UNDERSTANDING AND SAMPLING SPATIAL ECOLOGICAL PROCESS FOR BIODIVERSITY CONSERVATION IN HETEROGENEOUS LANDSCAPES

By

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ABSTRACT

Landscape change and biodiversity decline is a global problem and has sparked world-wide initiatives promoting biological conservation techniques such as reintroductions, protected area networks, and both preservation and restoration of landscape connectivity. Despite the increasing abundance of such working landscapes (i.e. “human-modified” landscapes), we know relatively little about their ecological mechanics; these landscapes can be vast, encompassing areas too large to obtain high resolution ecological data to test ecological process. To investigate the ecological mechanics of working landscapes, I use a small, tractable, landscape mesocosm situated in east-central Alberta, Canada, The Cooking Lake Moraine (a.k.a. the Beaver Hills Biosphere). The chapters within this dissertation quantify biodiversity across a hierarchy of measurements (from genes to communities) and investigate consistencies in ecological processes generating patterns in these biodiversity measurements across spatial scales. As a result, I investigate both a depth, and breadth, of spatial ecological processes underlying the efficacy of biodiversity conservation techniques in heterogeneous working landscapes. In Chapter I, I explore between-landscape functional connectivity by investigating the genetic contribution of reintroduced individuals to an ostensibly successfully reintroduced population within the mesocosm. I find that contemporary animals are the result of recolonization from adjacent sources rather than putative reintroduction founding individuals, indicating greater mesocosm functional connectivity to adjacent landscapes than previously thought. In Chapter II, I probe within-landscape functional connectivity by quantifying the contribution of protected areas, natural, and anthropogenic landscape features to animal movement across the mesocosm. I find that natural features had the largest effect on animal movements, despite the presence of protected areas. Chapter III investigates protected area network efficacy on biodiversity conservation by quantifying the contribution of protected areas, natural, and anthropogenic landscape features to mammalian functional diversity across multiple spatial scales within the mesocosm. I find that protected areas rarely predict functional diversity across spatial scales; instead natural features positively predict functional diversity at small spatial scales while anthropogenic features are negatively associated with biodiversity at large spatial scales. Finally, Chapter IV ties the previous three chapters together by testing implicit assumptions of the species occurrence data collected in each. I compare GPS collar data (Chapter II) to species occurrence data collected on wildlife cameras (Chapter III) to demonstrate that the magnitude of animal movements better predict species occurrence than the commonly assumed proximity of animal space use. Across chapters, two central themes emerge from this dissertation. First, the importance of natural features at small spatial scales, and anthropogenic features at large spatial scales, within the landscape matrix is predominant in predicting multiple measures of biodiversity. And second, we cannot assume predictable efficacy of conservation strategies or even the ecological process inferred from the data collected to test these strategies.

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GENERAL INTRODUCTION

Earth's biodiversity has gone through many changes. From a single source, it has diverged into an incredible variety of forms – and has done so rapidly multiple times in part the result of five big mass extinctions (Courtillot et al. 1996). Today's global decline in biodiversity may represent a sixth mass extinction (Wake et al. 2008; Barnosky et al. 2011), thought to be driven by an abundance of one single species – us, *Homo sapiens sapiens* (Ceballos et al. 2015). Biodiversity patterns provide insight into the processes determining biodiversity declines (Turner et al. 2001), and these processes are still not fully understood. However, observed patterns of biodiversity are dependent on the spatial and temporal scale of measurement (Wiens 1989; Levin 1992; Tscharntke et al. 2012). Strong inference across multiple scales may provide generalizable patterns of processes affecting biodiversity decline.

One cause of contemporary biodiversity decline is rapid human-driven land use change (*i.e.* landscape change; Maxwell et al. 2016). Correlated at large spatial scales to biodiversity declines (Kehoe et al. 2015), land use change results in ecosystem modifications, and an increasing abundance of heterogeneous 'working' landscapes – areas that are considered neither pristine wilderness nor urban centres, and are commonly composed of anthropogenic features intermixed with 'natural' features to produce highly heterogeneous spaces (a.k.a. 'human-modified', 'mixed-use' or 'human-dominated' landscapes; Tscharntke et al. 2012). Such land use change affects where species are (Laliberte & Ripple 2004; Wolf & Ripple 2017; Shackelford et al. 2017). Still, we know relatively little about the spatial ecological processes moderating these biodiversity patterns in increasingly abundant heterogeneous working landscapes (but see Tscharntke et al. 2012), how they change with scale (but see Holling 1991; Levin 1992), and how conservation initiatives play a role in species persistence (Rands et al. 2010).

Global initiatives attempt to conserve biodiversity in a number of ways and are being implemented across taxa at an unprecedented rate. For example, in 2016 alone, the International Union for Conservation of Nature (IUCN) lists 52-ongoing reintroductions of plants, invertebrates, fish, reptiles, birds, and mammals (Soorae 2016). The Convention on Biological Diversity Aichi Target 11 also mandates that countries implement 17% of their terrestrial area as protected by 2020 (CBD 2020) – a deadline which is rapidly approaching – and that these protected areas are functionally connected to mitigate the anticipated effects of climate change (Heller and Zavaletta 2009). However, two problems exist: 1) how conservation initiative efficacy is moderated by ecological process, and changes with biological hierarchies, spatial scales, and landscape heterogeneity is not well understood, and 2) the point-count data collected to test initiative efficacy incorporates implicit assumptions that affect interpretation of ecologic process driving biodiversity patterns. Addressing these problems is complicated by the fact that many of these conservation initiatives are implemented across landscapes too vast to quantify biodiversity, or it's drivers, in multiple resolutions across landscape extents – a requirement for understanding how efficacy changes across spatial scales and biological hierarchies. Using a heterogeneous landscape mesocosm, investigating multiple measures of biodiversity across types of conservation initiatives, and investigating consistencies in ecological process across spatial scales could serve as a prime example for understanding the spatial ecological processes moderating biodiversity patterns in heterogeneous landscapes globally.

The research in this dissertation focuses on inferring spatial ecological process behind observed biodiversity patterns, and the resulting efficacy of conservation initiatives. I utilize an exemplar heterogeneous working landscape of tractable size ensuring high data density across multiple spatial scales, biological hierarchies, and three conservation techniques (reintroduction, protected areas, and connectivity conservation). I quantify the relative effects of natural landscape features, anthropogenic disturbance, and conservation decisions on observed biodiversity. I then infer the ecological processes moderating these observed biodiversity patterns. Together, this work provides strong inference for understanding, and sampling, spatial ecological processes for biodiversity conservation in heterogeneous working landscapes.

The first three chapters within this dissertation each quantify a different metric of biodiversity across a mesocosm working landscape and infer spatial ecological process to the observed biodiversity pattern. The first chapter makes use of a reintroduction as a natural experiment to test functional connectivity of the mesocom landscape to adjacent landscapes by quantifying genetic diversity of contemporary fisher (*Pekania pennanti*). Functional connectivity is a measure of individual movements or geneflow across landscapes (Rudnick et al. 2012) and is a biodiversity conservation concern in the face of both anthropogenic, and climate, change (Hodgson et al. 2009). The second chapter builds off the first chapter by 'scaling-down' and looking at functional connectivity within the mesocosm. It uses individual variation in fisher movements as a measure of connectivity between a network of protected areas. Anthropogenic landscape changes drastically shorten animal movements (Fahrig 2007; Tucker et al. 2018), risk limiting functional connectivity between isolated populations (Fischer & Lindenmayer 2007), and the resulting species persistence on landscapes (Fahrig 2003). This chapter quantifies the natural, anthropogenic, and protected area contributions to within-mesocosm functional connectivity. The third chapter uses species occurrence data from remote wildlife camera traps to quantify the contribution of protected areas to generalized mammalian species diversity. Protected areas as a conservation strategy are promoted globally under the assumption that they facilitate biodiversity protection (CDC 2020; Watson et al. 2014), but the effect of the surrounding landscape can detrimentally influence their efficacy (Leroux & Kerr 2013) . Finally, the fourth chapter addresses implicit assumptions of the data collected in the previous three chapters, and data generally collected in ecological research; species occurrence data collected from stationary points in space. Rarely do researchers explicitly test the assumed relationships between measures derived from species occurrence data, and inferred ecological process, despite this being a prerequisite to accurate data interpretation. I compare fisher detections collected from a wildlife camera trap array (Chapter III) to detailed GPS movement data (Chapter II) to test whether population level patterns in species detections reflect the proximity of animal space-use (i.e. habitat selection or relative abundance) or, variation in magnitude of species movement across the mesocosm (i.e. functional connectivity).

Each chapter explicitly questions assumptions in ecological inference, with tangible ramifications to how biodiversity conservation and ecological research are conducted in future. In each case, strong inference is used to test hypothesized ecological mechanics of the mesocosm compared to alternative possibilities derived from theory. I search for generalizable patterns across multiple spatial scales of inference to draw strong conclusions about landscape function extendable to other heterogeneous working landscapes of various size. I quantify relatable biodiversity measures applicable to other animals and use methods accessible to many conservation practitioners. Together, I quantify and compare the impacts of anthropogenic land use change, relative to conservation techniques and natural landscape features, to elucidate ecological mechanisms consistently moderating biodiversity across the globe's increasingly abundant heterogeneous working landscapes.

Literature Cited

Barnosky AD, et al. 2011. Has the Earth’s sixth mass extinction already arrived? Nature 471(7336): 51.

Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences 114(30): E6089-E6096.

Courtillot V, Gaudemer Y. 1996. Effects of mass extinctions on biodiversity. Nature 381(6578): 146-148.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fahrig L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003–1015. Blackwell Publishing Ltd.

Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a syndissertation. Global ecology and biogeography 16(3):265-280.

Heller NE, Zavaleta ES. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological conservation 142(1):14-32.

Hodgson JA, Thomas CD, Wintle BA, Moilanen A. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46(5):964-969.

Holling CS. 1992. Cross-Scale morphology, geometry, and dynamics of ecosystems. Ecological monographs 62(4):447-502.

Kehoe L, Kuemmerle T, Meyer C, Levers C, Václavík T, Kreft H. 2015. Global patterns of agricultural land use intensity and vertebrate diversity. Diversity and Distributions 21:1308–1318.

Laliberte AS, Ripple WJ. 2004. Range contractions of North American Carnivore and Ungluates. AIBS Bulletin 54:123–138.

Leroux SJ, Kerr JT. 2013. Land Development in and around Protected Areas at the Wilderness Frontier. Conservation Biology 27:166–176.

Levin S. 1992. The Problem of Pattern and Scale in Ecology : Ecology 73:1943–1967.

Maxwell SL, Fuller RA, Brooks TM, Watson J. 2016. The ravages of guns, nets and bulldozers. Nature 536:143–145.

Rands MR et al. 2010. Biodiversity conservation: challenges beyond 2010. Science 329(5997): 1298-1303.

Rudnick DA, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps, C. Gerber LR, Hartter J, Jenness JS, Kintsch J, Merelender AM. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology 13:1–16.

Shackelford N, Standish RJ, Ripple W, Starzomski BM. 2017. Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. Conservation Biology. DOI: 10.1111/cobi.13036

Soorae PS. 2016. Global Re-introduction Perspectives, 2016: Case-studies from Around the Globe. IUCN/SSC Re-introduction Specialist Group & Environment Agency-Abu Dhabi.

Tucker MA, et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359(6374):466-469.

Tscharntke T, et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews 87:661–685.

Wake DB, Vredenburg VT. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences 105(1):11466-11473.

Watson JEM, Dudley N, Segan DB, Hockings M. 2014. The performance and potential of protected areas. Nature 515:67–73.

Wiens J. 1989. Spatial Scaling in Ecology. Functional Ecology 3:385–397.

Wolf C, Ripple WJ. 2017. Range contractions of the world ' s large carnivores. Royal Society Open Science 4:170052.

CHAPTER I

Distinguishing reintroduction from recolonization with genetic testing

Stewart, F.E.C., J.P. Volpe, J.S. Taylor, J. Bowman, P. Thomas, M. Pybus, and J.T. Fisher. 2017. Distinguishing reintroduction from recolonization with genetic testing. Biological Conservation 214:242-249.

Introduction

Reintroduction – the attempt to re-establish a species in part of its indigenous range (Pavlik 1996; IUCN 1998; IUCN/SSC 2013) – remains a popular management method in conservation biology after a century of use (Hayward & Sommers 2009; Seddon et al. 2014). Considerable contemplation is given to reintroductions as a conservation tool across taxa: in 2016, the Species Survival Commission Reintroduction Specialist Group of the International Union for Conservation of Nature (IUCN) highlighted 52 on-going case studies encompassing invertebrates, fish, amphibians, reptiles, birds, mammals, and plants (Soorae 2016). The number of reintroductions being conducted each year is increasing (Seddon et al. 2007), reflecting the conservation community's growing confidence in the strategy compared to other management options. Successful reintroductions are loosely defined as 'establishment of a self-sustaining population' (Seddon 1999; but see Beck et al. 1994; Sarrazin & Barbault 1996) and are most commonly undertaken in North America, Australia, and New Zealand (Fischer & Lindenmayer 2000). Often less empirical examination is given to the real probability for natural recolonization. Many reintroductions are performed in systems perceived to be highly isolated; however, natural recolonization is possible in many areas that demonstrate some form of contemporary, or importantly future, functional connectivity to adjacent populations (Kareiva 1990); that is, the ability for animals, or their genes, to move through the landscape (Rudnick et al. 2012). With both landscape and climate change altering the occurrence and distribution of biodiversity (Maxwell et al. 2016) the possibility of natural recolonization should be prioritized for many mobile species (Rout et al. 2013).

Context about the dynamics of reintroduced populations may be gleaned from the invasion biology literature. Species invasions and reintroductions are characterized by initiation and expansion stages prior to establishment (Shigesada & Kawasaki 1997; Armstrong & Seddon 2007). Invasive (or exotic) species rarely establish following a single introduction (Shigesada & Kawasaki 1997). In reintroductions, the probability of establishment can be greatly increased with planning and depends on a suite of limiting factors such as habitat availability and quality, predation, parasitism, and duration in captivity (Seddon et al. 2014). Invasion biology recognizes the 'Tens Rule' where 10% of introduced species establish and a further 10% of these spread (Jeschke & Strayer 2005). Reintroduction biology recognizes that roughly 20% of reintroductions have been self-described as "successful" (Griffith et al. 1989; Seddon et al. 2014); when compared to the Tens Rule, one might expect this rate may be overestimated and question why more conservation efforts are not being spent on determining the best alternative action.

"Success" is a contested term in reintroduction biology. Definitions vary with project objectives, life history of the species, and the temporal scale of observation (Griffith et al.1989; Beck et al. 1994; Sarrazin & Barbault 1996; Seddon 1999; Haskins 2015; Robert et al. 2015). The IUCN provides guidance (IUCN 1998; IUCN/SSC 2013), however no definition enjoys a consensus. There are no standards for comparison, and specifically no threshold for discriminating the successful establishment of reintroduced individuals from recolonization events (Robert et al. 2015); just because a species is present in a reintroduction location does not equate to a successful reintroduction. We define 'reintroduction success' as an instance where the reintroduced genetic lineage is maintained in the contemporary population. Using this definition, we question whether reintroduction success is as high as the 20% currently documented (Seddon et al. 2014). Do conservation biologists overestimate reintroduction success, and perhaps underestimate the frequency with which species naturally recolonize former ranges? To distinguish between reintroduction and recolonization success, reintroduction events need to be tested using genetic assessments within a critical time limit; too long and the results will be ambiguous due to accumulation of mutations and/or genetic drift (Nei et al. 1975), and too short risks false declaration of success.

As an example of this larger issue for conservation biologists globally (Olding-Smee 2005), we re-assessed a previously deemed "successful" fisher (*Pekania pennanti*) reintroduction to Alberta's Cooking Lake Moraine (CLM; 900km^2; Badry et al. 1997; Proulx & Genereux 2009; Proulx & Dickson 2014). The loss of fisher from 40% of its historic range has stimulated frequent reintroduction attempts, making it an attractive model to investigate the probability of reintroduction versus recolonization success (Lewis et al. 2012; Powell et al. 2012). Between 1990 and 1992, twenty fishers were opportunistically reintroduced to the CLM from Steinbach, Manitoba and Bancroft, Ontario, after being held in captivity at Vegreville, Alberta (1,300 and 3,300 km away, respectfully; Badry 1994; Badry et al. 1997; L. Roy, R. Toews, and J. Bowman pers com.). The CLM is an area where all evidence indicated the fisher was locally extirpated, due to overexploitation and land use change, for a minimum of 50 years (Badry et al. 1997). Fishers have frequently been reported by landowners within the CLM since 2007 (Pybus et al. 2009). The CLM is a forested 'terrestrial island' surrounded by a matrix of unsuitable agricultural habitat; extant fisher are hypothesized to be functionally isolated from adjacent Albertan populations (80-600 km away). The distinct genotypic signatures of Manitoba, Ontario, and native Alberta (Kyle et al. 2001) provide an opportunity to assess the degree of reintroduction vs. recolonization success by comparing alleles between reintroduction source populations, adjacent Albertan populations, and contemporary CLM samples. With an extant population, we test three non-mutually exclusive hypotheses about the outcome of the CLM reintroduction; 1) a successful reintroduction, wherein the genetic signature of one or both source populations (Ontario and Manitoba) is present within contemporary CLM samples, 2) inadvertent reinforcement, wherein an undetected population was occupying the CLM prior to reintroduction as indicated by unique alleles within CLM samples that do not appear in any other sampled population, or 3) natural recolonization, wherein contemporary fisher individuals are most closely related to animals from adjacent Albertan populations, without genetic evidence of Ontario or Manitoba fishers.

Methods

We investigated the ancestry of the contemporary CLM fisher population by comparing microsatellite genotypes to four possible source populations: two adjacent Albertan populations and the two reintroduction source populations (Figure 1.1). We consolidated the most recently collected samples from each population (2000 – 2014). Samples from reintroduction source populations were donated from the original trap-lines sampled in Steinbach, Manitoba (2014 skin; R. Toews pers. com.) and Bancroft, Ontario areas (2000 – 2003 muscle; *sensu* Carr et al. 2007; J. Bowman pers. com). CLM fisher DNA samples were collected from 64 stratified-random, non-invasive baited hair traps (*sensu* Fisher et al. 2011; 2013) in the winters of 2014 and 2016. Fisher populations adjacent to the CLM were sampled *via* muscle samples donated from fur-harvested individuals in Alberta's boreal forest north of Edmonton (2014), and isolated fisher

DNA samples recovered from baited hair traps in Alberta's Willmore Wilderness (Figure 1.1) in the Rocky Mountains (2006 - 2008; Fisher et al. 2011; 2013). All research was performed under the Canadian Council for Animal Care Guidelines (University of Alberta and University of Victoria permit #AUP00000518).

We extracted DNA from samples using the QIAGEN DNeasy Blood & Tissue Kit® and protocol (Hilden, Germany). We excluded hair samples that did not contain at least 1 guard hair root or 5 underfur hairs. Muscle and skin samples comprised a ~3 mm^3 clipping. Samples that produced weak or no amplification were analyzed a second time for confirmation, after which we culled 22.8 % (87/381) of samples that failed on both attempts. A set of 15-microsatellite loci was used to identify individuals and quantify genetic differentiation among individuals. Primers were developed by Duffy et al. 1998 (*Ggu101* and *Ggu216* in wolverine), Dallas & Piertney 1998 (*Lut604* in Eurasian otters), Davis & Strobeck 1998 (*Ma-1*, *Ma-2* and *Ma-19* in American marten, and *Ggu7* in wolverine), Jordan et al. 2007 (*MP144*, *MP182*, *MP055*, *MP114*, *MP175*, *MP227* and *MP247* in fisher), and Fleming et al. 1999 (*Mvis72* in mink and ermine). PCR reactions were performed in a volume of 15 µL containing 50 mM KCl, 160 µM dNTPs, and 0.1 % Triton X-100, with primers and *Taq* polymerase optimized to permit co-amplification (Paetkau et al. 1998). PCR thermal cycling ran in a Perkin Elmer 9600 with an initial denaturing step of 94°C for 1:20 min, 40 cycles of annealing and extension following 94°C for 20 s, 54°C for 25 s, and 72°C for 10 s, followed by 1:05 min at 72°C. Microsatellite error-checking followed Paetkau (2003) published protocol of reanalyzing mismatching markers in pairs of genotypes that are very similar.

We used three statistical methods to determine the most probable ancestry of contemporary CLM genotypes. First, we compared genetic differentiation between groups using

F_{ST} (Wright 1943), the probability of identity by descent based on allele frequency variation. F_{ST} values range from 0-1, with probability of identity by descent increasing as the value approaches zero. We determined F_{ST}, and whether these values were significantly different than zero, in the *diveRsity* package (Keenan et al. 2013) in R (R Foundation for Statistical Computing 2016). We determined the most probable grouping of samples by genotype-based relationships by qualitatively observing whether sample locations clustered on a biplot with a PCA (Genetix; Belkhir et al. 2004), and quantitatively using MCMC maximum likelihood clustering algorithm (Structure; Hubisz et al. 2009) as well as an assignment test (Geneclass2; Piry et al. 2004). Finally, allele occurrences across sampled populations were screened for any CLM alleles diagnostic of reintroduction or recolonization (Table 1).

Results

Both PCA and MCMC identified three distinct provincial clusters (Alberta, Ontario and Manitoba; Figure AI.1, Figure 1.2). Neither method suggested CLM samples were genetically isolated from Northern Alberta or Willmore Wilderness samples. Study areas contained 40 individuals from the CLM, 19 from Willmore Wilderness, 34 from Northern Alberta, 29 from Ontario, and 25 from Manitoba (Table A1.1). Genetic mark-recapture modeling demonstrates that CLM samples represent 47% of the contemporary estimated population (J. Burgar, unpublished data). Within Alberta, F_{ST} was 0.04 between the Willmore Wilderness and the other two study areas, and just 0.02 (marginally greater than zero) between northern Alberta and the CLM. The highest F_{ST} when comparing Alberta samples to other provinces was between Ontario and the Willmore Wilderness ($F_{ST} = 0.14$; Table A1.2).

Only 2 of 109 alleles (173 at *Ma*-2, and 136 at *Lut604*) were indicative of reintroduction success; they were found only in the CLM, Ontario, and Manitoba populations. These alleles occurred in few animals in the CLM but are common in Ontario samples, and are only one mutational step away from Albertan alleles (Table 1.1). We tested individual origins using the software Geneclass2 (Piry et al. 2004); no CLM individual showed a statistically meaningful departure from expectation for pure Alberta ancestry (lowest p-value = 0.05 which is not significant after correcting for small sample sizes). There were no alleles unique to the CLM, indicating that inadvertent reinforcement is unlikely. Together, these results provide strong support for recolonization of the CLM from northern Alberta and Willmore Wilderness areas rather than successful reintroduction of founder individuals from Ontario or Manitoba.

Discussion

All individuals used in the 1990s CLM fisher reintroduction experiments had experienced months or years of captivity prior to re-introduction, and few individuals remained close to release locations months after reintroduction (Badry 1994). Here we show evidence that fishers sampled from the Cooking Lake Moraine (CLM) were not derived from the individuals reintroduced from Ontario and Manitoba in the 1990s. Instead it appears that recolonization by Albertan fishers is responsible for the current CLM population. This observation is not uncommon; our review of all fisher reintroductions demonstrated that 47% have been given a different reintroduction status once genetic testing for reintroduction success was performed (Table 1.2).

Cryptic recolonization has been observed in other commonly reintroduced mammals. In a similar example, Kruckenhauser and Pinsker (2004) reviewed multiple Alpine Marmot

(*Marmota marmota*) reintroductions and demonstrated that three contemporary Austrian populations are more closely related to neighboring Austrian populations than putative founders from France. Hicks et al. (2007) concluded that dispersal is much higher in Elk (*Cervus elaphus*) than previously believed because of the astoundingly high genetic diversity within, and low genetic divergence between, western North America's reintroduced populations. Statham et al. (2012) document the unanticipated continental recolonization of native Red Fox (*Vulpes vulpes*) compared to the perceived reintroduction success from European sources. Such examples highlight two important considerations: 1) that many reintroductions are sub-optimal conservation strategies when compared to the ability of species to naturally recolonize historic ranges, and 2) that re-introductions may provide a catalyst for socially facilitated recolonization (Parker et al. 2007). In either case, promoting functional connectivity may be a more effective conservation goal.

Caveats

Within CLM samples, there were two alleles also found among eastern fishers but not among any other fishers from Alberta (Table 1.1). We suspect these CLM alleles are the products of independent mutations and are not identical by descent to the Ontario alleles, as they are only one mutational step away from other Albertan alleles; each allele may have been the result of a single microsatellite mutation (Waits & Paetkau 2005). Longer microsatellites mutate more frequently and rates can vary from 10^{-3} to 10^{-4} per locus per generation (Ellegren 2000). Ideally, genetic samples should be collected at multiple time points from reintroduction, source, and adjacent populations to document drift.

Post translocation genetic data does not distinguish the exact date, route, or mechanism by which individuals disperse and recolonize former ranges. Our genetic analysis has reduced the possibility of reintroduction success from eastern populations, yet a contemporary CLM population still exists. As in any cryptic recolonization event close to human habitation, there are two possible mechanisms to explain contemporary species occurrence: 1) "paw-power" reflecting multiple routes of natural dispersal, and 2) "horse-power" reflecting unknown (and unsanctioned) translocation. Our genetic analyses found eight of 109 alleles diagnostic of recolonization from northern Alberta and Willmore Wilderness, across 15 loci. We find it unlikely two of these alleles (*MP182* 175 and *Mvis72* 258) are explained by independent mutations because they do not conform to the loci's microsatellite allele sequence (Table 1.1). Fishers use areas of high forest cover compared to what is available (Badry 1994; Koen et al. 2007; LaPoint et al. 2013; Koen et al. 2014). Dispersal may happen through unsuitable habitat if distances are small and within a home territory (LaPoint et al. 2013); average dispersal distances are typically less than 30 km for either sex (6 – 29 km; Aubry and Raley 2006; Lofroth et al. 2010). However, mustelids can demonstrate amazing feats of dispersal (Carr et al. 2007; Moriarty et al. 2009). We cannot reliably distinguish between "paw-power" and "horse-power" mechanisms of provincial recolonization, but instead demonstrate that recolonization may be an important aspect of range stability. This conclusion suggests that maintaining and enhancing connectivity (and thus opportunities for natural recolonization) may in many cases be a better use of conservation resources than reintroductions.

Broad conservation implications

If cryptic recolonization is misinterpreted as reintroduction success, it implies that our concept of functional connectivity may be flawed. Functional connectivity is a species-specific concept, and describes how genes, individuals, or populations move through a landscape (Goodwin 2003; Garroway et al. 2008; Luque et al. 2012; Rudnick et al. 2012). However, if individuals are recolonizing areas that were previously perceived to be functionally disjunct from the rest of the species range, then individuals may be attracted to an anchoring site and move through landscape features more readily than predicted. We therefore recommend conservation biologists attempt to estimate the ability of species to recolonize former ranges by genetically testing past re-introductions, modeling habitat connectivity liberally, and not underestimating the dispersal ability of the study species. There may be situations where connectivity is detrimental to establishing populations (i.e. promoting connectivity with competitor or predator populations). However, if reintroductions are performed, and there is even a small chance of natural recolonization, we recommend investing, and tracking, the time and money into non-invasively sampling the genetic signatures of both reintroduced individuals and proximal populations across a series of time intervals. These genetic measurements inform landscape resistance modeling (Cushman et al. 2006; McRae et al. 2008; Rudnick et al. 2012; Zeller et al. 2012; Koen et al. 2014; 2016; Elliot et al. 2014), translocation evaluation (Bowman et al. 2016) including the need for assisted colonization in response to climate change (Rout et al. 2013), and provide a financial evaluation of performing reintroductions. Broadly, such emerging applications in landscape genetics and wildlife management have applicable ramifications on future biodiversity through corridor and conservation area planning (Spear et al. 2005; Balkenhol et al. 2009; Schwartz et al. 2010). The accurate quantification and perception of functional connectivity, which can be empirically documented through recolonization events, is paramount for decision making and implementing the best conservation management techniques.

Our results from the CLM fisher reintroduction (Table 1.1), fisher reintroduction genetics in general (Table 1.2), and a sample of mammalian reintroduction events from the literature demonstrate the importance of employing genetic data for comparing reintroductions and recolonizations as optimal conservation strategies. We recommend that given the large amount of money, political capital, public buy-in, and hard work invested in reintroductions – in addition to the great conservation importance of their outcomes – that if recolonization is even minutely probable, reintroduction be treated as a conservation experiment with genetic samples obtained and analyzed from all animals, non-invasive samples obtained from proximal and source populations, and results published that generate and disseminate an objective conclusion about reintroduction vs. recolonization success. Documenting the relative success of reintroductions and recolonizations across varying degrees of functional connectivity helps conservation biologists understand the efficacy of these conservation tools and quantify the potential of reintroductions providing a catalyst for socially facilitated recolonization, thereby saving valuable future conservation funds. Alternative conservation approaches – such as landscape management to facilitate functional connectivity – must be better assessed for long-term conservation and may fix some of the very problems that led to extirpation in the first place

Literature cited

Anderson B. 2002. Reintroduction of fishers (Martes pennanti) to the Catoosa Wildlife Area in Tennessee. Tennessee Wildlife Resources Agency, Crossville, Tennessee.

Armstrong DP, Seddon PJ. 2007. Directions in reintroduction biology. Trends in Ecology and Evolution **23**:20–25.

Aubry KB, Lewis JC. 2003. Extirpation and reintroduction of fishers (Martes pennanti) in Oregon: implications for their conservation in the Pacific states. Biological Conservation **114**:79–90.

Aubry KB, Raley CM. 2006. Ecological characteristics of fishers (Martes pennanti) in the sourthern Oregon Cascade range. USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA.

Badry MJ, Proulx G, Woodard PM. 1997. Home-range and habitat use by fishers translocated to the aspen parkland of Alberta. Pages 233–251 in G. Proulx, HN Bryant, and PM Woodard, editors. Martes: taxonomy, ecology, techniques and management.

Badry MJ, 1994. Habitat use by fishers (*Martes pennanti*) in the aspen parkland of Alberta. MSc dissertation. University of Alberta.

Baird R, Frey S. 2000. Riding Mountain National Park fisher reintroduction program 1994–1995. Riding Mountain National Park, Manitoba.

Balkenhol N, Gugerli F, Cushman SA, Waits LP, Coulon A, Arntzen JW, Holdregger R, Wagner HH. 2009. Identifying future research needs in landscape genetics: Where to from here? Landscape Ecology **24**:455–463.

Beck BB, Rapaport LG, Price MRS, Wilson AC. 1994. Reintroduction of captive-born animals *in* Creative Conservation (Olney, PJS, Mace GM, Feistner ATC, eds), pp.265 286, Chapman & Hall.

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F. 2004. GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France).

Benson DA. 1959. The fisher in Nova Scotia. Journal of Mammalogy **40**(3): 451-451.

Berg WE. 1982. Reintroduction of fisher, pine marten and river otter. Pg 159–175 in Sanderson GC, ed. Midwest furbearer management, North Central Section of The Wildlife Society, Bloomington, Illinois.

Bowman J, Greenhorn JE, Marrotte RM, McKay MM, Morris KY, Prentice MB, Wehtje M. 2016. On applications of landscape genetics. Conservation Genetics: 1-8.

Bradle BJ. 1957. The fisher returns to Wisconsin. Wisconsin Conservation Bulletin **22**(11): 9–11.

Brander RB, Books DJ. 1973. Return of the Fisher. Natural History **82(1)**: 52–57.

Carr D, Bowman J, Kyle C, Tully S, Koen EL, Robitaille J, Wilson P. 2007. Rapid Homogenization of Multiple Sources: Genetic Structure of a Recolonizing Population of Fishers. Journal of Wildlife Management **71**:1853–1861.

Cushman SA, McKelvey KS, Hayden J, Schwartz MK. 2006. Gene fow in complex landscapes: testing multiple hypotheses with Causal modeling. American Naturalist. **168**:1–14.

Dallas JF, Piertney SB. 1998. Microsatellite primers for the Eurasian otter. Molecular Ecology **7**:1248–1251.

Davie J. 1984. Fisher reintroduction project completion report. Alberta Forest, Lands, and Wildlife, Edmonton. 10p.

Davis CS, Strobeck C. 1998. Isolation , variability , and cross-species amplification of polymorphic microsatellite loci in the family Mustelidae. Molecular Ecology **7**:1776–1778.

Dilworth TG. 1974. Status and distribution of fisher and marten in New Brunswick. Canadian Field-Naturalist **88**(1):495–498.

Dodds DG, Martell AM. 1971. The recent status of the fisher, Martes pennanti (Erxleben), in Nova Scotia. Canadian Field-Naturalist **85**(1):62–65.

Dodge WE. 1977. Status of the fisher (Martes pennanti) in the conterminous United States. Unpublished report submitted to US Dept. of the Interior. On file with JC Lewis.

Drew RE, Hallett JG, Aubry KB, Cullings KW, Koepfs SM, Zielinski WJ. 2003. Conservation genetics of the fisher based on mitochondrial DNA sequencing. Molecular Ecology **12**:51-52.

Duffy AJ, Landa A, O'Connell M, Stratton C, Wright JM. 1998. Four polymorphic microsatellites in wolverine, *Gulo gulo*. Animal Genetics **29**:63–72.

Ellegren H. 2000. Microsatellite mutations in the germline: Implications for evolutionary inference. Trends in Genetics **16**:551–558.

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ. 2014. The devil is in the dispersers: Predictions of landscape connectivity change with demography. Journal of Applied Ecology **51**:1169–1178.

Fischer J, Lindenmayer DB. 2000. An assessment of the published results of animal relocations. Biological Conservation **96**:1–11.

Fisher JT, Anholt B, Volpe JP. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecology and Evolution **1**:517–528.

Fisher JT, Bradbury S, Anholt B, Nolan L, Roy L, Volpe JP, Wheatley M. 2013. Wolverines (Gulo gulo luscus) on the Rocky Mountain slopes: natural heterogeneity and landscape alteration as predictors of distribution. Canadian Journal of Zoology **91**:706–716.

Fleming MA, Ostrander EA, Cook JA. 1999. Microsatellite markers for American mink (Mustela vison) and ermine (Mustela erminea). Molecular Ecology **8**:1352–1354.

Fontana AJ, Teske IE. 2000. East Kootenay fisher reintroduction program. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk **24**:693–694.

Garroway CJ, Bowman J, Carr D, Wilson PJ. 2008. Applications of graph theory to landscape genetics. Evolutionary Applications **1**(4):620-630.

Goodwin BJ. 2003. Is landscape connectivity a dependent or independent variable? Landscape Ecology **18**:687–699.

Griffith B, Scott JM, Carpenter JW, Reed C. 1989. Translocation as a species conservation tool: status and strategy. Science (New York, N.Y.) **245**:477–480.

Hapeman P, Latch EK, Fike JA, Rhodes EO, and Kilpatrick CW. 2011. Landscape Genetics of Fishers (Martes pennanti) in the Northeast: Dispersal Barriers and Historical Influences. Journal of Heredity **102**:251–259.

Haskins KE. 2015. Alternative perspectives on reintroduction success. Animal Conservation **18**:409–410.

Hayward MW, Somers MJ. 2009. Reintroduction of Top-Order Predators. John Wiley & Sons. Oxford, UK.

Heinemeyer KS. 1993. Temporal Dynamics in the Movements, Habitat Use, Activity, and Spacing of Reintroduced Fishers in Northwestern Montana. MSc Dissertation. University of Montana.

Hicks JF, Rachlow JL, Rhodes OE, Williams CL, Waits LP. 2007. Reintroduction and genetic structure: Rocky Mountain elk in Yellowstone and the western states. Journal of Mammalogy, **88**(1), 129-138.

Hubisz MJ, Falush D, Stephens M, Pritchard JK. 2009. Inferring weak population structure with the assistance of sample group information. Molecular Ecology Resources **9**:1322–1332.

IUCN. 1998. Guidelines for Reintroductions. Prepared by the IUCN/SSC Reintroduction Specialist Group. IUCN http://www. iucnsscrsg.org/ (accessed 5 July 2016)

IUCN/SSC. 2013. Guidelines for reintroductions and other conservation translocations. Version 1.0. Gland, Switzerland. Available from http://www.issg.org/pdf/publications/RSG_ISSG-Reintroduction-Guidelines-2013.pdf (accessed 5 July 2016).

Irvine GW, Magnus LT, Bradle BJ. 1964. The restocking of fishers in lake state forests. Transactions of the North American Wildlife and Natural Resources Conference **29**:307–315.

Jeschke JM, Strayer DL. 2005. Invasion success of vertebrates in Europe and North America. Proceeding of The National Academy of Sciences **102**(20):7198-7202.

Jordan MJ, Higley JM, Matthews SM, Rhodes OE, Schwartz MK, Barrett RH, Palsbøll PJ. 2007. Development of 22 new microsatellite loci for fishers (Martes pennanti) with variability results from across their range. Molecular Ecology Notes **7**:797-801.

Kareiva P, Mullen A, Southwood R. 1990. Population dynamics in spatially complex environments: theory and data [and discussion]. Philosophical Transactions of the Royal Society B: Biological Sciences **330**(1257):175-190.

Kebbe CE. 1961a. Return of the fisher. Oregon State Game Commission Bulletin **16**:3-7.

Kebbe CE. 1961b. Transplanting fisher. Western Association of State Game and Fish Commissioners **41**:165–167.

Keenan K, McGinnity P, Cross TF, Crozier WW, Prodöhl PA. 2013. diveRsity: An R package for the estimation of population genetics parameters and their associated errors, Methods in Ecology and Evolution **4**(8):782-788.

Koen EL, Bowman J, Findlay C, Zheng L. 2007. Home Range and Population Density of Fishers in Eastern Ontario. Journal of Wildlife Management **71**:1484–1493.

Koen EL, Bowman J, Sadowski C, Walpole AA. 2014. Landscape connectivity for wildlife: Development and validation of multispecies linkage maps. Methods in Ecology and Evolution **5**:626–633.

Kohn BE, Payne NF, Ashbrenner JE, Creed WE. 1993. The fisher in Wisconsin. Wisconsin Department Natural Resources, Technical Bulletin No. 183.

Kruckenhauser L, Pinsker W. 2004. Microsatellite variation in autochthonous and introduced populations of the Alpine marmot (Marmota marmota) along a European west–east transect. Journal of Zoological Systematics and Evolutionary Research **42**(1), 19-26.

Kyle CJ, Robitaille JF, Strobeck C. 2001. Genetic variation and structure of fisher populations across North America. Molecular Ecology **10**:2341 – 2347.

LaPoint S, Gallery P, Wikelski M, Kays R. 2013. Animal behavior, cost-based corridor models, and real corridors. Landscape Ecology **28**:1615–1630.

Lewis JC. 2014. Post-release movements, survival, and resource selection of fishers (Pekania pennanti) translocated to the Olympic Peninsula of Washington. PhD dissertation. University of Washington.

Lewis JC, Powell R, Zielinski W. 2012. Carnivore Translocations and Conservation: Insights from Population Models and Field Data for Fishers (Martes pennanti). PLoS ONE **7**:e32726.

Lofroth EC, Raley CM, Higley JM, Truex RL, Yaeger JS, Lewis JC, Finley LL, Naney RH, Hale LJ, Krause AL. 2010. Conservation of Fishers (Martes pennanti) in South-Central British Columbia, Western Washington, Western Oregon, and California. USDI Bureau of Land Magement, Dever, Colorado, USA.

Luque S, Saura S, Fortin MJ. 2012. Landscape connectivity analysis for conservation: insights from combining new methods with ecological and genetic data. Landscape Ecology **27**:153–157.

Maxwell SL, Fuller RA, Brooks TM, Watson JE. 2016. Biodiversity: The ravages of guns, nets and bulldozers. Nature **536**(7615):143-145.

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology **89**:2712–2724.

Moriarty KM, Zielinski WJ, Gonzales AG, Dawson G, Boatner TE, Wilson KM, Schlexer FV, Pilgrim KL, Copeland JP, Schwartz MK. 2009. Wolverine confirmation in California after nearly a century: native or long-distnae immigrant? Northwest Science **83**(2):154-162.

Nei M, Maruyama T, Chakraborty R. 1975. The Bottleneck Effect and Genetic Variability in Populations. Evolution **29**:1–10.

Olding-Smee O. 2005. Dollars and Sense. Nature **437**:614–616.

Paetkau D, Shields GF, Strobeck C. 1998. Gene flow between insular , coastal and interior populations of brown bears in Alaska. Molecular Ecology **7**:1283–1292.

Paetkau D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology **12**(6):1375-1387.

Parker MW, Kress SW, Golightly R., Carter HR, Parsons EB, Schubel SE, Boyce JA, McChesney GJ, Wisely SM. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. Waterbirds **30**(1):17-28.

Pavlik BM. 1996. Defining and measuring success. In Restoring diversity, strategies for reintroduction of endangered plants: 127–155. Falk, D.A., Millar, C.I. & Olwell, M. (Eds). Covelo: Island Press.

Petersen LR, Martin MA, Pils CM. 1977. Status of fishers in Wisconsin. Wisconsin Department Natural Resources Report **92**: 1–14.

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity **95**:536–539.

Powell RA, Lewis JC, Slough BG, Brainerd SM, Jordan NR, Abramov AV, Monakhov V, Zollner PA, Murakami T. 2012. Evaluating translocations of martens, sables, and fishers: testing model predictions with field data in *Biology and conservation of martens, sables, and fishers: a new syndissertation* (KB Aubry, WJ Zielinski, MG Raphael, G. Proulx, and SW Buskirk, eds.). Cornell University Press, New York Pg 93-137.

Proulx G, and Dickson HL. 2014. Occurrence and Distribution of Fishers in the Central Aspen Parklands of Alberta. Canadian Wildlife Biology and Management **3**:15–21.

Proulx G, Genereux B. 2009. Persistence of a reintroduced Fisher, Martes pennanti, Population in Cooking Lake-Blackfoot provincial recreation area, Central Alberta. Canadian Field Naturalist **123**:178–179.

Pybus M, Lawrence G, Harris P. 2009. Fisher on the Cooking Lake Moraine, Alberta : Landowner Observations. NatureAlberta. pg 22–28.

R Foundation for Statistical Computing. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rego PW. 1989. Wildlife investigation: fisher reintroduction, 10/1/88-9/30/ 89. Project number W-49-R-14 performance report. Connecticut Department of Environmental Protection, Wildlife Division, Burlington. 7 p.

Rego PW. 1990. Wildlife investigation: fisher reintroduction, 10/1/89-9/30/ 90. Project number W-49-R-15 performance report. Connecticut Department of Environmental Protection, Wildlife Division, Burlington. 6 p.

Rego PW. 1991. Wildlife investigation: fisher reintroduction, 10/1/90-9/30/ 91. Project number W-49-R-16 performance report. Connecticut Department of Environmental Protection, Wildlife Division, Burlington. 3 p

Robert A, Colas B, Guigon I, Kerbiriou C, Mihoub JB, Saint-Jalme M, Sarrazin F. 2015. Defining reintroduction success using IUCN criteria for threatened species: A demographic assessment. Animal Conservation **18**:397–406.

Rosenberg NA, Burke T, Elo K, Feldman MW, Freidlin PJ, Groenen MA, Hillel J, Mäki Tanila A, Tixier-Boichard M, Vignal A, Wimmers K. 2001. Empirical evaluation of genetic clustering methods using multilocus genotypes from 20 chicken breeds. Genetics **159**(2): 699-713.

Rout TM, McDonald-Madden E, Martin TG, Mitchell NJ, Possingham HP, Armstrong DP. 2013. How to decide whether to move species threatened by climate change. PloS one **8**(10):p.e75814.

Roy KD. 1991. Ecology of reintroduced fishers in the Cabinet Mountains of northwest Montana. Dissertation, University of Montana, Missoula, Montana, USA

Rudnick DA, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps, C. Gerber LR, Hartter J, Jenness JS, Kintsch J, Merelender AM. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology **13**:1–16.

Sarrazin F, Barbault R. 1996. Reintroduction: Challenges and lessons for basic ecology. Trends in Ecology and Evolution **11**:474–478.

Schwartz M, Luikart G, McKelvey K, Cushman S. 2010. Landscape genomics: a brief perspective. Pages 193–221Spatial Complexity, Informatics, and Wildlife Conservation.

Seddon PJ. 1999. Persistence without intervention: Assessing success in wildlife reintroductions. Trends in Ecology and Evolution **14**:503.

Seddon PJ, Armstrong DP, Maloney RF. 2007. Developing the science of reintroduction biology. Conservation Biology **21**:303–312.

Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP. 2014. Reversing defaunation: Restoring species in a changing world. Science **345**:406–411.

Serfass TL, Brooks RP, Tzilkowski WM. 2001. Fisher reintroduction in Pennsylvania: Final report of the Pennsylvania fisher reintroduction project. Frostburg State University, Frostburg, Maryland.

Shigesada N, Kawasaki K. 1997. Biological Invasions: theory and practice. Invasions of alien species 2.1 Mammals. Pg 6-25

Soorae PS. 2016. Global Reintroduction Perspectives: 2016. Case-studies from around the globe. Gland, Switzerland: IUCN/SSC Reintroduction Specialist Group and Abu Dhabi, UAE: Environment Agency Abu Dhabi.

Spear SF, Peterson CR, Matocq MD, Storfer A. 2005. Landscape genetics of the blotched tiger salamander (Ambystoma tigrinum melanostictum). Molecular Ecology **14**:2553–2564.

Statham MJ, Sacks BN, Aubry KB, Perrine JD, Wisely SM. 2012. The origin of recently established red fox populations in the United States: translocations or natural range expansions? Journal of Mammalogy **93**(1): 52-65.

Vinkey R, Schwartz M, McKelvey K, Foresman K, Pilgrim K, Giddings B, LoFroth EC. 2006. When reintroductions are augmentations: the genetic legacy of fishers in montana. Journal of Mammalogy **87**(2):265-271.

Waits LP, Paetkau D. 2005. Noninvasive genetic sampling tools for wildlife biologists: A review of applications and recommendations for accurate data collection. Journal of Wildlife Management **69**(4):1419-1433.

Wallace K, Henry R. 1985. Return of a Catskill native. The Conservationist **40**: 17–19.

Weir RD. 2003. Status of the fisher in British Columbia. BC Ministry of Water, Land and Air Protection.

Williams RN, Rhodes OE, Serfass TL. 2000. Assessment of Genetic Variance Among Source and Reintroduced Fisher Populations. Journal of Mammalogy **81**:895–907.

Wright S. 1943. Isolation by Distance. Genetics **28**:114–138.

Zeller KA, McGarigal K, and Whiteley AR. 2012. Estimating landscape resistance to movement: A review. Landscape Ecology **27**:777–797

Tables and Figures

Table 1.1 Allele presence indicates support for population similarity and mechanism of contemporary fisher occurrence on Alberta's Cooking Lake Moraine. Allele similarities between populations are indicators of reintroduction versus recolonization success. However, alleles that adhere to the microsatellite allele sequence could be the result of a mutation rather than diagnostic of recolonization or reintroduction. Alleles indicating potential mutations are underlined, while alleles diagnostic of either reintroduction or recolonization are bolded.

	Microsatellite	**Diagnostic allele**	**CLM* (n = 40)**	**WW* (n = 19)**	**NA* (n = 34)**	**ON* (n = 29)**	**MB* (n = 25)**	**Microsatellite allele sequence**
REINTRODUCTION	Ma-2	173	1	-	-	14(3)	3	155, 167, 169, 171, 173, 175, 177, 179
	Lut604	136	3	-	-	9(1)	5	120, 122, 126, 128, 130, 132, 134, 136
RECOLONIZATION	Ggu216	152	2	4	4	-	-	152, 154, 158, 160, 162, 164, 166, 168, 170, 172
	MP144	199	20(3)	2	12(2)	-	-	167, 175, 179, 183, 187, 191, 195, 199, 203, 207
	MP175	179	4	-	3	-	-	151, 155, 159, 163, 167, 171, 175, 179
	MP182	175	17(1)	2	16(4)	-	-	166, **175**, 183, 187, 191, 195, 199, 203, 207
		203	1	-	1	-	-	

	207	1	-	2	-	-	
MP247	126	7	3(1)	16(3)	-	-	122, 126, 130, 134, 138, 142, 146
Mvis72	258	10	-	2	-	-	**258**, 274, 276, 278, 280, 282, 284

*CLM = Cooking Lake Moraine, WW = Willmore Wilderness in Alberta's Rocky Mountains, NA = Northern Alberta, ON = Ontario, MB = Manitoba. Units of measurement are the number of individuals sampled within each population. Numbers in brackets represent the number of homozygote individuals.

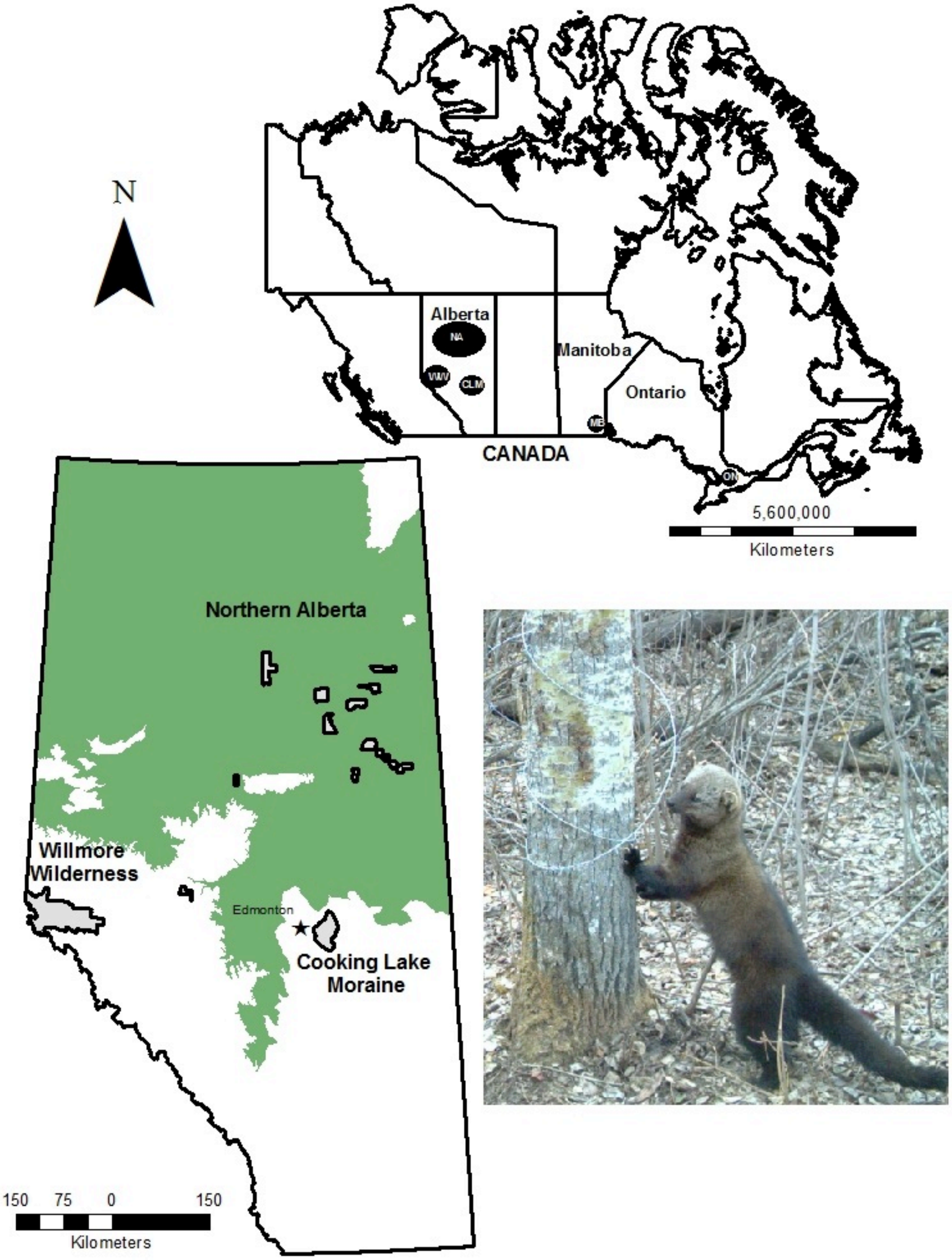
Table 1.2 Implication of genetic work on the status of fisher reintroduction success. Opportunistic genetic sampling provides the ability to re-assess reintroduction success of fisher populations[a]. A status being maintained (Y) demonstrates the genetic results support the original status of the reintroduction. Many genetic tests demonstrate either doubtful (N), or ambiguous (U), contribution of reintroduced individuals to the contemporary genetic population[b].

Release location	**Source location**	**Years**	**Status[a]**	**Genetic reference**	**Genetic method**	**Years after release**	**Status maintained[b]**	**Original References**
Nova scotia	Ranch	1947-1948	S	(Kyle et al. 2001)	microsats	53	Y	(Benson 1959; Dodds 1971)
Wisconsin	New York Minnesota	1956-1963	S	(Williams et al. 2000)	allozymes	37	U	(Irvine et al. 1964; Bradle 1957; Petersen et al. 1977; Kohn et al. 1993; Dodge 1977)
Ontario	Ontario	1956	U	N	na	na	na	(Berg 1982)
Ontario	Ontario (Parry Sound)	1956-1963	S	(Carr et al. 2007)	microsats	44	U	(Berg 1982)
Vermont	Maine	1959-1967	S	(Williams et al. 2000; Hapeman et al. 2011)	allozymes; microsats	33; 44	Y	(Berg 1982)
Oregon	British Columbia	1961	F	(Aubry & Lewis 2003)	microsats; mtDNA	22	Y	(Kebbe 1961a &b)
Michigan	Minnesota	1966-1968	S	N	na	na	na	(Brander & Brooks 1973; Irvine et al. 1964)
Nova Scotia	Maine	1963-1966	S	(Kyle et al. 2001)	microsats	35	Y	(Dodds & Martel 1971)
Wisconsin	Minnesota	1966-1967	S	(Williams et al. 2000)	allozymes	33	U	(Petersen et al. 1977; Kohn et al. 1993; Dodge 1977)
New Brunswick	New Brunswick	1966-1968	S	(Drew et al. 2003)	mtDNA	35	U	(Dilworth 1974; Lewis et al. 2012)
West Virginia	New Hampshire	1969	S	(Williams et al. 2000; Drew et al. 2003)	allozymes; mtDNA	31 35	U Y	(Berg 1982; Lewis et al. 2012)
Minnesota	Minnesota	1968	F	N	na	na	na	(Berg 1982; Lewis et al. 2012)
Maine	Maine	1972	U	(Drew et al. 2003; Hapeman et al. 2011)	mtDNA; microsats	39; 31	Y	(Lewis et al. 2012)
Manitoba	Manitoba	1972	F	N	na	na	na	(Berg 1982; Lewis et al. 2012)
New York	New York	1976-1979	S	(Hapeman et al. 2011)	microsats	32	Y	(Wallace & Henry 1985; Lewis et al. 2012)
Oregon	British Columbia Minnesota	1977-1981	S	(Drew et al. 2003; Aubry & Lewis 2003)	mtDNA; microsats	28; 28	Y	(Lewis et al. 2012)
Ontario	Ontario (Manitoulin Is)	1979-1981	S	(Carr et al. 2007)	microsats	26	Y	(Kyle et al. 2001; Lewis et al. 2012)

Ontario	Ontario (Bruce Peninsula)	1979-1981	S	(Carr et al. 2007)	microstats	27	U	(Kyle et al. 2001; Lewis et al. 2012)
Alberta	Alberta	1981-1983	F	N	na	na	Y	(Davie 1984)
Montana	Minnesota Wisconsin	1988-1991	S	(Drew et al. 2003; Vinkey et al. 2006)	mtDNA	12	N	(Roy 1991; Heinemeyer 1993)
Michigan	Michigan	1988-1992	S	N	na	na	na	(Lewis et al. 2012)
Connecticut	New Hampshire Vermont	1989-1990	S	(Williams et al. 2000; Hapeman et al. 2011)	allozyme; microsats	10; 21	Y	(Rego 1989; 1990; 1991; Lewis et al. 2012)
Alberta	*Ontario* *Manitoba*	*1990-1992*	*S*	*Stewart et al.*	*microsats*	*24*	*N*	(Badry et al. 1997b; Kyle et al. 2001; Proulx & Dickson 2014)
Manitoba	Manitoba	1994-1995	S	N	na	na	na	(Baird and Frey 2000)
Pennsylvania	New York New Hampshire	1994-1998	S	N	na	na	na	(Serfass et al. 2001)
British Columbia	British Columbia	1996-1998	F	N	na	na	na	(Fontana & Teske 2000; Weir 2003)
Tennessee	Wisconsin	2001-2003	S	N	na	na	na	(Anderson 2002)
Washington	British Columbia	2008-2011	S	N	na	na	na	(Lewis et al. 2014)
California	California	2009-2012	S	N	na	na	na	(Lewis et al. 2012)
Washington	British Columbia	2015-present	O	N	na	na	na	(J. Lewis pers. comm.)

[a] S = successful re-introduction, F = failed re-introduction, O = ongoing re-introduction,

[b] N = Status not maintained after genetic re-assessment, Y = Status maintained after genetic assessment, U = Unknown status after genetic assessment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CANADA
5,600,000
Kilometers
Northern Alberta
Willmore
Wilderness
Edmonton
Cooking Lake
Moraine
150 75 0 150
Kilometers

Figure 1.1 Fisher DNA samples were collected from 64 sample sites across Alberta's Cooking Lake Moraine (CLM) and compared to four candidate source populations; two adjacent populations in Alberta (Willmore Wilderness in the Rocky Mountains and scattered trap lines throughout northern Alberta) and reintroduction source populations (Manitoba and Ontario) to assess the success of a 1990/1992 fisher reintroduction. Alberta's boreal forest is highlighted in green and a fisher is depicted at a CLM sample site. CLM = Cooking Lake Moraine, NA = northern Alberta, WW = Willmore Wilderness, MB = Manitoba, ON = Ontario.

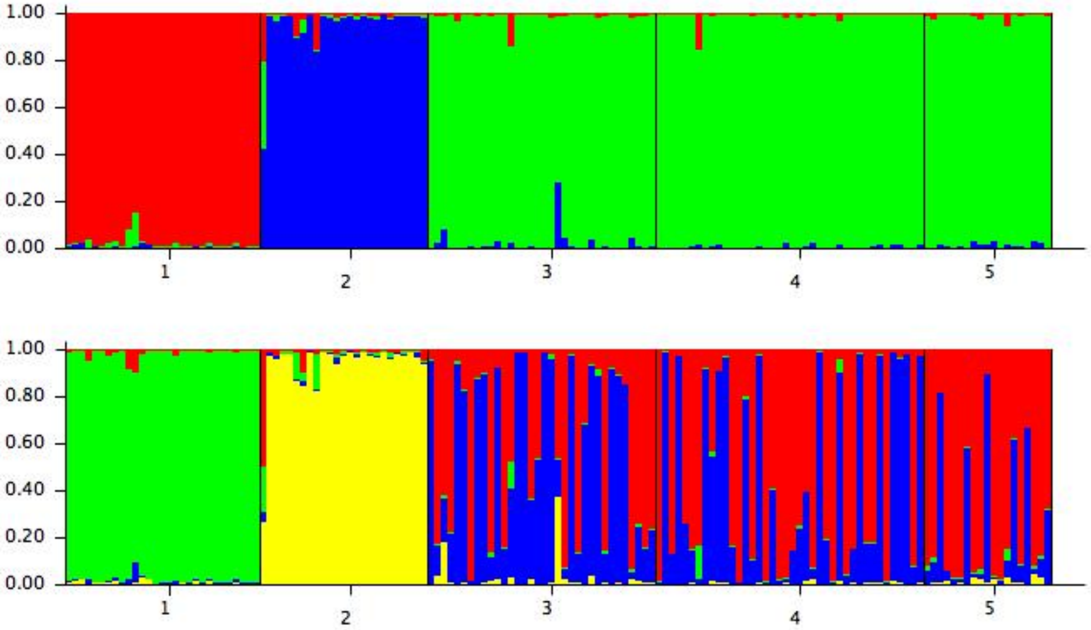

Figure 1.2 The probability of population structuring when 3 (upper; *k* = 3), or 4 (lower; *k* = 4), populations are assumed across 15-locus fisher genotype data. Each vertical line represents the probability of population assignment for an individual. Multiple runs under the same conditions converged, and further increases in *k* did not produce plausible clusters nor did they increase the likelihood meaningfully (Figure AI.2). In either situation, Cooking Lake Moraine samples are most closely related to samples from northern Alberta and the Willmore Wilderness. The populations are: 1 - Ontario; 2 - Manitoba; 3 - northern Alberta; 4 - Cooking Lake Moraine; and 5 - Willmore Wilderness in the Rocky Mountains.

CHAPTER II

It’s all in the matrix: natural habitat predicts functional connectivity within working landscapes

With Siobhan Darlington, John P. Volpe, Malcolm McAdie, and Jason T. Fisher

Introduction

Land use change is restructuring landscapes such that they integrate both natural and anthropogenic features. The resulting “working landscapes” – areas of interspersed natural and anthropogenic features (a.k.a. “mixed-use” or “human-dominated” landscapes; Tscharntke et al. 2012) – affect the abundance and persistence of many species. Landscapes may become structurally, but not functionally connected (Taylor et al. 1993; Rudnick et al. 2012) as land use change results in both habitat loss and fragmentation (Andren 1994) and affects the ability of species to connect habitats through movements or geneflow. For example, fragmentation and land use change alter the movement paths of birds (da Silveira et al. 2016), insects (Ng et al. 2017), amphibians (Sadler 2017), and mammals (Tucker et al. 2018), with the potential to rapidly affect species extinction risk (Fahrig 1991;2002). Studying animal movement patterns within working landscapes allows for an understanding of how animals use these rapidly changing landscapes, and could be used for refining conservation decisions to maintain biodiversity while reconciling both economic growth and landscape conversion.

Functional connectivity describes how easily species use a landscape; how individuals or their genes move between patches of habitat. Structural connectivity only refers to the physical connectedness of habitat patches – it does not comment on the ease, ability, or resistance of species movements (Forman 1995; Rudnick et al. 2012). The pattern of functional connectivity can be categorized, based on theoretical and empirical research, into three general types of analysis methods involving discrete assumptions of how animals navigate working landscapes: habitat corridors, least cost paths (LCP), and stepping stones. Adherence to these assumptions are often species specific, where the thresholds distinguishing each assumption changes with the demography (Elliot et al. 2014), evolutionary, and ecological history of the species (Fahrig 2007). Based in metapopulation theory, and enhanced by graph theory (Urban & Keitt 2001), the corridor method suggests that structurally connected habitats surrounded by a landscape matrix – the unsuitable landscape features for a given species (Turner et al. 2001) – will best facilitate functional connectivity of wildlife populations (Beier & Noss 1998; but see Haddad et al. 2000); it assumes structural connectivity predicts functional connectivity. Alternatively, derived from electrical circuit theory (McRae et al. 2008), the LCP method defines habitat by the 'cost' or 'effective distance' it imparts on animal movement. It views the landscape as a continuum of costs that correlate to the type, and density, of habitat features (Adriaensen et al. 2003); it does not consider habitat and matrix as binary, separate, entities. Stepping Stone theory, derived from Island Biogeography (MacArthur & Wilson 1967), is a subset of LCP that implies physically close, and large, patches of the same habitat type will best facilitate connectivity (Gilpin 1980); it acutely distinguishes between landscape matrix and habitat. Relative support for landscape connectivity methods can be inferred from measuring the pattern, rate, and directions of animal movement between patches (Tischendorf & Fahrig 2000a; 2000b; Goodwin 2003).

Without much thought about the theoretical frameworks, landscape connectivity conservation techniques commonly assume they achieve functional connectivity. Whether it be through development of protected areas, connectivity of these protected areas into networks (Saura et al. 2018) through wildlife corridors or highway overpasses (Clevenger & Waltho 2000), or greenway planning for changing cities (Beier et al. 2008), the promotion of global conservation initiatives underlines the support for conservation techniques in facilitating functional connectivity. However, rarely to we understand how functional connectivity works, and whether our assumptions are supported by real animal movements. Given (1) the rate at which habitat fragmentation and land use change is transforming landscapes (Haddad et al. 2015) and altering animal movements (Tucker et al. 2018), (2) the increasing acknowledgement of matrix importance on landscape connectivity (Baum et al. 2004) and biodiversity conservation (Leroux & Kerr 2013; Driscoll et al. 2013; Chapter III), and (3) the current global promotion of protected areas under the Convention on Biological Diversity Aichi Target 11 (CBD 2020), our assumptions regarding functional connectivity in working landscapes requires critical testing to inform effective future conservation decisions.

As an example of this global issue for wildlife management, we use a tractable landscape mesocosm (Odum 1984) – an area of representative global land use change to provide a link between empirical (e.g. Clark et al. 2015), modeling (e.g. Royle et al. 2013, Morin et al. 2017), and simulation (e.g. Fahrig 1991; Epperson et al. 2010) studies – which encompasses over 700 protected areas (PAs) comprising a PA network . We compare the adherence of observed functional connectivity to theoretical derivations as a test of common assumptions regarding connectivity in working landscapes. We employ the most extensive, and high resolution, GPS movement telemetry data yet collected from fisher (*Pekania pennanti*), a species subject to extensive connectivity research (Garroway et al. 2011, LaPoint et al. 2013, Koen et al. 2013), as an inference of functional connectivity (Figure 2.1). We analyze these data using the recently developed iSSA method (Avgar et al. 2016), which incorporates animal movement – measured as movement velocity and directionality (i.e. step length and tortuosity) – and habitat selection – measured as animal occurrence – into the same model, to ask: what aspects of working landscapes facilitate both animal habitat selection and movement, and how do protected areas play a part?

We test three non-mutually exclusive hypotheses to determine how habitat features affect functional connectivity in working landscapes. First, if corridors – land that allows passage between two or more areas (Beier et al. 2008) - provide connectivity, then we expect animals to take many short steps close to linear features or many steps within one type of habitat. We also expect each subsequent step to be within the same habitat feature as the previous step; animals select specific landscape features through which to continuously move. Second, if least cost paths provide connectivity, then we expect animal tortuosity and step length to vary with the density of habitat – without distinction between landscape matrix or protected areas; habitats that are costly to move through receive long straight steps as animals do not frequently select this habitat, while habitats that provide ease of movement receive small tortuous steps indicating a high residency time and frequent habitat selection. Finally, if stepping stones serve as the best method for functional connectivity, where PAs act as stepping stones across a relatively unused (and presumably unsuitable) matrix, we expect many tortuous and short steps within PAs and few longer steps outside of PAs; animals select PAs and the landscape matrix is costly for movement. We explicitly test the relative support of these three functional connectivity methods, and parameterize the components of functional connectivity in working landscapes to better inform effective future conservation decisions.

Materials and methods

Data collection across the mesocosm

The Beaver Hills Biosphere (BHB) covers approximately 1,596 km^2 of glacial moraine in east-central Alberta, Canada (53.381167°N, 113.062976°W; Figure 2.1). This heterogeneous landscape is composed primarily of native aspen parkland (*Populus tremuloides* and *P. balsamifera*), and interspersed small waterbodies, meadows, and patches of white spruce (*Picea glauca*). Seven hundred and sixty-three protected areas of varying size (mean = 784.1 ± 290 km^2), status (local from local conservation easements managed by non-government organizations to provincial and national parks; Chapter III), and isolation conserve these native features across the BHB, but are surrounded by extensive resource extraction in the form of oil and gas, agriculture, forestry, and rural-residential development. As a result, the matrix landscape surrounding the BHB's protected areas is a mosaic of private lands, roads, and agriculture that separate the BHB from tracts of contiguous forest in other parts of the province.

From November 2015 through February 2016 we used covered cage traps (Tomahawk 109, Tomahawk, WI) to live-capture 14 fisher (Stewart et al. 2018). We used a combination of ketamine (concentration = 100mg/ml, dose = 12 mg/kg) and midazolam (concentration = 5mg/ml, dose = 0.3 mg/kg) to sedate individuals; we monitored vital rates and fitted individuals with GPS tracking collars (E-obs Collar 1A; Grünwald, Germany). Collars contained a GPS microchip, ultra-high frequency transmitter for telemetry and data download, and tri-axial accelerometer; the GPS was programmed to take a GPS-fix every 5 minutes if the individual was moving greater than 10 cm/s. Spatial capture-recapture (Royle et al. 2013) modeling of these data estimate the BHB fisher population to be at most 62 individuals (5.74 fishers 100 km^{-2}; J.

Burgar, unpubl. data). We therefore obtained GPS telemetry data from at least 16% of the contemporary population.

All research was approved by the InnoTech Alberta Animal Care Committee (2070M-A02/048/15-P01) under the Canadian Council on Animal Care.

Integrated step selection analysis

Step lengths are defined as straight-line distances between successive GPS-fixes. They directly measure speed (i.e. m/5min) and can be used as an estimate of animal residency time within habitat features (i.e. the shorter steps the longer the residency time (Turchin 1998; Thurfjell et al. 2014). Using the *movement.ssf* function in GME (www.spatialeclogy.com/gme/), available fisher step lengths were sampled from a log normal distribution parameterized on used step lengths for the entire population (distribution shape = 3.68, distribution scale = 1.51) as well as for each individual (distribution shape varied between 3.31 – 4.45, distribution scale varied between 1.99 – 1.40). Step lengths were ln-transformed (*sensu* Prokopenko et al. 2016; ln*StepLength*) to decrease the tail length of this distribution. Available turn angles were sampled from a uniform distribution between –π and π radians (*sensu* Avgar et al. 2016) and are defined as the angular deviation between two headings; these values were cosine-transformed (cos*TurnAngle*), which transitions a circular measure (radians) into a linear measure between -1 and 1 (Barraquand & Benhamou 2008; Prokopenko et al. 2016); values approaching 1 represent linear movement (Benhamou 2004). Therefore, steps without a proceeding step (*i.e.* the first step collected for each individual) were removed from the analysis.

For each used GPS-fix, 10 random available steps and turn angles were generated, and compared in a used-available, or “case-control”, design (*sensu* Fortin et al. 2005; Figure 2.1B).

These observed steps and turn angles were assigned a “1”, whereas available (*i.e.* generated in GME) steps and turn angles a “0” and represent the response variable in our conditional logistic regressions (Avgar et al. 2016). We conducted two analyses: one examining selection by individuals, and another for the population of steps without identifying individuals.

Landscape features as model covariates

To test the role of landscape features in connectivity theory, we used ArcGIS v10.3 (ESRI, Redlands, CA, USA) Geographic Information System to quantify landscape heterogeneity. We used the LandSat digital map inventory from the Beaver Hills Biosphere (Land Management Framework 2015) to quantify the distance of fisher steps (m) to each landscape feature, as well as the density of landscape features (%), across 15 categories representing natural, anthropogenic, and protected area features; bare landscape, crops, deciduous forests, mixed forests, coniferous forests, wetlands, development, forage, grasslands, lakes, shrubs, protected areas, rail lines, roads, streams, and protected areas (Table 2.1). Landscape feature density was calculated as the raster density of a buffer around the end point of each step, where the mean fisher step length was the buffer radius (106 m; *i.e.* # of raster pixels/m^2). We scaled these measures to ensure comparison of coefficients within regression models; these scaled distance, and density, measures represent the predictor variables in our conditional logistic regressions.

Our final data set comprised 214,148 rows of data across 10 fisher individuals. Each row represented a used, or available, GPS fix. Each column comprised information about the step (used/available status, step length, turn angle, fisher ID, UTM coordinates, and strata of available steps) or the relationship of each step to landscape predictor variables – either the distance to, or density, of 15 landscape features (Table 2.1). This information totaled a data matrix of 214,148 rows by 42 columns.

Statistical analysis

We created statistical models to test each of the three landscape connectivity hypotheses: corridors, least cost paths, or stepping stones (Table 2.2). We developed a ‘core model’ of assumed habitat features explaining variation of fisher movement in a homogenous landscape and included this model, which incorporates the step length (ln*StepLength*) and cosine of the turn angle (cos*TurnAngle*) as predictor variables, within each of our connectivity hypotheses (Table 2.2). ln*StepLength* (m) represents the linear displacement between consecutive steps – a proxy for animal velocity as the time between steps is constant (m/5-minutes) – whereas the movement directionality, or tortuosity, is described by the cosine of the turning angle (Turchin 1998; Avgar et al. 2013). Including ln*StepLength* and cos*TurnAngle* as model predictors within a clogit regression extends the step selection function framework (Fortin et al. 2005; Thurfjell et al. 2014) into an integrated Step Selection Analysis (iSSA), accounting for animal movement velocity and directionality within selected habitat features (Avgar et al. 2016).

From previous research we expect tortuosity and velocity to affect fisher movement and fisher to select areas of deciduous forest, coniferous forest, and mixed forest, while remaining proximate to water bodies (Koen et al. 2007; Weir 2010; LaPoint et al. 2013; Aubry et al. 2013). We included the cos*TurnAngle*, ln*StepLength*, distance to wetlands, deciduous, coniferous, and mixed forests, as well as density of deciduous, coniferous, and mixed forests within a core model. If fisher movement and habitat selection on the BHB corresponds to a corridor model of functional connectivity, then we additionally predict each fisher step, as well as the previous step, to remain close to linear features (steams, rail lines, roads) – whether natural or anthropogenic – while selecting for areas of high habitat density (Table 2.1). We therefore included the distance of each step to linear features, the distance of the previous step to linear features, the density of habitat features around each step, the density of habitat features around the previous step, as well as core model covariates as predictors within our corridor model (Table 2.2).

Alternatively, if fisher display a least cost paths (LCP) pattern of movement and habitat selection, then we predict fisher to display tortuous and short step lengths within habitats of low resistance, and linear but long movements within habitats with high resistance; on top of our core model predictors, we included an interaction between habitat density and both the cos*TurnAngle* and ln*StepLength* as predictors within our LCP model. Finally, if fisher display a stepping stone pattern to movement and habitat selection, then we expect fisher to use discrete areas of protection and have a high residency time within these areas. They should display highly tortuous movements and short step lengths within these habitats; in addition to core model predictors, we included protected area presence (0/1) and interactions between protected area presence and both cos*TurnAngle* and ln*StepLength* within our stepping stone model.

To avoid model averaging (Cade 2015) we competed each of the three models (corridor model, LCP model, and stepping stone model) at both the population and individual levels in an Information Theoretic approach using Akaike Information Criterion values (AIC; Burnham and Anderson 2002; Table 2.2). We used the *clogit* function in the *Survival* package (Therneau 2015) in R (v3.2.2 R Foundation for Statistical Computing), to perform a total of 33 conditional logistic regressions (3 population models, one for each hypothesis, and 30 individual models – 3 for each individual). The response variable was steps observed (0/1), each strata was assigned to paired used:available steps, and fisher individual ID was specified as the model cluster within the population model (*sensu* Prokopenko et al. 2016). We performed a variance inflation analysis to remove predictor collinearity, and thoroughly explored our data (*sensu* Zuur et al. 2009) ensuring all *clogit* model assumptions were met. All statistical analyses were conducted in R (v3.2.2 R Foundation for Statistical Computing), and results are presented as mean ± SE unless otherwise specified.

Results

Of the 14 fisher captured and collared, we obtained GPS data from 10 individuals (5 males: 5 females; the 4 other collars either did not collect data, or were too damaged after deployment to be retrieved). These 10 collars collected a total of 19,578 GPS fixes, and an average of 32.97 days (minimum = 4.87 days, maximum = 90.79 days) of continuous movement data per individual. Fisher step length over a 5-min fix interval approximated a gamma distribution with many small steps (105.47 m ± 1.85 m, min = 0.06 m, max = 2972.0 m), and turn angles were on average positive, indicating significant directional movement behaviour (0.08 rad ± 0.0001 rad).

Individual and population models best support a corridors for functional connectivity

At both the individual and population scales the corridor model of functional connectivity received the most support. At the population scale, this model received 99% of the AIC weight of evidence, when competed against least cost path and stepping stone models. Across three population models, fisher selected for a high density of protected areas (PAs; $ß = 0.14 – 0.16$, $p < 0.0001$), providing support for our stepping stone predictions. Fisher ln*StepLength* also significantly varied with the density of protected areas, but the direction of this relationship fluctuated with the hypothesis tested (LCP; ß = 0.04 ± 0.005 p = 0.04, Stepping Stone; ß = -0.03 ± 0.0.005, p = < 0.0001); fisher had longer (LCP) or shorter (Stepping Stone) step lengths within protected areas than outside protected areas, limiting support for our predictions. The distance of fisher movement relative to protected areas, and the tortuosity of fisher movement within protected areas, were never significant predictors of observed fisher steps.

At the individual scale, the corridor model of functional connectivity also received the highest AIC weight of evidence across all individuals (86 – 99%), when competed against least cost path and stepping stone models. Across individual models, fisher seldom selected for protected area features; PA predictors (density, distance to, and interactions with either ln*StepLength* or cos*TurnAngle*) were rarely significant in top models. Only two of 10 top-individual models contained significant PA predictors; one fisher individual's movement and habitat selection significantly varied with PA density of the current (ß = 0.20 ± 0.04, p < 0.001) and previous (ß = 0.15 ± 0.04, p < 0.001) step, which supported our stepping stone predictions. The other fishers' movement and habitat selection also varied positively with PA density of the previous step (ß = 0.89 ±0.41, p = 0.04), but not of the current step. Of the other eight individual fishers, three individuals had PA predictors in their top models, but these parameters were never significant. Selection for the presence, and specific features, of protected areas differed between fishers. Instead, fisher always selected for at least one type of natural feature.

Natural landscape features best predict functional connectivity in working landscapes

The magnitude of selection for natural and anthropogenic features varied between individuals. However, at both individual and population scales, fisher consistently and significantly selected areas close to deciduous and mixed forest that were within areas of dense coniferous or mixed forest, and protected areas. Their previous step usually came from locations of dense protected area. Fisher consistently and significantly avoided open areas; areas close to, and/or of high density of wetlands, streams, lakes, forage, grass, bare, crops, development, and roads. Their previous step also significantly avoided these features – which encompass all anthropogenic features measured (Table 2.1).

Natural features within top models had the largest effect size at both the population and individual levels. Within the population model, PA parameter effect sizes accounted for 9.1% of the variation, while natural features accounted for 65.6% and anthropogenic features accounted for 25.3%. Across individual models, PA parameter effect sizes varied from 0 to 11.1% (24.1 ± 1.1%), while natural features varied from 26.1 to 99% (73.0 ± 7.2%), and anthropogenic features varied from 0 to 49.7% (24.6 ± 7.3%). Despite the functional connectivity analysis method tested, natural features (Table 2.1) accounted for the majority of the observed variation in fisher movement and habitat selection across the heterogeneous working landscape of Alberta's Beaver Hills Biosphere.

Discussion

A combination of natural and anthropogenic landscape features best predict functional connectivity, although protected areas play a minor role. Combined, these landscape features best support animals moving along functional corridors; they remain close to, and within, consistent habitat features from one step to the next. These results extend studies demonstrating an effect of the landscape matrix on PA efficacy (Baum et al. 2004; Prevedello et al. 2010; Leroux & Kerr 2013; Boesing et al. 2017) to highlight the importance of the landscape matrix in maintaining functional connectivity across a PA network. To best facilitate functional connectivity, PA networks should be integrated between corridors of natural landscape features rather than explicitly relying on the landscape matrix for promotion of landscape-scale functional connectivity.

Connecting and protecting land

The theory of Island Biogeography (MacArthur & Wilson 1967) first provided a framework for functional connectivity in terrestrial environments – the functional connectivity of discrete habitat patches depends on their size and isolation. In this framework, the space between habitat patches – the landscape matrix (Turner et al. 2001) – is important, but inhospitable. This may be the case of islands within an ocean, but increasingly the importance of the matrix in terrestrial studies is recognized as a continuum; it can provide varying degrees of facilitation, or impediment for functional connectivity (Baum et al. 2004; Saura et al 2018), species richness in remnant forest patches (Gascon et al. 1999), or protected area efficacy (Leroux & Kerr 2013). Boesing et al. (2018) highlight the importance of forests for matrix quality preventing abrupt losses in taxonomic diversity. However, matrix quality is only valuable if there is adequate remaining habitat within the landscape for it to influence: if habitat loss is above 80%, matrix quality no longer buffers extinction thresholds (Boesing et al. 2018). Andren (1994) demonstrated a similar finding across birds and mammals; he attributes this finding to the fact that above 70% of habitat loss, habitat fragmentation equates to habitat loss. Our findings build upon this previous research by demonstrating the importance of maintaining natural features both within protected areas, as well as within the landscape matrix. Across all models, fisher consistently avoided anthropogenic features, grasslands, shrub-lands and wetlands; they remained close to areas of coniferous, deciduous, and mixed forest. Prioritizing forest features between protected areas will best facilitate functionally connectivity within protected areas networks for this, and similar, species.

Although based on a limited sample size, the direction of predicted relationships between cos*TurnAngle*, ln*Steplength*, and the presence and density of protected areas provided limited support for a stepping stone model of functional connectivity. Opposing our predictions, fisher population models consistently displayed less tortuous ($ß = 0.02 \pm 0.02$, $p = 0.26 - 0.13$) and longer steps ($ß = 0.04 \pm 0.005$, $p < 0.001$) within protected areas; however this result varied in direction, magnitude, and significance when investigating individual models. This may be a result of individual variation in response to landscape features within the home territory, and in corridor movements between protected areas. In a similar study, LaPoint et al. (2013) demonstrate fisher movement data at local scales best supports a corridor model of functional connectivity, but more importantly, that fisher-defined corridors are composed of a variety of land cover types. As a result, protected area network functional connectivity can be additionally improved by incorporating individual behavioural data, rather than assuming a uniform response by individuals to structural connectivity. These ‘animal-defined’ corridors quantified in heterogeneous landscapes (Vogt et al. 2009) will help to parameterize the functional components of connectivity across seasons, and both natural (*e.g.* forest fires) and anthropogenic (*e.g.* crop rotation, development) disturbances (*sensu* LaPoint et al. 2013; Panzacchi et al. 2016; Abrahms et al. 2017).

Animal-defined corridors are an important concept in investigating connectivity across spatial scales, as the habitat predicting connectivity may change based on scale-specific ecological processes. Regionally, protected areas may enhance functional connectivity through dispersal and species range expansion (Turner et al. 2001). However, only 14.7% of the global terrestrial area is under protection, and only half of these areas are considered structurally connected. As a result, only 30% of countries currently meet the Aichi 2020 Target 11 (Saura et al. 2018). Therefore, achieving the majority of the globe's functional connectivity must be achieved through the quality of landscape matrices, rather than specifically protected areas.

Applications for conserving functional connectivity in working landscapes

The current global prioritization of protected area generation (CBD 2020) will be most effective for biodiversity conservation if protected areas are functionally connected into PA networks. Failure to implement effective PA networks for biodiversity conservation may not only result in financial devastation of global conservation funds, but result in protected areas of isolated populations with inadequate potential to mitigate existing biodiversity declines. The research presented here on a PA network mesocosm suggests limited value of PAs in maintaining landscape connectivity unless conservation consideration of natural features within the matrix receives greater attention. In addition to continual promotion of new protected areas under the Aichi Target 11 (CBD 2020), focusing on maintaining or restoring natural landscape features within the matrix of existing PA networks, or, creating PA networks within existing landscapes of high natural features, will only enhance the use of conservation funds. Increasing the extent and density of the global protected area network is not the only solution to connecting protected areas; in similar working landscapes, enhancing the conservation of natural landscape features between protected areas may facilitate connectivity within them.

Literature cited

Abrahms B, Sawyer SC, Jordan NR, McNutt JW, Wilson AM, Brashares JS. 2017. Does wildlife resource selection accurately inform corridor conservation? Journal of Applied Ecology **54**(2):412-422.

Adriaensen F, et al. 2003. The application of 'least-cost'modelling as a functional landscape model. Landscape and urban planning **64**(4):233-247.

Andren H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos **71**:355–366.

Aubry K, Raley C, Buskirk S, Zielinski W, Schwartz M, Golightly R, Purcell K, Weir R, Yaeger J. 2013. Meta-analyses of habitat selection by fishers at resting sites in the pacific coastal region. The Journal of Wildlife Management **77**:965–974.

Avgar T, Potts JR, Lewis MA, Boyce MS. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution **7**:619–630.

Avgar T, Mosser A, Brown GS, Fryxell JM. 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. Journal of Animal Ecology **82**(1):96-106.

Banks SC, Cary GJ, Smith AL, Davies ID, Driscoll D, Gill M, Lindenmayer DB, Peakall R. 2013. How does ecological disturbance influence genetic diversity? Trends in Ecology and Evolution **28**:670–679.

Barraquand F, Benhamou S. 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. Ecology **89**:3336–3348.

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT. 2004. The matrix enhances the effectiveness of corridors and stepping stones. Ecology **85**(10):2671-2676.

Beier P, Noss RF. 1998. Do habitat corridors provide connectivity?. Conservation biology **12(**6): 1241-1252.

Beier P, Majka DR, Spencer WD. 2008. Forks in the road: choices in procedures for designing wildland linkages. Conservation Biology **22**(4):836-851.

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? Journal of theoretical biology **229**(2):209-220.

Boesing AL, Nichols E, Metzger JP. 2017. Biodiversity extinction thresholds are modulated by matrix type. Ecography. DOI: 10.1111/ecog.03365

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Cade BS. 2015. Model averaging and muddled multimodel inferences. Ecology **96**(9): 2370-2382.

Clark JD, Laufenberg J, Davidson M, Murrow J. 2015. Connectivity Among Subpopulations of Louisiana Black Bears as Estimated by a Step Selection Function. Journal of Wildlife Management **79**:1347–1360.

Clevenger AP, Waltho N. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology **14**(1):47-56.

Convention on Biological Diversity. 2020. Target 11 – Technical Rationale extended (provided in document COP/10/INF/12/Rev.1). Accessed November 17, 2017. https://www.cbd.int/sp/targets/rationale/target-11/

da Silveira NS, Niebuhr BBS, de Lara Muylaert R, Ribeiro MC, Pizo MA. 2016. Effects of land cover on the movement of frugivorous birds in a heterogeneous landscape. PloS one **11(**6): p.e0156688.

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in ecology & evolution **28**(10):605-613.

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ. 2014. The devil is in the dispersers: predictions of landscape connectivity change with demography. Journal of Applied Ecology **51**(5):1169-1178.

Epperson BK et al. 2010. Utility of computer simulations in landscape genetics. Molecular Ecology **19**:3549–3564.

Fahrig L. 1991. Simulation methods for developing general landscape-level hypotheses of single-species dynamics. Ecological Studies 82:417-442.

Fahrig L. 2002. Effect of habitat fragmentation on the extinction threshold: a syndissertation. Ecological applications **12**(2):346-353.

Fahrig L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology **21**:1003–1015. Blackwell Publishing Ltd.

Forman RTT. 1995. Some general principles of landscape and regional ecology. Landscape Ecology **10**:133–142.

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320–1330.

Franklin JF, Lindenmayer DB. 2009. Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Sciences **106**(2):349-350.

Garroway CJ, Bowman J, Wilson PJ. 2011. Using a genetic network to parameterize a landscape resistance surface for fishers, Martes pennanti. Molecular Ecology **20**:3978–3988.

Gascon C. et al. 1999. Matrix habitat and species richness in tropical forest remnants. Biological conservation **91**(2-3):223-229.

Goodwin BJ. 2003. Is landscape connectivity a dependent or independent variable? Landscape Ecology **18**:687–699.

Haddad NM et al. 2015. Habitat fragmentation and its lasting impact on Earth ' s ecosystems. Science Advances **1**(2):e1500052.

Haddad NM, Rosenberg DK, Noon BR. 2000. On experimentation and the study of corridors: response to Beier and Noss. Conservation Biology **14**(5):1543-1545.

Koen E, Bowman J, Findlay C, Zheng L. 2007. Home Range and Population Density of Fishers in Eastern Ontario. Journal of Wildlife Management **71**:1484–1493.

Koen EL, Garroway CJ, Wilson PJ, Bowman J. 2013. The effect of map boundary on estimates of landscape resistance to animal movement. PLoSone **5**(7):e11785.

LaPoint S, Gallery P, Wikelski M, Kays R. 2013. Animal behavior, cost-based corridor models, and real corridors. Landscape Ecology **28**:1615–1630.

Leroux SJ, Kerr JT. 2013. Land Development in and around Protected Areas at the Wilderness Frontier. Conservation Biology **27**:166–176.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton University Press.

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology **89**:2712–2724.

Morin DJ, Fuller AK, Royle JA, Sutherland C. 2017. Model-based estimators of density and connectivity to inform conservation of spatially structured populations. Ecosphere **8**:e01623.

Ng K, Barton PS, Macfadyen S, Lindenmayer DB, Driscoll DA. 2017. Beetle's responses to edges in fragmented landscapes are driven by adjacent farmland use, season and cross habitat movement. Landscape Ecology **33**(1):109-125.

Odum EP. 1984. The Mesocosm. BioScience **34**:558–562. Oxford University Press.

Panzacchi M, et al. 2016. Predicting the continuum between corridors and barriers to animal movements using step selection functions and randomized shortest paths. Journal of Animal Ecology **85**(1):32-42.

Prevedello JA, Vieira MV. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation **19**(5):1205-1223.

Prokopenko CM, Boyce MS, Avgar T. 2016. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. Journal of Applied Ecology **54**(2):470-479.

R Foundation for Statistical Computing. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle JA, Chandler RB, Gazenski KD, Graves TA. 2013a. Spatial capture-recapture models for jointly estimating population density and landscape connectivity. Ecology **94**:287–294.

Royle JA, Chandler RB, Sollmann R, Gardner B. 2013b. Spatial capture-recapture. Academic Press.

Rudnick DA et al. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology **13**:1–16.

Sadler A. 2017. Determining How Varying Severity of Forest Fragmentation Effect Red-backed Salamander Movement Patterns. Dissertation. Allegheny College, USA.

Stewart FEC, Fisher JT, Burton AC, Volpe JP. 2018. Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. Ecosphere **9**(2):e02112.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity is a vital element of landscape structure. Oikos: 571-573.

Thurfjell H, Ciuti S, Boyce MS. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology **2**:26.

Therneau T. 2015. A Package for Survival Analysis in S. version 2.38, <URL: https://CRAN.R-project.org/package=survival>.

Tischendorf L, Fahrig L. 2000a. How should we measure landscape connectivity? Landscape Ecology **15**:633–641.

Tischendorf L, Fahrig L. 2000b. On the usage and measurement of landscape connectivity. Oikos **90**:7–19.

Tscharntke T, et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews **87**:661–685.

Tucker MA, et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science **359**(6374):466-469.

Turchin P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants (Vol. 1). Sunderland: Sinauer Associates.

Turner MG, Gardner RH, O'neill RV. 2001. Landscape ecology in theory and practice (Vol. 401). New York: Springer.

Urban D, Keitt T. 2001. Landscape connectivity: A graph-theoretic perspective. Ecology **82**:1205–1218.

Vogt P, Ferrari JR, Lookingbill TR, Gardner RH, Riitters KH, Ostapowicz K.,2009. Mapping functional connectivity. Ecological indicators **9**(1):64-71.

Weir RD. 2010. Ecology of fishers in the boreal mixedwood forests of northeastern British Columbia: year end report. British Columbia Government.

Zuur A, Ieno E, Elphick C. 2009. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1**:3–14.

Tables and Figures

Table 2.1 Distance to (*Dist*), and density around (*Dens*), the end of both used and available fisher steps were quantified across 15 landscape features within the Beaver Hills Biosphere.

Category	Landscape feature	Feature type	Description
Natural features	Bare	Polygonal	Distance to, and density, of exposed land
	Deciduous forests	Polygonal	Distance to, and density, of deciduous forest; native natural forest stands of primarily aspen or balsam poplar
	Coniferous forests	Polygonal	Distance to, and density, of coniferous forest; native natural forest stands of primarily white or black spruce
	Mixed forests	Polygonal	Distance to, and density, of mixed forests; native natural forest stands of mixed deciduous and coniferous species
	Wetlands	Polygonal	Distance to, and density, of water bodies; wetlands and ephemeral lakes
	Grasslands	Polygonal	Distance to, and density, of grassland; native natural grass cover
	Lakes	Polygonal	Distance to, and density, of water bodies; lakes
	Shrubs	Polygonal	Distance to, and density, of shrub-land; native natural shrub cover
	Streams	Linear	Distance to, and density, of water bodies; streams and small rivers
Anthropogenic features	Development	Polygonal	Distance to, and density, of built-up land (e.g. residential, municipal, or commercial)
	Crops	Polygonal	Distance to, and density, of annual and perennial crops

	Forage	Polygonal	Distance to, and density, of pastures and forages
	Rail lines	Linear	Distance to, and density, of rail transport lines
	Roads	Linear	Distance to, and density, of hard roads, vegetated roads, and trails
Protected areas	Protected areas	Polygonal	Distance to, and density, of parks and protected areas; protected area of any status (e.g. public lands, provincial parks, provincial recreation areas, national parks, conservation areas, and NGO sites

Table 2.2 Parameters within each *clogit* model describing hypothesized frameworks for landscape connectivity across the Beaver Hills Biosphere. Across both individual and population models, the corridor hypothesis was best supported.

Hypothesis	**Model Covariates**
Corridors	*Core model* + *Dist*(each linear features) + *Dens*(each habitat feature) + *Dist*$_{t-1}$(each linear features) + *Dens*$_{t-1}$(each habitat feature)
Least Cost Paths	*Core model* + *Dens*(all habitat features):cos*TurnAngle* + *Dens*(all habitat features):ln*StepLength*
Protected Area Stepping Stones	*Core model* + Protected area presence/absence + Protected area presence/absence:cos*TurnAngle* + Protected area presence/absence:ln*StepLength*

*All models involved a set of Core model variables that we hypothesized would be generally important to fisher movement: CosTurnAngle + lnStepLength + Dist(DECID) + Dens(DECID) + Dist(CONIF) + Dens(CONIF) + Dist(MIXED) + Dens(MIXED) + Dist(WATER)

: denotes an interaction

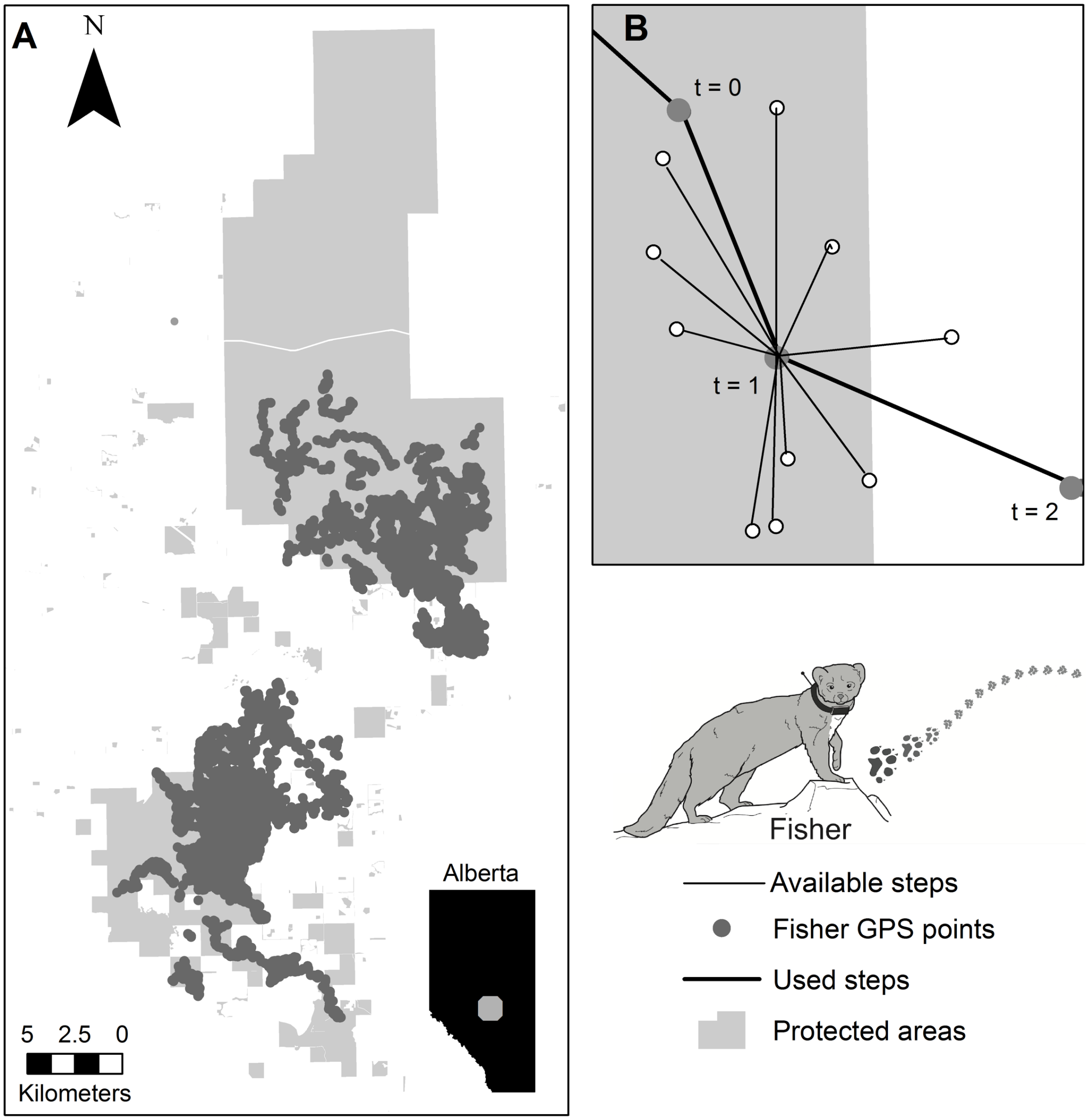

Figure 2.1 Fisher GPS telemetry locations were collected across the protected area network of the Beaver Hills Biosphere in east-central Alberta, Canada (A). For each used GPS step, 10 random available steps and turn angles were generated. These points were compared in a used-available, or "case-control", design to determine the density and configuration of habitat features predicting used points (B).

CHAPTER III

Protected area networks are only as effective as the working landscapes they conserve

With John P. Volpe, Glynnis A. Hood, Brian R. Eaton, Dragomir Vujnovic, and Jason T. Fisher

Introduction

Protected area (PA) networks – interconnected areas dedicated and managed for the long-term conservation of nature, ecosystem services, and associated cultural values (IUCN 2008) – are increasingly implemented globally, driven by the Convention on Biological Diversity's Aichi Target 11 of 17% global terrestrial area protection by 2020 (CBD 2020). PA networks are a conservation tool hailed as an effective way to conserve biodiversity in the Anthropocene (Bruner et al. 2001, Brooks et al. 2006; Le Saout et al. 2013), and have been implemented across some of the world's most iconic landscapes (*e.g.* North America's Yellowstone to Yukon (Y2Y), Europe's Natura 2000, Western Australia's Macro-Corridor network). However, the assumption that PAs conserve biodiversity is rarely tested (but see Geldmann et al. 2013), and extending this assumption to PA networks is made more difficult by their sheer size. Assuming PAs unambiguously conserve biodiversity – with exception to notable ongoing theoretical arguments (*e.g.* SLOSS; Simberloff & Abele 1982, Santini et al. 2016) – may have led to the generation of many 'paper parks': PAs that exist for political rather than conservation purposes (Dudley & Stolton 1999; Watson et al. 2014; Di Minin & Toivonen 2015). Empirical evidence of PA network efficiency is needed to prevent development of 'paper networks' under the rapidly approaching CBD 2020 deadline – which would merely multiply the detrimental effects of paper parks across landscapes.

Biodiversity conservation is globally challenged by habitat fragmentation and loss through agriculture, urbanization, and resource extraction (Maxwell et al. 2016). Ongoing landscape change results in increasing prevalence of working landscapes – areas shared by wildlife and by humans, neither pristine wilderness nor urban centers – and are commonly composed of anthropogenic features intermixed with ‘natural’ features to produce highly heterogeneous spaces (a.k.a. 'human-modified' or 'human-dominated' landscapes; Tscharntke et al. 2012). Despite the increasing prevalence of these landscapes, little is known about their ecological mechanics, making PA network implementation for effective biodiversity conservation difficult (see Amarasekare 2003; Leibold et al. 2004; Tscharntke et al. 2012; Tscharntke et al. 2008). However, from existing PA networks we can learn how different habitats support species within them, how species distributions vary spatially with natural heterogeneity and anthropogenic disturbance, and how biodiversity is maintained both locally and at larger spatial scales spanning the entire network. The mesocosm research approach provides a valuable bridge between ecological inferences on small scales (*i.e.* controlled experiments) and the real world (*i.e.* natural systems; Odum 1984). To test PA network efficacy, we use a ‘landscape mesocosm’ to quantify biodiversity across a tractable model PA network.

To make widely useful inferences about biodiversity conservation that are relatable among systems, biodiversity needs to be quantified in a generalizable way. Functional diversity metrics (functional richness, evenness, and dispersion) are translatable among systems (Tilman et al. 1997; Tilman 2001), and better predict ecosystem function than species-based indices (Gagic et al. 2015). They compare the role and position of species within an ecosystem (*i.e.* n-dimensional utilized niche space; Hutchinson 1957). Functional richness represents the cumulative roles occupied by all species investigated, functional evenness the uniformity of these roles (see Mason et al. 2005; Villeger et al. 2008 for equations), and functional dispersion represents the difference between averaged and individual species in their roles (see Laliberte & Legendre 2010 for equations). These generalized measures standardize biodiversity across species and ecosystems, making biodiversity relatable to ecosystems around the world.

Determining the size of the ecological neighborhoods that affect species – or functional diversity – at a point in space is an unresolved ecological challenge (Pickett & Cadenasso 1995; Wheatley and Johnson 2009). We know that species occurrence at a point in space is affected by more than immediate resources (Fahrig 2001); for example, species integrate information on mates, competitors, and prey from unknown distances away (Zeller et al. 2014). These resources are in turn affected by anthropogenic disturbance (Fahrig 2003). One approach is to model a variety of scales, and determine which scale best fits the collected data (*sensu* Findlay & Houlahan 1997; Fisher et al. 2011; McGarigal et al. 2016). Examining functional diversity-habitat relationships at multiple spatial scales, and across a tractable PA network mesocosm, would be beneficial for both theoretical and applied conservation biology. It would (1) identify the best spatial scale to implement PA networks for biodiversity conservation, (2) compare how different habitat features (native vegetation, anthropogenic features, and PA configuration and status) differentially contribute to biodiversity across spatial scales, and (3) provide a reference point for extrapolation of PA network efficacy to other landscapes of varying size and species composition.

As a test of PA network conservation efficacy, we studied a mesocosm PA network as a model for PA networks in working landscapes globally and test the importance of PA implementation versus measures of landscape composition and native vegetation conservation across multiple scales. If PA networks within multi-use landscapes are important for biodiversity conservation then functional diversity should increase with both the i) proportion of native vegetation, and ii) proportion, proximity, and conservation status of protected areas, among all spatial scales investigated. Moreover, anthropogenic development in the surrounding landscape should have little to no effect. However, if retention or mitigation of native vegetation or anthropogenic features is more important for biodiversity conservation than implementation of PA networks, then there should be no relationship between the proportion, proximity, or conservation status of protected areas and functional diversity metrics. We explicitly test the assumed conservation value of PA networks and identify the most important features for optimizing their conservation efficiency across landscapes.

Methods

Mesocosm data collection

Most terrestrial protected area networks (PA networks) share some common characteristics: several protected areas of various sizes and degrees of human footprint are spatially clustered within a matrix of unprotected or ‘mixed-use’ landscape (Dudley & Stolton 1999). The Beaver Hills Biosphere (BHB) is a tractable mesocosm reflecting this structure. It is approximately 1,596 km^2, and is situated in east-central Alberta, Canada (53.381167 ˚N, 113.062976 ˚W; Figure 3.1). Composed of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) forest with patches of white spruce (*Picea glauca*), open meadows, and small permanent water bodies, these natural features are primarily preserved by 763 protected areas of varying size (mean = 784.1 ± 290 km^2) and status (local from local conservation easements managed by non-government organizations to provincial and national parks; Chapter II). Together, these protected areas cover 598 km^2, or 37% of the BHB landscape. The intervening landscape matrix has experienced extensive resource extraction in the forms of timber, oil and gas, transmission lines, rural residential, and municipal development, and encompasses 998 km^2, or 63% of the landscape. The resulting exurban heterogeneous landscape sits in a matrix of agricultural land and is spatially disjunct from tracts of contiguous forests to the north and west (Patriquin 2014).

Several conservation areas cover the BHB forming a relatively small, but diverse, network of multiple protected areas embedded within a region of high economic value (Figure 3.1). Combined, the landscape hosts a diverse mammal community characteristic of many working landscapes around the globe (Figure 3.2). A century of increasing habitat loss and fragmentation for agriculture, paired with ongoing predator persecution (Alberta's Wildlife Predator Compensation Program; see Laliberte & Ripple 2004; Wolf & Ripple 2017 for historic carnivore ranges), results in few top predators, a diversity of mesocarnivores, abundant ungulate species, as well as species listed as sensitive (fisher, *Pekania pennanti*; American badger, *Taxidea taxus*) and at-risk (long-tailed weasel, *Mustela frenata*; Alberta Status Listing 2015).

To quantify mammalian functional diversity across this heterogeneous protected area network, we used a systematic study design of 4 x 4 km grid cells (64 total; Figure 3.1), which is representative of the average home-range size of female fishers (Linden et al. 2017; Burgar et al. in review). Each cell contained a camera trap (CT; Reconyx™ models PC85 and PC900) to record multi-species mammal occurrence (Burton et al. 2015). These were positioned to photograph the area surrounding a tree baited with a commercial sent lure (O'Gorman's™ Long Distance Call) and 5 kg of beaver meat (Fisher & Bradbury 2014; Stewart et al. 2018). Camera traps were deployed for two sampling seasons; January through June 2014, and January through April 2016, for a total of 10 monthly surveys. All data were collected under Canadian Council of Animal

Care permits approved by the University of Alberta and University of Victoria Animal Care Committees (AUP00000518).

Quantifying functional diversity metrics

We calculated the relative abundance of each species at each camera site as the number of species-specific photos, divided by the total number of all species photos taken at the site. In the R package *FD* (Laliberté et al. 2014), this site-specific species abundance matrix is compared to a functional-trait matrix. From these matrices a functional-trait weighted abundance matrix is created to calculate dissimilarity of different trait types. A principal co-ordinates analysis (PCoA) is then used to compute a functional diversity metric for each site (Laliberte et al. 2014). In mammals, movements can confound abundance metrics (Steenweg et al. 2016; Broadley 2017; Stewart et al. 2018), probability of species detections (Stewart et al. 2018), and body size is related to species-specific scales of habitat selection (Holling 1992; Haskell et al. 2002; Fisher et al. 2011); therefore, we used mammal home-range size and body mass as functional traits within the *FD* analysis (McGill et al. 2006).

Quantifying habitat features across the mesocosm

To test whether protected area (PA) networks explained variance in functional diversity metrics, we used ArcGIS v10.3 (ESRI, Redlands, CA, USA) Geographic Information System to calculate the proportion of habitat features (natural features, anthropogenic features, and PA features; Table 3.1) around camera sites. We used LandSat digital map inventories from the Alberta Biodiversity Monitoring Institute (ABMI; Landcover Map 2014) to quantify the eight primary landcover features in this landscape: water, grassland, shrub-land, cultivation, development, coniferous forest, deciduous forest, and mixed forest. We quantified human footprint variables (ABMI; Human Footprint Map 2014) describing anthropogenic linear features (hard roads, vegetated roads, trails, seismic lines, pipelines, and transmission lines) and anthropogenic block features (rural residential homes and oil well sites). Although there is some spatial dependence between linear, block, and development features, linear features are more spatially continuous within this landscape, and block features distinguish rural-residential homes and well pads from areas of rural-residential development. From the Beaver Hills Biosphere LandSat digital map inventory (Land Management Framework 2015), we quantified aspects of PAs: proportion of area around the camera protected by PAs, legal PA designation (status), and site isolation (measured as the distance of a camera trap to the nearest PA; Table 3.1).

We posited that the effect of PAs on mammalian diversity would diminish with distance. To test this effect of spatial scale on diversity-habitat relationships, we quantified habitat (natural features, anthropogenic features, and protected area features) at multiple spatial scales around each camera. We held the resolution (spatial grain) of habitat features constant and varied the spatial extent at which we quantified habitat around each camera site. We calculated the percent area of all features (Table 3.1) around a camera site within buffers of increasing size, from 250 m – 5,000 m radii in 250 m increments, generating habitat variables at 20 different concentric spatial scales (*sensu* Fisher et al. 2011). Finally, we calculated the percent disturbed landscape (sum of cultivation, development, linear and block features) within a 500 m buffer around each camera site to compare the average amounts of disturbance within each protected area status (Figure 3.3).

The importance of protected areas in predicting mammal functional diversity

To test our hypothesis that the proportion, proximity, and conservation status of protected areas best predict diversity-habitat models, we used model selection to rank three candidate sets of generalized linear models in an information theoretic framework (Burnham & Anderson 2002). Prior to European colonization, the BHB was a glacial moraine composed of knob and kettle wetlands, aspen and coniferous forests (Patriquin 2014); we therefore expect that coniferous, deciduous and mixed forested areas, along with water, would be consistently significant features in top models. We also expect management features that ostensibly conserve these native habitats (*i.e.* protected areas) to be related to greater mammalian functional diversity. We therefore predict that the proportion, proximity, and/or conservation status of protected areas will be significant features in all models.

We created three candidate model sets, each with a functional diversity metric as the response, and habitat variables measured within a spatial scale (natural features, anthropogenic features, and protected areas; Table 1) as the predictors. Each candidate model set contained 20 models, one representing each spatial scale. The response variables were assessed for an appropriate probability distribution (*sensu* Zuur 2010). Functional richness was modeled using a gamma family function (inverse link), whereas evenness and dispersion were modeled using a Gaussian family functions. We used the *stepAIC* function of the *MASS* package (Ripley et al. 2013), which uses a step-wise procedure that ranks model Akaike Information Criterion values (AIC; Burnham & Anderson 2004) to determine the best fit model for each spatial scale, and observed the consistency of predictor variables across spatial scales.

Spatial scales best predicting mammal functional diversity

To determine the best-supported spatial scale explaining mammal functional diversity, we compared the AIC weights of the models created at each spatial scale within each candidate model set. The model(s) within a set with the highest AIC weight were identified as the best-supported model, and hence 'characteristic scale' (*sensu* Holland et al. 2004) for predicting mammalian function diversity. All statistical analyses were performed in R v3.4.2 (R Foundation for Statistical Computing 2017) and we tested for adherence to all model assumptions prior to statistical analyses (*sensu* Zuur 2010). Results are presented as mean ± standard error unless otherwise specified.

Results

We obtained repeat detections, measured as any photo taken over 10 months of observations, for 15 mammal species across 64 camera sites: coyote (*Canis latrans*; 40170 photos), fisher (*P. pennanti*; 27496 photos), red fox (*Vulpes vulpes*; 1800 photos), moose (*Alces alces*; 22369 photos), elk (*Cervus canadensis*; 3912 photos), white-tailed deer (*Odocoileus virginianus*; 18912 photos), mule deer (*O. hemionus*; 2481 photos), least-, short-, and long-tailed weasel (*M. nivalis*, *M. ermina*, and *M. frenata*; 11, 1189, and 804 photos respectfully), northern flying squirrel (G*laucomys sabrinus*; 3712 photos), red squirrel (*Tamiasciurus hudsonicus*; 8194 photos), snowshoe hare (*Lepus americanus*; 6596 photos), striped skunk (*Mephitis mephitis*; 67 photos), and porcupine (*Erethizon dorsatum*; 93 photos; Fig. 2). These detections totaled 137,807 photos over 18,118 camera trap days, with 91% (or 125,856) of photos collected in protected areas protected areas. On average 2,153 ± 168 mammalian photos were recorded at each camera site. There was no significant correlation between the number of photos recorded at each camera site and the distance of the site to the nearest protected area. More photos were recorded at sites with little disturbance (Pearson correlation: r = -0.28, p = 0.03, df = 62), and at sites on the east side of the study area (Pearson correlation: r = 0.26, p = 0.03, df = 62).

Mammalian functional diversity metrics varied among sites (functional richness = 2.81 ± 0.15, functional evenness = 0.33 ± 0.02, functional dispersion = 0.82 ± 0.03). Mammalian evenness and mammal dispersion were significantly correlated (Pearson correlation; *r* = 0.56, *df* = 64, p < 0.0001), whereas mammal richness was not correlated with either mammalian evenness (Spearman rank correlation; rho = -0.11, *df* = 64, *p* = 0.38) or mammalian dispersion (Spearman rank correlation; rho = 0.15, *df* = 64, *p* = 0.23).

Protected areas rarely explain mammal functional diversity

The BHB mesocosm is composed of 763 PAs, which range in size from multiple small conservation easements at 1.2 m^2 up to Elk Island National Park at 134,464.5 km^2 (mean = 784.1 km^2 ± 290 km^2; Figure 3.1). Despite this substantial and complex network, we determined that protected areas rarely explained observed functional diversity metrics. The exception is for functional dispersion at large scales: at small scales species are similar in their ecological roles, whereas at large spatial scales species differentiate their ecological roles the farther sites are from protected areas, although this effect was not significant (Figure 3.4B).

Localized natural features promote functional diversity and widespread anthropogenic features suppress it

Natural features generally have a positive relationship with functional diversity metrics across all spatial scales (Figure 3.4A-C). However, natural features best explain functional diversity at small scales (scales < 2000m), and these are generally positive relationships: functional evenness significantly increases with deciduous and coniferous forests at small scales (Figure 3.4C) and are also important for functional dispersion (Figure 3.4B) and richness (Figure 3.4A).

Anthropogenic features generally have a negative relationship with functional diversity metrics across all spatial scales, the exception being linear features at some small (Figure 3.4C) and intermediate scales (Figure 3.4B). Anthropogenic features best predict functional diversity at large scales (scales > 2000m), and these are generally negative relationships: functional richness decreases with linear features (Figure 3.4A), functional dispersion decreases with development (Figure 3.4B), and functional evenness decreases with both cultivation and development (Figure 3.4C).

Mammal functional diversity is explained by both near and distant landscape features

No single scale best explains functional evenness, diversity, or richness diversity metrics. Model AIC weights were spread more or less across all scales of mammal diversity, with no model explaining more than 40% of the weight of evidence (Figure 3.4A-C). Best-fit models carrying the most weight of evidence were 4250 m for functional richness (AIC_W = 12%, null deviance = 27.97, *df* = 61 df; residual deviance = 27.95, *df* = 60), 3500 m for functional dispersion (AIC_W = 39%, null deviance = 4.55, *df* = 63; residual deviance = 3.69, *df* = 59), and 500 m for functional evenness (AIC_W = 25%, null deviance = 1.24, *df* = 63; residual deviance = 1.03, *df* = 61). It appears landscape features near to, and farther from, camera sites were equally important in explaining mammalian functional diversity (Appendix 2).

Discussion

Protected areas (PAs) are not significant predictors of mammal functional diversity across the BHB's PA mesocosm. Instead, a combination of natural and anthropogenic features best explain functional diversity. Moreover, features up to 5 km away were as important as features close by; what happens outside of protected areas, affects biodiversity inside protected areas. We found within this PA network what others have found for single PAs: habitat features surrounding PAs are critical to their function (DeFries et al. 2010; Leroux & Kerr 2013). For PA networks to conserve biodiversity, the working landscape between PAs must also work to maintain biodiversity.

Protected areas and biodiversity conservation

Assuming that PA networks are effectively designed for biodiversity conservation, these results suggest that the value of PAs within a PA network is dependent on the composition and configuration of the surrounding landscape: what happens outside of a PA affects the conservation value of the PA within the PA network. As a result, the effective area of a PA network might be either larger, or smaller, than what is mapped (Weins 2009; DeFries et al. 2010). Baker (2016) found that the effective conservation area of three parks in the southern United States was much smaller than mapped – all carnivores avoided the edge of the protected areas and were sensitive to human disturbance within protected areas. The conservation value of new PAs, either as stand-alone areas or as one component of a PA network, is dependent on the natural and anthropogenic features in the surrounding landscape. If PA networks are instead designed as "paper networks", the ineffectiveness of paper parks networks may also be extended across spatial scales.

The escalating extent and density of global anthropogenic disturbance makes landscapes of high habitat loss and fragmentation increasingly abundant (Foley et al. 2005). These landscapes frequently experience a "ghost of predation past", where large predators have experienced prosecution from human-wildlife conflict (Berger 1999; Woodroffe et al. 2005) or range contraction correlated to post-European settlement (Laliberte & Ripple 2006). Our study takes place on such a landscape and is therefore relevant to many landscapes globally being considered for PA networks. Only 3.6% of mammalian geographic ranges are situated within protected areas in highly suitable habitat – the other 96.4% are in areas of high anthropogenic disturbance. This disturbance is directly related to extinction risk (Crooks et al. 2017), where both protected areas, and the landscape surrounding them, need to be better managed to improve natural habitats (DeFries et al. 2010) . For example, Shackelford et al. (2017) found evidence for a trade-off between mammalian conservation and development at large scales. Our research highlights managers need to be considering land use decisions at all spatial scales to prevent significant species extinctions in the face of rapid landscape change.

Processes moderating biodiversity in working landscapes

Ecological processes change among spatial scales (Wiens 1989; Dunning et al. 1992; Holling 1992; Levins 1992; Liebold et al. 2004; Tscharntke et al. 2012), and hence so do biodiversity-habitat relationships (Fahrig 2003; Hewitt et al. 2010). The consistency of AIC weights between our scale models (Figure 3.4.) demonstrates the importance of considering multiple scales when implementing PA networks within landscapes. At small scales, natural habitat is the most important for conserving biodiversity; at larger scales mitigating anthropogenic features is the most important. Foundational theoretical research predicts this divide between biotic and abiotic process governing ecological patterns at small vs. large scales (summarized in Tscharntke et al. 2012), and are consistent with our findings; at large scales, abiotic features override local interacting biotic features, and this divide can be amplified when measured at the community level (Ricklefs 1987). We contend landscape-scale anthropogenic features might be overriding local natural features – whether within or between PAs – that are beneficial to biodiversity.

Alternatively, either (1) beta diversity, and or (2) landscape-moderated functional trait selection (Tscharntke et al. 2012), may be moderating biodiversity-habitat relationships with the BHB mesocosm. The dissimilarity of local communities across the BHB may determine the landscape scale biodiversity patterns and override potential negative relationships between biodiversity and habitat fragmentation, habitat loss, or anthropogenic features at local scales (Tscharntke et al. 2012). For example, in an elegant example of controlled habitat loss and habitat fragmentation, Rubene et al. (2015) found that beta diversity best predicted local wild bee and wasp species richness when compared to either habitat loss or fragmentation. In a similar conclusion to ours, they infer that conservation efforts are most effective when applied at multiple spatial scales. However, landscapes can also moderate the functional traits of species: this moderation can shape the functional role of species found at smaller scales within the landscape (Tscharntke et al. 2012) and may be moderating the functional diversity-habitat relationships observed on the BHB mesocosm. Gamez-Virues et al. (2015) highlight the importance of a diversity of land cover types at landscape scales for maintaining diverse functional traits at local scales. They show the simplification of landscapes by agriculture (especially monocultures) filters out functional traits at both local and landscape scales, and that this ‘biotic homogenization’ is a significant contributor to biodiversity decline.

Recommendations for future conservation

In light of the CBD 2020 targets, newly implemented protected areas will have the highest biodiversity conservation value if (1) placed in landscapes with little anthropogenic disturbance, or (2) are accompanied by significant restoration efforts in the surrounding working landscape matrix. To be effective, conserving natural features, and mitigating anthropogenic disturbance, within and around protected area networks is required. More importantly, managing anthropogenic footprint between protected areas will increase the conservation value of existing, as well as new, protected areas networks. Although important components of conservation, protected area networks are not a stop-gap fix within already disturbed landscapes; land use decisions must prioritize conserving natural features for biodiversity scaling relationships to avoid extending the ineffectiveness of ‘paper parks’ into ‘paper networks’.

Literature cited

Alberta Wildlife Predator Control Compensation Program. 2017. Accessed June 22, 2017. http://aep.alberta.ca/fish-wildlife/wildlife-damage-control-programs/wildlife-predator-compensation-program.aspx

Alberta Status Listing. 2015. Alberta Wild Species General Status Listing. Accessed June 1, 2017. http://aep.alberta.ca/fish-wildlife/species-at-risk/albertas-species-at-risk-strategy/general-status-of-alberta-wild-species/documents/SAR-2015WildSpeciesGeneralStatusList-Mar2017.pdf.

Amarasekare P. 2003. Competitive coexistence in spatially structured environments: a syndissertation. Ecology Letters **6**:1109–1122.

Baker AD. 2016. Impacts of Human Disturbance on Carnivores in Protected Areas of the American Southwest. University of Louisiana at Lafayette, PhD dissertation.

Berger J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. Proceedings. Biological sciences **266**:2261–7. The Royal Society.

Broadley K. 2017. The implications of animal movement on camera detections as a means to monitor density. University of Alberta.

Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL. 2006. Global biodiversity conservation priorities. Science (New York, N.Y.) **313**:58–61.

Bruner AG, Gullison RE, Rice RE, da Fonseca GAB. 2001. Effectiveness of Parks in Protecting Tropical Biodiversity. Science **291**(5501):125-128.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Burnham KP, Anderson DR. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research **33**:261–304.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675–685.

Convention on Biological Diversity. 2020. Target 11 – Technical Rationale extended (provided in document COP/10/INF/12/Rev.1). Accessed November 17, 2017. https://www.cbd.int/sp/targets/rationale/target-11/

Crooks KR, Burdett CL, Theobald DM, King SRB, Di M, Rondinini C. 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proceedings of the National Academy of Sciences **114**(29):7635-7640.

DeFries R, Karanth K, Pareeth S. 2010. Interactions between protected areas and their surroundings in human-dominated tropical landscapes. Biological conservation **143**(12): 2870-2880.

Di Minin E, Toivonen T. 2015. Global Protected Area Expansion : Creating More than Paper Parks. BioScience **65**:637–638.

Dudley N, Stolton S. 1999. Conversion of paper parks to effective management: developing a target. Report to the WWF-World Bank Alliance from the IUCN/WWF Forest Innovation Project.

Dunning JB, Danielson BJ, and Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. Oikos:169-175.

Findlay CS, Houlahan J. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation biology **11**(4):1000-1009.

Fisher JT, Anholt B, Volpe JP. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecology and Evolution **1**:517–528.

Fisher JT, Bradbury S. 2014. A multi-method hierarchical modeling approach to quantifying bias in occupancy from noninvasive genetic tagging studies. The Journal of Wildlife Management **78**:1087-1095.

Gagic V, et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society of London B: Biological Sciences **282**(1801):20142620.

Geldmann J, Barnes M, Coad L, Craigie ID, Hockings M, Burgess ND. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation **161**:230–238.

Haskell JP, Ritchie ME, Olff H. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature **48**:527–530.

Holland JD, Bert DG, Fahrig L. 2004. Determining the spatial scale of species' response to habitat. BioScience **54**:227-233.

Holling CS. 1992. Cross-Scale morphology, geometry, and dynamics of ecosystems. Ecological monographs **62**(4):447-502.

Laliberte AS, Ripple WJ. 2004. Range contractions of North American Carnivores and Ungluates. AIBS Bulletin **54**(2):123-138.

Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology **91**:299–305.

Laliberté E, Legendre P, Shipley B. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. https. cran. r-project. org.

Le Saout S, Hoffmann M, Shi Y, Hughes A, Bernard C, Brooks TM, Bertzky B, Butchart SH, Stuart SN, Badman T, Rodrigues AS. Protected areas and effective biodiversity conservation. 2013. Science **342**(6160):803-5.

Leibold MA, et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters **7**:601–613.

Leroux SJ, Kerr JT. 2013. Land Development in and around Protected Areas at the Wilderness Frontier. Conservation Biology **27**:166–176.

Linden DW, Fuller AK, Royle JA, Hare MP. 2017. Examining the occupancy-density relationship for a low density carnivore. Journal of Applied Ecology **54**(6):2043-2052.

Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence : the primary components of functional diversity. Oikos **111**(1):112–118.

Maxwell SL, Fuller RA, Brooks TM, Watson J. 2016. The ravages of guns, nets and bulldozers. Nature **536**:143–145.

McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution **21**.

Patriquin D. 2014. Landscape of Hope: The influence of place and social capital on collaborative action in sustainable management. University of Alberta PhD dissertation.

Pickett ST, Cadenasso ML. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science **269**(5222):331-334.

R Foundation for Statistical Computing. 2017. R: A language and environment for statistical Computing. Vienna, Austria

Ricklefs R. 1987. Community diversity: relative roles of local and regional processes. Science **235**:167–171.

Ripley B, Venables B, Bates D, Hornik K, Gebhardt A. 2013. Package "MASS." CRAN Repos.

Rubene D, Schroeder M, Ranius T. 2015. Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. Biological Conservation **184**:201-208.

Santini L, Saura S, Rondinini C. 2016. Connectivity of the global network of protected areas. Diversity and Distributions **22**:199–211.

Shackelford N, Standish RJ, Ripple W, Starzomski BM. 2017. Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. Conservation Biology. DOI: 10.1111/cobi.13036

Simberloff D, Abele LG. 1982. Refuge Design and Island Biogeographic Theory: Effects of Fragmentation. The American Naturalist **120**:41–50.

Steenweg R, Whittington J, Hebblewhite M, Forshner A, Johnston B, Petersen D, Shepherd B, Lukacs PM. 2016. Camera-based occupancy monitoring at large scales : Power to detect trends in grizzly bears across the Canadian Rockies. Biological Conservation **201**:192–200.

Stewart FEC, Fisher JT, Burton AC, Volpe JP. 2018. Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. Ecosphere. DOI: 10.1002/ecs2.2112

Tilman D. 2001. Functional diversity. Encyclopedia of biodiversity **3**(1):109-120.

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science **277**:1300–1303.

Tscharntke T et al. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews **87**:661–685.

Tscharntke T, Sekercioglu CH, Dietsch T V., Sodhi NS, Hoehn P, Tylianakis JM. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology **89**:944–951.

Villeger S, Mason N, Mouillot D. 2008. New multidimensional functional diversity indives for a multifaceted framework in functional ecology. Ecology **89**:2290–2301.

Watson JEM, Dudley N, Segan DB, Hockings M. 2014. The performance and potential of protected areas. Nature **515**:67–73.

Wheatley M, Johnson C. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity **6**(2):150-159.

Wolf C, Ripple WJ. 2017. Range contractions of the world's large carnivores. Royal Society Open Science **4**(7):170052.

Woodroffe R, Thirgood S, Rabinowitz A. eds., 2005. People and wildlife, conflict or co-existence? (No. 9). Cambridge University Press.

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM. 2014. Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioralstate: pumas as a case study. Landscape Ecology **29**(3):541-557.

Tables and Figures

Table 3.1 Habitat features hypothesized to explain mammal diversity across the Beaver Hills Biosphere mesocosm

Category	Habitat features	Description
Natural features	Deciduous forest	Proportion of deciduous forest; native natural forest stands of primarily aspen or balsam poplar
	Coniferous forest	Proportion of coniferous forest; native natural forest stands of primarily white or black spruce
	Mixed wood forest	Proportion of mixed wood forest; native natural forest stands of both deciduous and coniferous
	Wetlands	Proportion of water bodies; wetlands, lakes, and streams
	Grassland	Proportion of grassland; native natural grass cover
	Shrub-land	Proportion of shrub-land; native natural shrub cover
Anthropogenic features	Linear	Proportion of linear features; lines of urban footprint (e.g. hard roads, vegetated roads, tails, seismic lines, pipelines, and transmission lines)
	Block	Proportion of block features; blocks of urban footprint (e.g. well pads and rural residential)
	Cultivation	Proportion of cultivation; agricultural lands used for cultivation
	Development	Proportion of development; residential – industrial lands (e.g. current country-residential and industrial developments)
Protected areas	Protected Area	Proportion of protected areas; protected area of any status (e.g. public lands, provincial parks, provincial recreation areas, national parks, conservation areas, and NGO sites)
	Status	Status of land protection at each camera site location: 0 – Private land, 1 – Public/county lands, 2 – Provincial conservation land, 3 – National park, 4 – Provincial recreation land, 5 – Non-governmental organization lands
	Distance	Proximity of a camera site to the nearest protected area.

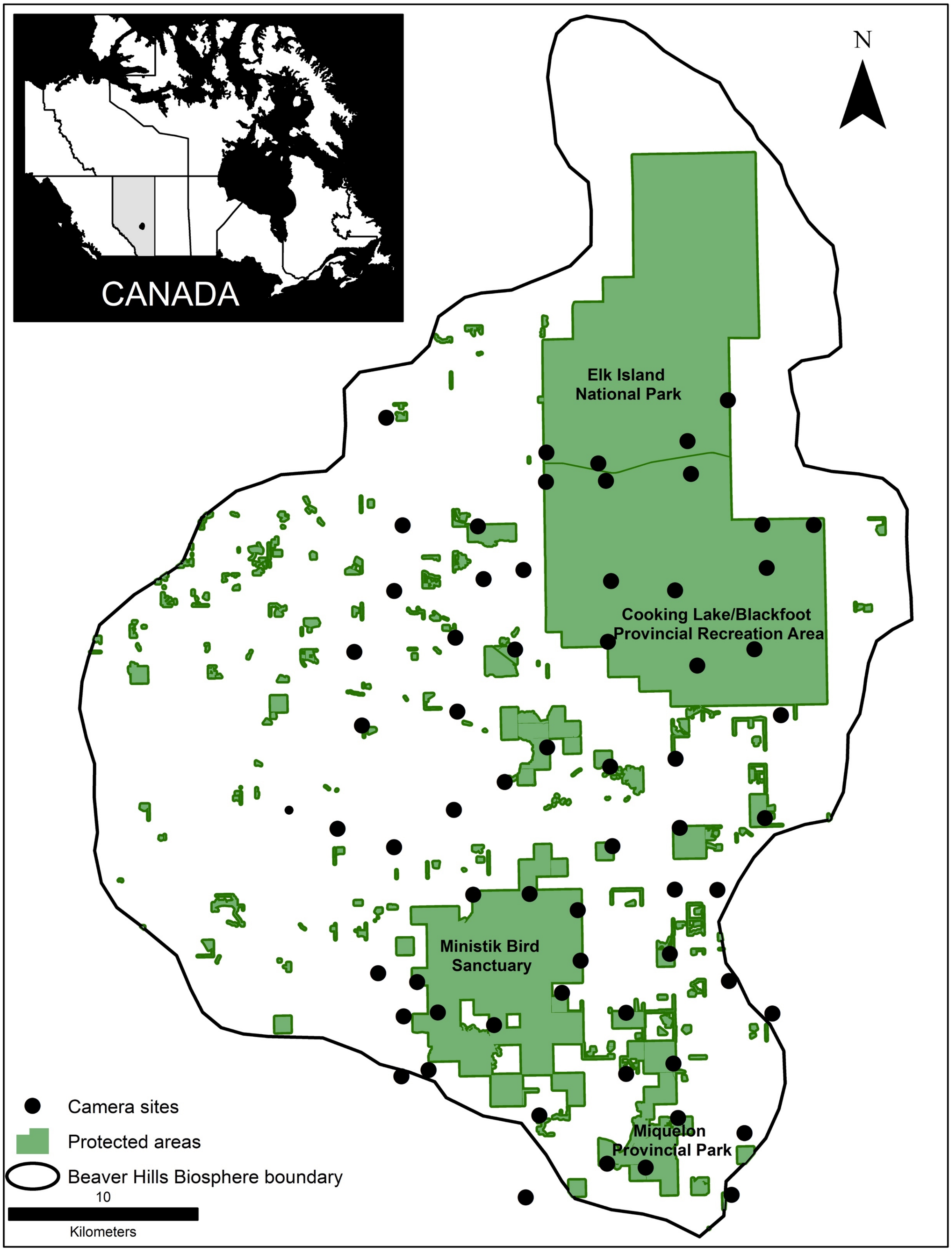

Figure 3.1 Sixty-four wildlife camera sites were deployed across the protected area network within the Beaver Hills Biosphere of east-central Alberta, Canada. Large national parks, and

provincial parks and recreation conservation lands are identified. All smaller protected areas represent public/county lands or Non-government organization lands. Private lands are white.

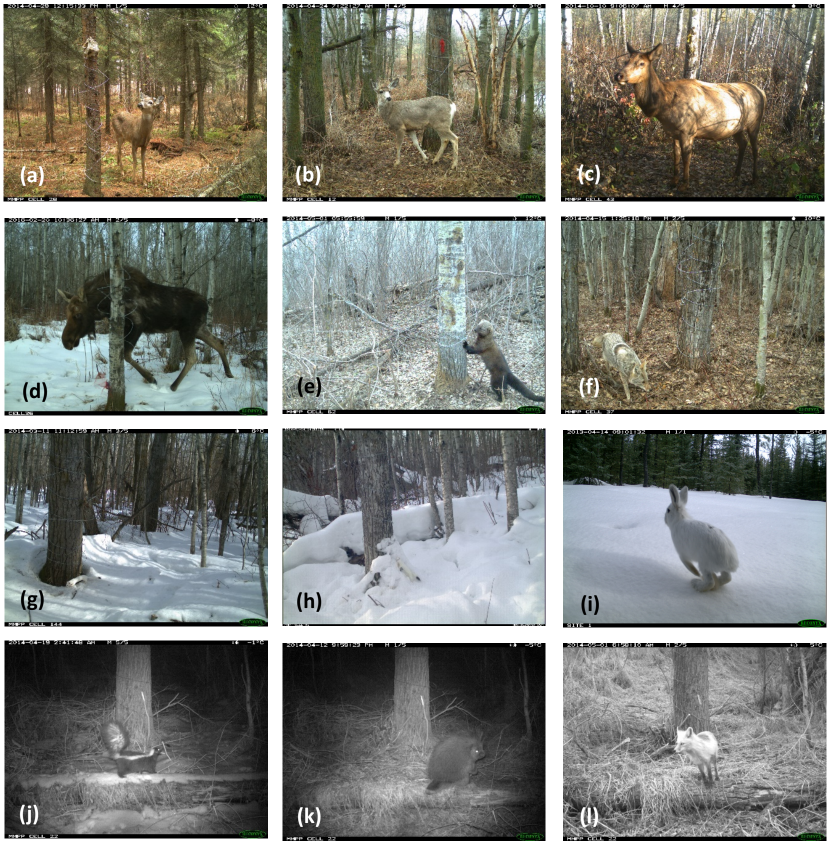

Figure 3.2 Wildlife cameras documented repeat occurrences of (a) while tailed deer, (b) mule deer, (c) elk, (d) moose, (e) fisher, (f) coyote, (g) long-tailed weasel, (h) sort-tailed weasel, (i) snowshoe hare, (j) striped skunk, (k) porcupine, (l) red fox, as well as red squirrels, northern flying squirrels, and least weasels.

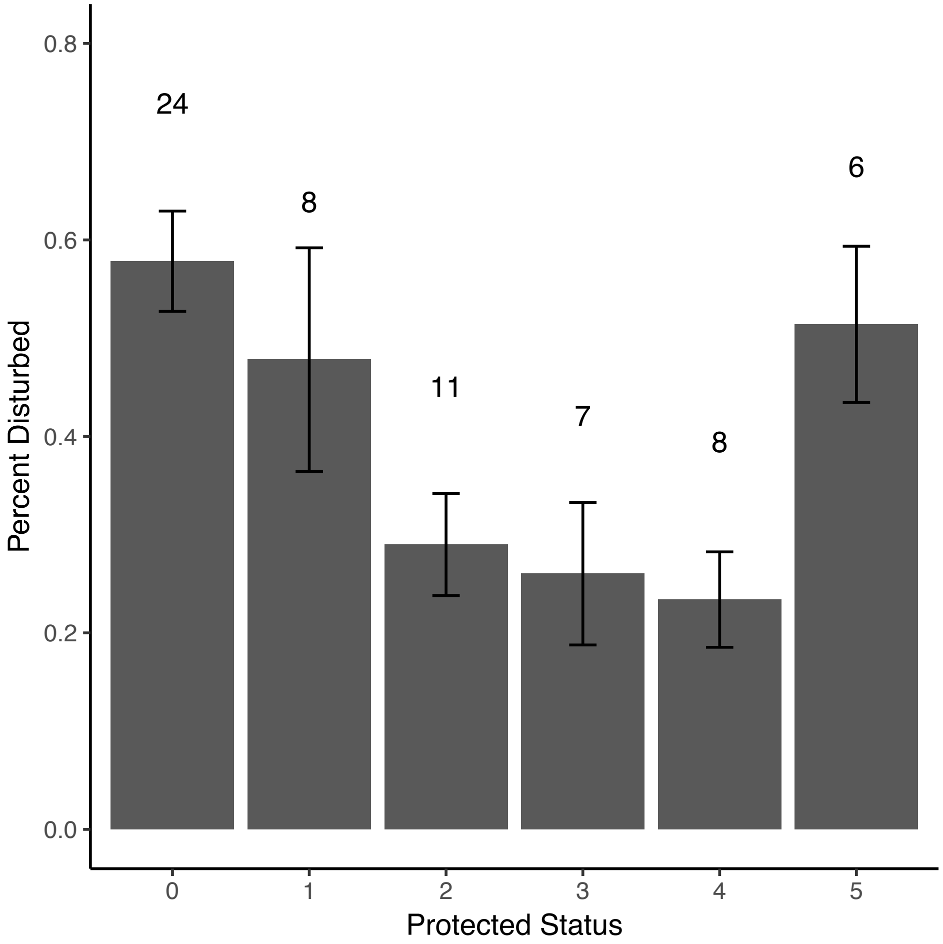

Figure 3.3 The averaged percent disturbed landscape (cultivation, development, linear and block features) within a 500-m buffer of camera sites grouped by protected area status. Statuses refer to 0 – private land, 1 – public/county lands, 2 – Provincial conservation lands, 3 – National Parks, 4 – Provincial recreation lands, and 5 – Non-government organization lands. Bars and whiskers represent means +/- standard errors, and numbers above bars represent the number of camera sites (N) within each status

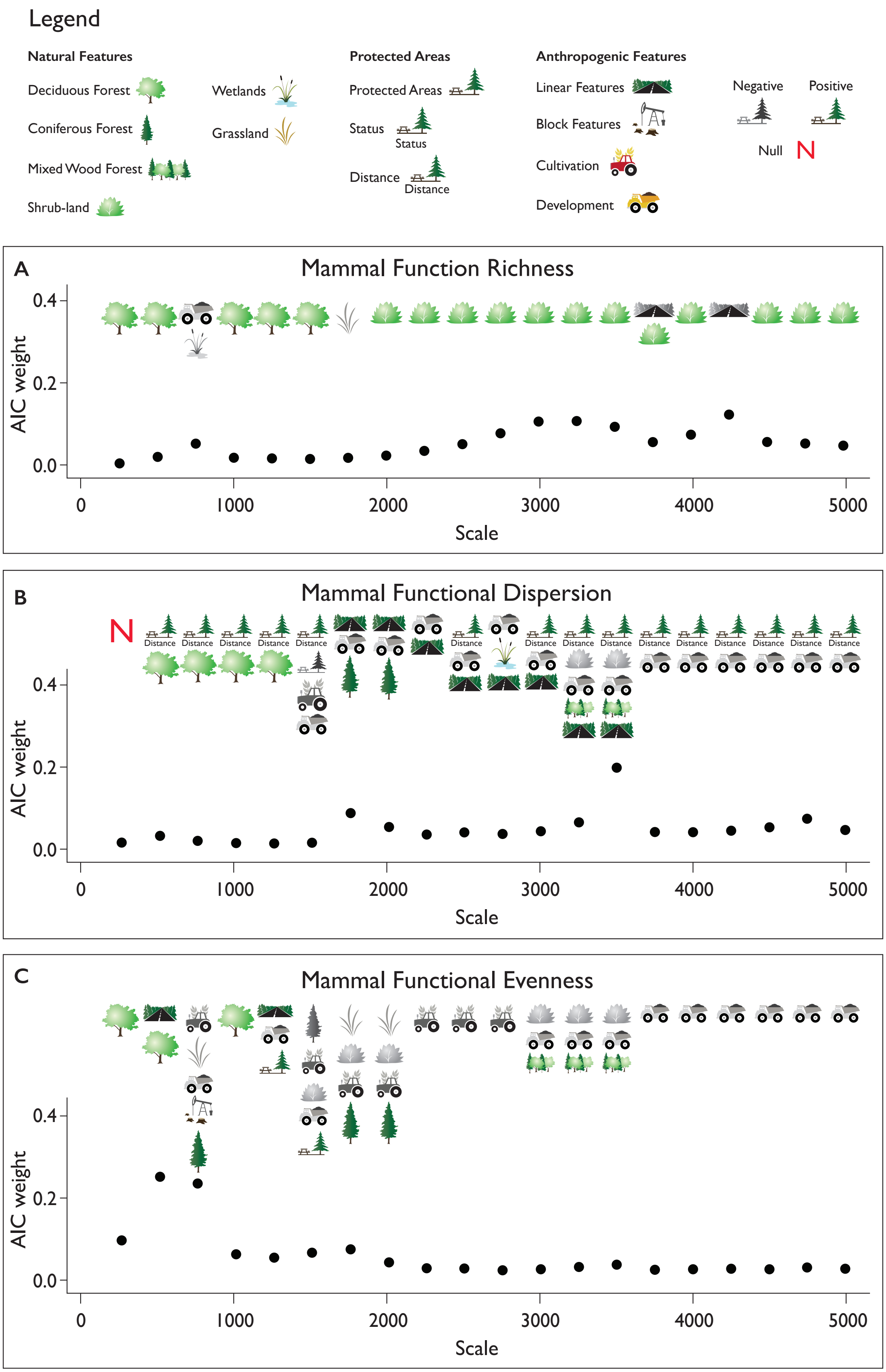
Legend
Natural Features
Deciduous Forest
Coniferous Forest
Mixed Wood Forest
Shrub-land
Wetlands
Grassland
Protected Areas
Protected Areas
Status
Status
Distance
Distance
Anthropogenic Features
Linear Features
Block Features
Cultivation
Development
Negative
Positive
Null
N
A
Mammal Function Richness
AIC weight
0.0
0.2
0.4
0
1000
2000
3000
4000
5000
Scale
B
Mammal Functional Dispersion
N
Distance
AIC weight
0.0
0.2
0.4
0
1000
2000
3000
4000
5000
Scale
C
Mammal Functional Evenness
AIC weight
0.0
0.2
0.4
0
1000
2000
3000
4000
5000
Scale

Figure 3.4 Across a heterogeneous working landscape, mammal functional richness (A), dispersion (B), and evenness (C) were best predicted by positive relationships with natural features at small scales, and negative relationships with anthropogenic features at large scales. When compared across spatial scales, model AIC weights were similar and demonstrate the importance of considering biodiversity-habitat relationships at all scales when implementing conservation and management considerations.

CHAPTER IV

Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use

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Introduction

Animal ecologists quantify populations and communities by counting animals across space and time. Point-surveys of individuals or species are commonly collected from stationary sampling locations (*i.e.* survey sites) through a variety of field methods (avian point count surveys, mist-netting surveys, live-trapping surveys, camera trap surveys, *etc.*) and are generally referred to as species occurrence data (SOD): the sequence of species detections at a single position in space and time (Scott et al. 2002). However, although mobile animals move in and around survey sites, rarely does the interpretation of SOD explicitly consider the influence of animal movement. Movement – changes in location through time – is a dynamic space-time process that makes it difficult to accurately characterize where and when animals are located, and how the cumulative locations of individuals over time define patterns of population distribution and relative abundance (Hooten et al. 2017), as is the goal of point-count surveys.

Ecological inferences derived from SOD assume that spatial variation in species occurrence among survey sites represents variation in relative abundance, whereas temporal variation in species occurrence within a survey site reflects variation in the proximity of animal space use (*i.e.* the “activity centre” of Royle et al. 2013; also see Turchin 1998, MacKenzie 2006, Burton et al. 2015). However, rarely have researchers explicitly tested the assumed relationships between measures derived from SOD (*e.g.* occurrence, detection probability, or occupancy – occurrence corrected for detection probability) and inferred ecological processes (abundance or density, space use, and habitat selection) despite this being a prerequisite to accurate data interpretation (Burton et al. 2015). A few studies have attempted to incorporate individual movement data empirically into estimates derived from SOD by combining occurrence from both point-count and telemetry datasets (*e.g.* Gopalaswamy et al. 2012, Sollmann et al. 2013; Popescu et al. 2014). However, a basic and general question remains: How does variability in the magnitude of species movement, versus variability in the proximity of species space use, affect a survey's ability to sample a population? This question focuses on species rather than individual identification – a common goal of point-counts surveys – and therefore assumes that movement and space use from a random sample of individuals are representative of the population.

One approach to investigate assumptions inherent in species occurrence data is to statistically relate occurrence data from common survey methods to simultaneously collected movement data around survey sites. Developments in Global Positioning System (GPS) technology enable biologists to obtain detailed individual movement patterns through GPS telemetry rather than relying on traditional tracking techniques (Kays et al. 2015, but also see Ranacher et al. 2016). Each GPS point collected from a GPS collar on an active animal is considered an animal location, and its distance to survey sites can be quantified. With the survey site as the sampling unit, we define the proximity of species space use as the mean distance between a survey site (*e.g.* camera trap) and all GPS locations, regardless of individual animal identity, collected through space and time (P_j; analogous to the Royle et al. 2013 "activity centre", but quantified at the population rather than individual level);

$$P_j = \frac{1}{N}\sum_{i \to N} d_i \qquad (Eq. 1)$$

Where N is the total number of GPS locations collected across all individuals within the study, i represents each GPS location, and d_i is the distance between a survey site, j, and i. Again, with the survey site as the sampling unit, we define the magnitude of species movement (M_j) as the variation in d_i through space and time (Figure 4.1);

$$M_j = \frac{1}{N-1} \sum_{i \to N} (d_i - P_j)^2 \quad (Eq. 2)$$

This framework ensures that each survey site has a value for both P and M.

For mammals, camera traps are increasingly used to obtain SOD for a variety of ecological research and conservation applications across increasingly large spatial and temporal scales (Burton et al. 2015; Steenweg et al. 2017). However, cameras lack the high resolution of individual movement patterns that can be derived from radio- or GPS-telemetry (Pacifici et al. 2017). Therefore, cameras and telemetry provide fundamentally different kinds of information, and our objective was to use one method to assess assumptions inherent in the other.

We used fisher (*Pekania pennanti*) detection data collected from a camera trap array, paired with data collected from concurrent overlapping GPS-collared fishers, to test whether variability in species detection frequency is better explained by the proximity of species space use (P_j), or variation in the magnitude of species movement (M_j), across three temporal detection resolutions (survey-wide presence-absence, monthly and weekly detections). Movement variability will dictate how frequently animals become available for detection at a point sample (camera trap), particularly for wide-ranging species sampled in continuous habitat (Efford & Dawson 2012). For this reason, we hypothesized that variability in the frequency (or probability) of species occurrence would be better explained by the magnitude of fisher movements around a site, M_j, than by the proximity of fisher space use to the site, P_j. As the temporal sampling resolution of the species detections increases (from survey presence-absence to monthly or weekly counts) there should be an increasing sensitivity to the magnitude of fisher movement relative to a site: binary presence-absence data should be least sensitive to movement, as the species must be detected only once during the entire survey to be considered present. We therefore predict that variability in M_j will better explain survey-wide presence-absence than monthly or weekly counts.

Currently, typical point-surveys assume that SOD are representative of animal activity in space and time, thus making implicit assumptions about animal movement, to which resulting ecological inferences could be sensitive (Burton et al. 2015; Neilson et al. 2018). We sought to explicitly quantify the contribution of animal movement to variations in SOD and evaluate how the inference of ecological process might change if the magnitude of species movement, rather than proximity of species space use, is the better predictor of species occurrence data.

Methods

Study system and data collection

Fisher are a medium-sized (2 - 7 kg; F. Stewart, unpublished data) Mustelid native to North American forests (Powell 1982). They have moderate body and home range size (Lindstedt et al. 1986) representative of mammal species investigated in many previous camera trap surveys (Burton et al. 2015), making them an attractive model for evaluating the contribution of movement parameters to species occurrence data. We sampled fisher occurrence in central Alberta, Canada, in an area known as the Cooking Lake Moraine (CLM; Figure 4.2). This 1,596 km^2 landscape of rolling knob-and-kettle topography supports a diverse mammal community

(Chapter III) and is dominated by small wetlands, with trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and scattered pockets of spruce (*Picea glauca* and *P. mariana*). It is a patchwork of exurban development, agriculture, protected forested areas, and privately owned green space. It is surrounded by unsuitable agricultural lands on all sides, making this a fairly closed population.

We established 64 camera trap sites in a 4 x 4 km^2 systematic grid cell array across the CLM (Figure 4.2). At each site the camera photographed the area surrounding a tree baited with ~5 kg of beaver meat and a commercial scent lure (O'Gorman's™ Long Distance Call). Fisher detections were recorded using Reconyx™ infra-red cameras (models PC900 and PC85; *sensu* Fisher et al. 2014). Camera traps were deployed from December 2015 to April 2016 and checked monthly. From these temporally continuous data we binned fisher detections weekly (0-15), monthly (0-4), and as presence-absence (0/1) across the whole survey.

We live-trapped and GPS-collared 10 fisher individuals (5 male: 5 female) from November 2015 through March 2016. We distributed traps in a stratified random design that aimed to sample animals distributed as randomly as possible relative to camera traps, and assumed collared animals are representative of the true distribution of fishers in this population. Fisher were captured in covered cage traps (Tomahawk 109 live-trap, Tomahawk, WI) and sedated with a combination of ketamine (100 mg/ml, 12 mg/kg) and midazolam (5 mg/ml, 0.3 mg/kg). We fitted fisher with GPS tracking collars (E-obs Collar1A™; Grünwald, Germany) containing a GPS microchip, a tri-axial accelerometer, and ultra-high frequency transmitter for telemetry and data download. The GPS was programmed with a 5-minute fix schedule when the accelerometer recorded a speed greater than 10 cm/s.

All data were collected under Canadian Council of Animal Care permits approved by InnoTech Alberta (2070M-A02/048/15-P01), and the University of Alberta and University of Victoria (AUP00000518) Animal Handling and Care Committees.

Statistical methods

We used both regression and occupancy modelling frameworks to test whether fisher detections across the camera trap array were more closely related to the proximity of fisher space use (P_j) or magnitude of fisher movement (M_j) around each camera trap. Our basic response data format involved a site by weekly fisher detection matrix at each camera trap; this SOD is denoted as Y_{jt}, the presence/absence (or count) of any fisher detected at camera trap j in each survey t. When investigating temporal variation in SOD, this matrix was collapsed into monthly counts (0-4) and total survey presence-absence (0/1). Our predictor data set is comprised of two main variables measured at the site level; M_j and P_j. We measured the distance d_i (in metres) between each camera (N = 64) and all GPS-telemetry points, and then calculated summary statistics of these distances – minimum, maximum, mean (P_{jt}; Eq 1.), and standard deviation (M_{jt}; Eq 2.) – using the Generate Near Table tool in ArcGIS 10.4.1 (ESRI, Redlands, CA). Mean, standard deviation, minimum, and maximum distance metrics are all highly correlated (Table A3.1); to avoid multicollinearity, we did not include more than one metric as a predictor variable within each of our models.

We treated the mean of distances d_i between the camera and all GPS locations (i) as a measure of fisher space use proximity P to camera site j (Eq 1.). We hypothesized that camera detection frequencies (Y_j) would be negatively related to fisher proximity of space use (P_j): if fishers are physically situated close to a camera site, there will be more detections than if fishers are situated far from a camera site (Figure 4.1). We predicted a negative relationship between camera detection frequencies and fisher minimum distance to be a sampling artifact – fisher must *de facto* be close to the camera to be detected, but this is not particularly informative. To quantify the magnitude of fisher movement (M_j) relative to a camera trap, we calculated the standard deviation of the distances d_i between camera trap *j* and all GPS locations (M_j; Eq. 2). We hypothesized that camera detection frequencies would demonstrate a negative quadratic relationship with fisher movement magnitude (M_j): high or no variability in fisher movements would result in fewer detections as it would represent fewer opportunities for fisher to pass through a camera field of view (Burton et al. 2015), whereas intermediate variation in animal movements should result in more camera detections (Figure 4.1). We conducted two analyses to test both spatial and temporal assumptions of SOD.

Spatial variation in species occurrence data

Ecologists assume that spatial variation in species occurrence data reflects variation in relative abundance across survey sites; sites with many detections are situated in habitats with high frequency of animal use. We hypothesized that species detections were better explained by variation in the magnitude of species movement (M_j; Eq 2.) than the proximity of species space use (P_j; Eq 1.), such that:

$$Y_j \sim \alpha + ßM_j + \varepsilon$$

To test this hypothesis we regressed camera detection data, against the mean (*i.e.* proximity of space use; P_j), standard deviation (*i.e.* magnitude of movement; M_j), and maximum distances of fisher GPS locations relative to all camera traps using generalized linear models in R (v3.3.3, R Foundation for Statistic Computing 2017).

Another way to consider SOD is as serial, binomial, detection histories – for example, the detection history 01110 observes three occurrences in five sessions. In the original formulation of occupancy modeling, detections of stationary species are obtained at discrete patches closed to movement, and hence the zeros in detection histories are considered as error – a failure to detect a species when present. Detection histories are used to estimate probability of detection given presence (p) using maximum likelihood estimation (MacKenzie et al. 2002). For mobile animals in continuous habitat, p represents frequency of site-use (Efford & Dawson 2012), with zeros entrained by both error and by the movement of the animal around the sampling site (see Burton et al. 2015 Figure 1). We hypothesized that variability in site detection probability (p) is explained by the magnitude of animal movement (M_j), whereas probability of site occupancy (ψ) is explained by proximity of animal space use (P_j). We predict:

$$\psi(.)p(M_j) \quad \text{and} \quad \psi(P_j)p(.)$$

Where each camera site (N = 64) is the sampling unit. We competed a null model, $\psi(.)p(.)$, against models that assumed occupancy (ψ), detection probability (p), or both, varied as a function of movement magnitude (M_j), and proximity of space use (P_j). Further, we predict p to change with the temporal resolution of sampling (monthly or weekly counts as sample replicates). All occupancy models were performed in PRESENCE software v11.7 (Hines 2006) and competed in an information-theoretic framework based on AIC scores (Burnham & Anderson 2002).

Temporal variation in species occurrence data

Temporal variation in species occurrence data – for example, a monthly 0111 detection history – is assumed to reflect changes in animal movements, which induces variations in the proximity of animal space use around the survey point. If this is true, we predict that sensitivity to the effects of the proximity of species space use (P_j), or magnitude of species movement (M_j), on SOD should increase with temporal sampling resolution: survey presence-absence should be least sensitive, as the species must become available only once during an entire survey to be considered present. Within both our regression and occupancy frameworks, models involving monthly counts as the response variable should better fit the data than models involving survey presence-absence data, but models involving weekly counts as the response variable should fit the data best.

To investigate the effects of temporal resolution on SOD, we competed suites of models with occurrence data measured as survey presence-absence (0/1), monthly counts (0-4), or weekly counts (0-15) of fisher detections. For these generalized linear models, we used the residual deviance to compare model fit as a measure of model sensitivity. Survey presence-absence data were modelled using a binomial family function (logit link), and weekly count data were modeled using a Poisson family function (log link). Monthly count models used a multinomial regression in the R package *nnet* (version 7.3-12, Venables & Ripley 2002), an extension of logistic regression for response variables with count data (0-4) that is not Poisson distributed (Zuur et al. 2007). Suites of regression models within each temporal resolution were competed using Akaike Information Criterion scores (AIC; Burnham & Anderson 2002). For occupancy models, we compared two suites of temporal models where species detection histories were composed of either four monthly or 15 weekly detection histories. We used the residual deviance (-2 log likelihood) to compare model fit. Results are presented as mean ± standard error unless otherwise specified.

Results

Sixty-four cameras were deployed for a total of 102 days (6,528 trap days) and collected 95,128 photos (*i.e.* animal detections) from December 2015 through early April 2016. Of these detections 12,156 were of fisher. Fisher were observed on 43 of 64 cameras (naïve occupancy = 0.67). From 10 GPS-collared individuals we obtained 28,088 fixes with 2,808 ± 1,137 fixes per individual. GPS fixes were on average 15,188 ± 1,281 m away from any camera (Figure 2). Microsatellite analysis from hair samples collected throughout the study revealed that at least 32 fishers occupied the CLM during the winter of 2015/2016 (Stewart et al. 2017). We therefore obtained GPS information from 31% of the minimum known population.

Spatial variation in species occurrence data

Variability in fisher SOD was best explained by variation in the magnitude of movement (M_j), rather than the proximity of space use relative to cameras (P_j). As predicted, a quadratic model with (M_j) better explained variation in fisher occurrence than did linear relationships. In no models did the proximity of space use (P_j) explain SOD better than a null model (Figure 4.3A).

Similarly, within the occupancy modelling framework, detection probability (p) was best explained by the magnitude of movement (M_j), rather than the proximity of species space use (P_j) relative to cameras. We competed a total of 45 monthly and 45 weekly models involving all possible combinations of maximum, mean (P_j), and standard deviation (M_j) distances as both occupancy (ψ) and/or detection probability (p) covariates (Table A3.2). The best-supported models all suggested the magnitude of movement (M_j) best explained detection probability (p). The proximity of space use (P_j) best explained site occupancy (ψ) only when M_j was included as a detection covariate (Table 4.1).

Temporal variation in species occurrence data

The relationship between species occurrence and magnitude of movement (M_j) demonstrates a consistent negative quadratic pattern across all temporal resolutions (survey, monthly, and weekly; Figure 4.3B-D). In contrast to our temporal prediction, binary presence-absence was more sensitive to M_j than were monthly or weekly species detections (model residual deviance = 72.58 for survey presence-absence temporal resolution; 76.65 for monthly temporal resolution; and 165.72 for weekly temporal resolution; Figure 4.3B).

Estimated occupancy varied slightly with temporal resolution (monthly: $\psi = 0.68$, $p = 0.65$; weekly: $\psi = 0.64$, $p = 0.32$). AIC ranking of occupancy models differed between monthly and weekly temporal resolutions, however, top models always involved movement magnitude (M_j) as an occupancy (ψ) and/or detection probability (p) covariate (Table 4.1). For monthly models, p did not vary with survey month but did vary with M_j (ER model 1 and 2 = 3.87), and ψ varied with the maximum distance between a GPS fix and the camera (ER model 2 and 3 = 70.1). For weekly models, p varied by survey week and M_j (ER model 7 and 8 = 1.96), and ψ varied with M_j (ER model 6 and 7 = 9.3). In contrast to our temporal prediction, occupancy models measured on a monthly temporal resolution demonstrate more sensitivity to this relationship than models measured on a weekly temporal resolution (monthly models deviance ranged between 255 - 300; weekly models deviance ranged between 790 – 857; Table 4.1).

Discussion

Species occurrence data (SOD) from camera traps better reflect the degree to which animals move, rather than the space that animals use. Variation in the magnitude of movement (M_j)

around a camera trap, rather than proximity of space use (P_j) to the camera trap, best explained species detections regardless of the temporal sampling resolution. Similarly, M_j best explained detection probability, and P_j only explained occupancy probability when M_j was included as a detection probability covariate. In addition, presence-absence was more sensitive to M_j than were monthly or weekly counts (Figure 4.3).

The role of movement in species detections is an implicit assumption in species occurrence research (Turchin 1998; MacKenzie 2006; Royle et al. 2013; Burton et al. 2015), and the conservation strategies derived therefrom (Morin et al. 2017; Royle et al. 2017), but rarely is movement explicitly quantified. We therefore recommend that the magnitude of species movement receive greater consideration when analyzing species occurrence data from stationary surveys. These results may be especially important for species with large movements relative to the size of the study area (*cf*. Efford & Dawson 2012).

Considerable debate on the relationships between SOD, density, and abundance is waged within the ecological literature (Steenweg et al. 2016; Linden et al. 2017, Broadley 2017; Parsons et al. 2017), with ramifications for conservation and management (Fuller et al. 2016). Previous work acknowledges the potential for a non-linear relationship between occupancy and abundance when animals display variable movement patterns between detection devices (Efford & Dawson 2012; Noon et al. 2012), and spurs calls for research that tests the assumptions of animal movement within these relationships (Ellis et al. 2014; Steenweg et al. 2016). In our test, temporal and spatial variations in species occurrence at a sampling site reflected the magnitude of animal movements, rather than the explicitly assumed variation in proximate space use and variation in relative abundance, respectfully (Turchin 1998; MacKenzie 2006; Royle et al. 2013; Burton et al. 2015). New methods are in continual development for different ways to think about the continuous sampling of camera trap data, and the resulting inferences on abundance and movement (*e.g.* Moeller 2017; Neilson et al. 2018).

The method of sampling also influences species occurrence data. For example, considerable debate exists about the use of attractants in trap studies, as this method may affect both animal movement and detection probability. Bait is required for thousands of point-count surveys; of hundreds of camera trap studies reviewed by Burton et al. (2015), two thirds targeted the camera at some form of attractant, with bait or lure being used in one third of the studies. The effect of bait will vary by target species, and for elusive carnivores such as the fisher, is argued to be the most effective use of research funds (du Preez et al. 2014). We do not expect bait to have affected detection probability in this study, as spatially-explicit capture-recapture modeling (Royle et al. 2013) did not detect any effect of trap behaviour at the population level (J. Burgar, in review). However, investigating the tortuosity of GPS movement paths of individuals relative to baited sites would be a valuable test of whether maximizing detection probability with bait truly comes at the expense of inflating species detections by increasing movement at a sampling site, relative to movements on the surrounding landscape.

Challenging the consistency of multiple data types represents an alternate tactic for addressing assumptions inherent in SOD. Popescu et al. (2014) demonstrated that camera traps reflected fisher space use in California, as fisher telemetry relocations correlated to the probability of detection by cameras; however, the spacing of cameras was much denser than in our study. In another methods comparison example, Chauvenet et al. (2017) demonstrated that distance sampling provided more accurate European boar (*Sus scrofa*) density estimates than spatially-explicit individual camera-based models because distance sampling was more robust to heterogeneity in boar group size. Our results build upon this literature in two ways: (1) by assessing animal space use and movement as separate, though associated, processes, and (2) assessing multiple measures of SOD – occurrence and detectability-corrected occupancy.

SOD methods in general, and camera traps specifically, often measure occurrence of multiple species simultaneously. Two-thirds of reviewed camera studies compared relative abundance of multiple species by contrasting observed detection rates of each (Burton et al. 2015). For example, O'Brien et al. (2003) demonstrate European wild boar to be more abundant than either Malay tapir (*Tapirus indicus*) or Sambar deer (*Cervus unicolor*) across multiple areas. Similar conclusions have been made across continents and across methods, where more vagile species receive higher frequencies of detection when compared to less vagile species, and are inferred as being more abundant (Gompper et at al. 2006; Monterroso et al. 2013; Monterroso et al. 2014; Carreras-Duro et al. 2016). However, our research suggests frequency of detections is not an accurate or robust index of relative abundance across species, as it is likely conflated by differences in species' propensity for movement. We recommend that "relative abundance" as a population index needs to be standardized by some measure of species movement propensity, such as expected home range size or movement rate (Broadley 2017), to ensure it is a meaningful metric for species comparisons within, and between, studies. Moreover, devices with consistent capacity for animal detection need to be deployed in a sampling density reflective of the movement ecology of each species (*sensu* Linden et al. 2017). Species detection rates are affected by many factors other than abundance; the expected relationships between sampling design, detectability, and ecological inference will be species specific (Burton et al. 2015), and likely influenced heavily by species density (Kjellander et al. 2004; Broadley 2017).

We demonstrate the ubiquity and importance of movement when interpreting different temporal resolutions of SOD (survey presence-absence, monthly and weekly counts). This relationship is reflected in sampling design literature. For example, MacKenzie & Royle (2005) suggest the temporal resolution of SOD should scale with species rarity: surveying more sites less frequently is more efficient for rare species, whereas surveying few sites more frequently may be better for conspicuous species. These trade-offs in survey effort have been considered across bats (Weller & Lee 2007), birds (Bried et al. 2011), reptiles (Sewell et al. 2012), and plants (Garrard et al. 2008). Much less frequently has movement variability been considered when interpreting the SOD generated by those designs, but this could be evaluated with the methods described here.

We demonstrate that inferences from ecological investigations using SOD may reflect the magnitude of species movement better than species space use. This result has important implications for how we interpret projections from wildlife distribution (or ecological niche) models (Peterson 2003), how we model future biodiversity projections from landscape and climate change (Anderson et al. 2006: Elith et al. 2009), and how we understand large-scale ecological patterns and processes.

Literature cited

ArcGIS. 2016. E.S.R.I., Environmental Systems Research Institute, Redlands, CA.

Anderson P, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**(2):129-151. 353

Broadley K. 2017. The implications of animal movement on camera detections as a means to monitor density. MSc dissertation, University of Alberta.

Bried JT, Langwig KE, Dewan AA, Gifford NA. 2011. Habitat associations and survey effort for shrubland birds in an urban pine barrens preserve. Landscape and Urban Planning **99**(3):218-225

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Boutin S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**(3):675-685

Carreras-Duro J, Moleó M, JBarea-Azcón JM, Ballesteros-Duperón E, Virgós E. 2016. Optimization of sampling effort in carnivore surveys based on signs: A regional scale study in a Mediterranean area. Mammalian Biology-Zeitschrift für Säugetierkunde **81**(2):366 205-213

Chauvenet AL, Gill RMA, Smith GC, Ward AI, Massei G. 2017. Quantifying the bias in density estimated from distance sampling and camera trapping of unmarked individuals. Ecological Modeling **350**:79–86 du Preez BD, Loveridge AJ, Macdonald DW. 2014. To bait or not to bait: a comparison of camera-trapping methods for estimating leopard Panthera pardus density. Biological Conservation **176**:153-161.

Efford MG, Dawson DK. 2012. Occupancy in continuous habitat. Ecosphere **3**(4):1-15.

Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual review of ecology, evolution, and systematics **40**:677-697.

Ellis M, Ivan J, Schwartz M. 2014. Spatially explicit power analyses for occupancy-based monitoring of wolverine in the U.S. Rocky Mountains. Conservation Biology **28**:52–62.

Fisher JT, Wheatley M, Mackenzie D. 2014. Spatial patterns of breeding success of grizzly bears derived from hierarchical multistate models. Conservation Biology **28**(5):1249–1259. 378

Fuller AK, Linden DW, Royle JA. 2016. Management decision making for fisher populations informed by occupancy modeling. The Journal of Wildlife Management **80**(5):794-802. 381

Garrard GE, Bekessy SA, McCarthy MA, Wintle BA. 2008. When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. Austral Ecology **33**(8):986-998. 384

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin **34**(4):1142-1151. 387

Gopalaswamy AM, Royle JA, Delampady M, Nichols JD, Karanth KU, Macdonald DW. 2012. Density estimation in tiger populations: Combining information for strong inference. Ecology **93**(7):1741–1751. 390

Hines JE. 2006. PRESENCE2: software to estimate patch occupancy and related parameters. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA. http://www.mbr-pwrc.usgs.gov/software/presence.htmli 393

Hooten MB, Johnston DS, McClintock BT, Morales JM. 2017. Animal movement: statistical models for telemetry data. CRC research press. ISBN: 13:978-1-4665-8214-9

Kjellander P, Hewison AJM, Liberg O, Angibault J, Bideau E, Cargnelutti B. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus L.*): a comparison of two long-term studies. Oecologia **139**:478-485

Kays R, Crofoot MC, Jetz W, Wikelski, M. 2015. Terrestrial animal tracking as an eye on life and planet. Science **348**(6240):1222–1232.

Linden DW, Fuller AK, Royle JA, Hare MP. 2017. Examining the occupancy–density relationship for a low-density carnivore. Journal of Applied Ecology **54**(6):2043-2052.

Lindstedt SL, Miller BJ, Buskirk SW. 1986. Home Range, time, and body size in mammals. Ecology **67**(2):413–418.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**(8):2248–2255. 407

MacKenzie DI, Royle JA. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of applied Ecology **42**(6):1105-1114.

MacKenzie DI. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press.

Moeller AK. 2017. New Methods to Estimate Abundance from Unmarked Populations Using Remote Camera Trap Data. Masters of Science Dissertation. University of Montana.

Monterroso P, Castro D, Silva TL, Ferreras P, Godinho R, Alves PC. 2013. Factors affecting the (in) accuracy of mammalian mesocarnivore scat identification in South western Europe. Journal of Zoology **289**(4):243-250. 414

Monterroso P, Rich LN, Serronha A, Ferreras P, Alves PC. 2014. Efficiency of hair snares and camera traps to survey mesocarnivore populations. European journal of wildlife research **60**(2):279-289.

Morin DJ, Fuller AK, Royle JA, Sutherland C. 2017. Model-based estimators of density and connectivity to inform conservation of spatially structured populations. Ecosphere **8**(1):e01623. 10.1002/ecs2.1623 420

Neilson EW, Avgar T, Burton AC**,** Broadley K, Boutin S. Animal movement affects interpretation of occupancy models from camera trap surveys of unmarked animals. Ecosphere **9**(1). DOI: 10.1002/ecs2.2092

Noon BR, Bailey LL, Sisk TD, McKelvey KS. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology **26**:432–441

O'Brien TG, Kinnaird MF, Wibisono HT. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation **6**(2):131-139.

Pacifici K, Reich BJ, Miller DAW, Gardner B, Stauffer G, Singh S, McKerrow A, Collazo JA. 2017. Integrating multiple data sources in species distribution modeling: a framework for data fusion. Ecology **98**(3):840-850.

Parsons AW, Forrester T, McShea WJ, Baker-Whatton MC, Millspaugh JJ, Kays R. 2017. Do occupancy or detection rates from camera traps reflect deer density? Journal of Mammalogy **98**(6):1547-1557.

Peterson AT. 2003. Predicting the geography of species' invasions via ecological niche modeling. The quarterly review of biology **78**(4):419-433.

Popescu VD, de Valpine P, Sweitzer RA. 2014. Testing the consistency of wildlife data types before combining them: The case of camera traps and telemetry. Ecology and Evolution **4**(7):933–943.

Powell RA. 1982. The fisher: life history, ecology, and behavior. University of Minnesota Press.

R Foundation for Statistical Computing. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranacher P, Brunauer R, Trutschnig W, Van der Spek S, Reich S. 2016. Why GPS makes distances bigger than they are. International Journal of Geographical Information Science **30**(2):316-333.

Royle JA, Chandler RB, Sollmann R, Gardner B. 2013. Spatial capture-recapture. Academic Press.

Royle JA, Fuller AK, Sutherland C. 2017. Unifying population and landscape ecology with spatial capture–recapture. Ecography **40**: 001-012.

Sewell D, Guillera-Arroita G, Griffiths RA, Beebee TJ. 2012. When is a species declining? Optimizing survey effort to detect population changes in reptiles. PloS One **7**(8):e43387.

Scott JM, Heglund JH, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds.). 2002. Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Washington, DC, 868 pp. ISBN 1-55963-787-0.

Sollmann R, Gardner B, Parsons AW, Stocking JJ, McClintock BT, Simons TR, Pollock KH, O'Connell AF. 2013. A spatial mark–resight model augmented with telemetry data. Ecology **94**:553–559.

Steenweg R, Whittington J, Hebblewhite M, Forshner A, Johnston B, Petersen D, Shepard B, Lukacs PM. 2016. Camera-based occupancy monitoring at large scales: Power to detect trends in grizzly bears across the Canadian Rockies. Biological Conservation **201**:192–200.

Steenweg R. Hebblewhite M, Kays R, Ahumada J, Fisher JT, Burton AC, Townsend SE, Carbone C, Rowcliffe JM, Whittington J, Brodie J. 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment **15**(1):26-34.

Stewart FEC, Volpe JP, Taylor JS, Bowman J, Thomas PJ, Pybus MJ, Fisher JT. 2017. Distinguishing reintroduction from recolonization with genetic testing. Biological Conservation **214**:242-249.

Turchin P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants (Vol. 1). Sunderland: Sinauer Associates.

Zuur A, Ieno EN, Smith GM. 2007. Analyzing ecological data. Springer Science & Business Media.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Weller TJ, Lee CD. 2007. Mist net effort required to inventory a forest bat species assemblage. Journal of Wildlife Management **71**(1): 251-257.

Tables and Figures

Table 4.1 Selection of top occupancy models for fisher in Alberta's Cooking Lake Moraine across both monthly and weekly sampling periods.

Model[a]	**AIC**[b]	**ΔAIC**	**AIC weight**	**Model Likelihood**	**K**[c]	**-2LL**[d]
Monthly sampling						
1. ψ (MAXIMUM),$p(M_j)$	263.51	0.00	0.79	1.00	4	255.51
2. ψ (MAXIMUM),$p(M_j$+ SURVEY)	266.22	2.71	0.20	0.26	7	252.22
3. ψ (.),$p(M_j)$	274.74	11.23	0.00	0.00	3	268.74
4. ψ (P),$p(M_j)$	274.82	11.31	0.00	0.00	4	266.82
5. ψ (.),p(.)	304.93	41.42	0.00	0.00	2	300.93
Weekly sampling						
6. ψ (M_j),$p(M_j$ + SURVEY)	826.95	0.00	0.77	1.00	18	790.95
7. ψ (MAXIMUM),$p(M_j$ + SURVEY)	831.42	4.47	0.08	0.11	18	795.42
8. ψ (.),$p(M_j$ + SURVEY)	831.82	4.87	0.07	0.09	17	797.82
9. ψ (P_j),$p(M_j$ + SURVEY)	832.54	5.59	0.05	0.06	18	796.54
10. ψ (.),p(.)	861.69	34.74	0.00	0.00	2	857.69

[a] Occupancy (ψ) and detection probability (p) were either constant (.), varied by SURVEY, or varied by the MAXIMUM, STANDARD DEVIATION (M_j), or MEAN (P_j) distance between a camera trap and GPS fixes.
[b] Akaike Information Criterion.
[c] Number of parameters in the model
[d] -2logliklihood of the model (deviance)

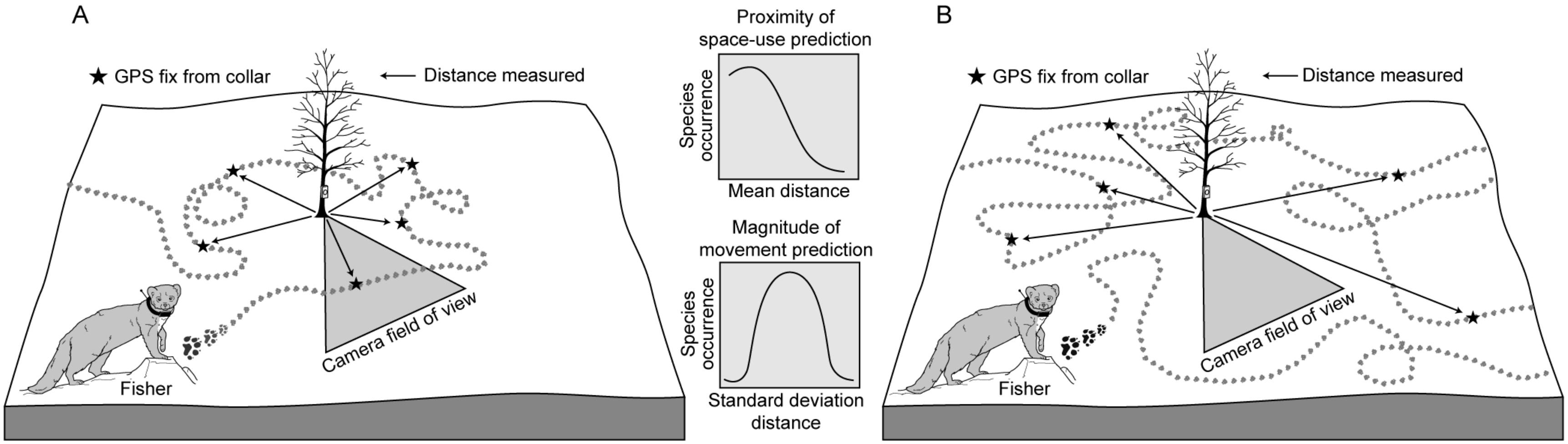

Figure 4.1 Species occurrence data is the result of species detection within the detection zone of a stationary survey device. We tease apart population-level contributions of the magnitude of animal movement and proximity of space use to the detection of species at camera traps by comparing the mean distance between GPS locations of all sampled individuals and each camera trap (P_j; proximity of space use) and standard deviation of distances between GPS locations and a camera trap (M_j; movement magnitude) of fisher (*Pekania pennanti)* GPS telemetry fixes. Panel (A) represents a camera site with high proximity of space use [small P_j], low movement magnitude [small M_j], and high detection probability within the camera's field of view. Panel (B) represents a camera site with low proximity of space use [large P_j] and high movement magnitude [large M_j] resulting in low detection probability within the camera's field of view.

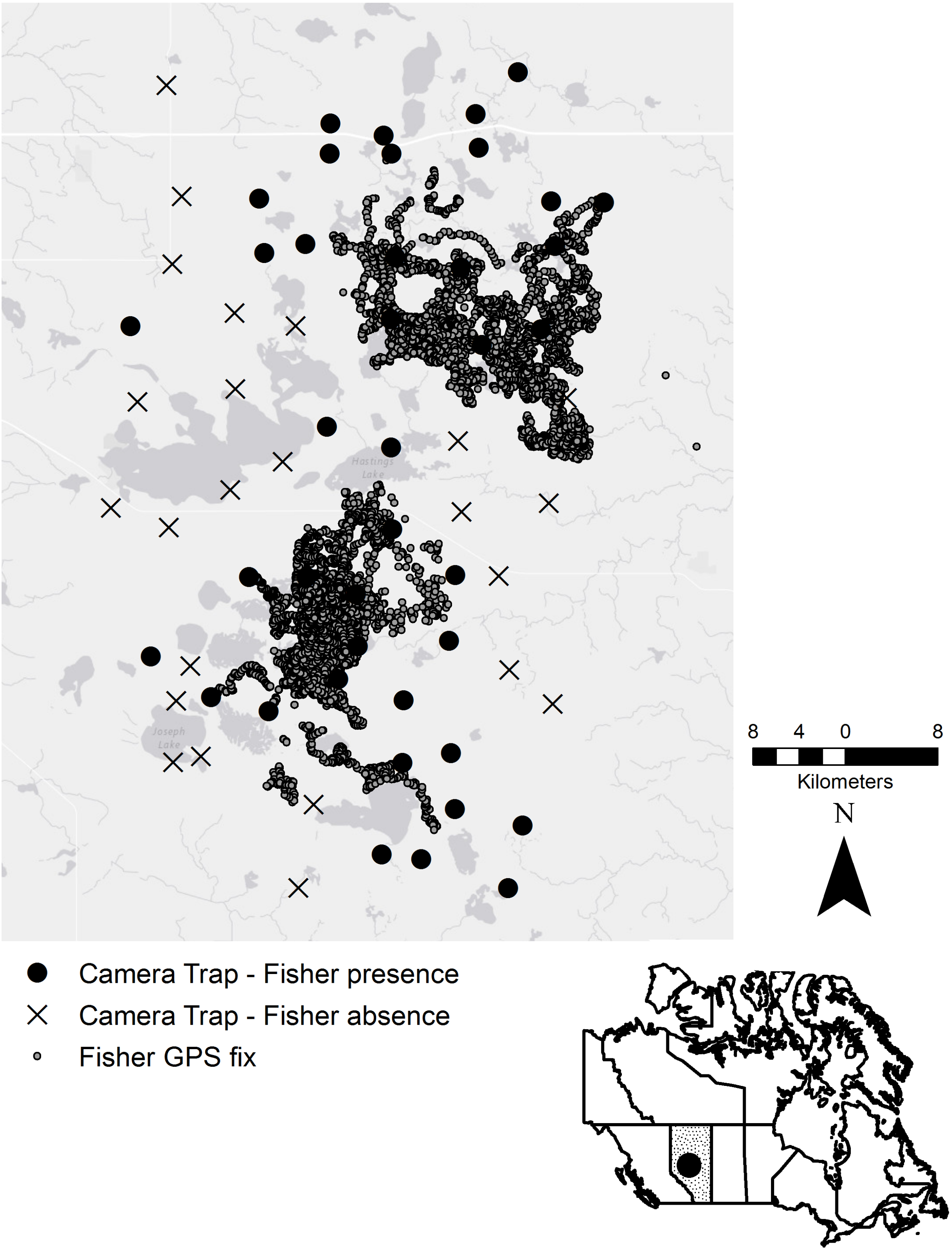
Hastings Lake
Joseph Lake
8 4 0 8
Kilometers
N
● Camera Trap - Fisher presence
× Camera Trap - Fisher absence
• Fisher GPS fix

Figure 4.2 Fisher GPS fixes from 10 individuals are overlaid on the spatial distribution of 64 camera trap sites deployed through winter 2015/2016 on Alberta's Cooking Lake Moraine. For spatial reference, dark patches refer to lakes and rivers where as white lines refer to roads.

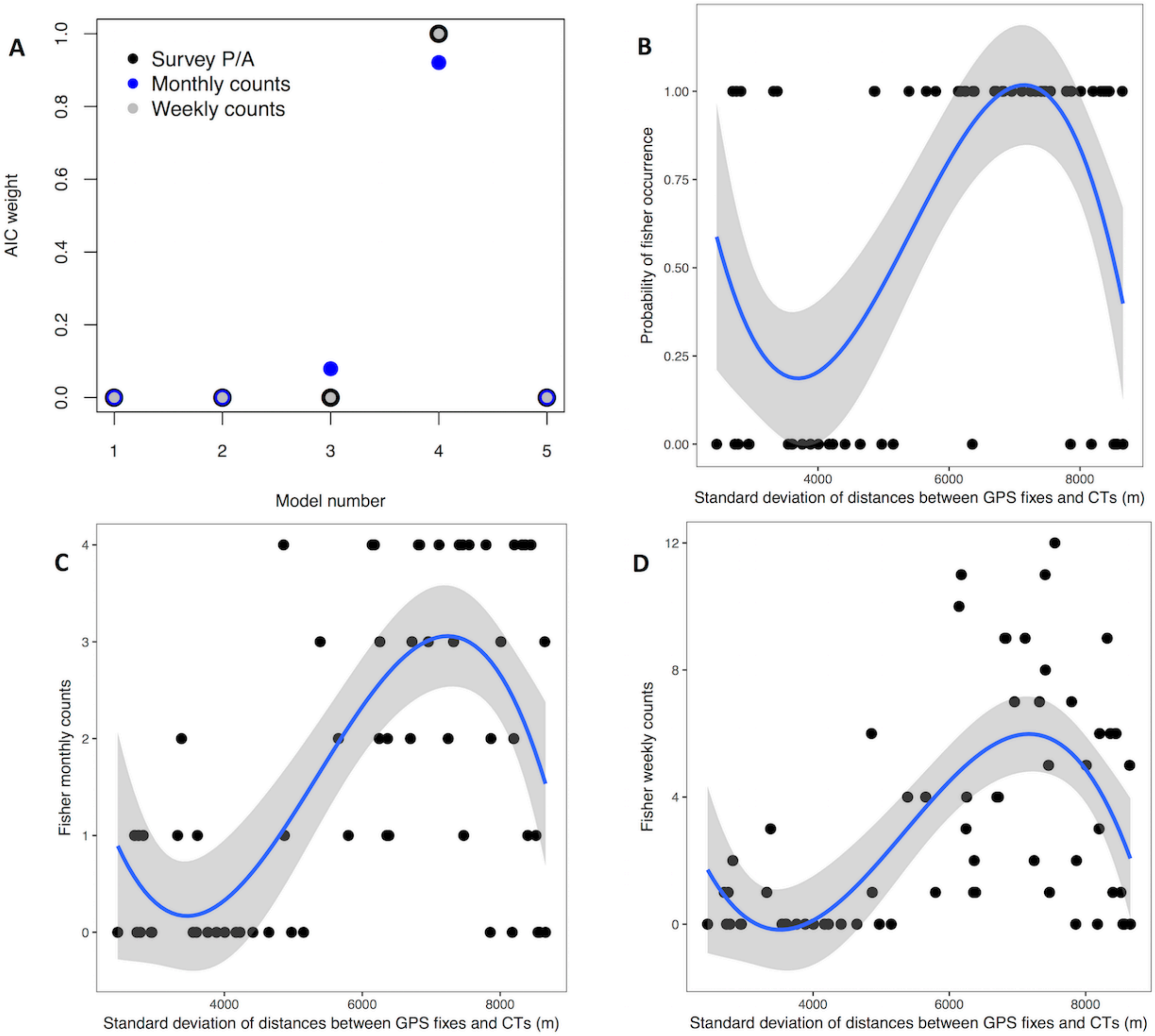

Figure 4.3 Generalized linear models across three temporal resolutions all demonstrate that the standard deviation of the distances between GPS collar fixes and camera traps best predict the probability of species presence-absence, monthly counts, and weekly counts. Models presented in panel (A) include fisher SOD as the response variable, with predictors of: 1- null model, 2 – mean distance (*i.e.* proximity of space use; P_j), 3 – standard deviation distance (*i.e.* movement magnitude; M_j), 4 – standard deviation distance quadratic, and 5 – maximum distance. Panels (B-D) demonstrate the top model from panel (A) at each temporal resolution (survey presence-absence, monthly counts, and weekly counts).

GENERAL CONCLUSION

This dissertation contributes both a depth, and a breadth, to our understanding of spatial ecological process in heterogeneous landscapes. It comments on how our land use actions affect spatial ecological processes, with the ability to either facilitate, or impede, conservation efficacy. The dissertation employs strong inference (Platt 1964) across a mesocosm landscape (Odum 1984) to draw generalizable implications for biological conservation in heterogeneous working landscapes. These inferences, and their conservation outcomes, are important for understanding how to sample, how to understand, and how to best conserve biological diversity in highly heterogeneous, human-dominated, landscapes.

Across chapters, I dive deep into three hierarchies of biodiversity; variation in genes, variation in individual movements, and variations in functional diversity. I use mammals as a model system for this investigation and focus specifically on fisher for genetic and individual metrics. Fisher are a model organism for our investigations as they have been reintroduced broadly across North America (summarized in Lewis et al. 2012) received extensive investigation for questions around functional connectivity (Carr et al. 2007; Garroway et al. 2011; LaPoint et al. 2013; Koen et al. 2015), species occurrence investigations through multiple statistical methods (Heinemeyer 1993; Proulx et al. 1994; Harrison et al. 2004; Bowman et al. 2006; Weir & Corbould 2006; Jordan et al. 2011; Lapoint et al. 2014; Fuller et al. 2016; Linden et al. 2016; 2017), and are representative of many mammal species investigated in camera trapping studies (Burton et al. 2015). Through employing this model system I use multiple methods to explore ecological spatial patterns across biological hierarchies. From genes to communities, I demonstrate a consistent effect of both biotic and abiotic environments on genetic diversity (Chapter I), diversity of movements (Chapter II), and functional diversity (Chapter III).

In each case natural features in the surrounding landscape are positively correlated, and anthropogenic features are negatively correlated, with biodiversity measures (with minimal exceptions). Protected areas themselves do not seem to be significant in predicting biodiversity; it is the natural features within protected areas, and in the surrounding landscape, that are the features of importance.

Across chapters I also look broadly at ecological patterns across spatial scales; from the scale of individual camera sites (Chapter IV) to multiple landscapes within a province (Chapter I). I search for consistencies in ecological patterns across scales to infer generalizable effects of landscape heterogeneity on ecological process. C.S. Holling (1992) pioneered the search for generalizable ecological processes structuring ecosystems. He made a call for studies to use model-systems in cross-scale analyses, a spectrum of disturbance across landscapes, analysis of remote imagery across spatial scales to quantify landscape configuration and composition, and a hierarchy of biological decisions across spatial scales. Employing all of these concepts I demonstrate consistently that biological diversity is positively associated with natural features at small spatial scales, and negatively associated with anthropogenic features at large spatial scales; individual fisher use localized natural features to move and stay far away from most anthropogenic features (Chapter I and II), and mammalian diversity is positively associated with natural features near wildlife cameras, but negatively associated with anthropogenic features far away from cameras (Chapter III).

Investigating biological depth, as well as ecological breadth, within this dissertation has lead to one generalizable conclusion: the biotic and abiotic environment surrounding a point count (*i.e.* a stationary survey site) are important in determining ecological process inferred from the data collected. Specifically, greater emphasis needs to be placed on the biotic and abiotic features within landscape matrices – the matrix can have a moderating effect on conservation practice and biological diversity across spatial scales. The matrix is increasingly recognized as an integral feature in heterogeneous landscapes (summarized in Driscoll et al. 2013). However, my dissertation extends this knowledge to demonstrate the integrity of matrix configuration and composition as important across biological hierarchies, spatial scales, and networks of protected areas, not just individual protected areas. Inadvertently, through the targeted investigations within this dissertation focused on specific conservation strategies or landscape areas, I began to form a conceptual model of an integration these targets, *i.e.* the matrix; how it affects multiple measures of biodiversity, how it determines ecological process across spatial scales, and how it moderates efficacy of targeted conservation initiatives. The matrix is a crucial component of landscape complementation, to go hand in hand with multiple types of biodiversity conservation.

Ironically, the fourth chapter within this dissertation suggests that increased functional connectivity may influence the ecological processes we infer from species occurrence data. Species occurrence data best reflects the magnitude of animal movement better than the proximity of animal space use (Chapter IV). Therefore, increasing the room for animals to roam may also increase the magnitude of animal movements (Tucker et al. 2018), and the frequency of species occurrence data collected from stationary survey devices (*e.g.* camera traps, mist-nets, pit-fall traps, etc). However, this relationship, and inferences derived from it (Linden et al. 2017; Nielson et al. 2018), is integrally intertwined with population density (Broadley 2017), and therefore requires continual investigation as animal densities change through time.

Throughout this dissertation I have learnt to question assumptions of how ecology works across spatial scales, biological hierarchies, and our conservation decisions. Although we must continue to investigate the biological patterns we observe, acknowledging that protected areas, corridors, and matrix are all important components of an integrated, and complimented landscape (Dunning et al. 1992) – a landscape where each component influences other components across multiple spatial scales and biological hierarchies – will help us to better understand, and sample, ecological processes within the complex systems of heterogeneous landscapes.

Literature Cited

Auffret AG, Plue J, Cousins SA.,2015. The spatial and temporal components of functional connectivity in fragmented landscapes. Ambio **44**(1):51-59.

Bowman J, Donovan D, Rosatte RC. 2006. Numerical Response of Fishers To Synchronous Prey Dynamics. Journal of Mammalogy **87**:480–484.

Broadley K. 2017. The implications of animal movement on camera detections as a means to monitor density. MSc dissertation, University of Alberta.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675–685.

Carr D, Bowman J, Kyle C, Tully S, Koen E, Robitaille J, Wilson P. 2007. Rapid Homogenization of Multiple Sources: Genetic Structure of a Recolonizing Population of Fishers. Journal of Wildlife Management **71**:1853–1861.

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in ecology & evolution **28**(10):605-613.

Dunning JB, Danielson BJ, and Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. Oikos:169-175.

Fischer J, Lindenmayer DB, Manning AD. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment **4**(2):80-86.

Fuller AK, Linden DW, Royle JA. 2016. Management decision making for fisher populations informed by occupancy modeling. The Journal of Wildlife Management **80**(5):794-802. 381

Garroway CJ, Bowman J, Wilson PJ. 2011. Using a genetic network to parameterize a landscape resistance surface for fishers, Martes pennanti. Molecular Ecology **20**:3978–3988.

Harrison DJ. Fuller AK, Proulx G. eds. 2004. Martens and fishers (Martes) in human-altered environments: an international perspective. Springer Science & Business Media.

Heinemeyer KS. 1993. Temporal Dynamics in the Movements, Habitat Use, Activity, and Spacing of Reintroduced Fishers in Northwestern Montana.

Holling. 1992. Cross-Scale morphology, geometry, and dynamics o ecosystems. Ecological Monographs **62**:447–502.

Jordan MJ, Barrett RH, Purcell KL. 2011. Camera trapping estimates of density and survival of fishers Martes pennanti Original article Camera trapping estimates of density and survival of fishers Martes pennanti. Wildlife Biology **17**:266–276.

Koen EL, Bowman J, Wilson PJ. 2015. Node-based measures of connectivity in genetic networks. Molecular Ecology **16**(1):69-79.

Lapoint S, Belant J, Kays R. 2015. Mesopredator release facilitates range expansion in fisher. Animal Conservation **18**(1):50-61.

LaPoint S, Gallery P, Wikelski M, Kays R. 2013. Animal behavior, cost-based corridor models, and real corridors. Landscape Ecology **28**:1615–1630.

Lewis J, Powell R, Zielinski W. 2012. Carnivore Translocations and Conservation: Insights from Population Models and Field Data for Fishers (Martes pennanti). PLoS ONE **7**:e32726.

Linden DW, Fuller AK, Royle JA, Hare MP. 2016. Examining the occupancy-density relationship for a low density carnivore. bioRxiv.

Linden DW, Fuller AK, Royle JA, Hare MP. 2017. Examining the occupancy-density relationship for a low density carnivore. Journal of applied ecology **54**:2034–2052.

Neilson EW, Avgar T, Burton AC, Broadley K, Boutin S. Animal movement affects interpretation of occupancy models from camera trap surveys of unmarked animals. *Ecosphere* **9**(1). DOI: 10.1002/ecs2.2092

Odum EP. 1984. The Mesocosm. BioScience **34**:558–562. Oxford University Press.

Platt JR.1964. Strong inference. Science **146**(3642):347-353.

Proulx, Kolenosky, Brady, Drescher, Seidel, Cole. 1994. Post-Release movements of translocated fishers:1–8.

Tucker MA, et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science **359**(6374):466-469.

Weir RD, Corbould FB. 2006. Denisty of fishers in the sub-boreal spruce biogeoclimatic zone of British Columbia. Northwestern Naturalist **87**:118–127.

APPENDIX I

Supplementary information from Chapter I

Table A1.1 Measurements of fisher genetic variability at 15 microsatellite loci sampled within Alberta, Ontario, and Manitoba.

Population	**Sample Size (N)**	**Mean number of alleles per locus (N_x)**	**Mean expected heterozygosity (H_E)**
Alberta’s Cooking Lake Moraine (CLM)	40	5.1	0.72
Alberta’s Willmore Wilderness (WW)	19	4.5	0.70
Northern Alberta (NA)	34	5.5	0.69
Ontario (ON)	29	5.7	0.69
Manitoba (MB)	25	5.0	0.70

Table A1.2 Pairwise Fst values from 15 microsatellite loci were all significantly different than zero for Alberta's Cooking Lake Moraine, Northern Alberta, Alberta's Willmore Wilderness, Ontario, and Manitoba fisher populations.

	ON	**MB**	**NA**	**CLM**
MB	0.117			
NA	0.119	0.100		
CLM	0.125	0.105	0.019	
WW	0.135	0.099	0.042	0.041

ON = Ontario, MB = Manitoba, NA = Northern Alberta, CLM = Cooking Lake Moraine, WW = Willmore Wilderness

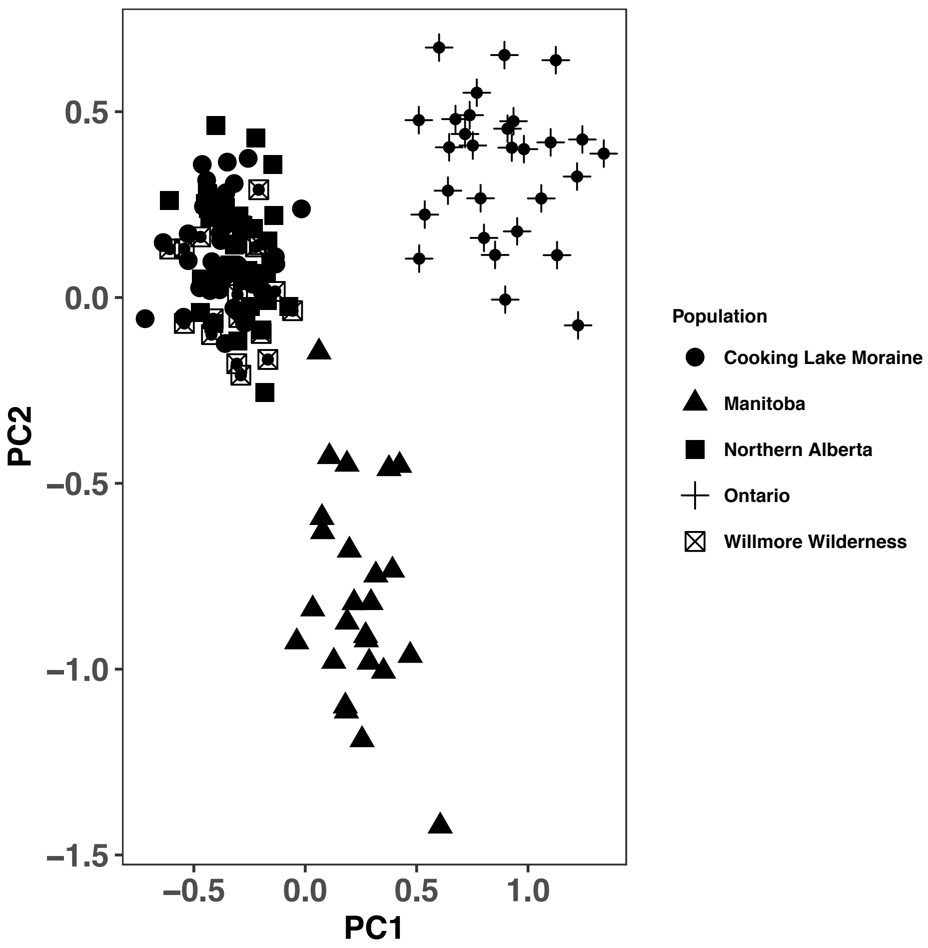

Figure A1.1 Principle components of allele frequencies from 15 microsatellite loci cluster into three groups. Alberta’s Cooking Lake Moraine, Northern Alberta, and Alberta’s Willmore Wilderness samples cluster into one distinct group.

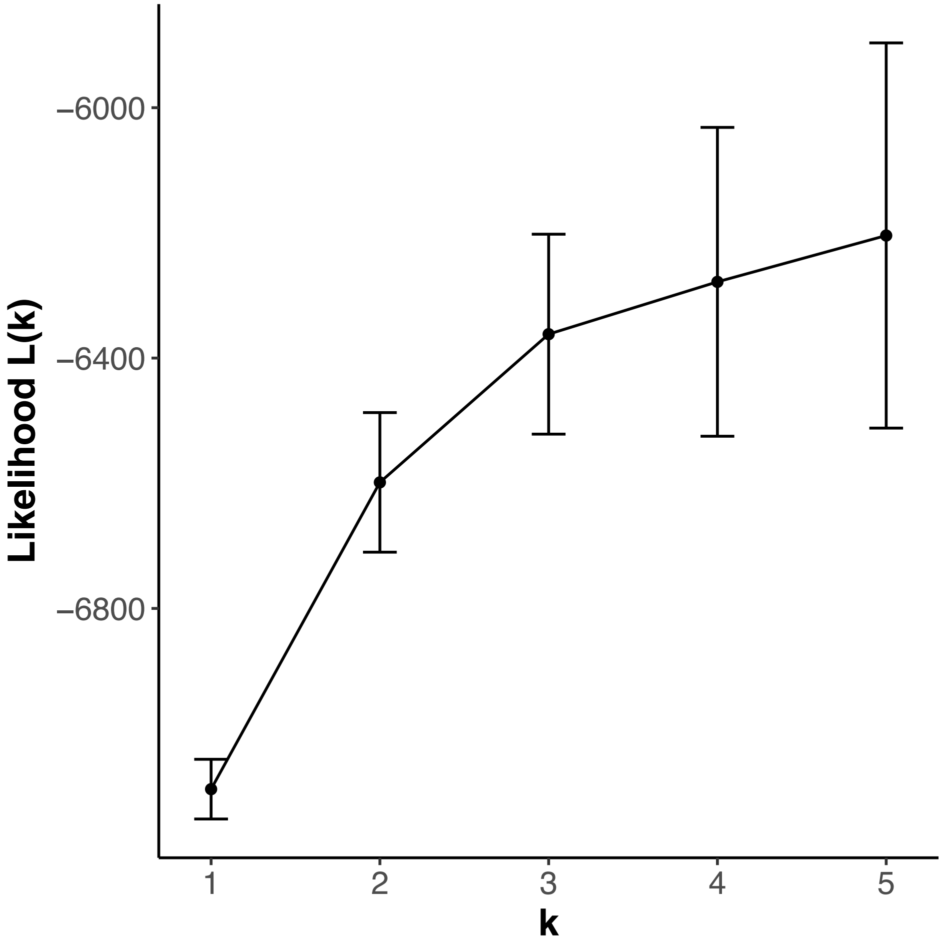

Figure A1.2 Likelihood curve from STRUCTURE output of all fisher genetic samples (n = 147) across five potential population clusters (*k*). Burnin and MCMC periods between 10,000 and 1000,000 did not influence likelihood estimations or variances. We used the rate of change in the likelihood estimates and their variance between runs (Rosenberg et al. 2001) to estimate *k*.

APPENDIX II

Supplementary information from Chapter III

Table A2.1 Regression model output from across scale functional richness-, functional dispersion-, and functional evenness-habitat models.

Richness

Scale	Intercept	Deciduous forest	Coniferous forest	Mixedwood forest	Wetland	Grassland	Shrubland	Linear	Block	Development	-2LL	AICc	Weight
4250	0.36							-0.279			-116.04	238.49	0.12
3250	0.29						1.59				-116.17	238.75	0.11
3000	0.30						1.55				-116.32	238.79	0.10
3500	0.30						1.60				-116.51	2389.05	0.09
2750	0.30						1.42				-116.56	239.43	0.07
4000	0.30						1.61				-116.90	239.52	0.07
4750	0.30						1.63				-116.90	240.21	0.05
4500	0.30						1.63				-116.95	240.21	0.05
2500	0.31						1.21				-115.85	240.31	0.05
3750	0.29						1.78	-2.85E-08			-117.02	240.39	0.05
5000	0.30						1.64				-115.95	240.45	0.05
750	0.46				-0.28				-8.67		-117.37	240.59	0.04
2250	0.31						1.02				-117.81	241.15	0.03
2000	0.32						0.81				-118.02	242.02	0.02
500	0.28	0.15									-118.15	242.44	0.02
1000	0.28	0.16									-118.18	242.71	0.01

1750	0.39	-0.39										-118.25	242.77	0.01
1250	0.28	0.16										-118.25	242.89	0.01
1500	0.29	0.16										-118.38	243.17	0.01
250	-446.99	447.86	449.21		447.70	447.79	447.87	447.87			447.85	-116.45	257.05	<0.01

Dispersion

Scale	Intercept	Deciduous forest	DistToPA	PA	Cultivation	Development	Coniferous forest	Linear	Wetlands	Mixedwood forest	Shrubland	-2LL	AICc	Weight
3500	1.18		1.01E-04			-5.98		3.81			-2.08	2.45	11.08	0.21
1750	0.94					-3.43	4.63	3.67				-1.3	13.72	0.07
5000	1.07		9.7-E05			-3.34						-2.63	13.94	0.07
4750	1.04									1.63	-3.39	-1.52	14.08	0.06
3250	1.14		9.63E-05			-5.45		3.59		1.28	-1.71	0.86	14.27	0.06
4250	1.04		9.01E-05			-3.03						-2.83	14.35	0.05
3750	1.03		9.03E-05			-2.79						-2.9	14.48	0.05
4000	1.03		8.97E-05			-2.87						-2.9	14.55	0.05
4500	1.03									1.48	-3.09	-1.87	14.79	0.04
500	0.62		9.06E-05									-3.11	14.91	0.04
3000	1.04		8.40E-05			-4.84		4.05				-1.99	15.02	0.03
2500	1.01		8.32E-05			-4.47		4.19				-2.09	15.22	0.02
750	0.63	0.31	9.86E-05									-3.65	15.98	0.01
250	0.82											-6.23	16.63	0.01
1000	0.64	0.31	9.57E-05									-4.11	16.91	0.01
2250	0.96					-1.16		-3.57E-08				-4.24	17.71	0.01
1250	0.64	0.33	9.73E-05									-4.26	17.21	0.01

2000	0.89					-1.16	4.66	-3.25E-08				-3.15	17.34	0.01
1500	1.02		8.95E-05	-0.18	-0.47	-1.14						-2.15	17.79	0.01
2750	0.88					-1.41		-5.31E-08	0.39			-3.47	17.99	<0.01

Evenness

Scale	Intercept	Deciduous forest	Linear	Block	Coniferous forest	Cultivation	Development	Grassland	Shrubland	PA	Mixedwood forest	-2LL	AICc	Weight
500	0.16	0.24	0.65									41.22	-73.76	0.25
750	0.36			8.78	2.04	-0.19	-0.15	-0.27				44.13	-72.27	0.14
250	0.23	0.17										39.19	-71.98	0.12
1750	0.40				3.10	-0.21		-0.35	-0.69			41.88	-70.29	0.05
1250	0.33		2.17				-1.13			0.09		40.48	-69.93	0.04
1500	0.39		1.70		2.57	-0.14	-1.03		-0.45			42.72	-69.45	0.03
2000	0.41				0.29	-0.24		-0.36	-0.61			41.14	-68.81	0.02
3500	0.45						-1.44		-0.76		0.89	39.88	-68.73	0.02
1000	0.39		1.83		1.73	-0.18	-0.67	-0.32	-0.39			43.66	-68.71	0.02
2250	0.37					-0.22						37.54	-68.68	0.02
2500	0.37					-0.22						37.37	-68.35	0.02
4750	0.44						-1.35					37.33	-68.27	0.02
4500	0.43						-1.3					37.30	-68.21	0.01
5000	0.44						-1.36					37.27	-68.14	0.01
4250	0.43						-1.22					39.21	-68.03	0.01
3250	0.44						-1.38		-0.67		0.82	37.52	-68.00	0.01
4000	0.42						-1.14					37.11	-67.83	0.01

2750	0.37	-0.20				37.05	-67.69	0.01
3750	0.42		-1.08			37.04	-67.68	0.01
3000	0.43		-1.31	-0.57	0.78	39.14	-67.25	0.01

APPENDIX III

Supplementary information from Chapter IV

Table A3.1 Correlation values between summary statistics of the distance (m) between GPS telemetry points and camera traps.

	Mean (P_j)	**Standard deviation (M_j)**	**Minimum**
Mean (P_j)			
Standard deviation (M_j)	0.38*		
Minimum	0.51***	-0.45**	
Maximum	0.29*	0.33*	0.16

*$p < 0.05$
**$p < 0.005$
***$p < 0.0005$

Table A3.2 All occupancy models for fisher in Alberta's Cooking Lake Moraine across both *monthly* and *weekly* sampling periods.

Model^a	AIC^b	ΔAIC	AIC wgt	Model Likelihood	K^c	-2LL^d
Monthly sampling						
ψ (MAXIMUM),$p(M_j)$	263.51	0.00	0.79	1.00	4	255.51
ψ (MAXIMUM),$p(M_j$ + SURVEY)	266.22	2.71	0.20	0.2579	7	252.22
ψ (.),$p(M_j)$	274.74	11.23	0.00	0.00	3	268.74
ψ (P_j),$p(M_j)$	274.82	11.31	0.00	0.00	4	266.82
ψ (M_j),$p(M_j)$	276.69	13.18	0.00	0.00	4	268.69
ψ (.),$p(M_j$ + SURVEY)	277.32	13.81	0.00	0.00	6	265.32
ψ (P_j),$p(M_j$ + SURVEY)	277.4	13.89	0.00	0.00	7	263.40
ψ (M_j),$p(M_j$ + SURVEY)	279.18	15.67	0.00	0.00	7	265.18
ψ (M_j),p(MAXIMUM)	293.58	30.07	0.00	0.00	4	285.58
ψ (M_j),p(.)	296.43	32.92	0.00	0.00	3	290.43
ψ (M_j),p(MAXIMUM + SURVEY)	296.53	33.02	0.00	0.00	7	282.53
ψ (M_j),$p(P_j)$	298.03	34.52	0.00	0.00	4	290.03
ψ (M_j),$p(P_j$ + SURVEY)	300.77	37.26	0.00	0.00	7	286.77
ψ (.),p(.)	304.93	41.42	0.00	0.00	2	300.93
Weekly sampling						
ψ (M_j),$p(M_j$ + SURVEY)	826.95	0.00	0.77	1.00	18	790.95
ψ (MAXIMUM),$p(M_j$ + SURVEY)	831.42	4.47	0.08	0.11	18	795.42
ψ (.),$p(M_j$ + SURVEY)	831.82	4.87	0.07	0.09	17	797.82
ψ (Mean),$p(M_j$ + SURVEY)	832.54	5.59	0.05	0.06	18	796.54
ψ (M_j),$p(M_j)$	833.89	6.94	0.02	0.03	4	825.89
ψ (MAXIMUM),$p(M_j)$	838.16	11.21	0.00	0.00	4	830.16
ψ (.),$p(M_j)$	838.63	11.68	0.00	0.00	3	832.63
ψ (P_j),$p(M_j)$	839.31	12.36	0.00	0.00	4	831.31
ψ (M_j),p(MAXIMUM + SURVEY)	845.64	18.69	0.00	0.00	18	809.64
ψ (M_j),$p(P_j$+ SURVEY)	849.37	22.42	0.00	0.00	18	813.37
ψ (M_j),p(MAXIMUM)	851.67	24.72	0.00	0.00	4	843.67
ψ (M_j),p(.)	853.8	26.85	0.00	0.00	3	847.8
ψ (.),p(MAXIMUM + SURVEY)	853.83	26.88	0.00	0.00	17	819.83
ψ (MAXIMUM),p(MAXIMUM + SURVEY)	854.67	27.72	0.00	0.00	18	818.67
ψ (M_j),$p(P_j)$	855.27	28.32	0.00	0.00	4	847.27
ψ (P_j),p(MAXIMUM + SURVEY)	855.45	28.5	0.00	0.00	18	819.45
ψ (.),$p(P_j$ + SURVEY)	857.29	30.34	0.00	0.00	17	823.29
ψ (MAXIMUM),$p(P_j$ + SURVEY)	858.07	31.12	0.00	0.00	18	822.07
ψ (P_j),$p(P_j$ + SURVEY)	858.9	31.95	0.00	0.00	18	822.9
ψ (.),p(MAXIMUM)	859.91	32.96	0.00	0.00	3	853.91
ψ (MAXIMUM),p(MAXIMUM)	860.75	33.8	0.00	0.00	4	852.75

ψ (P_j),p(MAXIMUM)	861.52	34.57	0.00	0.00	4	853.52
ψ (.),p(.)	861.69	34.74	0.00	0.00	2	857.69

[a] Occupancy (ψ) and detection probability (p) were either constant (.), varied by SURVEY, or varied by the MAXIMUM, STANDARD DEVIATION (M_j), or MEAN (P_j) distance between a camera trap and GPS fixes.

[b] Akaike Information Criterion.

[c] Number of parameters in the model

[d] -2logliklihood of the model (deviance)