slope at camera locations. The derivative of the slope within a neighbourhood of eight cells, scaled between -1 and 1, was used to measure surface curvature as an index of ruggedness. Finally, we measured the mean slope along the line connecting each location to the nearest settlement and to the nearest commercial plantation because we expected that a higher slope to human-dominated land would enable animals to come closer to it.

Sampling covariates included survey effort, as well as characteristics of the camera location. We measured effort in three ways. We computed the total number of trap-days at every location to test whether it influenced the probability of detection. Because camera density varied over the study area, we also computed the local density of camera using a circular moving window with a radius of 300m, 600m, 1200m and 2400m. We also combined these above two indices, by weighting the local camera density by the number of trap-days. For local characteristics, we measured the number of trails intersecting in front of the camera, and mean trail width, as we expected these to influence probability of detection (*e.g.,* Sunquist 1981).

5.2.4 Temporal segregation covariates

We assigned each tiger event into one of 12 time intervals centered on noon, and used this variable as a continuous covariate. We also categorized time of the day into three time periods: day (one hour after sunrise to one hour before sunset), twilight (one hour on either side of sunrise and sunset) and night (one hour after sunset to one hour before sunrise; times taken from Earth Systems Research Laboratory, National Oceanic and Atmospheric Administration, USA). For locations where tigers were not detected, hour from noon was assigned at random and categorical time period was assigned at random.

5.2.5 Individual variation & body state covariates

We visually identified individual tigers based on stripe patterns (Karanth, 1995). Stripe patterns differ between each flank of the same individual and so only individuals that exposed both flanks in a single event could be identified with certainty in subsequent events based on either flank (T-1 and T-7; Table 5.2). Other identities were conditional on the flank that was used as the basis; for example, we suspected that T-2 and T-3 were the same individual. Some other tigers could not be identified to individual level due to photographic limitations. Further, 60% of tiger events were of T-1. Because of these uncertainties and small sample sizes, we categorized tiger identity into three categories for subsequent analysis: T-1, all other tigers that were identified based on at least one flank (T2 to T8; hereafter, T-OTH) and unidentified tigers that could not be assigned to either of the above categories (T-UID).

To quantify infirmity, we used a qualitative index of body state (an ephemeral quantity, as opposed to a more chronic condition; *sensu* McNamara & Houston, 1990). We based this index on the stomach-fullness index of Bertram (1975), which used visual inspection of the side profile of lions to assess the amount of recent feeding. Bertram's (1975) index has been used for assessing the short-term body state of lions where the direct and invasive measurement of such traits (*e.g.,* weight or stomach contents) was not possible (*e.g.,* Kissui & Packer, 2004; Packer *et al.,* 2011). Following this method, we visually inspected the profile of each tiger photograph, and categorized tigers into one of three classes: good, poor and unknown state. Tigers in poor body state were distinguished from those in good body state by an acute upward slope from the belly to the hindquarters, associated with a clear depression in front of the femur (Fig. 5.2; Bertram 1975). If these characteristics could not be assessed for any event (for example, if only the head was photographed), we assigned body state to be unknown. Similar non-invasive qualitative indices are also used for other large mammals such as Asian elephants (*Elephas maximus*; Wemmer *et al.,* 2006) and grey whales (*Eschrichtius robustus*; Bradford *et al.,* 2012). While such indices usually involve direct observation of animals, direct observations are not feasible for low-density tiger populations in closed forest habitat. Around 42% of tiger detections could not be assigned to body state (Table 5.2). For all the locations where tigers were not detected, we assigned individual identity and body condition at random.

5.2.6 Logistic regression models for habitat use

We modelled tiger presence at a resolution of 100m with mixed-effects logistic regression models that compared locations where tigers were detected (hereafter, used) and were not detected (hereafter, available). Because of unbalanced sample sizes, we used individual identity category (three levels; above) and body state (three levels; above) as random intercepts. We did not use hierarchical models that explicitly estimate detection probability (reviewed by MacKenzie *et al.,* 2006) because our data do not meet the assumptions of these models, especially the crucial assumption of closure (Welsh *et al.,* 2013). Instead, we used statistical methods that were suited to our biological question (Banks-Leite *et al.,* 2014), and directly incorporated sampling covariates that we expected to influence detection probability (above).

We first built the best model that incorporated only spatial habitat covariates, because these covariates are well-known to influence tiger presence (*e.g.,* Karanth *et al.,* 2011); our main interest in this study was in evaluating whether the addition of temporal, individual and infirmity covariates improved fit compared to this null model. After building the best spatial model, we added to it one of the temporal, individual or infirmity covariates, to build the best temporal, individual and infirmity model. Finally, we combined covariates selected in the best spatial, temporal, individual and infirmity models to develop the best global model of tiger use.

We built models using a forward selection approach based on AIC, whereby we added covariates sequentially until this no longer led to a reduction in the AIC score greater than 2 per parameter (Arnold, 2010). We also used likelihood-ratio tests to compare nested models. We scaled continuous covariates before analysis and screened covariates for collinearity (Spearman rank correlation, $|r_s| > 0.6$). For covariates measured at multiple scales, we used the scale that maximized explanatory power between used and available data. We included quadratic and biologically-meaningful two-way interaction terms. Individual identity category and body state were used only as interaction terms in the fixed-effects part of the models. We evaluated model fit using the methods of Nakagawa & Schielzeth (2013).

5.2.7 Linear discriminant analysis

To further investigate the interaction between individual and body state with respect to spatial and temporal covariates, we used linear discriminant analysis (LDA; Legendre & Legendre, 1998). LDA maximizes the factors that differ between groups while minimizing those that differ within groups, as long as group membership is known (in this case, the three pairs of individual identity and body state category defined above). Our intention was to develop a multivariate representation of how habitat use by T-1 changed with body condition, and how it differed from other identified tigers.

We screened all covariates for collinearity and transformed all variables to better meet assumptions of normality (natural log transformation for curvature, square root transformation for all others). We evaluated statistical significance of the discriminant analysis using Wilk's lambda, which evaluates the proportion of the variance not explained by the model and compares that to the appropriate F distribution. We used only locations where tigers were detected for this analysis.

5.2.8 Temporal activity patterns

To further investigate the interaction between individual category and body state with respect to temporal activity patterns, we evaluated the overlap between tigers and their prey species, as well as with humans. We used three tiger identity-body state combinations: T-1 in good state, T-1 in poor state, and all other identified tigers (T-OTH) in good state. For each of these classes, we evaluated temporal overlap in activity patterns with humans, gaur and a combined index of all other smaller prey (above). For each of the nine resulting pairs of activity times, we used the methods of Ridout & Linkie (2009) to fit kernel density functions to activity times, and computed temporal overlap using the coefficient of overlap (Δ_1), which estimates the area under both activity curves of a pair. We estimated 95% confidence intervals for Δ_1 using a bootstrap procedure with 10,000 resamples, conducted in R package overlap (Meredith & Ridout, 2014). We used only locations where tigers were detected for this analysis.

5.3 Results

A total of 73 tiger detections occurred at 50 locations, at a rate of approximately one event per 504 trap-days. Prey use was calculated from 1589 gaur events, 6672 sambar events, 2449 pig events, 1843 muntjac events and 431 events of bonnet macaque; human use from 4560 events of people on foot, 394 events of livestock and 320 events of vehicle use.

The best spatial habitat model for tigers included gaur use, distance to settlement and distance to major road, all three of which positively influenced tiger use (model 1a; Table 5.3). At locations used by tigers, gaur use was 490% higher than available locations, and these locations were 83% further from settlements and 67% further from major roads than available locations ($P < 0.001$ in all cases; Fig. 5.3a). The addition of temporal variables improved model fit over the purely spatial model (ΔAIC = 8.40; $\chi^2 = 12.42$, $P = 0.002$), and the best temporal model (model 2a) included the main effect of time as a continuous variable. The interactive effect of time with distance to settlement (model 2b) was not large enough to decrease AIC or increase log likelihood substantially when other covariates were controlled for (ΔAIC = 0.3; $\chi^2 = 2.40$, $P = 0.13$). However, when time was considered by itself, tigers used areas 26% closer to settlements at night compared to day (Wilcoxon rank sum test, $W = 401$, $P = 0.02$; Fig. 5.3b).

The best individual variation model (model 3a; Table 5.3) modestly improved fit over the spatial model (ΔAIC = 4.9; $\chi^2 = 8.94$, $P = 0.01$), but less so than the addition of temporal covariates. While T-1 used areas that were 18% closer to settlements on average than other tigers (Fig. 5.3c), this was not statistically significant ($W = 445$, $P = 0.42$). The addition of body state covariates caused the greatest drop in AIC (ΔAIC = 10.80; $\chi^2 = 14.86$, $P < 0.001$ for model 4a). All tigers used areas that had higher gaur use than available; however, tigers in good state used areas that had 980% higher gaur use, while for tiger in poor state this was only 45% higher ($W = 294$, $P = 0.03$; Fig. 5.3d).

The final global model incorporated the additional effect of time and the interaction between individual identity and distance to settlement compared to the top infirmity model (model 5a, Table 5.3). In this model, we pooled individual categories T-OTH and T-UID as part of the intercept, because much of the individual variation was driven by T-1 and pooling the other two identity categories decreased AIC. We also dropped the interaction between gaur use and distance to settlement, because and this terms was no longer statistically significant ($P > 0.2$) and dropping it decreased AIC. The global model fit better than the best infirmity model ($\Delta\text{AIC} = 12.6$; $\chi^2 = 16.71$, $P < 0.001$). Coefficients of the global model are given in Table 5.4; both the marginal and conditional R^2 values indicated adequate fit (Table 5.3).

The interactive effect of individual identity and individual state were demonstrated by the linear discriminant analysis (Fig. 5.4a), and indicated considerable within-individual variability for T-1. This individual was separated from other tigers by the first linear discriminant (explaining 78% of variance), but itself varied along the second discriminant axis depending on its body state. Overall, T-1 used locations that were correlated with lower gaur use and higher use by smaller prey such as sambar and pig (see Table 5.5 for factor loadings). However, the avoidance of gaur-rich areas varied with body state (Fig. 5.4b): T-1 in poor state used areas that had 67% more gaur than available, but used areas with 837% more gaur when in good state ($W = 445$, $P = 0.05$, $W = 376$, $P = 0.003$ respectively). T-1 in poor state also used areas that were closer to settlements (Fig. 5.4a & Table 5.5), but these areas had a higher mean slope to the nearest settlement. Indeed, detections of T-1 while in good state were further from settlements than available ($W = 353$, $P = 0.02$) but were not significantly different from available when in poor condition ($W = 384$, $P = 0.42$; Fig. 5.4c).

The interaction between individual identity category and body state with respect to spatial prey characteristics was partly reflected in temporal overlap too (Fig. 5.4d). T-1 in poor state was less active at the times when gaur were active, compared to all other tigers in good state ($\Delta_1 = 0.64$, 95% CI 0.55

– 0.72; Δ_1 = 0.86, 95% CI 0.81 – 0.90 respectively). While the trend was similar for other prey species, confidence intervals overlapped each other. Similarly, confidence intervals for the coefficient of overlap with human activity did not exclude each other across individual-state categories.

5.4 Discussion

This study evaluated four hypotheses concerning tiger presence in a multiple-use landscape: the spatial habitat hypothesis (which we considered to be the null hypothesis), temporal segregation hypothesis, individual variation hypothesis and infirmity hypothesis. We tested the following predictions: tigers would use areas with high prey use and low human impact; they would avoid humans in time; and that individual identity or body state would determine tolerance of human activity or the targeting of prey. We found that the interaction between body state and gaur use resulted in the greatest improvement of fit to the best spatial model, suggesting that tiger infirmity may be more important than temporal segregation and individual identity in determining tiger presence in the study area. Although there was some evidence for tigers approaching closer to settlements at night, the global model supported only the finding that tigers were less active during the day overall, when other variables were controlled for. Individual identity was part of the global model, but only with respect to T-1; this individual approached significantly closer to settlements than others did. Overall, these results indicate that variation in habitat use occurs at the population level, between individuals and within individuals, which together shape tiger presence in the Shencottah Gap. Connectivity across the gap may currently depend on the behavioral flexibility demonstrated by a single individual tiger, which may be a function of its body state.

Spatial habitat attributes – particularly, prey use and human impacts – influence habitat use across carnivore taxa (MacDonald, 1983; Carbone & Gittleman, 2002), including in spotted hyenas (Kruuk 1972), Iberian lynx (*Lynx pardinus*; Palomares *et al.,* 2001), and lions (Packer *et al.,* 2013), and these habitat preferences may be exhibited across scales. At the scale of the home range, despotic individuals (*sensu* Fretwell, 1972) may displace subordinate animals away from highest-quality habitat – such as reserves – into more marginal, multiple-use habitat (reviewed by Elfstrom *et al.,* 2012). But even within this constrained space, most individuals may still prefer areas with relatively high prey and low human use (*e.g.,* cougars, Dickson & Beier, 2002; tigers, Karanth *et al.,* 2011). In poor-quality areas that are subject to multiple human uses, prey attributes may be particularly important, as seen in the five-fold difference in mean gaur use at tiger presence locations compared to available locations (see also Karanth *et al.,* 2004).

Carnivore presence in multiple-use areas is further challenged by the temporal distribution of human activity, to which carnivores may respond by avoiding humans in time. Temporal segregation of carnivores has been observed in coyotes (Kitchen *et al.,* 2000), wolves (Ciucci *et al.,* 1997; Theuerkauf *et al.,* 2003) and lions (Valeix *et al.,* 2012), and has been invoked as a means of co-existence between dense human populations and tigers (Carter *et al.,* 2012). However, carnivore activity patterns may also simply track their nocturnal or crepuscular prey (Linkie & Ridout, 2011), or be determined by the need to avoid thermal stress during the day (Seidensticker, 1976), and not necessarily by temporal avoidance of humans (Theuerkauf, 2009). Our results do not strongly suggest that tigers reduce daytime activity to avoid humans; instead, they may be tracking the activity patterns of their prey species (particularly gaur). However, we suggest that the rugged terrain of this landscape may enable tigers to use areas that are closer to settlements, by using slope to enhance spatial separation.

Individual carnivores may be forced to move through or live in low-quality habitat by dominant conspecifics (Parker & Sutherland, 1986), and must often exhibit behavioral flexibility to survive (Knopff *et al.,* 2014). Genetic studies (*e.g.,* Joshi *et al.,* 2013) show that some individual tigers can disperse over surprisingly hostile landscapes; others may even establish home ranges in densely populated regions (ca. 200 people km^{-2}; Athreya *et al.,* 2014). These individual animals may be critical to connectivity between reserves. Yet, individual behavior is not necessarily constant (*e.g.,* Pruitt *et al.,* 2011), and can vary with state (*sensu* McNamara & Houston, 1990). The combination of individual variability and state-dependent use of habitat may lead to tolerance of a much broader range of land uses than the population average, and lead to more connectivity between populations than expected. For example, Tigas *et al.,* (2002) attributed 58% of highway crossings by bobcats (*Lynx rufus*) in a fragmented region to a single individual male.

It may be argued that body state is a consequence of poor habitat quality within a home range, rather than a predictor for habitat use. We are unable to quantify home ranges and availability within them with our data. But we compared predicted gaur use (see Chapter 3 for model) within a convex hull containing all detections of T-1 to predicted gaur use in the rest of the study area (both of which excluded settlements and commercial plantations). Mean gaur use was 36% higher within T-1's convex hull than outside (0.041 day^{-1} vs 0.030 day^{-1}; $t = 29.0$, d.f. = 23342.7, $P < 0.001$), suggesting that lack of access to gaur-rich habitat was not the major driver of habitat use for this individual, at least over the pooled time period of this study.

The state-dependent behavior of individual carnivores is often associated with conflict. For example, lion attacks on people in Tanzania peaked at times of low vulnerability of ungulate prey (Packer *et al.,* 2011), and lion attacks on livestock outside reserves in India peaked during drought (Saberwal *et al.,* 1994). These findings are supported by historic observations of conflict animals (*e.g.,* Corbett, 1944). We did not come across any instance of human-tiger conflict during our study, and tiger conflict in this landscape appears to be much lower than conflict with herbivores (Sharma, 2010). If individual carnivores are shy and secretive, the probability of conflict may be low (Athreya *et al.,* 2014). Carnivore conflict may also be caused by several other factors, including the pace of land use change, prey depletion, the density of carnivores, and the creation of attractive secondary habitat by human activity (*e.g.,* Boomgaard 2001; Patterson 2003; Packer *et al.,* 2005). In our study area, the apparent low levels of conflict may simply be due to the low density of tigers overall. Because habitat restoration in human-dominated areas can increase conflict (Gurung *et al.,* 2008), we suggest that in human-dominated areas that are important for their connective value, increasing the densities of the largest felids may neither be necessary nor desirable. Instead, management measures may be better directed towards enhancing connectivity for the few behaviorally flexible individuals that do occur in such areas, while responding quickly and effectively to conflict situations. Achieving this delicate balance will require monitoring that takes into account the variability among and within individuals.

Our study suggests that the potential for habitat use and connectivity may be underestimated if population-level means derived from protected reserves are used to predict carnivore presence outside reserves (Knopff *et al.,* 2014). 'Super-dispersers' may be unusually important for movement between populations (Baguette & Van Dyck, 2007); we suggest that 'super-flexible' individuals may also hold a disproportionate influence on connectivity, and hence the survival of their species in a fragmented world (St. Clair *et al.,* in press). While qualitative, our methodological approach takes advantage of non-invasive photographic methods that are already in wide use, and is easily applicable to existing photograph databases (*e.g.,* those used by Jhala *et al.,* 2011). We believe the assignment of body state can be further refined with larger sample sizes, and converted into more quantitative, rigorous indices (perhaps by modifying existing software that fits three-dimensional models to animal photographs; Hiby *et al.,* 2009). At small scales, predictive models incorporating individual and condition-dependent effects could then be used to anticipate connectivity and conflict. Conversely, body state may be used as an index to identify high-quality habitat for regional conservation planning at large resolutions and extents, thereby supplementing models based on occurrence (*e.g.,* Pilfold *et al.,* 2014). More generally, behavioral flexibility may be a conservation commodity that can provide important insights into carnivore conservation in areas of mixed land use (St. Clair *et al.,* in press).

5.5 Tables

Table 5.1 Four hypotheses and consequent predictions for the correlates of tiger presence in multiple-use areas, with examples from the carnivore literature.

Hypothesis	Predictions	Literature examples
Spatial habitat	Tiger use increases with prey use and decreases with human impact	Kruuk 1972; MacDonald 1983; Dickson & Beier 2002; Karanth *et al.,* 2011
Temporal segregation	Tiger use of areas with high human impact increases by night and decreases by day	Boitani 1982; Ciucci *et al.,* 1997; Kitchen *et al.,* 2000; Valeix *et al.,* 2012
	Tiger use of high-prey areas increases by night and decreases by day	
Individual variation	Individual tigers vary in the prey species they target	McCullough 1982; Ross *et al.,* 1997; Estes *et al.,* 2003; Knopf *et al.,* 2014
	Individual tigers vary in the human impact they tolerate	
Infirmity	Tigers in poor body state target smaller prey than those in good body state	Corbett 1944; Saberwal *et al.,* 1994; Patterson *et al.,* 2003; Yeakel *et al.,* 2012
	Tigers in poor body state tolerate higher human impact than those in good body state	

Table 5.2 Summary of camera-trap tiger detections by individual identity, sex and body state in the Shencottah Gap, India between 2011 and 2013. Individual category refers to the binning of individual identities for use in statistical models and tests.

Individual identity	Sex	Identified flank	Individual category	Events	Body state		
					Good	Poor	Unknown
T-1	F	Both	T-1	44	14	14	16
T-2	M	Left	T-OTH	6	5	0	1
T-3	M	Right	T-OTH	4	2	0	2
T-4	F	Left	T-OTH	4	3	0	1
T-5	U	Right	T-OTH	2	1	0	1
T-6	U	Left	T-OTH	1	0	0	1
T-7	F	Both	T-OTH	1	1	0	0
T-8	U	Left	T-OTH	1	1	0	0
Unidentified	U	-	T-UID	10	1	1	8
Totals				73	28	15	30

Table 5.3 Best mixed-effects logistic regression models based on spatial habitat covariates, temporal covariates, individual identity covariates and body state covariates to compare the spatial habitat, temporal segregation, individual variation and infirmity hypotheses for tigers camera-trapped in the Shencottah Gap, India between 2011 and 2013. All models contained a random intercept for tiger body state and for tiger identity category. Bolded terms differ between models within each hypothesis set.

Model name	Fixed effects	AIC	ΔAIC[a]	Log likelihood	K	Marginal R^2	Conditional R^2
	Spatial habitat hypothesis						
1a	Gaur + setdist + setdist^2 + roadist + numtrail + trapdays + setdist x roadist + **gaur x setdist**	279.8	0.0	-128.9	9	0.61	0.69
1b	Gaur + setdist + setdist^2 + roadist + numtrail + trapdays + **setdist x roadist**	282.2	2.4	-131.1	8	0.51	0.60
1c	Gaur + setdist + setdist^2 + roadist + numtrail + trapdays + **setdist x gaur**	293.8	14.0	-136.9	8	0.53	0.62
	Temporal segregation hypothesis						
2a	All spatial variables + **timehour** + **timehour^2**	271.4	0.3	-122.7	11	0.62	0.70
2b	All spatial variables + timehour + timehour^2 + **setdist x timehour**	271.1	0.0	-121.6	12	0.64	0.72
2c	All spatial variables + timehour + timehour^2 + **roadist x timehour**	272.5	1.4	-122.3	12	0.63	0.71
2d	All spatial variables + timehour + timehour^2 + **people** + **people x timehour**	273.0	1.9	-121.5	13	0.63	0.71
	Individual variation hypothesis						
3a	All spatial variables + **identity x setdist**	274.9	0.0	-124.5	11	0.62	0.72
3b	All spatial variables + **identity x roadist**	281.3	6.4	-127.7	11	0.62	0.70
3c	All spatial variables + **identity x gaur**	283.2	8.3	-128.6	11	0.65	0.72

	Infirmity hypothesis						
4a	All spatial variables + **bodystate x gaur**	269.0	0.0	-121.5	11	0.78	0.83
4b	All spatial variables + **bodystate x setdist**	272.9	3.9	-123.5	11	0.65	0.72
4c	All spatial variables + **bodystate x roadist**	277.0	8.0	-125.5	11	0.64	0.71
	All hypotheses – global						
5a	Gaur + setdist + setdist^2 + roadist + numtrail + trapdays + setdist x roadist + bodystate x gaur + **timehour** + **timehour^2** + **identity x setdist**	256.3	0.0	-113.1	13	0.71	0.82
5b	Gaur + setdist + setdist^2 + roadist + numtrail + trapdays + setdist x roadist + bodystate x gaur + **timehour** + **timehour^2**	260.9	4.6	-116.5	12	0.73	0.79
5c	Gaur + setdist + setdist^2 + roadist + numtrail + trapdays + setdist x roadist + bodystate x gaur + **identity x setdist**	266.5	10.2	-119.2	12	0.71	0.79

Gaur, gaur use; setdist, distance to settlement; roadist, distance to major road; numtrail, number of intersecting trails; trapdays, number of trap days; bodystate, body state; identity, tiger identity category; AIC, Akaike Information Criterion; K, number of parameters.

[a] Comparisons within hypothesis set.

Table 5.4 Standardized coefficients of fixed effects and variance of random intercept terms in the best global model (model 5a of Table 5.3) comparing locations where tigers were and were not detected in the Shencottah Gap, India between 2011 and 2013.

Model term	Coefficient (SE)	*Z*	*P*
Fixed effects			
Intercept	-3.90 (0.92)	-4.3	<0.001
Gaur use	1.58 (0.45)	3.5	<0.001
Distance to settlement	2.23 (0.55)	4.1	<0.001
Distance to settlement^2	-1.20 (0.35)	-3.5	<0.001
Distance to major road	0.16 (0.29)	0.5	0.59
Distance to settlement X distance to major road	0.94 (0.29)	3.2	0.002
Body state X gaur use			
Good X gaur	1.50 (0.92)	1.6	0.10
Poor X gaur	-1.63 (0.69)	-2.4	0.02
Individual identity X distance to settlement			
T-1 X distance to settlement	-1.14 (0.47)	-2.4	0.02
Hour from noon	0.72 (0.24)	3.1	0.003
Hour from noon^2	-0.51 (0.20)	-2.6	0.01
Number of trails	0.35 (0.17)	2.0	0.04
Number of trap-days	0.53 (0.17)	3.1	0.002
Random effects			
Variance for tiger identity category	1.77		

Variance for tiger body state	0.10

Table 5.5 Correlation coefficients of selected variables ($|r_s| > 0.25$; three highest coefficients on each axis bolded) with the two axes produced by linear discriminant analysis (Fig. 5.4a) comparing the following combinations of individual tiger identity and body state: T-1 in good state, T-1 in poor state and all other tigers (T-OTH) in good state in the Shencottah Gap, India from 2011 to 2013.

Covariate	Linear discriminant 1	Linear discriminant 2
Gaur use	-0.30	**-0.29**
Sambar use	**0.55**	-0.05
Bonnet macaque use	0.25	0.26
Distance to settlement	-0.36	-0.26
Eco-climatic distance	**0.56**	0.22
Proportion of commercial plantation	0.02	**0.29**
Slope	0.30	0.08
Slope to settlement	**0.35**	0.17
Proportion of forestry plantation	0.28	-0.16
Pig use	0.30	0.16
Number of trails	-0.12	**0.31**
Path width	0.27	0.13

5.6 Figures

Figure 5.1 Location of Shencottah Gap, India, in the multiple-use region separating Periyar Tiger Reserve (PTR) from Kalakkad-Mundanthurai Tiger Reserve (KMTR) and Shendurney Wildlife Sanctuary (SWLS) in Kerala state, showing major land use types.

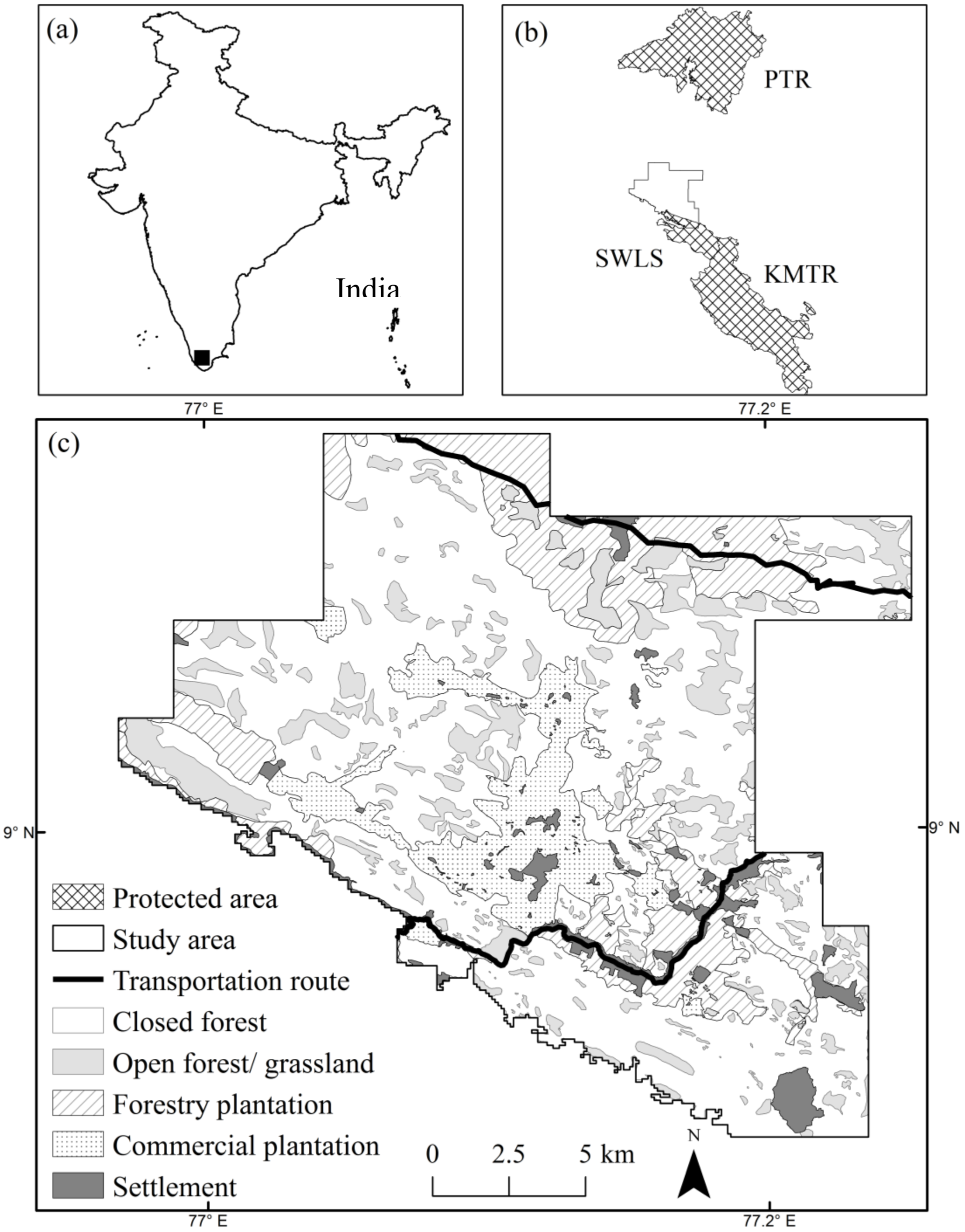


Figure 5.2 Examples of tigers classified into good body state (a and c) and poor body state (b and d) using camera trap data collected from the Shencottah Gap, India between 2011 and 2013. See Table 5.2 for tiger identities.

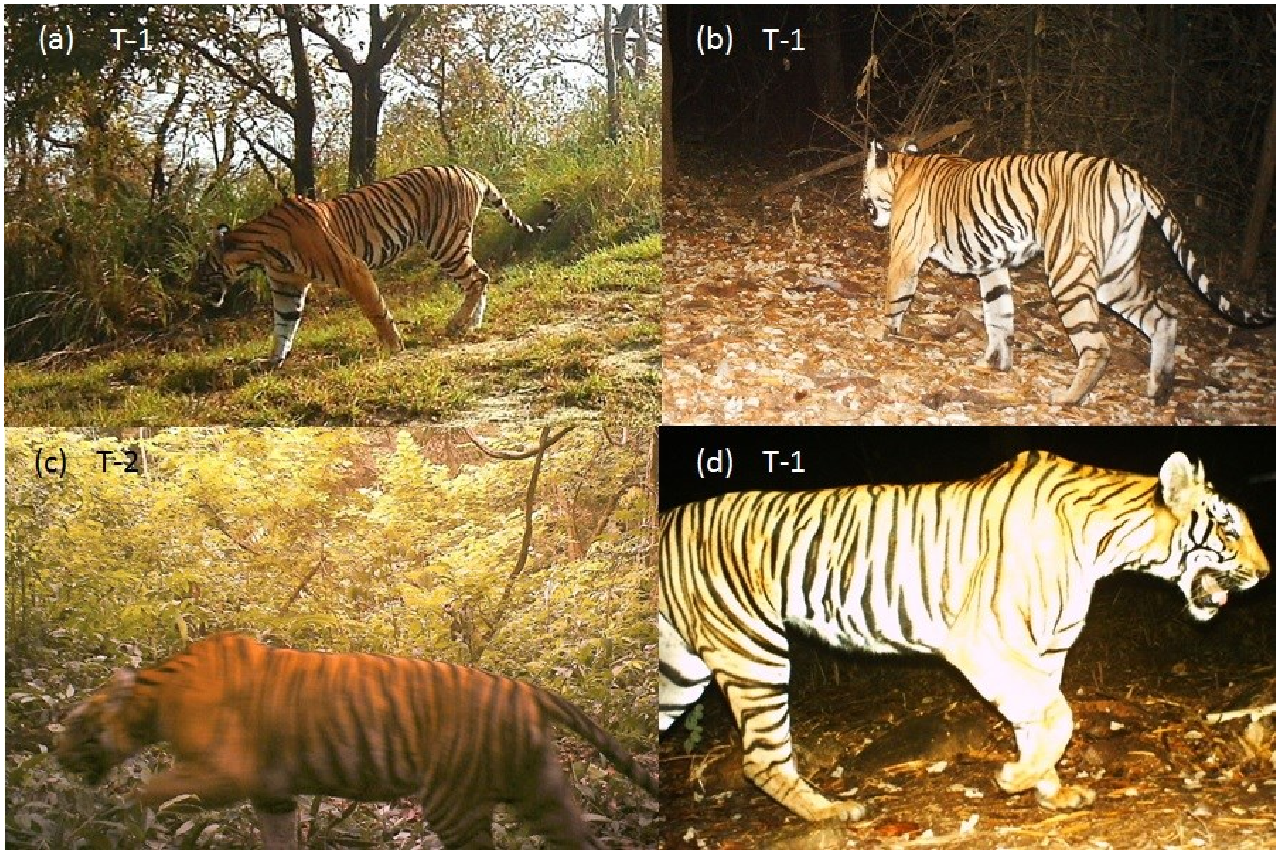
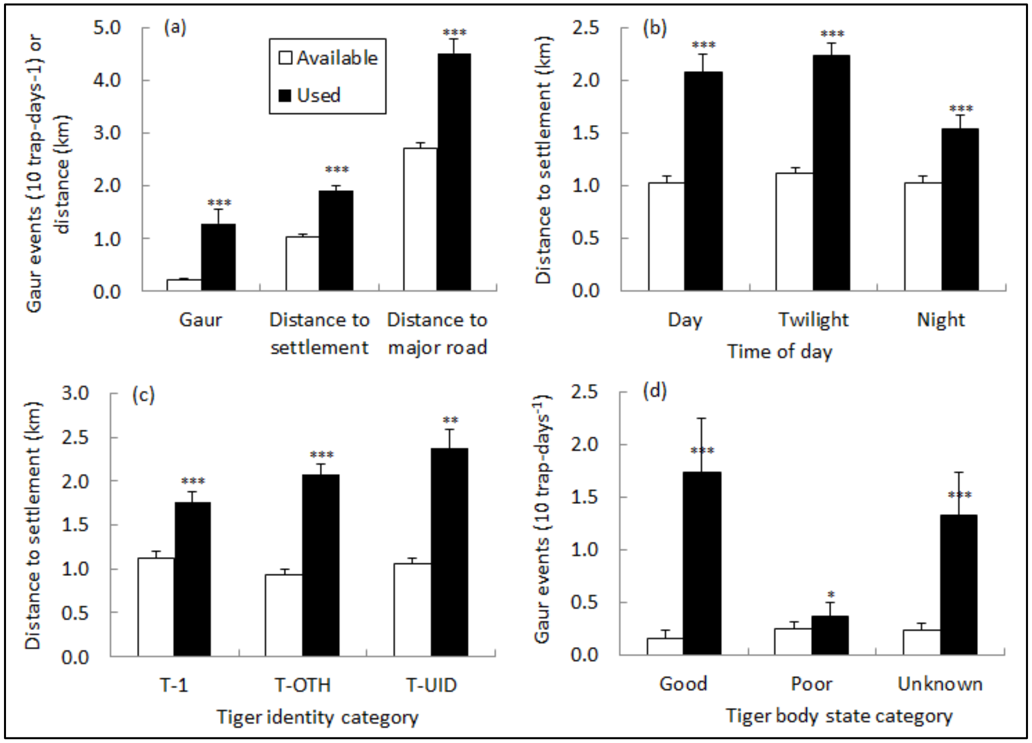
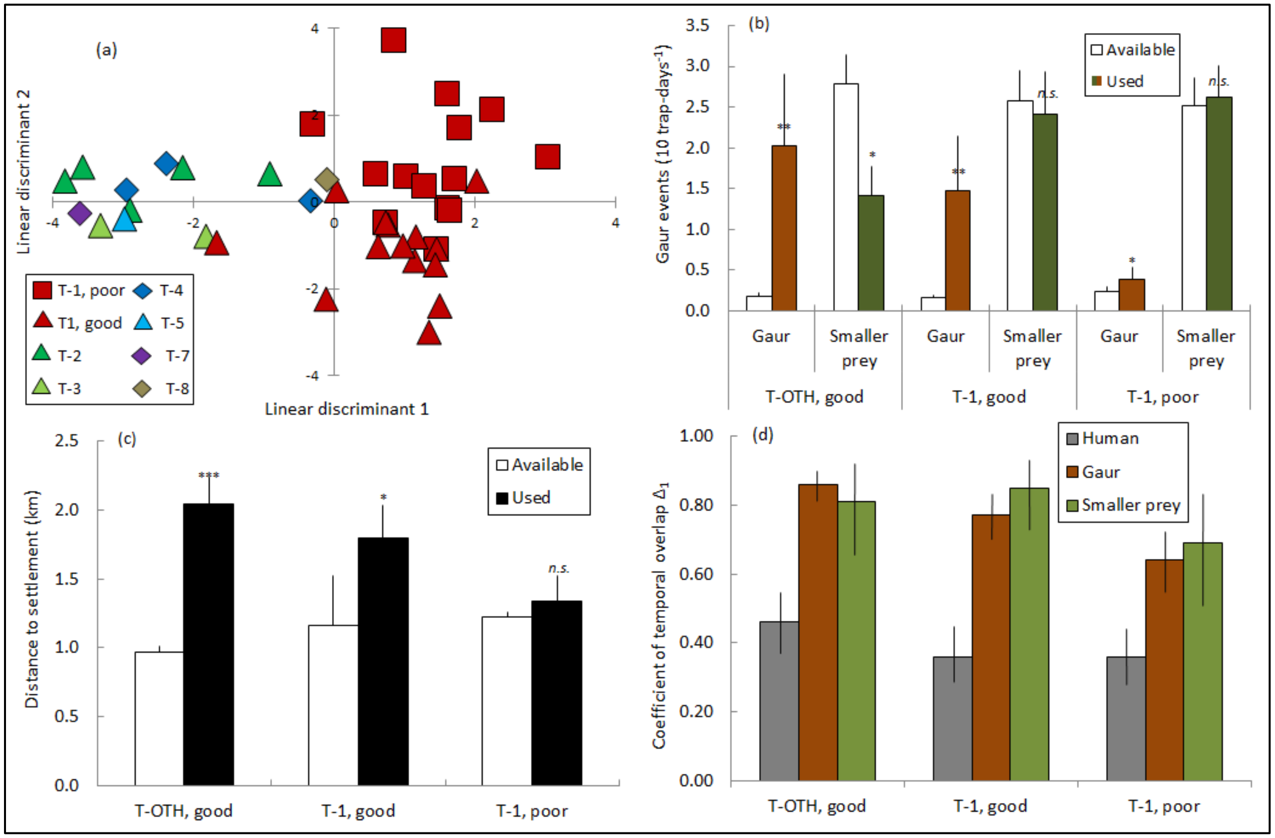


Figure 5.3 Effect sizes for (a) spatial habitat covariates for all tiger events, (b) temporal segregation with respect to distance from settlement for all tiger events, (c) interactive effect of individual identity with distance to settlement and (d) interactive effect of body state with respect to gaur use in the Shencottah Gap, India between 2011 and 2013.



Statistical significance of used *vs*. available locations (Wilcoxon rank sum test): ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; *n.s.*, $P > 0.05$.

Figure 5.4 (a) Linear discriminant analysis depicting within and between-individual variation in tiger habitat use in the Shencottah Gap, India, with respect to body state and individual identity class (individuals other than T-1 are depicted only for information, but were grouped together for analysis; factor loadings in Table 5.5). Variation among these categories with respect to (b) gaur use and (c) distance to settlement, with standard errors, is also provided. Temporal overlap between tigers in the three individual-body state categories with humans, gaur and smaller prey species with 95% confidence intervals is provided in (d).



Statistical significance of used *vs*. available locations (Wilcoxon rank sum test): ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; *n.s.*, $P > 0.05$.

Statistical significance of linear discriminant analysis: $F = 1.92$, d.f. = 36, $P = 0.02$; 83% correct classification of events.

Chapter 6

6 General discussion

6.1 Summary of results

My thesis objectives were to (a) examine the correspondence between areas that are important for habitat use, and areas that are potentially important for movement, of elephants and gaur; (b) evaluate whether habitat use models developed for elephants and tigers were correlated to the frequency of detection or the presence of other mammals; (c) evaluate how different mammals may be grouped by the position as well as the variance of their niches with respect to habitat characteristics and, (d) examine how spatial habitat, temporal segregation, individual variation and infirmity may influence tiger presence in multiple-use areas. In doing so, my intention was to investigate the opportunities and the challenges of connectivity conservation in multiple-use areas, develop generalizable inferences, and formulate specific management recommendations for my study site. I describe below the main findings from each data chapter of my thesis.

The first major result from Chapter 2 was that there was only low overlap between the areas important for habitat use and the areas contributing to potential movement. Further, the location of modelled corridors varied with the resolution of analysis; at the larger resolution, the eastern corridor was emphasized, while the smaller resolution emphasized both corridors. The scale-integrated habitat models produced corridors that were more flexible than the large-resolution models, and more compact than the small-resolution models; these potentially reflect a realistic scenario of multi-scale habitat selection (*e.g.,* Mortelliti & Boitani, 2008). Finally, the least cost paths across the linear transportation routes incorporated very poor habitat, suggesting that the corridor across the Shencottah Gap may not currently be functional for elephants and gaur.

The results from Chapter 3 suggested that elephants, tigers and gaur detections were highly correlated with each other; consequently, these species may serve as effective surrogates for each other. The congruence with other threatened species was less straightforward; Nilgiri langur was correlated to tiger habitat use, and sloth bears and pangolins tended towards hump-shaped distributions with both flagships. Importantly, however, dholes and sambar were negatively correlated to one or both of the flagship species. The diversity of threatened species increased with habitat use by the flagship species when the locally-abundant sambar was included, but this trend was less regular when it was excluded. Overall, these results show only modest support for the umbrella capacity of elephants and tigers for the mammals that I examined.

The results from Chapter 4 added some details to the above findings, by clustering species into functional types. When clustered by their marginality and tolerance, four main functional types emerged. These clusters ranged from an extreme degree of specialization (lion-tailed macaque) to the widely-distributed sambar and wild pig. Interestingly, threatened species were much more widely distributed along the marginality-tolerance space than expected, suggesting that at least some of them are able to make use of a wide variety of habitat types. When clustered by habitat associations, four more groups were identified; the three most important groups consisted of those species that required closed forest, those that required grassland and those that used anthropogenic habitat. The covariates that most influenced marginality varied by species; however, the covariates affecting tolerance were generally anthropogenic covariates such as house density. These covariates may currently restrict connectivity across the Shencottah Gap.

Chapter 5 also produced results that are relevant for tiger connectivity in the Shencottah Gap. At the population level, tigers preferentially used areas that were further from human infrastructure and were used more by gaur. However, the use of gaur-rich areas was mediated by infirmity; poor body state led to decreased use of such areas. One individual tiger was found closer to settlements than others were; tiger activity peaked during mornings and evenings, but temporal segregation with humans did not appear to play a major role in tiger habitat use. The individual tiger that was most frequently detected in the study area exhibited considerable variation in habitat use depending on its body state. Overall, this study suggests that connectivity may be determined by individual behavior that is dependent on body state.

6.2 Implications for the landscape approach

6.2.1 Connectivity through corridors and the matrix

The results from my thesis suggest that in multiple-use areas, both the matrix and corridors must be considered together in modelling efforts if conservation outcomes are to be balanced. When habitat fragmentation is low – such as in variegated (*sensu* McIntyre & Hobbs, 1999) parts of the landscape – habitat loss may be more important than fragmentation (Flather & Bevers, 2002; Fahrig, 2003). In such areas (*e.g.*, the northern parts of the Shencottah Gap), conservation efforts should focus on preventing habitat loss, which may promote both occupancy and connectivity (Pimentel *et al.,* 1992; Franklin, 1993; Hodgson *et al.,* 2009). In more fragmented or relict areas – such as those closer to the national highway – conservation efforts may be better targeted to enhancing connectivity (Andren, 1994; Fahrig, 2002), because restoring large amounts of habitat may be prohibitively expensive (James *et al.,* 1999).

These inferences are supported by the results from Chapter 5: the individual tiger that made most use of the Shencottah Gap, and appeared to be resident in it, was also the one that came closest to crossing. While tigers may conceivably disperse directly from Periyar or Shendurney, I suggest that animals that are resident in the matrix may also play a crucial role in fostering connectivity.

6.2.2 Role of flagship species in matrix conservation

Apart from fostering connectivity, the presence of large carnivores such as tigers in multiple-use areas may be a key determinant of conservation investment (*e.g.,* Seddon & Leech, 2008). Yet, large carnivores may only rarely occur in multiple-use areas (Sunarto *et al.,* 2012), and may be missed easily. I suggest that large herbivores that are similarly sensitive to human impacts may serve as effective surrogates for large carnivores such as tigers. Elephants and tigers both prefer relatively undisturbed habitat (Sukumar, 1989; Karanth & Sunquist, 2000) and exhibit negative demographic responses to poaching (Sukumar *et al.,* 1998; Chapron *et al.,* 2008). But elephants are more detectable than tigers even at low densities due to high cue production (up to 18 defecations and 80 kg of dung per day; Vanculyenberg, 1977). Similar characteristics may have made African elephants (*Loxodonta africana*) appropriate surrogates outside protected areas for several species including rarely-detected lions (*Panthera leo*) in Tanzania (Epps *et al.,* 2011). Similar arguments may also apply for the relatively shy gaur (Choudhury, 2002), in addition to it being a species that is preferentially targeted by tigers (Karanth & Sunquist, 1995).

Although detections of elephants, tigers and gaur were correlated, many other species, especially threatened ones, exhibited unclear trends. This result is similar to the findings of some studies that found low or mixed evidence for the effectiveness of umbrella species (*e.g.*, Andelman & Fagan, 2000; Caro *et al.,* 2004; Bilfochi & Lode, 2005; Ozaki *et al.,* 2006; Cushman *et al.,* 2010), but unlike others that did find positive evidence of their effectiveness (Launer & Murphy, 1994; Suter *et al.,* 2002; Sergio *et al.,* 2006; Branton & Richardson, 2011; Branton & Richardson, 2014). Overall, it appears that the effectiveness of umbrella species may depend on scale (Bohning-Gaese, 1997), and effectiveness may be a relative measure than a binary one (Mortelliti *et al.,* 2009). I suggest that much more empirical research is required to test the utility of umbrella species in conservation applications; however, this result does not detract from the role of elephants and tigers as flagship species.

6.2.3 Variation among species in matrix use

Elephants appeared to perform slightly worse than tigers as umbrella species; for example, Nilgiri langur detections were correlated to tiger habitat use, but not elephant habitat use. This may have been because elephants appear to occupy a wider niche than tigers in this landscape (slightly lower marginality and much higher tolerance). This tendency towards more generalist habitat use may therefore make them less effective as umbrella species than the more restricted tigers (*e.g.,* Ozaki *et al.,* 2006).

However, the most restricted species by far was the lion-tailed macaque, which depends on wet evergreen forest (Singh *et al.,* 2002). Conserving this species may therefore require strict protection, at least at a small scale, of the patches of evergreen forest that remain in this landscape (Santosh *et al.,* 2013). At the other extreme, dholes present a different conservation challenge because of their use of anthropogenic habitat (*e.g.,* tea and rubber plantations): their conservation will likely need to include appropriate management of such privately-owned areas. The conservation of wide-ranging African painted dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) outside protected areas in Africa presents similar challenges (Marker & Dickman, 2004; Lindsey *et al.,* 2005), and requires complex agreements with private landowners and communities (reviewed by Brandon & Wells, 1992; Dickman *et al.,* 2011). The results from my thesis suggest that a wide range of conservation initiatives may need to be undertaken in multiple-use areas, depending on variation in habitat use among species.

6.2.4 Variation among individuals in matrix use

Individual identity influenced how close tigers came to settlements, and body state influenced their use of gaur-rich areas. Large carnivores in a poor body state that approach settlements are often associated with conflict (*e.g.,* Packer *et al.,* 2005; Packer *et al.,* 2011; Das, 2012). However, I did not come across tiger-human conflict during the period of the study, for which I suggest four potential reasons.

Tigers did not seem to avoid humans through temporal segregation, though this is sometimes suggested as a means for coexistence (Carter *et al.,* 2012). Instead, idiosyncratic variation between individuals may influence conflict; for example, individual variation influenced cougar (*Puma concolor*) attacks on sheep (Ross *et al.,* 1997); leopard attacks on people (Athreya *et al.,* 2011) and crop-raiding by elephants (Hoare, 1999). It is also possible that the relatively high sambar densities near settlements constitute adequate alternative prey; sambar are commonly predated upon by tigers (*e.g.,* Ramesh et al. 2012). Subordinate carnivores may also use such areas as refugia against dominant conspecifics (Elfstrom *et al.,* 2014). A final possibility is that conflict may be low simply because tiger density is low; this has been suggested as an important reason for low tiger-human conflict in Russia (Carroll & Miquelle, 2006).

6.3 Study limitations and further work

I describe below some limitations of this study and how they may be overcome, as well as some potential for further analyses involving the data used in this thesis.

My evaluation of the umbrella capacity of elephants and tigers (Chapter 3) was at a small, local scale; however, this differs from their use in the 'classic' sense (Caro, 2010). Umbrella species are often selected because they require large areas for population viability (Noss *et al.,* 1996; Simberloff, 1998; Carroll *et al.,* 2001), implying that the use of species as umbrellas should be based on assessments of population and home range sizes. Although such assessments are rare, Berger (1997) reported that the area occupied by a viable population of black rhino (*Diceros bicornis*) was inadequate to maintain viable populations of other large mammals. Similarly, Cushman *et al.* (2010) did not find clear correlations between the abundance of indicator species of birds and the abundance of other taxa at the scale of river basins. While I am unable to evaluate population sizes and home range extents, I can potentially re-examine the data at a coarser resolution.

Perhaps a more serious shortcoming of my analysis of umbrella capacity is that I did not consider taxa other than mammals; for example, vascular plants and amphibians are the main reasons for the designation of the Western Ghats as a biodiversity hotspot (Myers *et al.,* 2000). Further, I did not include ecological processes or services. For example, elephants may play an important role in dispersing seeds (*e.g.,* Cochrane, 2003), and there may exist several synergies between carbon sequestration and biodiversity conservation (*e.g.,* Larsen *et al.,* 2011). Incorporating such data would be a logical next step in this analysis.

A more statistical limitation applies to Chapter 4, where I combined direct sightings, detections of sign and camera photos in a single analysis. These data are fundamentally different from each other: sign surveys constitute a single sweep through the study area, while camera trap data consists of repeated measurements at the same location. Yet, several databases are based on such variable information (Hirzel *et al.,* 2002), and conservation decisions may have to be made based on these imperfect data (*e.g.,* IUCN, 2010). Apart from this potential drawback, there also appears to be some evidence that the covariates influencing gaur use may change over space; for example, gaur were grouped with sloth bears in terms of their niche characteristics in Chapter 4, but were strongly correlated with elephants within the more disturbed subset of the landscape (Chapter 3). Habitat selection may not necessarily be uniform over space (*e.g.,* Mysterud & Ims, 1998), and there was some evidence of this from Chapter 2: gaur approached closer to settlements when they were within the Shendurney Wildlife Sanctuary that in multiple-use forest.

The ecology of dholes in multiple-use areas is an intriguing question for further investigation. Camera trap data (but not sign surveys) indicated that dholes were negatively correlated to tigers (Chapter 3); however, it is not clear whether this is a consequence of competitive dominance in a resource poor area, or that of differential prey selection. Srivathsa *et al.* (2014) did not report any spatial separation between tigers and dholes in a prey-rich reserve, but Steinmetz *et al.* (2013) detected evidence consistent with spatial avoidance in degraded areas with low prey density. Low prey densities may mediate niche overlap (*e.g.,* Colwell & Futuyama, 1971), and perhaps intra-guild predation too (Polis *et al.,* 1989). However, dholes also target smaller prey than tigers, such as sambar; consequently, their distribution may reflect sambar habitat preferences. An approach based on Structural Equation Models (Grace *et al.,* 2010) may potentially enable comparison of the bottom-up (prey-driven) hypothesis versus the top-down (competitor-driven) hypothesis for dhole occurrence, which is important because dholes are among the least well known of the canids (Srivathsa *et al.,* 2013), despite their endangered status (Durbin *et al.,* 2008).

My analysis of tiger habitat use (Chapter 5) involves several limitations as well. The tiger dataset was small, but this may be unavoidable in studies on an endangered large carnivore outside reserves (*e.g.,* Athreya *et al.,* 2014). A second limitation is set by the ordinal nature of body-state classification; I believe this method can be further refined, using larger databases of photos (*e.g.,* Jhala *et al.,* 2011) and may potentially be automated as well (*e.g.,* by modifying existing 3-dimensionsl software; Hiby *et al.,* 2009). It may also be possible to apply this method to a subset of the elephant photographs in my database, particularly since ordinal scales of body-state already exist for elephants (*e.g.,* Wemmer *et al.,* 2006).

6.4 Summary

The conservation of tropical biodiversity is increasingly determined by the need to balance conservation and development needs in large landscapes that are subject to multiple uses (DeFries *et al.,* 2005; Naughton-Treves *et al.,* 2005). This landscape approach to conservation has been implemented by multiple organizations and governments, with mixed results for both conservation and development (Kremen *et al.,* 1994; Newmark & Hough, 2000). These experiences suggest that wildlife conservation in multiple-use landscapes does not necessarily involve ‘win-win’ situations, but consists instead of a series of ‘hard choices’ (McShane *et al.,* 2011). Three such trade-offs may be particularly important.

In multiple-use areas, corridors are often modelled in the face of growing threats from human impacts (Beier & Noss, 1998). Although corridor modeling methods are certainly subjected to several cautions (*e.g.,* Beier *et al.,* 2009; Beier *et al.,* 2011), including identification of both 'patches' and 'corridors' (Chetkiewicz & Boyce, 2009), the attraction of corridors to society may be in the small area they occupy. Consequently, corridor conservation must not come at the cost of managing the matrix for biodiversity (Harrison & Bruna, 1999), or *vice-versa*, in working landscapes.

Unfortunately, the conservation of wildlife in multiple-use areas may be complicated by differing species responses, which may require management measures that conflict with development needs (McNeely, 1993; Rao & Geisler, 2008). Although a complex socio-political issue like this cannot be easily solved, I suggest that explicitly defining the needs of wildlife conservation in the design of such schemes can help bring about more realistic expectations and transparency (Newmark & Gough, 2000).

Because human-wildlife conflict is a major determinant of conservation in multiple-use areas (Karanth & Gopal, 2005), managers may be challenged to maintain a high enough level of animals use to support occupancy and connectivity, but low enough to minimize conflict (Linnell *et al.,* 2005). To this end, a much greater focus on individual animals and their state may be required. For example, standard protocols for dealing with conflict tigers in India already include individual identification via camera traps (NTCA, 2013); *a priori* quantification of individual habitat preferences may allow for faster response to such conflict. These efforts may also benefit from further investigation into how to increase movement through bottlenecks regions, without increasing residence (Andreassen *et al.,* 1996; Tischendorf & Wissell, 1997).

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Appendices

Appendix 2.1 Details of covariates used in resource selection models at macro and micro scales.

Covariates measured in the field: We collected covariates expected to influence detection probability and habitat use once per 0.1 km segment along the sampled route. Habitat covariates included: broad habitat type, which we subsequently classified into five categories relevant to the focal species of this study - closed forest, grassland dominated, forestry plantation (teak, acacia, eucalyptus, bamboo), commercial plantation (rubber, tea, cardamom), and settlement/ farmland; leaf litter depth, recorded at four locations within a single 1 m^2 quadrat in each sampled segment; and all signs of human impacts on a continuous basis (including logging, minor forest product extraction, livestock presence, quarrying and snares). We also visually estimated the percentage of each 1 m^2 quadrat that was covered in soil, stones, vegetation and leaf litter as an index of detectability. To aid in subsequent land use classification (below), we also physically mapped out the boundaries of all settlements and commercial plantations within the most heterogeneous part of the study area (300 km^2) using a hand-held GPS unit.

Derivation of covariates for analysis: Because of the unavailability of an accurate land use map of this area, we generated an approximate, field-verified alternative. We used a combination of physical mapping in the field (above), data from the management plans of Thenmala and Achenkovil Divisions (KFD, 2010, MOEF, 2006), Google Earth and large scale vegetation maps (Ramesh *et al.,* 1997) to trace out polygons representing closed forest, grassland, forestry plantations, commercial plantations and settlements/farmland. We verified and modified these polygons using habitat categorizations measured at 12082 locations in the field (above), and rasterized the resulting polygons to a resolution of 100 m. For macro cells, we summarized these land use categories in terms of the proportion of a cell covered by each category. We also computed the proportion of each cell covered by three pooled categories: natural areas (closed forest and grasslands), forestry plantations, and human dominated areas (commercial plantations and settlements/ farmland). To incorporate effects at a scale larger than that of the macro cell, we also computed the mean value of each of the above pooled quantities for a 3 x 3 cell neighbourhood around each macro cell. At the micro resolution, we assigned each cell to both the finer and coarser land use types as each of these as a factor covariate in analysis, and kept closed forest as the reference category.

Because our land use categorization is approximate and does not distinguish between different kinds of forests, we also used the eco-climatic distance (Krishnaswamy *et al.,* 2009) as an index to deciduousness. This index represents the Mahalanobis distance of the vegetation in a particular cell from a reference category of wet evergreen forest, and has been shown to correlate well with forest types in south India. We derived this index using Enhanced Vegetation Index data from MODIS (Oak Ridge National Laboratory Distributed Active Archive Center 2011) at a 250-m resolution. For macro cells, we took the mean value of the eco-climatic distance; for the micro scale, we took the mean value of the raster cells that were intersected by the micro cells. We considered leaf litter depth to be an index of productivity, and interpolated litter depth values from 7731 field measurements to un-sampled locations within the study area at a resolution of 0.1 km using ordinary kriging. Interpolation results were verified by cross validation, and indicated good predictive power (root mean squared error < 0.001). We took the mean leaf litter depth predicted by the kriging models as the candidate covariate for both macro and micro cells.

Similarly, we also considered the presence of human impacts to be an indicator of habitat quality, and interpolated presence or absence of these impacts using indicator kriging. Interpolation results were verified by cross validation, and indicated good predictive power (root mean squared error < 0.001). For macro cells, we summed the predicted number of human impacts; for the micro cells, we used this as a binary variable of presence or absence. We also mapped the point locations of all houses within the study area using Google Earth. We summed the number of houses contained within a macro cell, while we used the presence or absence of houses in each micro cell as a binary variable. We measured the Euclidean distance from the centroid of each macro and micro cell to the nearest settlement, as well as to the nearest human-dominated area. We also measured the Euclidean distance from the centroid of each macro and micro cell to the nearest major road (NH 208 and Shencottah-Achenkovil-Punalur road). We corrected all distance measurements for terrain, using a linear interpolation based on a digital elevation model (DEM) derived from 90-m LANDSAT data (USGS 2008). We also used this DEM to estimate slope, a steady-state wetness index (compound topographic index; Gessler *et al.,* 1995), and a roughness index (Jenness, 2013) at a 90-m resolution. For all three of these indices, we took the mean values of all rasters that intersected both macro and micro cells. To reflect potential differences in management, we considered the effect of whether the cell was located north or south of the linear barriers, and whether a cell was within or outside a protected area. We conducted all the above spatial analysis in ArcGIS 10.1 (ESRI, Redlands, USA) and Geospatial Modeling Environment 0.7.2.1 (Beyer 2012). To quantify the effect of ground cover on sign detectability, we summed the proportion of each quadrat in a segment that was covered by stones, leaf litter and vegetation, and used the mean value of this variable for each macro and micro cell. For micro cells, we also used sampling effort as a potential candidate covariate.

Appendix 2.2 Model fit for macro-resolution and micro-resolution models for elephant and gaur.

	Macro model		Micro model	
	Elephant	Gaur	Elephant	Gaur
Overdispersion ($\hat{c}$)	1.3	1.2		
Mc Fadden's pseudo R^2	0.13	0.14		
Spearman rank correlation r_s (five-fold cross validation)			0.98 (p <0.001)	0.99 (p <0.001)

Appendix 2.3 Correlation (Kendall's rank correlation, τ_b) between habitat quality rank based on resource selection functions, and current flow rank derived by running circuit theoretical models on predicted habitat quality rank, for dispersal corridor models for elephant and gaur at the macro resolution, micro resolution and scale-integrated resolution.

	Elephant τ_b	Gaur τ_b
Macro-resolution	0.25, $P < 0.001$	0.21, $P < 0.001$
Micro-resolution	0.21, $P < 0.001$	0.19, $P < 0.001$
Scale-integrated resolution	0.27, $P < 0.001$	0.23, $P < 0.001$

Appendix 3.1 Details of mixed-effects negative binomial regression models used for modeling camera trap data for gaur, for use in predicting gaur use at un-sampled sign survey locations. The model was validated with independent sign survey data, and the correlation (r_s) between the number of signs detected in each predicted decile (corrected for effort) and decile rank was 0.98 (S = 4, $P < 0.001$).

Fixed effects	Coefficient (SE)	*t*	*P*
Intercept	-4.10 (0.14)	-30.40	< 0.001
Building density[a]	-0.64	0.25	0.01
Distance to major road	0.32 (0.12)	2.63	0.009
Distance to settlement	0.28 (0.13)	2.18	0.03
Proportion of commercial plantation[b]	-0.29 (0.13)	-2.21	0.03
Proportion of open forest/ grassland[c]	0.37 (0.10)	3.95	< 0.001
Slope	-0.35 (0.10)	-3.48	< 0.001
Slope^2	0.19 (0.09)	2.22	0.03
Random effects			
Variance of sampling grid cell	1.35		

[a] 300-m buffer

[b] 2400-m buffer

[c] 300-m buffer

Appendix 3.2 Trend in a species heterogeneity index (Shannon-Weaver *H*) across elephant and tiger habitat quality quintile, based on counts of seven threatened and 14 non-threatened species from camera trap data.

Elephant

Quantile	Threatened		Non-threatened	
	H	SE (H)	H	SE (H)
1	0.18	0.03	1.11	0.05
2	0.37	0.04	1.18	0.05
3	0.38	0.04	1.07	0.06
4	0.53	0.04	1.19	0.05
5	0.47	0.04	1.01	0.05

Tiger

Quantile	Threatened		Non-threatened	
	H	SE (H)	H	SE (H)
1	0.34	0.04	1.10	0.05
2	0.40	0.04	1.14	0.05
3	0.60	0.05	1.24	0.05
4	0.67	0.05	1.17	0.06
5	0.66	0.04	0.92	0.05

Appendix 4.1 Marginality and tolerance scores from Ecological Niche Factor Analysis comparing cells that were sampled for each of 14 species with cells that were not sampled, to quantify potential biases in sampling intensity.

Species	Acronym	Sampled cells	Un-sampled cells	Marginality	Tolerance
Tiger	TGR	5474	60414	0.45	13.31
Leopard	LPD	5474	60414	0.43	12.54
Dhole	DHL	5474	60414	0.43	12.47
Bear	BER	11984	53904	0.11	14.19
Elephant	ELP	11984	53904	0.11	14.35
Gaur	GAR	11984	53904	0.11	14.20
Sambar	SBR	11984	53904	0.11	14.07
Pig	PIG	11984	53904	0.11	14.35
Muntjac	MJK	11984	53904	0.11	14.16
Chevrotain	CHV	11984	53904	0.11	14.11
Lion-tailed macaque	LTM	11642	54246	0.10	13.79
Nilgiri langur	NLG	11642	54246	0.10	14.57
Bonnet macaque	BNT	11984	53904	0.10	14.05
Giant squirrel	GSQ	11642	54246	0.11	14.25

Appendix 4.2 Correlation (Pearson's r; $|r| > 0.3$ depicted in bold) of all covariates to the marginality axis of an Ecological Niche Factor Analysis comparing sampled cells to un-sampled cells for 14 species, to quantify potential biases in sampling intensity with respect to covariates. Footnotes indicate scale of covariate measurement. See Appendix 4.1 for species acronyms.

	Threatened species								Non-threatened species					
Covariate	ELP	GAR	SBR	TGR	DHL	BER	LTM	NLG	LPD	PIG	MJK	CHV	GSQ	BNT
Closed forest	**-0.41**[d]	**-0.44**[b]	**-0.43**[d]	0.05[c]	0.07[d]	**-0.41**[d]	-0.26[a]	**-0.45**[d]	0.10[a]	**-0.42**[d]	**-0.43**[a]	**0.43**[a]	**-0.46**[a]	**-0.45**[a]
Open forest/grassland	0.00[d]	0.00[d]	-0.02[a]	-0.25[d]	-0.28[b]	0.00[d]	-0.11[a]	-0.01[a]	-0.25[d]	-0.03[a]	0.00[d]	0.00[d]	-0.01[a]	0.00[d]
Forestry plantation	**0.49**[b]	**0.54**[a]	**0.43**[c]	0.20[b]	0.10[d]	**0.52**[a]	**0.37**[c]	**0.40**[d]	0.18[c]	**0.49**[b]	**0.54**[a]	**0.54**[a]	**0.55**[a]	**0.39**[d]
Commercial plantation	0.01[c]	0.02[c]	0.04[a]	-0.09[a]	-0.09[a]	-0.01[d]	0.03[a]	-0.06[d]	-0.03[d]	-0.01[d]	-0.01[d]	0.04[a]	0.04[a]	-0.01[d]
Settlement	0.21[c]	0.11[b]	0.24[d]	0.17[c]	0.08[a]	0.11[b]	0.19[d]	0.23[c]	0.07[a]	0.22[c]	0.05[a]	0.05[a]	0.12[b]	0.05[a]
Eco-climatic distance	0.24[d]	0.06[a]	0.27[d]	-0.04[d]	-0.04[a]	0.26[d]	0.04[a]	0.29[c]	-0.01[b]	0.22[c]	0.11[a]	0.06[a]	0.05[a]	0.28[d]

House density	0.02[c]	0.03[c]	-0.11[a]	0.03[b]	-0.05[a]	-0.07[b]	-0.04[b]	0.00[c]	-0.05[a]	0.03[c]	0.03[c]	0.03[c]	0.00[c]	-0.08[b]
Distance to settlement	**-0.30**	**-0.31**	**-0.33**	-0.16	-0.17	**-0.31**	**-0.36**	-0.29	-0.17	**-0.31**	**-0.32**	**-0.32**	-0.28	**-0.34**
Distance to commercial plantation	0.08	0.07	0.06	-0.11	-0.11	0.07	-0.09	0.14	-0.11	0.07	0.07	0.07	0.14	0.07
Distance to road	-0.14	-0.15	-0.15	-0.21	-0.22	-0.14	-0.24	-0.10	-0.22	-0.15	-0.15	-0.15	-0.10	-0.16
Slope to settlement	-0.21	-0.21	-0.20	-0.29	-0.29	-0.21	-0.26	-0.23	-0.29	-0.21	-0.21	-0.21	-0.22	-0.22
Slope to commercial plantation	-0.15	-0.16	-0.15	-0.20	-0.21	-0.16	-0.19	-0.16	-0.21	-0.16	-0.16	-0.16	-0.16	-0.17
Slope	**-0.52**	**-0.52**	**-0.50**	**-0.77**	**-0.78**	**-0.51**	**-0.64**	**-0.51**	**-0.78**	**-0.51**	**-0.52**	**-0.52**	**-0.50**	**-0.55**
Curvature	-0.19	-0.18	-0.18	-0.23	-0.24	-0.18	-0.18	-0.20	-0.24	-0.18	-0.18	-0.18	-0.19	-0.19

[a] 300 m, [b]600 m, [c]1200 m, [d] 2400 m

Appendix 4.3. Correlation (Pearson's *r; |r|* > 0.3 depicted in bold lettering) of all covariates to the marginality axis of an Ecological Niche Factor Analysis comparing sampled cells where each of 14 species was detected or not detected. See Appendix 4.1 for species acronyms and Appendix 4.2 for scale of covariate measurement.

Covariate	Threatened species								Non-threatened species					
	ELP	GAR	SBR	TGR	DHL	BER	LTM	NLG	LPD	PIG	MJK	CHV	GSQ	BNT
Closed forest	**0.44**	0.05	**-0.49**	**0.46**	-0.13	-0.26	**0.49**	**0.39**	0.30	-0.25	**0.44**	**0.36**	**0.51**	**0.36**
Open forest/grassland	-0.05	**0.36**	**0.30**	-0.20	0.30	**0.49**	-0.22	-0.08	-0.11	-0.21	-0.30	-0.28	-0.21	-0.28
Forestry plantation	-0.08	-0.05	0.21	**-0.31**	-0.16	-0.04	-0.28	-0.21	-0.19	0.29	-0.17	-0.13	-0.19	-0.26
Commercial plantation	**-0.30**	**-0.36**	-0.20	-0.14	-0.10	**-0.32**	-0.11	-0.20	0.27	0.15	0.24	-0.13	-0.22	0.28
Settlement	**-0.33**	**-0.37**	**0.34**	-0.28	-0.21	-0.18	-0.19	-0.21	**-0.37**	0.18	-0.19	-0.14	-0.26	-0.05
Eco-climatic	**-0.40**	-0.10	**0.48**	-0.22	0.24	0.24	**-0.50**	**-0.36**	-0.20	0.20	-0.26	-0.20	**-0.39**	-0.08

distance														
House density	**-0.32**	**-0.39**	-0.12	-0.22	-0.13	-0.23	-0.13	-0.20	-0.22	0.29	0.10	0.25	-0.21	0.21
Distance to settlement	**0.43**	**0.37**	**-0.39**	0.19	**-0.55**	0.18	0.06	**0.45**	-0.23	**-0.33**	-0.15	-0.23	**0.37**	**-0.35**
Distance to commercial plantation	0.21	**0.36**	-0.04	**-0.43**	**-0.32**	**0.50**	-0.20	0.11	**-0.48**	-0.27	**-0.47**	**-0.45**	-0.01	**-0.53**
Distance to road	0.17	0.18	-0.19	-0.05	**-0.34**	**0.31**	0.11	0.27	**-0.37**	**-0.45**	**-0.32**	**-0.52**	-0.08	**-0.39**
Slope to settlement	0.18	0.03	-0.01	**0.33**	0.15	0.00	0.26	0.26	0.26	-0.25	**0.31**	0.28	0.29	0.19
Slope to commercial plantation	0.21	0.17	0.10	0.28	0.11	0.24	0.30	0.24	0.18	-0.25	0.19	0.09	0.29	0.04
Slope	-0.07	-0.28	0.10	-0.06	-0.12	-0.03	0.21	**0.32**	0.11	**-0.34**	0.15	0.01	0.18	0.03

Curvature	0.01	0.16	0.09	0.21	**0.41**	0.07	0.24	0.12	0.21	-0.02	0.13	0.15	0.03	0.04

Appendix 4.4. Loadings on two principal component axes that together explained 73% of the variance of covariate correlations with the marginality axis for 14 mammals. These components are reflected in Figure 4.2b.

Covariate	Principal component 1	Principal component 2
Closed forest	-0.80	0.51
Open forest/ grassland	0.21	-0.84
Forestry plantation	0.83	-0.39
Commercial plantation	0.30	0.82
Settlement	0.81	0.04
Eco-climatic distance	0.84	-0.33
House density	0.57	0.68
Distance to settlement	-0.72	-0.49
Distance to commercial plantation	-0.15	-0.95
Distance to road	-0.54	-0.76

Slope	-0.56	0.27
Curvature	-0.23	0.13
Slope to commercial plantation	-0.90	-0.20
Slope to settlement	-0.81	0.48

Appendix 4.5 Correlation (Pearson's *r; |r|* > 0.3 depicted in bold lettering) of all covariates with the first specialization axis of an Ecological Niche Factor Analysis comparing sampled cells where each of 14 species was detected or not detected. Only the absolute value of the correlation coefficient is meaningful. See Appendix 4.1 for species acronyms and Appendix 4.2 for scale of covariate measurement.

	Threatened								Not threatened					
Covariate	ELP	GAR	SBR	TGR	DHL	BER	LTM	NLG	LPD	PIG	MJK	CHV	GSQ	BNT
Closed forest	-0.14	0.06	0.12	-0.06	-0.14	-0.03	-0.20	0.02	0.02	0.17	0.03	0.11	**-0.57**	-0.06
Open forest/grassland	-0.15	0.02	-0.06	-0.07	-0.01	-0.05	-0.16	0.01	0.05	0.27	**-0.43**	-0.07	**-0.49**	**0.51**
Forestry plantation	-0.05	0.10	0.02	-0.04	-0.20	-0.02	0.12	0.04	0.06	0.10	0.01	-0.04	**-0.49**	**-0.64**
Commercial	**-0.81**	**-0.84**	**-0.82**	-0.06	0.00	**-0.56**	0.13	**-0.54**	-0.04	0.09	-0.07	-0.11	**-0.43**	-0.09

plantation														
Settlement	0.28	**0.40**	0.16	**-0.50**	**0.58**	-0.06	-0.19	-0.25	**-0.38**	-0.26	**0.86**	**0.92**	-0.03	-0.14
Eco-climatic distance	0.17	0.04	-0.26	-0.04	-0.02	0.05	0.01	-0.01	-0.05	**0.75**	0.04	0.12	0.01	0.15
House density	0.23	0.26	**-0.43**	**0.85**	**-0.75**	**0.82**	**-0.90**	**0.80**	**0.90**	0.00	-0.14	-0.14	0.01	-0.07
Distance to settlement	0.22	0.07	0.12	-0.04	0.10	0.07	-0.18	-0.03	0.01	**-0.37**	0.16	0.09	0.01	**-0.48**
Distance to commercial plantation	-0.27	-0.19	0.06	-0.06	0.00	-0.05	0.16	0.04	-0.15	0.14	-0.14	-0.17	-0.02	0.17
Distance to road	0.10	0.06	0.14	-0.05	-0.14	0.00	0.04	-0.03	0.00	0.16	-0.08	-0.16	0.01	0.08

Slope to settlement	-0.10	-0.06	0.00	0.03	-0.03	-0.01	-0.04	0.01	-0.04	0.17	-0.01	-0.12	0.00	0.00
Slope to commercial plantation	0.03	0.01	-0.06	0.04	-0.03	0.09	0.02	0.03	0.08	-0.10	0.03	0.04	0.00	0.05
Slope	0.01	0.06	0.04	-0.04	0.00	-0.02	0.00	0.01	-0.02	0.13	-0.03	-0.05	0.00	-0.12
Curvature	0.01	-0.01	0.03	-0.04	0.00	-0.01	0.02	0.01	0.01	0.14	-0.02	0.00	0.00	-0.02