

Movement ecology of fishers (*Pekania pennanti*) within a semi-urban landscape

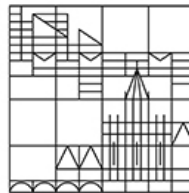
Dissertation submitted for the degree of Doctor of Natural Sciences

presented by:

Scott Daniel LaPoint

at the

Universität
Konstanz



Faculty of Sciences
Department of Biology

Oral examination: 9 October 2013

First supervisor: Martin Wikelski

Second supervisor: Roland Kays

“If I could walk with the animals, talk with the animals... what a wonderful world this would be!”
– Rex Harrison as “Doctor Dolittle”

Summary	11
Zusammenfassung	15
Chapter 1: General introduction	19
BACKGROUND and INTRODUCTION	21
DISSERTATION OUTLINE.....	26
Chapter 2: Eastern fisher (<i>Pekania pennanti</i>) range expansion may be facilitated by a mesopredator release	31
ABSTRACT.....	33
INTRODUCTION	34
METHODS	37
Fisher range regional divisions	37
Predator range overlap	38
Fisher diet.....	38
Fisher body size	41
RESULTS	42
DISCUSSION	45
FUTURE DIRECTIONS	49
CONCLUSION.....	50
ACKNOWLEDGEMENTS	50
Appendix.....	51

Chapter 3: Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity	61
ABSTRACT.....	63
INTRODUCTION	64
STUDY AREAS	66
MATERIALS and METHODS.....	66
Study species, capture protocols, and tag attachment	66
Tag details.....	67
RESULTS	71
Tag performance	71
Animal movement.....	71
DISCUSSION	73
MANAGEMENT IMPLICATIONS.....	76
ACKNOWLEDGEMENTS	77
Chapter 4: Fisher activity patterns within a developed landscape	79
ABSTRACT.....	81
INTRODUCTION	81
METHODS	83
RESULTS	85
DISCUSSION	86
CONCLUSIONS.....	92
ACKNOWLEDGEMENTS	92
Chapter 5: Animal behavior, cost-based corridor models, and real corridors	95
ABSTRACT.....	97
INTRODUCTION	97

METHODS	100
Study species and area	100
Movement data.....	101
Cost-based corridor mapping	101
Identifying animal-defined corridors	105
Corridor model validation.....	108
Corridor composition	109
RESULTS	110
DISCUSSION	116
ACKNOWLEDGEMENTS	122
Chapter 6: General discussion	125
CARNIVORES in the CAPITAL	127
IMPLICATIONS, CONSERVATION VALUE, and FUTURE DIRECTIONS	128
CONCLUSION.....	130
References.....	133
Acknowledgements	151
Author contributions	153
Curriculum vitae	155
Publications produced during this dissertation	161
Declaration	163

Habitat fragmentation and urbanization are ubiquitous threats to mammals, forcing species to either become locally extinct or to adapt. The challenge for species to adapt is great, partly because of the wide disparity between the quickness of these anthropogenic forces and the rate at which species can adapt through evolutionary processes. Yet some species are adapting to fragmented, potentially novel, urban landscapes. Until now however, our ability to investigate species responses to these threats remained practically infeasible, due to the technological limitations of monitoring free-ranging animals. However, the field of movement ecology is spurring interest in these questions, driving rapid technological improvements in biotelemetry methods, offering biologists unprecedented opportunities. I capitalized on these opportunities during my dissertation work and investigated a species whose responses to habitat fragmentation apparently varies greatly across its geographic range, hoping to explore hypotheses concerning the ecological and behavioral responses of a carnivore to these anthropogenic forces.

This dissertation is an attempt to better understand the behavior and ecology of fishers (*Pekania pennanti*) that have recently colonized the previously considered inhospitable, semi-urban landscape surrounding Albany, New York, USA. Within this dissertation, I compare the species historic, most-contracted, and current geographic range, and show that fishers have re-colonized much of their historical eastern range, (including suburban landscapes within the Northeastern United States), yet remain in isolated fragments within their historic western range (Chapter 2). Understanding how this species can successfully colonize a suburban landscape, but remain threatened elsewhere, motivated the field-based portion of this dissertation.

I hypothesized that fishers in my study area have adapted their behaviors (e.g., the timing of their activity and their movement-habitat patterns) in response to human activities. To test

these hypotheses, I captured and fitted 33 free-ranging fishers across a habitat fragmentation continuum during three winter field seasons. I deployed state-of-the-art GPS-tracking collars, equipped with tri-axial accelerometers and remote downloading capabilities and managed these recorded data via movebank.org. It was necessary to develop a novel system for collecting the temporal and spatial high-resolution data that would be required to test this hypothesis. Our accelerometer-informed GPS-fix attempt schedule (described in Chapter 3) achieved great success in both extending the deployment duration of our GPS-tracking collars while simultaneously recording more locations, ultimately yielding more realistic fisher movement tracks.

It appears that these fishers are facilitating their survival within this semi-urban landscape through adjustments in the timing of their activity and their movement patterns. Our accelerometers yielded activity data (i.e., overall dynamic body acceleration) that suggests that these fishers are nocturnal and are avoiding automobile traffic volume peaks by ceasing their activity earlier when these peaks occur earlier in the morning. Fishers also appear less selective in their habitat requirements here than reported in the literature, utilizing all forest cover types available to them rather than particular forest characteristics. However, my study animals rarely utilized only one forest patch, due to their small area, and instead crossed roads and other features nightly to move between multiple forest patches. From my model of fisher behavior, it appears that fishers are utilizing movement corridors to move between these patches. Unfortunately however, two popular approaches for identifying potential corridors (i.e., least-cost path analysis and circuit theory) poorly predicted the location of these corridors. Further, an independent set of animal movement data, derived from camera trap detections, validated my model predictions and confirmed that the other two models performed relatively poorly.

In summary, the work presented within this dissertation tells an encouraging story of persistence and resourcefulness, offering hope for the conservation of imperiled wildlife. The fisher has been thought to be highly, negatively impacted by human activities and landscape disturbance, yet their recent colonization of suburban areas suggests the contrary. I am confident that the results of future efforts similar to those outlined here will be vital to conservation efforts. Given the rate and ubiquity of threats to wildlife, we must improve our understanding of how some species are coping with these threats so that we can identify the traits that allow them to do so.

Habitatfragmentierung und Verstädterung sind allgegenwärtige Bedrohungen für Säugetiere, die lokal aussterben, wenn sie sich nicht anpassen können. Die Herausforderung für die Arten ist jedoch enorm, unter anderem aufgrund der zeitlichen Diskrepanz zwischen der Schnelligkeit, der anthropogenen Umweltveränderungsprozessen und der Geschwindigkeit, mit der sich Arten evolutiv verändern. Dennoch gibt es Arten, denen es gelingt, sich an fragmentierte und teilweise völlig neuartige städtische Landschaften anpassen. Bisher war es fast unmöglich zu beobachten, wie Arten auf diese Gefahren reagieren, da technische Schwierigkeiten die Beobachtung freilebender Tiere kaum gestatteten. Der Bereich der Movement Ecology verstärkt jedoch das Interesse an diesen Fragestellungen, wodurch eine schnelle technologische Entwicklung biotelemetrischer Methoden angestoßen wurde, die Biologen noch nicht dagewesene Möglichkeiten eröffnen. Die Untersuchung einer Art, die eine breite Reaktionsnorm auf veränderte Landschaftsformen zeigt, sollte geeignete Rahmenbedingungen bieten, die die Überprüfung von Hypothesen zur ökologischen und verhaltensbiologischen Reaktion wilder Arten auf solche anthropogenen Veränderungen erlaubt.

Diese Arbeit stellt einen Beitrag dar, die ökologischen- und Verhaltensanpassungen von Fischmardern (*Pekania pennanti*) besser zu verstehen, die es den Tieren ermöglicht haben, eine Gegend zu besiedeln, in der sie bisher nicht vorgekommen sind, nämlich die semi-urbane Landschaft um Albany im Bundesstaat New York, USA. In dieser Arbeit habe ich die historische und aktuelle geografische Verbreitung quantifiziert und belege, dass, obwohl Fischmarder fast ihr gesamtes östliches Verbreitungsgebiet inklusive der sub-urbanen Landschaften in den nordöstlichen Vereinigten Staaten re-kolonisiert haben, ihre Vorkommen in ihrem historischen westlichen Verbreitungsgebiet auf isolierte Fragmente beschränkt sind. Die Frage, warum diese

Art in einigen Gebieten gefährdet bleibt, obwohl sie in anderen Regionen erfolgreich die Vorstädte kolonisiert, war Grundlage für den auf Feldarbeiten basierenden Teil dieser Dissertation.

Ich habe in meiner Untersuchung die Hypothese aufgestellt, dass Fischmarder ihr Verhalten (also z.B. ihre Aktivitätszeiten und ihr Bewegungsmuster) an die menschliche Umwelt angepasst haben. Um diese Hypothese zu überprüfen, habe ich im Laufe von drei Wintern 33 wilde Fischmarder in unterschiedlich gestörten Landschaften gefangen. Die Tiere wurden mit modernen GPS-Halsbändern ausgestattet. Dieses neuartige, für diese Untersuchung entwickelte System kann zeitlich und räumlich sehr hochaufgelöste Daten speichern, die zu der Überprüfung der Hypothese notwendig sind. Die Halsbänder können auch die Beschleunigung in drei Achsen aufnehmen und können aus einiger Entfernung ausgelesen werden. Die Daten wurden auf der online-Plattform Movebank.org ausgewertet. Die beschleunigungsabhängige Aufzeichnung von GPS-Positionen (siehe Kapitel 3) hat erfolgreich dazu beigetragen, die Lebenszeit der GPS-Halsbänder zu verlängern und dabei mehr Positionen aufzunehmen, was dazu geführt hat, ein realistischeres Bild der Bewegungsmuster von Fischmardern zu erhalten.

Es hat sich herausgestellt, dass Fischmarder in den sub-urbanen Landschaften überleben, indem sie ihre Aktivitätszeiten und Bewegungsmuster anpassen. Die Daten unsere Beschleunigungsmesser legen nahe, dass diese Fischmarder nachtaktiv sind und auf die Stoßzeiten des automobilen Verkehrs und des damit verbundenen Lärms reagieren. Auch scheinen sie hier weniger wählerisch zu sein, was ihre Habitatsansprüche angeht. Anders als in der Literatur dargestellt, da sie alle und nicht nur einige ausgewählte Waldtypen nutzen. Jedoch haben die von mir untersuchten Tiere aufgrund der geringen Größe nur selten eines, sondern oft mehrere Waldgebiete genutzt, indem sie sich nachts zwischen den Waldfragmenten bewegt

haben. Um die Verbindung zwischen diesen Gebieten zu untersuchen erstellte ich ein ComputermodeLL, dass darauf schließen lässt, dass die Fischmarder zwischen den Waldinseln bestimmte Korridore nutzen. Die zwei gängigen Berechnungsmodelle zur Identifizierung möglicher Korridore, (Least-cost Path Analysis und Circuit Theorie), haben jedoch die Positionen der Fischmarder nur sehr ungenügend berechnet. Mein Modell wurde hingegen zusätzlich von unabhängig erhobenen Bewegungsdaten, die aus automatischen Kamerafallen berechnet wurden, bekräftigt und bestätigt, dass die anderen beiden Modelle sich nur als sehr bedingt geeignet erwiesen.

Zusammenfassend kann man sage, dass die hier vorgestellten Ergebnisse eine ermutigende Geschichte von Beständigkeit und Anpassungsfähigkeit erzählen, die Anlass zur Hoffnung für den Schutz gefährdeter Tiere bietet. Die Verbreitung der Fischmarder war dramatisch zurückgegangen und es wurde angenommen, dass diese Art durch menschliche Aktivitäten und Landschaftsveränderungen extrem negativ beeinflusst wird. Die aktuelle Besiedelung vorstädtischer Gebiete durch diese Art legt jedoch das Gegenteil nahe. Ich bin sicher, dass die Ergebnisse zukünftiger Untersuchungen ähnlich der hier vorgestellten Arbeit wesentlich für Schutzmaßnahmen sein werden. In Anbetracht der allgegenwärtigen und vielfältigen Bedrohung der Tierwelt müssen wir die Perspektive der Tiere berücksichtigen und einen Paradigmenwechsel im Naturschutz anstreben, der die Komplexität des individuellen Verhaltens mit einbezieht und diese Komplexitäten im Naturschutz berücksichtigt.

General introduction

BACKGROUND and INTRODUCTON

Human activities often affect substantial changes across ecosystems, pushing resident species toward extinction or forcing them to adapt (Wilcox and Murphy 1985; Saunders et al. 1991; Turner 1996; Fahrig 1997, 2003). Habitat fragmentation is especially threatening to native wildlife species, particularly when it leads to the conversion of natural landscapes into a matrix of less suitable habitat patches; i.e., urbanization (McKinney 2002). Whereas many cannot (McKinney 2002), some species are indeed able to adapt to these anthropogenic changes, either because of a pre-adaptation, or through new, rapid evolutionary change (Henle et al. 2004; Prange et al. 2004; Fischer and Lindenmayer 2007; Harveson et al. 2007; Gehrt et al. 2010).

These anthropogenic threats have temporal and spatial components: human activities affect changes in the spatial configuration of the landscape and these activities occur at predictable times within a 24-hour period (McKinney 2002, Longcore and Rich 2004; Beier 2006; Shochat et al. 2006). Thus, animals facing these threats must adapt their movement behaviors and the timing of their activities. For example, coyotes (*Canis latrans*) have adjusted the timing of their activities to avoid peak human activity periods and utilize a wide range of available land cover types, allowing them to successfully colonize suburban and urban landscapes across their geographic range (McClennen et al. 2001). However, our understanding of whether other species have similarly adapted their behaviors is limited, as only very recently have biologists been able to accurately quantify these behavioral adaptations of free-ranging individual.

Fortunately, the emerging field of Movement Ecology (Nathan et al. 2008) is spurring the miniaturization and complexity of biotelemetry technology, and new analytical tools for identifying behaviors of free-ranging animals (Nathan et al. 2012) and for discerning animal

behavior using movement data-based models (Fauchald and Tveraa 2003; Morales et al. 2004; Jonsen et al. 2005; Gurarie et al. 2009; Kranstauber et al. 2012). As a result, the amount of animal movement data is rapidly increasing and being made available to both quantify animal responses to habitat fragmentation and urbanization and to test model predictions of their responses (Wikelski et al. 2007; Wikelski and Kays 2012). These movement models, coupled with improved spatial and temporal resolution of GPS-derived animal movement data (e.g., Brown et al. 2012), are improving our understanding of the mechanistic links between animal behavior, space use, and survival in dynamic environments (Morales et al. 2010; Smouse et al. 2010; Bartoń et al. 2012; Buchmann et al. 2012). Given these technological and analytical advancements and the well-established threats of habitat fragmentation and urbanization to biodiversity, investigating wildlife species responses to these threats is both timely and necessary for successful conservation efforts.

Investigating the response of a once rare carnivore species to these threats may be exceptionally fruitful, especially when this carnivore demonstrates a wide disparity in its conservation status across its native range. Fishers (*Pekania pennanti* Erxleben 1777, formerly *Martes pennanti*) initially fared poorly in human dominated landscapes and went extinct in many parts of their range across North America (Powell 1993). They have subsequently expanded their range across most of their eastern range, including colonizing semi-urban areas of New York (LaPoint et al. 2013), but remain threatened across most of their western geographic range (Lewis et al. 2012). Understanding the ecology and behavior of fishers within the semi-urban areas of New York is the goal of this dissertation.

STUDY SPECIES AND AREA

The fisher is a medium-sized (females 2.0–2.5 kg; males 3.5–5.5 kg) member of the Mustelidae family native to the northern forests of North America (Powell 1993) (Figure 1). They are semi-arboreal generalist predators (Powell 1993; see Chapter 2). Little is known about their activity patterns and behavior, but they are presumably active throughout the 24-hour period (Weir and Corbould 2007). Fishers were once considered habitat specialists that required mature forests (Buskirk and Powell 1994), but more recent work suggests that fishers are less specialized in their forest-habitat requirements than previously thought (LaPoint et al. 2013).

During the 19th and early 20th centuries, their range contracted northward following the Euro-American colonization of North America and the subsequent land conversion, timber, and fur harvesting, leaving fishers in isolated refugia scattered throughout the southern portion of their range (Powell 1993; Lewis et al. 2012). By the early 20th century however, agricultural abandonment increased and forest clearing eased, particularly within much of their northeastern range (Pimm and Askins 1995). Across the United States, fisher trapping seasons were closed, first in Wisconsin (1921) and finally in California (1946), providing fishers with temporary relief from harvest (Powell 1993). Fisher populations have since expanded their north-central and northeastern ranges southward, aided by successful translocations (Lewis et al. 2012) and have even begun colonizing suburban woodlands in parts of their southeastern range (LaPoint et al. 2013). Unfortunately however, fishers still have the fourth most contracted geographic range of all North American carnivores (Laliberte and Ripple 2004) and their southwestern populations have been petitioned for protection under the U.S. Endangered Species Act (Center for Biological Diversity 2008). Fishers have been translocated 38 times throughout their range with much success (Lewis et al. 2012), yet the regional variation in fisher range expansion remains, sparking much discussion and debate among carnivore biologists.

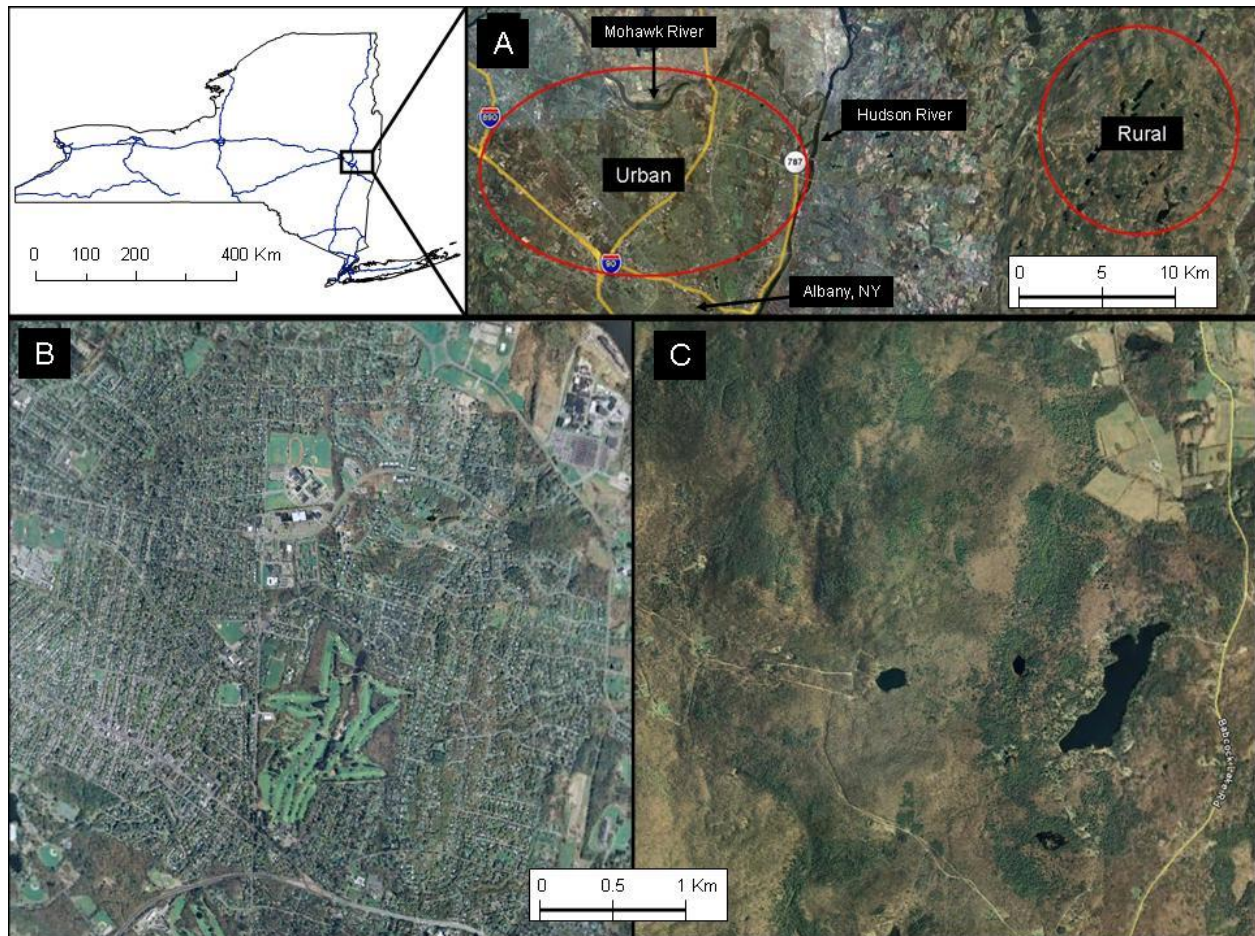
Figure 1. Images of the study species, fishers (*Pekania pennanti*). A sedated female (top left) and male (bottom left) and an alert male within a tree.



I studied fishers within two areas in eastern New York, USA (42°45' N, 73°51' E), to represent my wild (Rensselaer) and urban (Albany-Schenectady) study sites (Figure 2). The wild site, the Rensselaer Plateau in central Rensselaer County, ranges in elevation from 200 – 600 m and is predominantly forested (~85%) with typical northern hardwood and conifer trees species (e.g., eastern white pine *Pinus strobus*, eastern hemlock *Tsuga canadensis*, maples *Acer rubrum* and *A. sacharum*, oaks *Quercus rubra* and *Q. alba*, and paper birch *Betula papyrifera*). The road density is relatively low (1.33 km/km²; Rensselaer County Bureau of Research and Information Services 2009) with a human population density of approximately 29.9/km² (US Census 2012).

The urban site is a 350 km² developed area between the cities of Albany and Schenectady, bounded by the Mohawk and Hudson Rivers to the north and east, and by Interstates 90 and 890 to the south and west. The road density in the urban study area is nearly 4x higher than the wild site (4.77 km/km²; New York State Office of Cyber Security and Critical Infrastructure Coordination 2005; US Census Bureau 2012), with little change in elevation (0 – 100 m; United States Geological Survey). The area is characterized by residential and commercial land uses and is densely populated (438/km²; US Census 2012). Work within this area focused on forested fragments and other natural areas, including the Albany Pine Bush

Figure 2. Map of the study area showing (A) the proximity of the “urban” and “wild” study areas to each other, (B) a sample of the “urban” landscape near Albany, New York, USA, and (C) a sample of the “wild” landscape near Grafton, New York, USA.



Preserve, but also more developed and managed areas such as golf courses and cemeteries.

DISSERTATION OUTLINE

The motivation behind this dissertation research is to better understand the ecology and behavior of fishers inhabiting the developed landscape near Albany, New York, USA. I first quantified the fisher's geographic range expansion and tested hypotheses related to the mesopredator release hypothesis via changes in predator species richness over time, fisher dietary patterns, and fisher body size (see Chapter 2). This effort suggested that fishers in their eastern range (including my study area) have greatly expanded their range outward from refugia, and are possibly benefiting from a reduced predator community. However, it is quite clear that other, undocumented factors may also facilitate their range expansion, particularly habitat suitability.

I then focused my efforts on understanding when, where, and how fishers move by quantifying the daily activity patterns, habitat selection, and movement patterns of the fishers within my study areas. To do so required three years of field work, principally involving the capture and handling fishers, deploying state-of-the-art global positioning system (GPS) tracking collars equipped with accelerometers (see Chapter 3 for more details), and conducting camera trap surveys. However, because of the fragmented matrix of my urban study area and my desire to record between-patch movements of fishers, high spatial and temporal resolution movement data was clearly needed to achieve my objectives. In order to obtain this data, we developed a novel program for a behaviorally-informed, dynamic GPS location-fix attempt schedule (see Chapter 3). Simply, using the animal's level of activity (measured via the onboard accelerometer), we were able to dictate how frequently our GPS tracking collars recorded the location of our animals: more active equals more frequently. This new dynamic schedule nearly

doubled the battery life of our collars while simultaneously recording more locations during the fisher's activity, ultimately yielding biologically relevant insights that may have otherwise been undetected.

Chapter 4 describes the 'when' component of fisher movements. Using the raw recordings of the accelerometers of eleven individual fishers, I calculated their overall dynamic body acceleration (ODBA), and indicator of the level of activity of an individual. From these data, I was able to determine that these fishers are nocturnal. However, since fishers elsewhere in more "natural" habitats are reportedly active throughout the 24-hour period, I hypothesized that these urban fishers have adapting their activity patterns to avoid human activities during the day. Using automobile traffic volume data from the study area as a surrogate for human activity, I compared fisher's onset and cessation of activity with traffic volume peaks on weekdays versus weekends. Fisher's appear to cease their activity according to the onset of the morning traffic volume peak, with the earlier traffic volume peak on weekdays resulting in fisher's ceasing their activity earlier on weekdays than on weekends which have a delayed traffic volume peak. As the traffic volumes of both weekdays and weekends end at approximately the same time, we did not see a difference in the onset of fisher activities between weekdays and weekends. Further, fishers within the wild study area do not show these weekday-weekend patterns, perhaps because of their overall lower traffic volumes, and these fishers also remain active into the day longer than the urban fishers. These preliminary results suggest that the urban fishers are adapting to human activities by shifting the timing of their daily activities to avoid human activities.

The urban study is highly fragmented by roads and developments, often leaving potential fisher habitat (i.e., forests) in disconnected patches. Understanding what land cover types constituted the home ranges of the fishers within the landscape sought and how they moved

among and between these habitat patches is the focus of Chapter 5. I hypothesized that fishers selected for forest patches and that they connected the multiple forest patches that constitute their home ranges by utilizing corridors. I first quantified each fisher's habitat selection and found that they prefer forested habitats as expected, but they were often forced to move between several forest patches in order to acquire sufficient resources. I then developed a novel, simple model to identify corridors from animal behavior inferred from the movement data collected by the deployed GPS tracking collars. Next, I used the habitat selection information to run two models commonly used to predict and identify (yet rarely verified) conservation corridors. Finally, using remote camera traps, I quantified the number of passes made by several animal groupings through each predicted corridor type: my model (the "animal-defined" corridor model), least-cost path analysis, and circuit theory. Camera detection data suggested that the cost-based corridor models performed poorly in this landscape, whereas my model predicted corridors that received higher detection rates of every species grouping considered. The results of this chapter highlight the need to both validate corridor model predictions and to incorporate animal behavior into existing corridor models.

In the last chapter of this dissertation I review the major findings of each chapter and provide a broader perspective of this work. I discuss the limitations and conservation implications of my dissertation and offer suggestions for future research directions. In particular, I emphasize the potential value of a more animal-centric perspective of movement ecology for conservation biology.

Eastern fisher (*Pekania pennanti*) range expansion may be facilitated by a mesopredator release.

Scott LaPoint^{1,2}, Jerrold Belant³, and Roland Kays^{4,5}

submitted to Animal Conservation

¹ Max-Planck-Institute for Ornithology, Am Obstberg 1, D-78315 Radolfzell, Germany

² Department of Biology, University of Konstanz, Universitätsstraße 10, D-78464 Konstanz, Germany

³ Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA

⁴ North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, North Carolina 27601, USA

⁵ Department of Forestry and Environmental Resources, North Carolina State University, Box 8008, Raleigh, North Carolina 27695, USA

ABSTRACT

Today some eastern populations of fisher (*Pekania pennanti*) are making a strong comeback from historic range contractions, while other western populations continue to struggle. Here we investigate whether expanding fisher populations are benefiting from reductions in their carnivore predator community, as predicted by the mesopredator release. This hypothesis posits that local extinctions of the largest predators in an area “release” mesopredator populations from direct predation and competition, leading to an increase in their abundance, expansion of their range, and potentially shifts in their morphology and ecological niche. We show that the fishers range expansion appears to be facilitated by reductions in their predator community, especially in their southeastern range. Our meta-analysis of fisher diet also suggests that released fisher populations may benefit by complimenting their diverse diets with more large-bodied prey species, whereas range expansion appears limited by more specialized diets (e.g., northwestern populations) or those with diverse diets but which contain small amounts of large-bodied prey (e.g., populations along the Pacific coast). Further, measurements of museum specimens suggest that individuals within released populations are evolving larger body size, which may help them hunt larger prey species that are expected to be more available in the absence of larger carnivores. These three data sets all support the hypothesis that a reduced predator community is at least contributing to the geographic discrepancies in modern fishers range expansion. We discuss additional data needed to further test these hypotheses and suggest avenues for future research. The range expansion of the eastern fisher shows that protecting species and their refugia over time can allow them to adapt to changes in their environment, providing support for long-term conservation planning and hope for imperiled species.

INTRODUCTION

Anthropogenic forces such as habitat fragmentation, habitat loss, over-exploitation, and direct persecution have resulted in severe range contractions of many apex predator species (Channell and Lomolino 2000; Gittleman et al. 2001; Laliberte and Ripple 2004; Hemerik et al. 2007). Their local extinction can have widespread and complex effects on their food webs and ecosystems (Estes et al. 2011), including allowing populations of smaller predators to increase (i.e., mesopredator release; Crooks and Soulé 1999; Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2013). In turn, the “released” mesopredators may benefit from reduced interspecific killings (Palomares and Caro 1999), reduced competition for prey (Polis et al. 1989), or from reduced habitat selectivity due to a lower “fear” of predation (Laundré et al. 2001), potentially allowing the mesopredator to expand its range. However predicting the mesopredator release has been difficult because of numerous direct and indirect interactions and complexities within the ecosystem, and because mesopredators are likely also impacted by some of the same forces that lead to the reduction of the apex predators.

Fishers (*Pekania pennanti*) are mesopredators (females 2.0 – 2.5 kg; males 3.5 – 5.5 kg) native to the northern forests of North America (Powell 1993). Their range contracted northward following the Euro-American colonization of North America and the subsequent land conversion, timber, and fur harvesting, leaving fishers in isolated refugia scattered throughout the southern portion of their range (Lewis et al. 2012). By the early 20th century however, agricultural lands were being abandoned and forest clearing eased within much of their northeastern range (Pimm and Askins 1995). Across the United States, fisher trapping seasons were closed, first in Wisconsin (1921) and finally in California (1946), providing fishers with temporary relief from harvest (Powell 1993). Fisher populations have since expanded their

north-central and northeastern ranges southward, aided by successful translocations (Lewis et al. 2012) and have even begun colonizing suburban woodlands in parts of their southeastern range (LaPoint et al. 2013). Unfortunately, however, fishers still have the fourth most contracted geographic range of all North American carnivores (Laliberte and Ripple 2004). They remain threatened along the western coast of the United States, despite harvest bans and five translocation efforts (Lofroth et al. 2011; Lewis et al. 2012). Fishers have been translocated 38 times throughout their range with much success (Lewis et al. 2012), yet the regional variation in fisher range expansion remains, sparking much discussion and debate among carnivore biologists. Lewis et al. (2012) suggest that the success of a fisher translocation effort was partially predicted by whether the release occurred within the eastern or western range, and posited that predator-prey communities may be a contributing factor.

As a mesopredator, fishers themselves are at risk to being killed by larger carnivores, although records of adult fisher mortalities from predation events are rare. A group of coyotes (*Canis latrans*) killed a fisher in Maine (Krohn et al. 1994). In Montana, Roy (1991) documented eight fisher mortalities attributed to a diversity of fisher predators: three males to cougar (*Puma concolor*), one male and two females to coyote, one male to wolverine (*Gulo gulo*), and one female to lynx (*Lynx canadensis*). A lynx in British Columbia killed an adult female fisher (Weir and Corbould 2008). A fisher in Minnesota was killed by a female wolf (*C. lupus*), but was the only report of such an event known to the authors (Palacios and Mech 2011). Cougars and bobcat (*L. rufus*) have been documented as the most frequent natural mortality sources for male and female, respectively, fishers across the States of California, Oregon, and Washington (Wengert et al. in prep). Interspecific killings are common but often undocumented among carnivores (Palomares and Caro 1999) and are important factors that affect community

structure (Donadio and Buskirk 2006). Yet these killings are not without risks to the predator; indeed, fishers have been recorded killing lynx in Maine (Vashon et al. 2003). As these predators have been known to kill fishers, despite the risks, their presence within the landscape should hinder fisher populations, either through direct mortality or through indirect effects, such as increased competition for resources.

The regional variation in their range expansion makes the fisher an ideal study species to explore the factors that facilitate or hinder range expansion in carnivores. In this paper we investigate whether expanding fisher populations are benefiting from a reduced potential carnivore predator community. We first partitioned the fishers' geographic range into four regions and quantified each regions range expansion since their most contracted range. We then quantified the overlap of the fishers current range with the historic and current ranges of six of their potential predators: bobcat, cougar, lynx, coyote, wolf, and wolverine. If fishers have indeed experienced a release, theory suggests that they may also expand their ecological niche (Hutchinson 1957). Fishers could do this by consuming a greater diversity of food items, especially larger-bodied prey (Moreno et al. 2006), thereby increasing their energy intake efficiency (Gittleman and Harvey 1982; Carbone et al. 2007). Thus, we predicted that released fisher populations should have more diverse diets that also contain more large-bodied prey than fisher populations who have not experienced a release from their predators. Additionally, larger fishers should be better suited for targeting larger-bodied prey, as these individuals can reduce their prey handling time (Powell 1979) and should be better suited to defend their cache from intra-specific competitors (Arnott and Elwood 2009). Therefore, we investigated trends in fisher size (i.e., condylobasal length) across their range, predicting that the body size of released fisher populations should increase over time. Here we test these hypotheses with available data and

highlight areas in need of additional study, aiming to help guide conservation practitioners working to re-establish the fisher and other carnivore species.

METHODS

Fisher range regional divisions

We divided the fishers current geographic range (Lewis et al. 2012) into four regions whose boundaries were delineated based on ecoregions (U.S. Environmental Protection Agency 2010), genetics (Hall 1981; Drew et al. 2003), and probable range discontinuities (Lewis et al. 2012) (Figure 1). The Pacific region includes fisher populations within California and Oregon, corresponding to the probable subspecies (*P. pennanti pacifica*) range within the northwestern forested mountains ecoregion, but does not include data from the reintroduced population within northwestern Washington nor the ongoing translocations occurring in the northern Sierra Mountains of California, as the amount of time since individuals were released in these areas is insufficient to determine their re-establishment. The Northwest region includes fishers within western Montana and northern Idaho, and extends to the northern and westernmost extent of their current range and ends at the easternmost extent of the northwestern northern forests. The Central region includes the fishers range east of the Northwest region boundary and ends within Ontario at a probable range discontinuity during the species most contracted range (Lewis et al. 2012), including the states of Minnesota, Michigan, and Wisconsin. The Eastern region includes areas to the east of the Central region to the Atlantic Coast and southward along the Appalachian Mountains to West Virginia and including the satellite population within Tennessee.

Predator range overlap

We compared the percent overlap of the current fisher geographic range with the historic and current geographic ranges of their documented carnivore predators: bobcat, lynx, cougar, coyote, wolf, and wolverine. We digitized the current fisher range from Lewis et al. (2012) using ArcGIS (version 10.1; Environmental Systems Research Institute 2012). For the predator historic range maps, we used the same ranges as did Laliberte and Ripple (2004) and Prugh et al. (2009) which were based on field observations from the 18th and 19th century (Hall and Kelson 1959). We used shapefiles available from the IUCN (2012) as our source for predator current ranges. To quantify changes in the predator community, we first calculated the proportion of overlap of the fishers current range with each predators historic range and each predators current range. We also mapped the change in species richness over time by subtracting the current predator species richness from the historic to visualize the changes experienced by fishers. All spatial analyses were conducted using packages for program R (R Core Team 2013, version 3.0.1) packages *maptools* (vers. 0.8-25; Bivand and Lewin-Koh 2013), *PBSmapping* (vers. 2.66.53; Schnute 2013), *raster* (vers. 2.1-49; Hijmans 2013), *sp* (vers. 1.0-11; Pebesma and Bivand 2005), and *rgeos* (vers. 0.2-19; Bivand and Rundel 2013).

Fisher diet

The disappearance of larger carnivores should allow fisher populations to capitalize on the prey species that are now more available due to reduced competition with larger carnivores, particularly large-bodied prey (McKinney and Lockwood 1999; Gehring and Swihart 2003; Bowman et al. 2006; Prugh et al. 2009; Clavel et al. 2010; Hüner and Peter 2012). Thus, we hypothesized that the diets of fisher populations experiencing a mesopredator release should

contain greater proportions of larger-bodied prey items (i.e., mammals with mass >1 kg) within their diets than those populations that have not experienced a release. To test this hypothesis we quantified the diversity and the generality of fisher diets and compared the proportion of larger-bodied prey within their diets.

We conducted a literature survey, yielding 20 published studies, theses, and agency reports, including the 12 studies previously reviewed by Martin (1994) (Table 1). We quantified diet diversity using the Shannon-Weiner diversity index (H') (Zar 1996) on the full list of diet components identified within the study. The surveyed diet studies varied in their method for reporting fisher diet composition, thus to calculate H' , we standardized fisher diet compositions by calculating the % occurrence ($\%O_i$) (i.e., the number of samples that contained food item i , divided by the total number of occurrences of all food items; as recommended by van Dijk et al. 2007) from either the raw data presented in the study, or when the % frequency ($\%F_i$) (i.e., the number of times food item i was present divided by the total number of analyzed samples) was reported, by converting $\%F_i$ to $\%O_i$ by dividing F_i by the sum of frequencies for all food items. Because the studies also varied in the level of specificity of their food item identification (i.e., several studies attempted to identify diet components to the species level; e.g., Golightly et al. 2006, whereas others reported less specific categories; e.g., Powell 1977), we reclassified diet components into thirteen food item categories: insectivores, mice and voles (including bats and *Ochotona* spp.), tree squirrels (including *Arborimus* spp.), ground squirrels (excluding species with mass > 1 kg, e.g., woodchuck *Marmota monax*), rabbits (including *Sylvilagus* spp. and *Lepus* spp.), porcupine, carnivores, other large mammals (including food items listed as “carrion”, beaver *Castor canadensis*, muskrat *Ondatra zibethicus*, *Odocoileus* spp., moose *Alces*

	bird	carnivore*	fruit	ground squirrel	herpitle	insect	insectivore	large mammal*	mice & voles	porcupine*	rabbit*	tree squirrel	vegetation	O_i	H'	H'_{red}	large prey
Pacific ($W = 0.401$)	315	39	61	128	169	440	111	133	105	7	105	106	377	2096	2.923	2.272	0.135
Grenfell & Fasenfest, 1979	0	0	0	0	0	0	1	2	3	0	1	1	4	12	2.120	1.633	0.250
Zielinski <i>et al.</i> , 1999	90	2	18	13	41	113	9	8	41	0	1	24	0	360	2.233	1.877	0.031
Aubry & Raley, 2006	109	10	0	66	25	99	16	42	8	7	87	18	53	540	2.407	2.164	0.270
Golightly <i>et al.</i> , 2006	116	27	43	49	103	228	85	81	53	0	16	63	320	1184	2.571	2.175	0.105
Northwest ($W = 0.719$)	23	47	0	3	0	3	32	143	115	43	95	95	33	632	2.603	2.069	0.519
Jones, 1991	4	2	0	3	0	3	0	13	10	1	11	5	33	85	2.860	1.858	0.318
Weir <i>et al.</i> , 2005	19	45	0	0	0	0	32	130	105	42	84	90	0	547	2.617	1.928	0.550
Central ($W = 0.579$)	45	9	0	0	6	3	7	32	21	12	188	21	20	364	1.950	1.689	0.662
Powell, 1977 ¹	0	0	0	0	0	0	3	7	7	7	11	5	2	42	1.828	1.834	0.595
Leonard, 1980	22	1	0	0	1	0	4	20	12	5	43	14	0	122	2.484	1.771	0.566
Raine, 1987	23	8	0	0	5	3	0	5	2	0	134	2	18	200	1.347	1.202	0.735
East ($W = 0.528$)	214	34	171	19	3	59	293	473	380	168	294	281	340	2729	3.145	2.276	0.355
deVos, 1952	2	4	4	0	0	14	4	15	6	20	26	5	0	100	2.416	2.015	0.650
Hamilton & Cook, 1955	6	1	14	0	0	2	8	12	14	5	8	11	6	87	2.625	2.233	0.299
Coulter, 1966	34	18	26	3	3	12	34	152	58	74	82	53	0	549	2.790	2.114	0.594
Stevens, 1968 ¹	18	6	0	13	0	21	182	83	134	5	65	83	131	743	2.381	1.999	0.214
Clem, 1977	47	2	10	0	0	0	19	34	33	30	26	3	0	204	2.473	1.952	0.451
Kelly, 1977	4	0	4	0	0	0	5	0	17	0	3	8	0	41	2.275	1.586	0.073
Brown & Will, 1979 ¹	10	3	0	3	0	10	10	87	57	20	40	73	203	516	2.094	1.801	0.291
Arthur <i>et al.</i> , 1989	9	0	25	0	0	0	4	5	6	14	12	17	0	92	2.197	1.918	0.337
Giulano <i>et al.</i> , 1989	84	0	88	0	0	0	27	85	55	0	32	28	0	399	2.308	1.835	0.293
<i>Pekania pennanti</i> ($W = 0.314$)	597	129	232	150	178	505	443	781	621	230	682	503	770	5821	3.455	2.372	0.313

Table 1. Fisher diet studies listed by region and by date with the number of occurrences per food category (O_i) (sorted alphabetically), the diet diversity of the full food item list (H') and the reduced food item list (H'_{red}), and the proportion of the diet comprised of larger-bodied prey (i.e., mammals with mass > 1 kg; indicated with “*”). Unless reported as “bait” within the study, “large mammal” includes beaver, muskrat, deer (*Odocoileus* spp.), moose, reindeer, elk, and woodchuck. “Rabbit” includes *Sylvilagus* and *Lepus* spp. We excluded items listed as “unknown”, “remainder”, “other”, “rock”, or “trace materials”.

alces, reindeer *Rangifer tarandus*., elk *Cervus canadensis*, and woodchuck), bird (including eggs), herptiles, insects, fruit, and vegetation (Table 1). We excluded items listed as “unknown”, “remainder”, “other”, “rock”, or “trace materials”. We then calculated the diet diversity of each study using these reduced food item categories (H'_{red}) as described above and draw our conclusions from these values. The Shapiro-Wilk normality test suggested that H'_{red} was not normally distributed, so we used Wilcoxon rank sum tests to statistically compare diet diversity between regions.

We calculated Kendall’s coefficient of concordance (W) on the reduced food item categories to quantify the variability of food item contributions to the fisher’s diet and also to investigate whether these contributions varied between and within regions (Legendre 2005). To estimate Kendall’s W , food items (rows) are arranged by study (columns) and each food item is ranked by their proportion within each study. These rankings are then summed for each food item (row) and the variance of these ranking sums was estimated. For example, if the food item rankings are consistent across all studies, then the variance of the ranking sums (i.e., W) will be high, suggesting the diet is specialized. As W approaches 0, the food item rankings across diet studies approach dissimilarity (food item rankings are variable; i.e., opportunist or generalist diet), and as W approaches 1, the food item rankings become more similar (i.e., specialized diet) (Legendre 2005).

Fisher body size

We measured condylobasal length data on museum specimens across North America to investigate whether fisher body size has changed since their most contracted range. Earlier work suggested that fisher skull size varies geographically, with the Pacific and the Eastern

populations having the smallest skulls (Hagmeier 1959). However, data from more recent specimens were required to test our hypotheses. Condylobasal length is a commonly used body size metric since it is invariant with body condition and age in adults, and is associated with low measurement error (Meiri et al. 2005; Meiri et al. 2009). Condylobasal length measurements were taken by natural history museum staff or the authors using digital calipers to 0.1 mm precision. We only included sexed, adult (i.e., fused cranial sutures), wild caught specimens with locality data resolution to at least the township, but typically much more specific (see Appendix). For female specimens, we excluded individuals with condylobasal lengths greater than the 95% confidence interval, and for males we excluded condylobasal lengths that were less than the 5% confidence interval, under the assumption that these individuals may have been incorrectly sexed. We used a generalized linear model to determine whether fisher skull lengths have changed over time. We ran these models per sex for each region separately, with no interaction terms and an alpha of 0.05, and assumed skull lengths had a Gaussian distribution. We searched for non-normality in the residuals and used Cook's distance (D) to verify that no specimens had undue influence on the final model (i.e., specimens with potential measurement error) (Zar 1996).

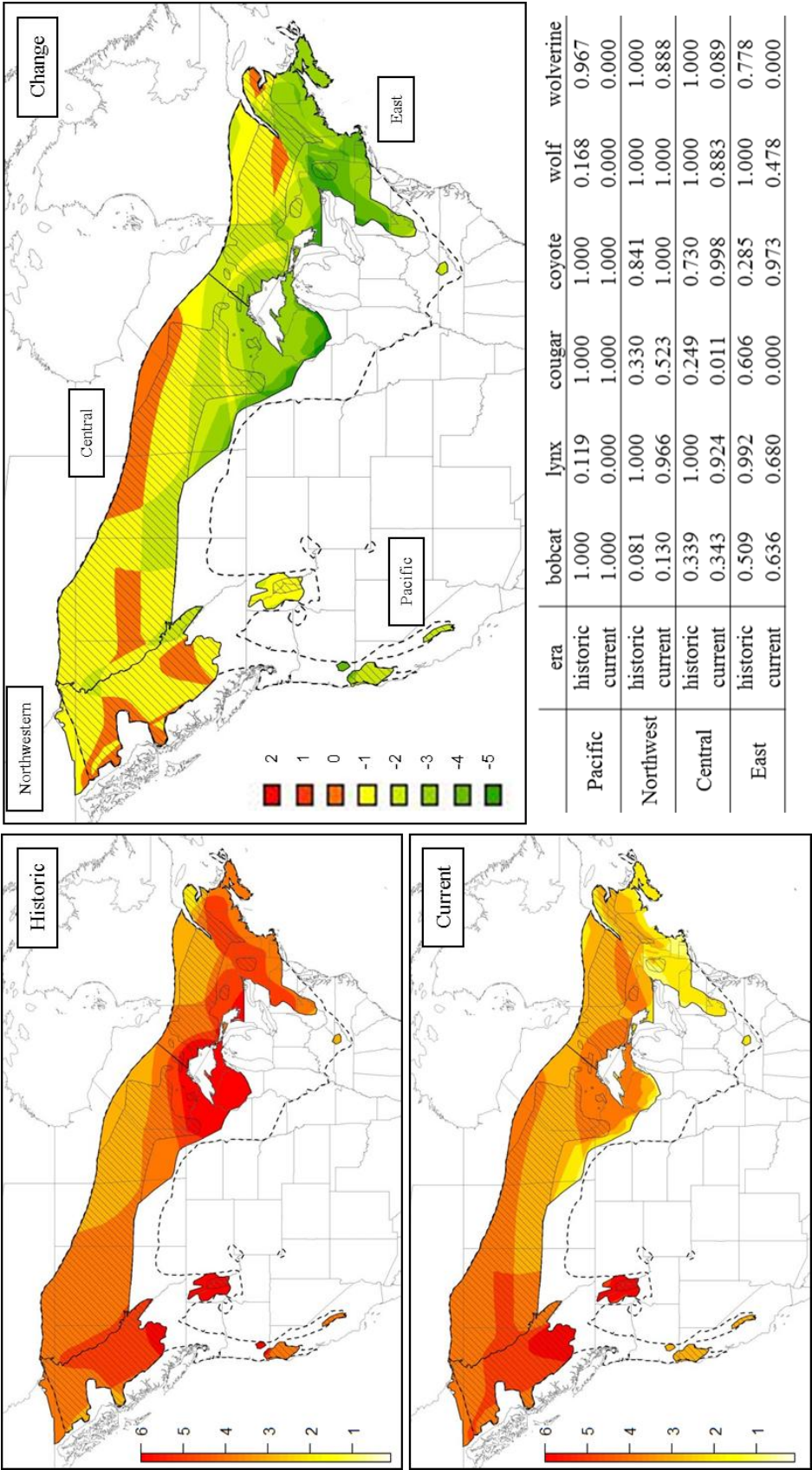
RESULTS

Overall, fishers have extended since their most contracted range by 57%, but the amount of range expansion varies between regions. Encouragingly, fishers in the Eastern and Central regions have increased their geographic ranges by 119% and 46%, respectively, although they do not yet fully occupy their historic ranges (Figure 1). Less encouraging however, fishers in the Pacific and Northwestern regions have expanded their ranges by 15% and 18%, respectively

(Figure 1). Fishers have also experienced changes in both the members of and overlap with their predator community (Figure 1). These changes match the predictions of the mesopredator release. The expanding Eastern fisher populations have experienced a 34% reduction in their predator species overlap, including the complete loss of cougar and wolverine and large range overlap reductions in both lynx and wolf (Figure 1). The Central region has also experienced a 25% reduction in their predator range overlap, with reductions again in both cougar and wolverine (Figure 1). Fishers within the Northwest region however, have experienced a 6% increase in their predator co-occurrence with only small reductions in their overlap with lynx and wolverine that may correspond with their relatively small amount of range expansion. Changes in the Pacific fisher predator community (29% reduction) are not consistent with the mesopredator release hypothesis however. Pacific fishers have experienced the complete loss of lynx, wolf, and wolverine, but continue to have complete overlap with bobcat, cougar, and coyote (Figure 1).

Two diet studies (i.e., Kuehn 1989 and Roy 1991) were excluded from our analyses because they did not report values from which we could calculate % occurrence. We were not able to replicate the H' values reported by Martin (1994), but our H' values were positively correlated with those reported by Martin (1994) ($r_s = 0.74$, $P = 0.008$) and our H'_{red} and H' estimates were also correlated ($r_s = 0.74$, $P < 0.001$). For the remaining 18 diet studies, we found no significant differences in H'_{red} between fisher population regions (Wilcoxon tests; $P > 0.3$) nor in their variances (F-test of variance; $P \geq 0.176$). Fishers are generalist predators across their range ($W = 0.314$), but the diversity of and the prominent food items within vary between regions (Table 1). Eastern fishers have the most diverse diet and appear to compliment this diversity by specializing ($W = 0.528$) on mammalian food items, particularly “large mammals”. Central

Figure 1. Historic (i.e., 19th century), current, and the change in predator species richness across the range of fishers. Dashed line indicates fisher historic range and diagonal lines indicate refugia. Table values indicate the historic and current proportion of each predator species range overlap with the current range of fishers, per region.



fishers have the least diverse diet, however it also contains the most large prey items.

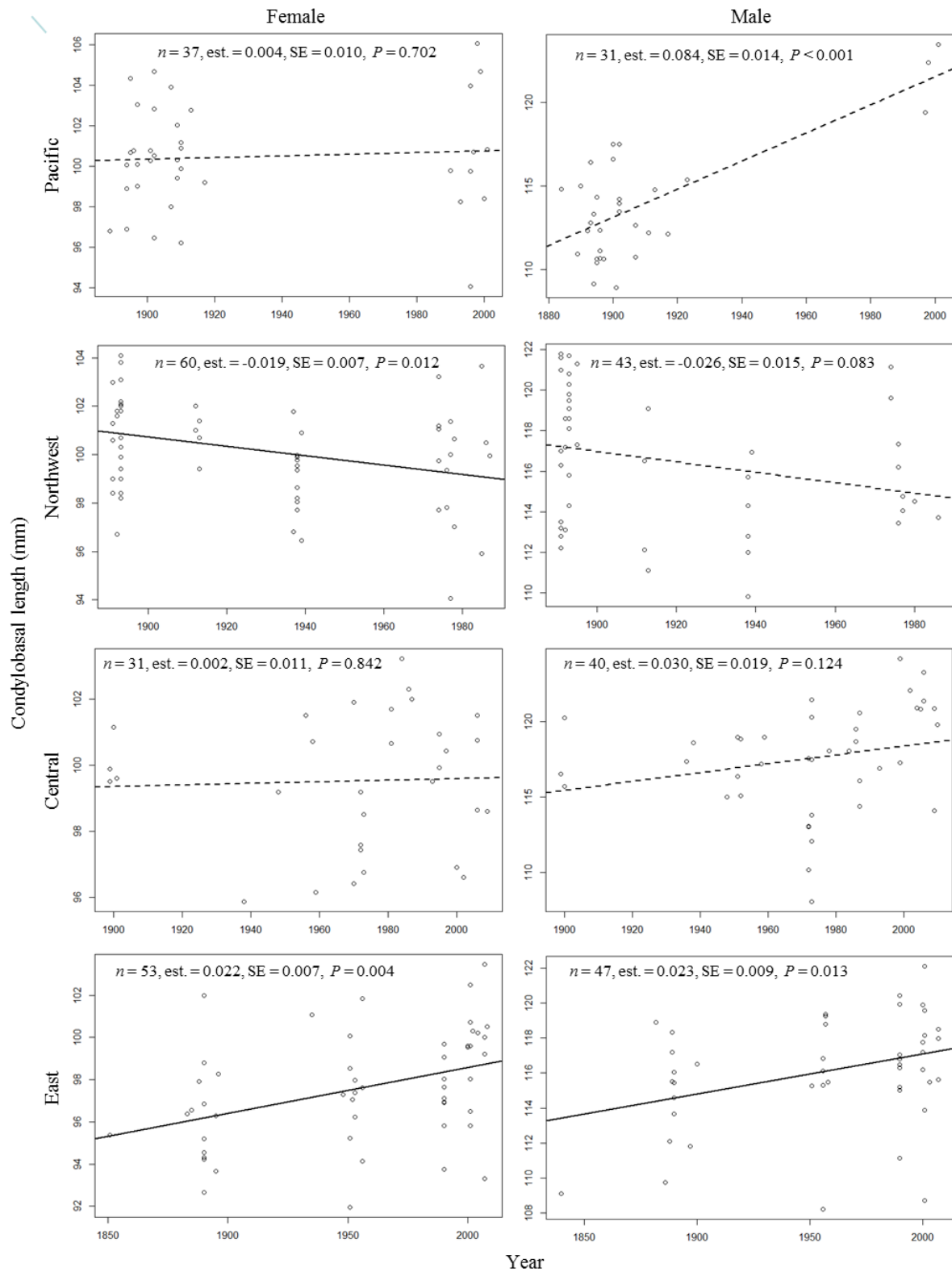
Northwestern fishers have specialized diets ($W = 0.719$) and appear to rely on four of the reduced food item categories, with only two of these categories being larger-bodied prey species. Pacific fishers appear to have diverse and unspecialized diets ($H'_{red} = 2.272$, $W = 0.4014$), but consume the least amount of larger-bodied prey items, instead relying heavily on insects and vegetation.

Condylobasal lengths for male fishers are 14% larger than those for females ($n = 162$, 116.15 mm, $SD. = 3.55$ mm, and $n = 181$, 99.37 mm, $SD = 2.64$ mm, respectively) (Appendix S1). As predicted, Eastern fisher body size has increased since the late 19th century (Figure 2). Northwest female skull lengths however have decreased over the last century (Figure 2). Both of these results are predicted if the populations have either experienced a mesopredator release (Eastern fishers) or an increase in the co-occurrence of larger predators (Northwestern fishers). However, we found no significant patterns for Central and Pacific fishers and for Northwest male fishers. Although the general linear model suggested Pacific male fisher skulls have increased in length (Figure 2), we consider this result spurious as we were only able to measure three specimens collected since 1930 from this area.

DISCUSSION

The fishers range expansion varies geographically with most expansions occurring southward, especially in their eastern ranges, while their western populations have expanded far less. The fisher's predator community has also changed in both composition and area of co-occurrence during this time. The limited range expansion of the Pacific fishers does not match our predictions, despite reductions in their predator community, bans on their harvest, and five

Figure 2. General linear model results showing changes in fisher skull (condylobasal) length over time. Sample sizes (n), model estimates (est.), standard error (SE) and P -values (P) indicated, with significant ($P < 0.05$; solid) and non-significant (dashed) trend lines.



translocation efforts. However, the fishers range expansion in the Eastern and Central regions appears coincident with reductions in the predator species richness and with reduced predator co-occurrence, particularly within the southern extents of these regions, thus supporting our predictions. Further, the relatively small amount of range expansion experienced by the Northwestern fishers may support our predictions as these fishers currently have more range overlap with their predator community than before. Thus, it appears that reductions in the predator community are facilitating fisher population range expansion, particularly within the southern extents of the Central and Eastern regions.

Released mesopredators are able to widen their dietary niche, allowing them to capitalize on the now relatively more available food items, particularly large-bodied prey species (Moreno et al. 2006). Consuming these larger-bodied prey species can facilitate range expansion for fisher as these species provide more energy per unit of effort (Powell 1979) and can be cached for future gains meals (Kuehn 1989; Powell 1993; Bowman et al. 2006; Hüner and Peter 2012). This is especially advantageous for dietary generalist, such as fishers, that are able to add large-bodied prey species to their already general diets (McKinney and Lockwood 1999; Gehring and Swihart 2003; Prugh et al. 2009; Clavel et al. 2010). The reduced predator community in the Eastern region may be especially beneficial to the fishers in this region as they consume a complimentary balance of food item diversity and larger-bodied prey, particularly rabbits and other “large mammals”. Fishers elsewhere may be more restricted by their diets, as they are either more specialized or contain only small amounts of larger-bodied prey species.

A mesopredator release can also affect body size or skull length increases in the “released” species (Dayan and Simberloff 1994; Simberloff et al. 2000) as these larger individuals can more efficiently kill larger prey species (Powell 1979) and are more able to

defend their cache from inter- and intra-specific competitors (Arnott and Elwood 2009). Supporting this, the size of the released Eastern fishers has increased over time. Interestingly, the skull size of female Northwestern fishers (who have experienced an increase in predator overlap), has decreased significantly; Northwestern male fishers show a similar but non-significant negative trend ($P = 0.083$). We believe these results are authentic and are not an artifact of translocation efforts because the source population and destination for most translocations (15 of the 17 Eastern and 5 of the 7 Northwestern translocations) were from within the same region (Lewis et al. 2012). Unfortunately, our interpretation from the Pacific fishers is limited due to the low number of recently collected specimens available to us, and we strongly encourage the continued deposition of specimens to natural history museum collections.

Although our results are all correlational, all three analyses support the predictions of the mesopredator release hypothesis, and the details suggest some insightful patterns. For example, coyote co-occur with fisher nearly completely, but do not appear to greatly hinder their populations given that both species have robust populations in the East (Kays et al. 2008). Cougar populations however, were extirpated from the eastern half of North America (Kays and Wilson 2010) yet co-occur with Pacific fisher completely, have expanded their Northwestern range, and are reportedly the most documented predator of adult male fishers along the Pacific coast (G.M. Wengert et al. in prep). These killings are not well predicted by the species relative body sizes alone (Donadio and Buskirk 2006); however, cougars seem prone to interspecific killings across their range: hog-nosed skunk (*Conepatus humboldtii*; Johnson and Franklin 1994), wolverine (Krebs et al. 2004), ocelot (*Leopardus pardalis*; Nuñez 1999), chulpeo fox (*Pseudalopex culpaeus*; Novaro 1997), chilla fox (*Pseudalopex griseus*; Yañez et al. 1986), and gray fox (*Urocyon cinereoargenteus*; Logan and Sweanor 2001).

FUTURE DIRECTIONS

We expect that numerous drivers are affecting the range expansion of fishers. For example, translocation efforts should facilitate their range expansion, yet a rigorous effort to explain why translocation efforts have been more successful in the east than in the west was inconclusive (Lewis et al. 2012). Another consideration is the chronology and expansion of Euro-American settlements across North America, as fisher populations in their eastern range may be receiving a two-fold advantage from this temporal effect: more time for their forests to recover and mature following reduced timber harvesting and agricultural abandonment, and more time for the fishers themselves to adapt to human activities. Other potential explanatory factors lack the data to be rigorously considered. For example, comparing fisher habitat selection preferences across their range should be a priority, given the differences between the ecological landscape and current land management regimes (Pimm and Askins 1995; Lofroth et al. 2010). However, doing so is currently unfeasible due to the variety of methods used to record fisher presence/absence and to quantify their habitat use and availability, and we encourage researchers to consider such issues in future studies. Rodenticide poisoning is a threat to fishers in California (Gabriel et al. 2012), yet has not been reported elsewhere (Stone et al. 1999), but clearly warrants direct future investigation. Fisher conservation efforts could also benefit from long-term population monitoring to determine survival estimates, and especially, mortality sources, and year-round diet studies that avoid seasonal diet composition biases. Finally, and especially important given our results, studying interactions between fishers and their co-occurring carnivore species will provide direct information on potential mesopredator release effects, including food web dynamics, resource partitioning, behavioural responses, and predator-prey dynamics.

CONCLUSION

Mesopredator increases often have negative impacts on their ecosystems (Crooks and Soulé 1999; Prugh et al. 2009; Ritchie and Johnson 2009). Here, however, we present an example of a once rare carnivore that is benefiting from the loss of its apex predators. The range expansion of the eastern fisher is encouraging for conservation practitioners aiming to restore the fisher to its previous range and highlights the importance of protecting species and their refugia over time.

ACKNOWLEDGEMENTS

We wish to thank the museum staff who kindly took condylobasal length measurements for this manuscript: D. Bogan, J. Bopp, K. Cassidy, A. Crosby, J. Diaz, C. Epps, P. Holahan, L. Kennes, M. Kimura-Sandoval, D. Oehlenschlager, J. Patton, C. Shores, and M. Wegan. We also thank the Max-Planck-Institute of Ornithology, the National Science Foundation (Grant 0756920 to RWK), and Mississippi State University's Forest and Wildlife Research Center for funding during this work. This manuscript benefited from conversations with D. Dechmann, R. Powell, and K. Safi.

Appendix. Fisher specimens used in our body size analysis.

region	era	institution	catalog #	sex	latitude	longitude	CBL	year
Pacific	historic	Smithsonian	87080	F	40.90085	-121.5	99	1897
Pacific	historic	Smithsonian	87081	F	40.80404	-121.632	100.1	1897
Pacific	historic	Smithsonian	A24025	F	39.68805	-123.483	96.8	1889
Pacific	historic	Smithsonian	92113	F	46.07065	-121.521	103.04	1897
Pacific	historic	Smithsonian	63908	F	46.07065	-121.521	96.9	1894
Pacific	historic	Smithsonian	70541	F	46.07065	-121.521	100.66	1895
Pacific	historic	Smithsonian	108213	F	46.07065	-121.521	100.76	1901
Pacific	historic	Smithsonian	116481	F	46.07065	-121.521	96.45	1902
Pacific	historic	Smithsonian	116653	F	47.40637	-123.141	100.26	1901
Pacific	historic	Smithsonian	119957	F	47.42871	-123.367	102.82	1902
Pacific	historic	Smithsonian	119959	F	47.42871	-123.367	104.68	1902
Pacific	historic	Smithsonian	119960	F	47.42871	-123.367	100.53	1902
Pacific	historic	Smithsonian	170606	F	47.40637	-123.141	98	1907
Pacific	historic	Smithsonian	170607	F	47.40637	-123.141	103.9	1907
Pacific	historic	Smithsonian	170610	F	47.40637	-123.141	102.03	1909
Pacific	historic	Smithsonian	170611	F	47.40637	-123.141	99.42	1909
Pacific	historic	Smithsonian	170612	F	47.40637	-123.141	100.31	1909
Pacific	historic	Smithsonian	170613	F	47.40637	-123.141	101.15	1910
Pacific	historic	Smithsonian	170614	F	47.40637	-123.141	99.88	1910
Pacific	historic	Smithsonian	170615	F	47.40637	-123.141	96.2	1910
Pacific	historic	Smithsonian	170616	F	47.40637	-123.141	100.89	1910
Pacific	historic	Smithsonian	227118	F	40.56582	-122.908	99.2	1917
Pacific	historic	Smithsonian	76615	F	46.07065	-121.521	100.75	1896
Pacific	historic	Smithsonian	64759	F	46.07065	-121.521	98.88	1894
Pacific	historic	Smithsonian	69972	F	46.07065	-121.521	100.05	1894
Pacific	historic	Oregon State Uni.	1235	F	43.75014	-122.468	102.76	1913
Pacific	historic	Smithsonian	76616	F	46.07065	-121.521	104.34	1895
Pacific	historic	Smithsonian	87084	M	46.07065	-121.521	110.6	1897
Pacific	historic	Smithsonian	51270	M	37.2049	-119.246	116.4	1893
Pacific	historic	Smithsonian	52821	M	37.53688	-119.656	112.8	1893
Pacific	historic	Smithsonian	81094	M	36.48093	-118.619	114.3	1895
Pacific	historic	Smithsonian	A30624	M	39.68805	-123.483	110.9	1889
Pacific	historic	Smithsonian	58109	M	42.73623	-123.423	109.11	1894
Pacific	historic	Smithsonian	64758	M	46.07065	-121.521	113.3	1894
Pacific	historic	Smithsonian	14395	M	40.79089	-121.847	114.8	1884
Pacific	historic	Smithsonian	24112	M	44.1722	-115.064	115	1890
Pacific	historic	Smithsonian	70927	M	46.07065	-121.521	110.62	1895
Pacific	historic	Smithsonian	70928	M	46.07065	-121.521	110.4	1895
Pacific	historic	Smithsonian	77873	M	46.07065	-121.521	112.35	1896
Pacific	historic	Smithsonian	81843	M	46.07065	-121.521	110.65	1896
Pacific	historic	Smithsonian	81951	M	46.07065	-121.521	111.1	1896

Pacific	historic	Smithsonian	99457	M	46.07065	-121.521	117.5	1900
Pacific	historic	Smithsonian	99652	M	46.07065	-121.521	116.58	1900
Pacific	historic	Smithsonian	107624	M	46.07065	-121.521	108.9	1901
Pacific	historic	Smithsonian	116480	M	46.07065	-121.521	114.22	1902
Pacific	historic	Smithsonian	116766	M	46.07065	-121.521	113.95	1902
Pacific	historic	Smithsonian	119958	M	47.42871	-123.367	117.5	1902
Pacific	historic	Smithsonian	119961	M	47.42871	-123.367	113.44	1902
Pacific	historic	Smithsonian	170608	M	47.40637	-123.141	112.65	1907
Pacific	historic	Smithsonian	170609	M	47.40637	-123.141	110.72	1907
Pacific	historic	Smithsonian	171002	M	37.74333	-119.576	112.2	1911
Pacific	historic	Smithsonian	227117	M	40.09979	-123.243	112.1	1917
Pacific	historic	Smithsonian	243790	M	46.42935	-121.973	115.36	1923
Pacific	historic	Smithsonian	44148	M	37.2049	-119.246	112.3	1892
Pacific	historic	Oregon State Uni.	1236	M	43.75014	-122.468	114.77	1913
Pacific	recent	Burke Museum	37530	F	47.09382	-122.277	99.79	1990
Pacific	recent	Burke Museum	60013	F	42.8782	-122.614	103.97	1996
Pacific	recent	Burke Museum	60016	F	42.909	-122.494	100.7	1997
Pacific	recent	Burke Museum	80877	F	42.9181	-122.392	104.66	1999
Pacific	recent	Burke Museum	80878	F	42.9181	-122.413	98.4	2000
Pacific	recent	Burke Museum	81058	F	42.6136	-122.452	100.84	2001
Pacific	recent	Burke Museum	80874	F	42.9327	-122.422	106.06	1998
Pacific	recent	MVZ Berkley	185230	F	37.652	-119.702	98.23	1993
Pacific	recent	MVZ Berkley	186281	F	36.12153	-118.651	94.06	1996
Pacific	recent	MVZ Berkley	186283	F	36.14346	-118.615	99.75	1996
Pacific	recent	Burke Museum	60014	M	42.5356	-122.101	119.39	1997
Pacific	recent	Burke Museum	81034	M	42.7876	-122.57	123.48	2001
Pacific	recent	Burke Museum	77855	M	42.9327	-122.413	122.4	1998
Northwest	historic	Smithsonian	180159	F	56.59937	-124.633	102	1912
Northwest	historic	Smithsonian	180161	F	56.59937	-124.633	101	1912
Northwest	historic	Smithsonian	A47981	F	54.53674	-124.507	101.8	1892
Northwest	historic	Smithsonian	53846	F	54.53674	-124.507	103.8	1893
Northwest	historic	Smithsonian	53847	F	54.53674	-124.507	102	1893
Northwest	historic	Smithsonian	53848	F	54.53674	-124.507	100.7	1893
Northwest	historic	Smithsonian	71071	F	54.53674	-124.507	102	1893
Northwest	historic	Smithsonian	203785	F	55.70652	-126.245	99.4	1913
Northwest	historic	Smithsonian	203786	F	55.70652	-126.245	101.4	1913
Northwest	historic	Smithsonian	203787	F	55.70652	-126.245	100.7	1913
Northwest	historic	Smithsonian	56955	F	54.53674	-124.507	100.3	1893
Northwest	historic	Smithsonian	56956	F	54.53674	-124.507	102.2	1893
Northwest	historic	Smithsonian	56957	F	54.53674	-124.507	98.4	1893
Northwest	historic	Smithsonian	56958	F	54.53674	-124.507	102.1	1893
Northwest	historic	Smithsonian	56959	F	54.53674	-124.507	99	1893
Northwest	historic	Smithsonian	56960	F	54.53674	-124.507	99.4	1893

Northwest	historic	Smithsonian	71061	F	54.53674	-124.507	104.1	1893
Northwest	historic	Smithsonian	71062	F	54.53674	-124.507	103.8	1893
Northwest	historic	Smithsonian	71063	F	54.53674	-124.507	102.2	1893
Northwest	historic	Smithsonian	71064	F	54.53674	-124.507	103.1	1893
Northwest	historic	Smithsonian	71068	F	54.53674	-124.507	99.9	1893
Northwest	historic	Smithsonian	71069	F	54.53674	-124.507	98.2	1893
Northwest	historic	Smithsonian	180162	F	56.59937	-124.633	102	1912
Northwest	historic	Smithsonian	A 44502	F	54.53674	-124.507	101.3	1891
Northwest	historic	Smithsonian	A 44504	F	54.53674	-124.507	99	1891
Northwest	historic	Smithsonian	A 44506	F	54.53674	-124.507	98.4	1891
Northwest	historic	Smithsonian	A 44523	F	54.53674	-124.507	100.6	1891
Northwest	historic	Smithsonian	A 47871	F	54.53674	-124.507	96.7	1892
Northwest	historic	Smithsonian	53844	F	54.53674	-124.507	101.8	1893
Northwest	historic	Smithsonian	A 44524	F	54.53674	-124.507	103	1891
Northwest	historic	Smithsonian	A 47881	F	54.53674	-124.507	101.6	1892
Northwest	historic	Smithsonian	A 44497	M	54.53674	-124.507	112.2	1891
Northwest	historic	Smithsonian	A 47872	M	54.53674	-124.507	117.2	1892
Northwest	historic	Smithsonian	180160	M	56.59937	-124.633	112.1	1912
Northwest	historic	Smithsonian	53842	M	54.53674	-124.507	118.6	1893
Northwest	historic	Smithsonian	53843	M	54.53674	-124.507	119.1	1893
Northwest	historic	Smithsonian	53845	M	54.53674	-124.507	120.8	1893
Northwest	historic	Smithsonian	56951	M	54.53674	-124.507	119.5	1893
Northwest	historic	Smithsonian	56952	M	54.53674	-124.507	121.7	1893
Northwest	historic	Smithsonian	56954	M	54.53674	-124.507	114.3	1893
Northwest	historic	Smithsonian	180158	M	56.59937	-124.633	116.5	1912
Northwest	historic	Smithsonian	71065	M	54.53674	-124.507	120.3	1893
Northwest	historic	Smithsonian	71066	M	54.53674	-124.507	118.1	1893
Northwest	historic	Smithsonian	71067	M	54.53674	-124.507	119.8	1893
Northwest	historic	Smithsonian	71070	M	54.53674	-124.507	115.8	1893
Northwest	historic	Smithsonian	77144	M	54.53674	-124.507	121.3	1895
Northwest	historic	Smithsonian	77145	M	54.53674	-124.507	117.3	1895
Northwest	historic	Smithsonian	203782	M	55.70652	-126.245	119.1	1913
Northwest	historic	Smithsonian	203783	M	55.70652	-126.245	111.1	1913
Northwest	historic	Smithsonian	A 44496	M	54.53674	-124.507	121.6	1891
Northwest	historic	Smithsonian	A 44498	M	54.53674	-124.507	116.3	1891
Northwest	historic	Smithsonian	A 44499	M	54.53674	-124.507	117	1891
Northwest	historic	Smithsonian	A 44500	M	54.53674	-124.507	113.5	1891
Northwest	historic	Smithsonian	A 44501	M	54.53674	-124.507	113.2	1891
Northwest	historic	Smithsonian	A 44525	M	54.53674	-124.507	121	1891
Northwest	historic	Smithsonian	A 44526	M	54.53674	-124.507	112.8	1891
Northwest	historic	Smithsonian	A 44527	M	54.53674	-124.507	121.8	1891
Northwest	historic	Smithsonian	A 47874	M	54.53674	-124.507	113.1	1892
Northwest	historic	Smithsonian	A 47875	M	54.53674	-124.507	118.6	1892

Northwest	recent	Royal BC Museum	2443	F	55.87454	-126.477	96.8	1937
Northwest	recent	Royal BC Museum	2491	F	53.85	-126.267	101.78	1937
Northwest	recent	Royal BC Museum	3534	F	56.09923	-126.804	99.97	1938
Northwest	recent	Royal BC Museum	3535	F	56.03063	-126.109	98.19	1938
Northwest	recent	Royal BC Museum	3536	F	56.03063	-126.109	98.05	1938
Northwest	recent	Royal BC Museum	3537	F	56.03063	-126.109	97.72	1938
Northwest	recent	Royal BC Museum	4282	F	56.47669	-126.741	99.36	1938
Northwest	recent	Royal BC Museum	4283	F	56.47669	-126.741	98.65	1938
Northwest	recent	Royal BC Museum	4288	F	56.47669	-126.741	99.78	1938
Northwest	recent	Royal BC Museum	4704	F	50.8108	-121.323	96.44	1939
Northwest	recent	Smithsonian	275923	F	50.79871	-119.038	100.9	1939
Northwest	recent	Smithsonian	275924	F	56.47669	-126.741	99.9	1938
Northwest	recent	Royal BC Museum	3533	F	56.09923	-126.804	99.53	1938
Northwest	recent	Royal BC Museum	10288	F	52.28991	-121.369	97.02	1978
Northwest	recent	Royal BC Museum	10292	F	52.41686	-121.488	99.36	1976
Northwest	recent	Royal BC Museum	14003	F	53.5539	-124.802	100.64	1978
Northwest	recent	Royal BC Museum	21045	F	58.3478	-128.589	101.38	1977
Northwest	recent	Royal BC Museum	21046	F	55.66082	-123.981	94.06	1977
Northwest	recent	Royal BC Museum	21052	F	50.22392	-119.23	100	1977
Northwest	recent	Royal BC Museum	21071	F	52.41686	-121.488	97.81	1976
Northwest	recent	U. of Wisc. Madison	22604	F	54.5352	-114.417	99.75	1974
Northwest	recent	U. of Wisc. Madison	22606	F	54.5352	-114.417	103.22	1974
Northwest	recent	U. of Wisc. Madison	22608	F	54.5352	-114.417	101.18	1974
Northwest	recent	U. of Wisc. Madison	22623	F	54.5352	-114.417	97.72	1974
Northwest	recent	U. of Wisc. Madison	22624	F	54.5352	-114.417	101.07	1974
Northwest	recent	Conner Museum	33344	F	47.25389	-115.907	95.9	1985
Northwest	recent	Conner Museum	33347	F	45.86983	-115.762	99.95	1987
Northwest	recent	Conner Museum	33348	F	45.75254	-115.275	100.5	1986
Northwest	recent	Conner Museum	33349	F	45.79754	-115.49	103.65	1985
Northwest	recent	Royal BC Museum	2821	M	56.47669	-126.741	114.29	1938
Northwest	recent	Royal BC Museum	2820	M	56.47669	-126.741	109.81	1938
Northwest	recent	Royal BC Museum	4279	M	56.47669	-126.741	111.99	1938
Northwest	recent	Royal BC Museum	4286	M	56.47669	-126.741	112.78	1938
Northwest	recent	Royal BC Museum	4308	M	56.47669	-126.741	115.7	1938
Northwest	recent	Royal BC Museum	4746	M	49.07398	-121.102	116.93	1939
Northwest	recent	Royal BC Museum	13996	M	52.41686	-121.488	117.35	1976
Northwest	recent	Royal BC Museum	13999	M	52.13215	-122.075	114.77	1977
Northwest	recent	Royal BC Museum	14002	M	53.88138	-125.841	113.44	1976
Northwest	recent	Royal BC Museum	21056	M	53.88138	-125.841	114.04	1977
Northwest	recent	Royal BC Museum	13995	M	52.41686	-121.488	116.2	1976
Northwest	recent	U. of Wisc. Madison	22605	M	54.5352	-114.417	119.6	1974
Northwest	recent	U. of Wisc. Madison	22633	M	54.5352	-114.417	121.15	1974
Northwest	recent	Conner Museum	33343	M	47.0105	-116.253	114.5	1980

Northwest	recent	Conner Museum	33351	M	45.46693	-116.323	113.7	1986
Central	historic	U. of Wisc. Madison	8786	F	47.66785	-93.5965	99.89	1899
Central	historic	U. of Wisc. Madison	8785	F	47.66785	-93.5965	99.51	1899
Central	historic	U. of Wisc. Madison	8781	F	47.55079	-93.5684	101.15	1900
Central	historic	Smithsonian	115970	F	49.82964	-95.2017	99.6	1901
Central	historic	U. of Wisc. Madison	8784	M	47.66785	-93.5965	116.52	1899
Central	historic	U. of Wisc. Madison	8783	M	47.55079	-93.5684	120.26	1900
Central	historic	U. of Wisc. Madison	8782	M	47.55079	-93.5684	115.7	1900
Central	recent	Royal BC Museum	3584	F	55.709	-121.635	95.86	1938
Central	recent	Royal Sask. Museum	M1273	F	52.85	-102.383	96.15	1959
Central	recent	Bell Museum	2626	F	47.5672	-92.3975	99.19	1948
Central	recent	Bell Museum	4376	F	47.8689	-92.3155	100.71	1958
Central	recent	Bell Museum	3986	F	47.5011	-91.2148	101.51	1956
Central	recent	U. of Wisc. Madison	36667	F	45.3	-89.3	100.76	2006
Central	recent	U. of Wisc. Madison	36638	F	45.3	-89.3	98.63	2006
Central	recent	U. of Wisc. Madison	36637	F	45.3	-89.3	101.51	2006
Central	recent	U. of Wisc. Madison	34601	F	45.7	-89.16	99.92	1995
Central	recent	U. of Wisc. Madison	33821	F	45.7	-89.16	100.95	1995
Central	recent	U. of Wisc. Madison	23952	F	45.84878	-89.7443	98.51	1973
Central	recent	U. of Wisc. Madison	21311	F	45.654	-90.3686	100.65	1981
Central	recent	U. of Wisc. Madison	21698	F	46.16688	-90.0633	103.23	1984
Central	recent	Michigan St. U.	MR.33238	F	46.18144	-89.2082	101.7	1981
Central	recent	Michigan St. U.	MR.16548	F	46.33539	-88.4934	96.4	1970
Central	recent	Michigan St. U.	MR.16547	F	46.32166	-89.9096	101.9	1970
Central	recent	Burke Museum	80951	F	46.18	-88.539	96.6	2002
Central	recent	Michigan DNR	F00-40	F	46.2	-87.6	96.9	2000
Central	recent	Michigan DNR	F93-265	F	46.2	-87.6	99.5	1993
Central	recent	Michigan DNR	F09121	F	46.2	-87.6	98.6	2009
Central	recent	Michigan DNR	F8700004	F	46.2	-87.6	102	1987
Central	recent	Michigan DNR	F86-6	F	46.2	-87.6	102.3	1986
Central	recent	U. of Wisc. Madison	27919	F	44.31871	-90.3708	100.43	1997
Central	recent	Bell Museum	12235	F	47.9478	-89.7806	96.75	1973
Central	recent	Bell Museum	12236	F	47.9667	-89.7667	97.43	1972
Central	recent	Bell Museum	12237	F	47.9667	-89.7667	99.18	1972
Central	recent	Bell Museum	12239	F	47.9667	-89.7667	97.58	1972
Central	recent	Royal BC Museum	3583	M	55.709	-121.635	118.6	1938
Central	recent	Royal BC Museum	14011	M	56.12536	-121.314	118.07	1978
Central	recent	Royal Sask. Museum	M598	M	50.567	-101.967	118.96	1951
Central	recent	Royal Sask. Museum	M913	M	53.2	-105.767	115.09	1952
Central	recent	Royal Sask. Museum	M922	M	53.2	-105.767	118.86	1952
Central	recent	Royal Sask. Museum	M1238	M	52.85	-102.383	117.21	1958
Central	recent	Bell Museum	1179	M	48.0076	-91.4671	117.36	1936
Central	recent	Bell Museum	2797	M	47.9529	-91.4585	115.01	1948

Central	recent	Bell Museum	3104	M	48.1911	-93.8064	116.38	1951
Central	recent	Bell Museum	4479	M	48.1864	-94.1831	118.97	1959
Central	recent	Smithsonian	349626	M	47.4616	-91.0559	108.05	1973
Central	recent	Burke Museum	34270	M	47.6172	-91.3547	113.03	1972
Central	recent	U. of Wisc. Madison	28021	M	45.22019	-88.007	120.93	2004
Central	recent	U. of Wisc. Madison	36651	M	45.3	-89.3	123.28	2006
Central	recent	U. of Wisc. Madison	21697	M	46.16688	-90.0633	118.08	1984
Central	recent	U. of Wisc. Madison	27897	M	46.17244	-91.7982	116.92	1993
Central	recent	U. of Wisc. Madison	36650	M	45.3	-89.3	121.36	2006
Central	recent	Michigan DNR	F09-144	M	46.2	-87.6	120.9	2009
Central	recent	Michigan DNR	F09-151	M	46.2	-87.6	114.1	2009
Central	recent	Michigan DNR	F8700024	M	46.2	-87.6	116.1	1987
Central	recent	Michigan DNR	F8700201	M	46.2	-87.6	114.4	1987
Central	recent	Michigan DNR	F02-286	M	46.2	-87.6	122.1	2002
Central	recent	Michigan DNR	F99-176	M	46.2	-87.6	124.2	1999
Central	recent	Michigan DNR	F99-99	M	46.2	-87.6	117.3	1999
Central	recent	Michigan DNR	F10-204	M	46.2	-87.6	119.8	2010
Central	recent	Michigan DNR	F86-2	M	46.2	-87.6	118.7	1986
Central	recent	Michigan DNR	F87120	M	46.2	-87.6	120.6	1987
Central	recent	Michigan DNR	F86-693	M	46.2	-87.6	119.5	1986
Central	recent	Science Mus. of MN	N/A	M	46.64159	-94.936	120.85	2005
Central	recent	Science Mus. of MN	Z74:1:1	M	48.41076	-93.213	117.5	1973
Central	recent	Bell Museum	12233	M	47.6346	-90.7086	120.31	1973
Central	recent	Bell Museum	12234	M	47.9478	-89.7806	110.16	1972
Central	recent	Bell Museum	12240	M	47.9667	-89.7667	117.55	1972
Central	recent	Bell Museum	12242	M	47.9667	-89.7667	113.05	1972
Central	recent	Bell Museum	12243	M	47.4677	-91.0384	121.46	1973
Central	recent	Bell Museum	12389	M	48.0131	-94.6826	112.07	1973
Central	recent	Bell Museum	13104	M	47.59643	-91.4965	113.8	1973
East	historic	Smithsonian	188240	F	43.80631	-74.7022	95.37	1851
East	historic	Smithsonian	81963	F	43.87589	-73.7304	98.28	1896
East	historic	Smithsonian	a03727	F	44.01074	-73.9508	94.22	1890
East	historic	Smithsonian	a03081	F	44.01074	-73.9508	94.56	1890
East	historic	Smithsonian	a03080	F	44.01074	-73.9508	95.21	1890
East	historic	Smithsonian	188229	F	45.30707	-69.0334	94.3	1890
East	historic	Smithsonian	a3082	F	44.01074	-73.9508	92.67	1890
East	historic	Smithsonian	188236	F	43.97245	-74.3872	97.91	1888
East	historic	Smithsonian	188238	F	43.74531	-74.8411	96.37	1883
East	historic	Smithsonian	188234	F	43.97245	-74.3872	96.84	1890
East	historic	Smithsonian	76431	F	49.32442	-67.5999	102	1890
East	historic	Smithsonian	81214	F	49.32442	-67.5999	93.67	1895
East	historic	Smithsonian	81216	F	49.32442	-67.5999	96.3	1895
East	historic	Smithsonian	188222	F	49.32442	-67.5999	96.55	1885

East	historic	Smithsonian	a03283	F	56.79984	-93.5647	98.79	1890
East	historic	Smithsonian	188242	M	43.77453	-75.2151	109.11	1840
East	historic	Smithsonian	188231	M	43.97245	-74.3872	116.05	1890
East	historic	Smithsonian	188233	M	43.97245	-74.3872	113.67	1890
East	historic	Smithsonian	188237	M	43.97245	-74.3872	116.05	1890
East	historic	Smithsonian	188232	M	43.97245	-74.3872	114.6	1890
East	historic	Smithsonian	75520	M	49.32442	-67.5999	115.45	1890
East	historic	Smithsonian	102570	M	48.50925	-72.2245	116.52	1900
East	historic	Smithsonian	188221	M	49.32442	-67.5999	118.9	1882
East	historic	Smithsonian	188223	M	49.32442	-67.5999	109.76	1886
East	historic	Smithsonian	188225	M	49.32442	-67.5999	115.5	1889
East	historic	Smithsonian	188226	M	49.32442	-67.5999	112.12	1888
East	historic	Smithsonian	188227	M	49.32442	-67.5999	117.19	1889
East	historic	Smithsonian	188228	M	49.32442	-67.5999	118.34	1889
East	historic	Smithsonian	99437	M	49.32442	-67.5999	111.82	1897
East	recent	Cornell Uni.	9396	F	44.55172	-74.0568	97.63	1956
East	recent	Cornell Uni.	7965	F	44.22395	-74.4641	97.38	1953
East	recent	Cornell Uni.	8016	F	43.69199	-74.9253	96.23	1953
East	recent	Cornell Uni.	9407	F	44.3239	-74.3285	94.13	1956
East	recent	Cornell Uni.	9408	F	44.55172	-74.0568	101.85	1956
East	recent	Cornell Uni.	7941	F	44.43836	-74.2526	97.98	1953
East	recent	Cornell Uni.	6244	F	43.14257	-74.7865	95.23	1951
East	recent	Cornell Uni.	6853	F	43.32222	-74.9789	97.07	1952
East	recent	Cornell Uni.	6245	F	44.55302	-74.9395	100.06	1951
East	recent	Cornell Uni.	6246	F	44.55302	-74.9395	98.53	1951
East	recent	Cornell Uni.	6159	F	42.70063	-74.0337	91.95	1951
East	recent	Cornell Uni.	5864	F	44.23569	-74.3169	101.08	1935
East	recent	Smithsonian	287846	F	46.55599	-81.032	97.3	1948
East	recent	New York State Mus.	14557	F	43.04092	-74.1375	100.31	2002
East	recent	New York State Mus.	14803	F	42.76194	-74.1342	100.23	2004
East	recent	New York State Mus.	14280	F	43.87667	-74.2508	99.6	2001
East	recent	New York State Mus.	14281	F	43.87667	-74.2508	98.04	2001
East	recent	New York State Mus.	14282	F	43.87667	-74.2508	96.49	2001
East	recent	New York State Mus.	15568	F	43.15733	-73.6257	100	2007
East	recent	New York State Mus.	13534	F	43.08608	-74.0617	95.82	2001
East	recent	New York State Mus.	13535	F	43.08608	-74.0617	102.49	2001
East	recent	New York State Mus.	13536	F	43.08608	-74.0617	100.72	2001
East	recent	New York State Mus.	13608	F	43.08608	-74.0617	99.55	2000
East	recent	New York State Mus.	15567	F	43.14581	-73.7203	99.2	2007
East	recent	New York State Mus.	15569	F	43.14581	-73.7203	93.3	2007
East	recent	New York State Mus.	15562	F	43.14581	-73.7203	103.47	2007
East	recent	New York State Mus.	13661	F	43.22799	-74.0567	99.6	2000
East	recent	Cornell Uni.	21211	F	42.06489	-76.0122	100.51	2008

East	recent	Royal Ont. Museum	98674	F	45.677	-79.178	99.08	1990
East	recent	Royal Ont. Museum	98656	F	45.17	-79.138	98.04	1990
East	recent	Royal Ont. Museum	98666	F	45.201	-78.95	99.68	1990
East	recent	Royal Ont. Museum	98658	F	45.262	-79.165	97.65	1990
East	recent	Royal Ont. Museum	98659	F	45.262	-79.165	93.74	1990
East	recent	Royal Ont. Museum	98673	F	45.3	-79.083	97.12	1990
East	recent	Royal Ont. Museum	98675	F	45.3	-79.083	95.82	1990
East	recent	Royal Ont. Museum	98671	F	45.783	-79.25	96.94	1990
East	recent	Royal Ont. Museum	98676	F	45.516	-79.302	96.9	1990
East	recent	Royal Ont. Museum	98664	F	44.958	-79.561	99.08	1990
East	recent	Cornell Uni.	6237	M	42.70063	-74.0337	115.27	1951
East	recent	Cornell Uni.	9906	M	42.34064	-75.1652	119.35	1957
East	recent	Cornell Uni.	9917	M	44.4395	-74.23	115.47	1958
East	recent	Cornell Uni.	9385	M	42.85333	-76.7489	108.23	1956
East	recent	Cornell Uni.	9817	M	44.43836	-74.2526	118.77	1957
East	recent	Cornell Uni.	9391	M	44.63367	-74.4574	116.84	1956
East	recent	Cornell Uni.	9394	M	44.22395	-74.4641	115.29	1956
East	recent	Cornell Uni.	9631	M	44.127	-73.96	116.13	1956
East	recent	Cornell Uni.	9920	M	44.63367	-74.4574	119.24	1957
East	recent	New York State Mus.	13605	M	43.08608	-74.0617	117.75	2000
East	recent	New York State Mus.	13532	M	43.11565	-74.043	122.1	2001
East	recent	New York State Mus.	13533	M	43.11565	-74.043	119.88	2000
East	recent	New York State Mus.	13539	M	43.11838	-74.0513	118.15	2001
East	recent	New York State Mus.	15563	M	43.23166	-73.6682	118.51	2007
East	recent	New York State Mus.	14517	M	42.77985	-73.8459	115.48	2003
East	recent	New York State Mus.	15565	M	43.15733	-73.6257	117.97	2007
East	recent	New York State Mus.	14235	M	43.87667	-74.2508	113.87	2001
East	recent	New York State Mus.	13533	M	43.11565	-74.043	119.88	2000
East	recent	New York State Mus.	13663	M	43.08608	-74.0617	108.73	2001
East	recent	New York State Mus.	13607	M	43.08608	-74.0617	116.18	2000
East	recent	New York State Mus.	13538	M	43.08608	-74.0617	119.57	2001
East	recent	New York State Mus.	13603	M	43.08608	-74.0617	117.75	2000
East	recent	New York State Mus.	13604	M	43.08608	-74.0617	117.2	2000
East	recent	New York State Mus.	15561	M	43.14581	-73.7203	115.61	2007
East	recent	Royal Ont. Museum	98637	M	45.55	-79.437	117.04	1990
East	recent	Royal Ont. Museum	98633	M	45.865	-79.486	116.78	1990
East	recent	Royal Ont. Museum	98628	M	44.339	-78.85	120.43	1990
East	recent	Royal Ont. Museum	98640	M	45.3	-79.083	115.19	1990
East	recent	Royal Ont. Museum	98646	M	45.099	-79.663	116.3	1990
East	recent	Royal Ont. Museum	98625	M	45.463	-78.891	115.01	1990
East	recent	Royal Ont. Museum	98629	M	44.339	-78.85	111.15	1990
East	recent	Royal Ont. Museum	98650	M	45.839	-79.082	119.94	1990
East	recent	Royal Ont. Museum	98634	M	44.958	-79.561	116.49	1990

Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity

Danielle D. Brown¹, **Scott LaPoint**^{2,3}, Roland Kays^{2,4}, Wolfgang Heidrich⁵, Franz Kümme⁵, and Martin Wikelski^{3,6}

Wildlife Society Bulletin (2012) 36: 139–146

¹ Animal Behavior Graduate Group, University of California, Davis, CA, 95616, USA

² New York State Museum, 3140 CEC, Albany, NY, USA

³ Max-Planck-Institute for Ornithology, Am Obstberg 1, D-78315 Radolfzell, Germany

⁴ Smithsonian Tropical Research Institute, Panamá, Republic of Panamá

⁵ e-obs GmbH, 82031 Grünwald, Germany

⁶ Department of Biology, University of Konstanz, Universitätsstraße 10, D-78464 Konstanz, Germany

ABSTRACT

Tracking animal movement using Global Positioning System (GPS) technology is an increasingly popular method for studying animal ecology, behavior, and conservation. To date, most GPS location schedules have been set at regular intervals. If intervals are too long, they under-sample the details of movement paths, and if too short, they oversample resting sites and deplete the unit's battery without providing new information. We address this problem by creating a dynamic GPS schedule that is linked to the activity level of the animal via an accelerometer onboard the tracking tag. We deployed traditional and accelerometer-informed GPS tags on northern tamanduas anteater (*Tamandua mexicana*) in tropical forest in the Republic of Panama (2009–2010), and on fisher (*Pekania pennanti*) in temperate forest in New York, USA (2009–2011). These species are medium-sized forest-dwellers that frequently use tree cavities, ground burrows, and thick vegetation for resting and foraging, all traits that make them particularly challenging for GPS tracking. The accelerometer-informed tags performed better than the traditional GPS tags: they attempted 73.6% more locations per day, achieved 61.7% higher location success rates, spent 28.2% less time searching for satellites, made 67.4% fewer redundant location attempts in places where animals were inactive, and ultimately provided more data for a given battery size. The resulting tracks of animal movement had high temporal resolution, revealing aspects of their behavior and ecology that would have been missed by traditional tags, especially for the fast-moving fisher. By dynamically linking the location schedule to animal movement rate, accelerometer-informed GPS tags reduce the trade-off between collecting detailed movement data and recording movement data for a longer period of time.

INTRODUCTION

The use of Global Positioning System (GPS) technology in wildlife research to address a variety of basic and applied scientific questions is growing rapidly (Bograd et al. 2010, Cagnacci et al. 2010). Technological developments in the past decade have dramatically improved and miniaturized GPS telemeters (tags), yet standard tags still consume considerable energy acquiring each location, and so a basic trade-off between battery life and sampling intensity remains (Hansen and Riggs 2008). Tags must be sufficiently lightweight and compact that they do not affect animal behavior, which limits the initial power supply on all but the largest species (Burdett et al. 2007). The fixed sampling schedule used by the vast majority of existing tags can produce high resolution data (e.g., one location every 1–15 min) for a very short period of time (hours to days, depending on battery size; Moreau et al. 2009, Recio et al. 2010) or lower resolution data (e.g., 4–6 locations each day) for several months (Heard et al. 2008, Swanepoel et al. 2010). In some tags, the GPS schedule can be adjusted by the researcher after tag deployment and can, theoretically, optimize data collection during certain seasons or times of day (Tomkiewicz et al. 2010). However, changes in sampling intensity must either be based on previous knowledge of the species' behavior or must be a reaction to a behavior change that has already occurred in the field and, thus, are not always advantageous. Therefore, at least when choosing the initial GPS schedule, most researchers must generally balance tag longevity with data resolution.

Tags with long intervals between GPS location attempts will obviously under-sample the actual path moved by an animal, providing less detail on their behavior and habitat use. Tags with short intervals between GPS location attempts will record these movement details, but will also effectively oversample areas where animals are resting, a waste of the device's limited

battery life (Adrados et al. 2003). Furthermore, GPS tags on resting animals often perform poorly either because the animals cover the GPS antenna by lying down (Bowman et al. 2000, Moen et al. 2001) or because they are resting in locations with poor satellite reception due to a dense forest canopy (Bourgoin et al. 2009) or other physical cover (e.g., subterranean dens or tree cavities; Swanepoel et al. 2010). This issue is especially critical for smaller animals that must carry a correspondingly smaller battery, and are, therefore, a priori more limited in the total number of GPS location attempts, and are even more likely than large animals to rest in refuges with little chance of satellite reception (Liow et al. 2009, Blackie 2010). The microprocessors inside most GPS tags, including those used in the present study, can conserve battery life by aborting the location attempt if no satellites have been found within a specified period (i.e., time-out or search time). Nevertheless, selecting shorter time-out periods to preserve battery life increases the rate at which the tag will abandon location attempts in sites of biological importance (feeding sites, territorial boundaries, etc.) due to temporary inaccessibility of satellites (Mattisson et al. 2010). Here we introduce a dynamic GPS location schedule that is synchronized with an accelerometer (ACT) activity sensor in order to obtain fine-scale location data when an animal is moving and minimize excessive location attempts while an animal is resting. This solution lessens the trade-off between power and longevity, while simultaneously reducing data loss. We present the accelerometer-based GPS scheduling rules and compare the performance between accelerometer-informed GPS tags and traditional GPS tags deployed on free-ranging fishers (*Pekania pennanti*) and northern tamandua anteaters (*Tamandua mexicana*).

STUDY AREAS

We deployed tags on northern tamanduas and fishers located at two separate study sites: northern tamanduas in the Republic of Panama and fishers in New York, USA. We tracked tamanduas on Barro Colorado Island (BCI, 9°9' N, 79°51' W), a 15.6-km² hilltop island in Gatun Lake, formed by the damming of the Chagres River that created the Panama Canal. The island had a broad, flat central plateau with steep ridges and valleys (20–30° slopes). The vegetation was closed-canopy lowland tropical moist forest (Dietrich et al. 1982). We tracked fishers in suburban forests around Albany, New York (42°45' N, 73°51' E), a relatively flat 350-km² developed area, with a matrix of residential and commercial land uses, interspersed with mixed and northern deciduous and coniferous forest patches.

MATERIALS and METHODS

Study species, capture protocols, and tag attachment

Northern tamanduas are 4–6-kg, semi-terrestrial, ant- and termite-eating mammals distributed across a wide range of landscapes in Central and northwestern South America (Eisenberg 1989). They can be active throughout the 24-hour period (Montgomery and Lubin 1977) and may rest on the ground, in burrows or logs, on large tree limbs, or in tree cavities and tangles of vines (Emmons and Feer 1990). On BCI, we captured tamanduas by hand or with a dart rifle and net between April 2009 and April 2010. All capture, tagging, and monitoring protocols were approved by the University of California, Davis and the Smithsonian Tropical Research Institute Institutional Animal Care and Use committees (IACUC). We fitted 7 male and 8 female tamanduas with identical 60-g tags (63 mm × 70 mm × 13 mm) that we affixed to their lower

back using 5-minute epoxy. Tags remained deployed for an average of 13.4 days (range: 6–20). Tamanduas groomed off 13 of 15 tags before the batteries were depleted.

Fishers are medium-sized (2.0–5.5 kg) carnivores native to the northern forests of North America. They are generally active during both day and night and often use tree cavities, large branches, or vacant burrows for resting (Powell 1993). We captured fishers with live traps during 3 winters (November – March) between 2009 and 2011. Fisher capture and handling protocols were approved by the IACUC at the Max-Planck-Institute for Ornithology. We fitted 8 male and 4 female fishers with tracking collars, for an average tag deployment of 19.8 days (range: 4.1–49.8). The GPS unit dimensions for fisher collars were 50 mm × 25 mm × 18 mm, and male collars weighed 105 g with a 30-mm × 55-mm battery unit, while female collars weighed 65 g with a 20-mm × 54-mm battery unit. Following release, we regularly located individuals of both species using ultra-high frequency (UHF) radio tracking, so that the GPS data could be remotely downloaded. We calculated GPS location error using a large sample average from stationary deployment tests (fisher and northern tamandua) and immobile study animals (northern tamandua).

Tag details

All tags were manufactured by e-obs GmbH (Grünwald, Germany) and contained an identical GPS microchip (U-Blox LEA-4S), a UHF radio transmitter, and a tri-axial accelerometer. We compared the performance of 2 types of tags: one with a fixed GPS schedule typical of traditional wildlife studies (hereafter, fixed-GPS), and another with a GPS schedule dynamically linked to the activity of an animal as measured by the accelerometer sensor on the tag

(accelerometer-informed GPS; hereafter, ACTi-GPS). We deployed 4 ACTi-GPS and 11 fixed-GPS tags on northern tamanduas and 6 ACTi-GPS and 6 fixed-GPS tags on fishers.

Tri-axial accelerometers (ACT) simultaneously measure the pull of gravity (g) and accelerations due to changes in animal movement along 3 orthogonal axes: forward–backward horizontal motion (X-axis), left–right horizontal motion (Y-axis), and up–down vertical movements of the body (Z-axis). An accelerometer is a piezoelectric sensor (like a spring). When deformed, the sensor generates a wave-like voltage signal, measured in millivolts, that is proportional to the acceleration (change in velocity) it experiences (Dow et al. 2009). The raw output of an accelerometer is a unit-less ratio of the voltage due to acceleration and an internal reference voltage. This ratio can be transformed into acceleration (m/sec^2) once tag measurements have been calibrated (further details are provided in the technical manual available from e-obs at <http://www.e-obs.de>). For this study we utilized these raw voltage measures and did not convert the raw accelerometer output to actual acceleration (m/sec^2).

The accelerometers in both tag types did not record constantly, but were scheduled to record at 18.74 Hz in a short (3.5-sec) burst every 2 minutes or 3 minutes (see Table 1 for exact settings). This sampling frequency produced a population of 66 accelerometer measurements for each 3.5-second burst. In active animals, the values of these measurements are highly variable, while the measurements of resting animals show little variability (Shepard et al. 2010). The microprocessor in both types of tags can calculate the statistical variance of the measurements from each burst (i.e., the population variance). For each species, we used behavioral observations made during previous tag deployments to determine typical burst-variance values for 3 activity levels: resting, medium-, and high-intensity activity (Fig. 1). This pilot data showed similar variance patterns across all 3 ACT axes, so we used a single axis (X-axis for

Figure 1. Pilot accelerometer burst-variance data from accelerometer-informed (ACTi) Global Positioning System (GPS) tags deployed on 5 northern tamanduas in the Republic of Panama, 2009–2010. The burst variances of known behaviors (from visual observations of locomotion, feeding, and resting) were compared to identify the variance thresholds for changing between GPS location schedules. Note the differences in scale of the y-axes between the 3 graphs. Maximum and minimum variance values for each category are designated with an asterisk and X, respectively. Boxes demarcate 75%, 50%, and 25% of the variance data in each category, respectively. Upper and lower whiskers demarcate 95% and 5% of the variance data in each category, respectively. The threshold to switch from the low to medium resolution schedule was 200 (dashed line on right-hand side graph). The threshold to switch from the medium to the high resolution schedule was 10,000 (dashed line on center graph).

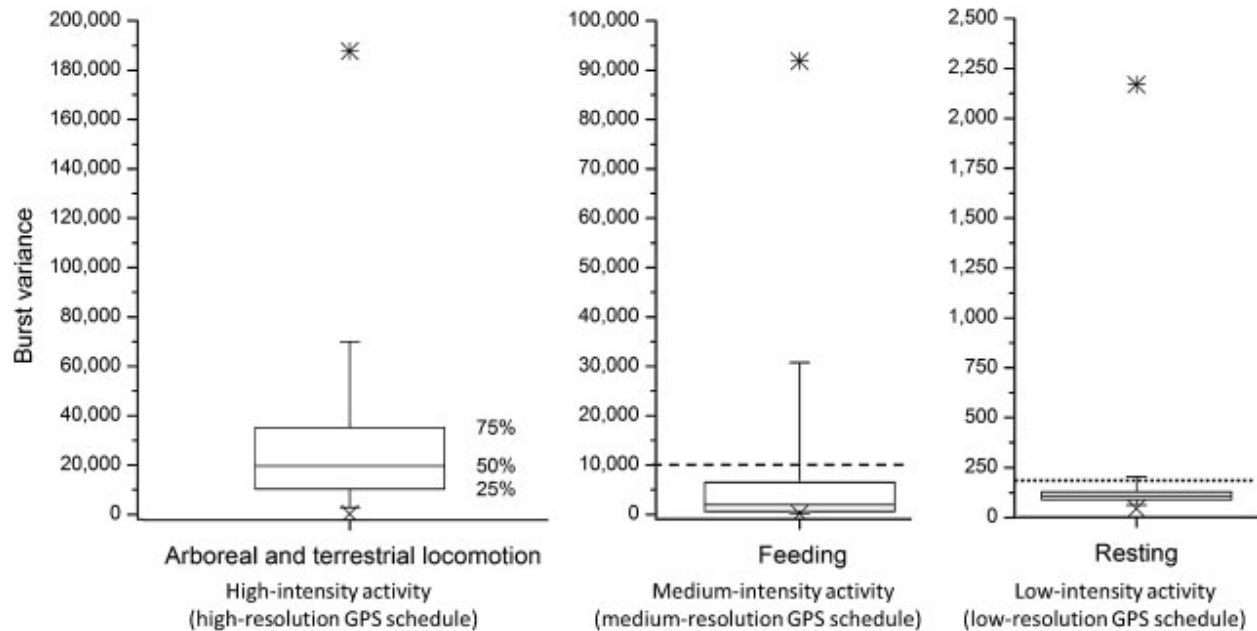


Table 1. Programmed settings of fixed-Global Positioning System (GPS) and accelerometer-informed (ACTi) GPS tags deployed on northern tamanduas in the Republic of Panama (2009–2010) and on fishers in New York, USA (2009–2011). All units are seconds unless otherwise specified. Global Positioning System time-out is the amount of time a unit was programmed to spend attempting to acquire a location before giving up.

		Northern tamandua		fisher	
		Fixed-GPS	ACTi-GPS	Fixed-GPS	ACTi-GPS
ACT sampling frequency interval		120	120	180	180
ACT sample rate/axis (Hz)		18.74	18.74	18.74	18.74
GPS sampling frequency (location schedule)	Fixed schedule	900	N/A	600	N/A
	High resolution	N/A	300	N/A	120
	Medium resolution	N/A	900	N/A	600
	Low resolution	N/A	4000	N/A	3600
GPS time-out		100	100	100 or 120	100 or 120

tamanduas, Z-axis for fishers) to identify 2 variance thresholds that delineated the 3 activity levels (Table 2).

We programmed the tag’s microprocessor to first calculate the variance of each accelerometer burst in real time and then relate this to a customized rule set to dynamically modify the GPS location attempt schedule. Simply, after calculating the population variance of each ACT burst, the onboard computer determined whether the variance values of a specified number of consecutive previous bursts (see Table 2) warranted a change in the GPS schedule from the schedule that was currently activated. The “default” GPS schedule in ACTi-GPS tags is the medium-resolution setting (Tables 1 and 2) and the decision to change schedules is based on whether variance values are above or below the low and high thresholds (Table 2). For example, in the tag settings for the northern tamanduas, a change from the medium- to the high-resolution schedule required only that the variance of the immediately preceding ACT burst be above the high threshold. At the next ACT sampling period, 120 seconds later, the algorithm would determine whether the variance values of the previous 3 bursts (180 sec) were below the high threshold; if not, the schedule would remain at high resolution until the next ACT sampling

Table 2. Thresholds and rule sets for the accelerometer-informed Global Positioning System (ACTi-GPS) location attempt schedule, as deployed on northern tamanduas in the Republic of Panama (2009–2010) and on fishers in New York, USA (2009–2011). The tag’s microprocessor determines the population variance of each ACT burst and compares the value to 2 threshold values (high and low) delineating 3 categorical activity levels: low (resting), medium, and high. The medium-intensity activity category includes all ACT variance values that fall between the resting threshold and the high-intensity activity threshold. After the variance calculation, the microprocessor follows user-programmed rules to count the number of preceding consecutive bursts whose variance values were above or below the thresholds and determine whether to change the GPS location schedule from the current resolution.

	thresholds		Rule set: no. of bursts that must pass a threshold to trigger a change in GPS location schedule			
	low-intensity (resting)	high-intensity (active)	medium to low	low to medium	medium to high	high to medium
Northern tamandua	< 200	> 10000	5	2	1	3
fisher	< 6400	> 48400	5	2	1	4

period and the decision algorithm would be run again. Therefore, changes in the GPS schedule were assessed over 1–5 ACT sampling intervals (120–600 sec) for northern tamanduas. Based on our rule sets, the location schedule for ACTi-GPS tags could be as short as an attempt every 120 seconds or as long as an attempt every 4,000 seconds. In contrast, we programmed the fixed-GPS tags to attempt a location every 600 or 900 seconds (Table 1). Both tag types also had a programmed time-out period (the amount of time the GPS would try to achieve a location before abandoning the attempt; Table 1).

RESULTS

Tag performance

Accelerometer-informed-GPS tags performed better than the traditional fixed-GPS tags in every performance category (Table 3). Accelerometer-informed-GPS tags improved the proportion of successful locations by an average of 62% across both species, and reduced the average time used to acquire a location by 39%, thus greatly improving the overall power efficiency of the tags. They also achieved more locations per day with a lower mean search time per location attempt. More locations were recorded during periods of activity; therefore, ACTi-GPS tags provided more accurate and realistic animal movement paths (Figs. 2 and 3) while reducing the amount of redundant information acquired by minimizing the number of locations attempted on resting animals.

Animal movement

Location data from a single fisher wearing an ACTi-GPS tag revealed several potential exploratory events (Fig. 2A, box 3), as well as movement bottlenecks (road crossing) and apparent movement corridors through habitat (Fig. 2A, box 2). Contrasting the movement path

Table 3. Performance comparison between fixed-Global Positioning System (GPS) and accelerometer-informed GPS (ACTi-GPS) tags deployed on northern tamanduas in the Republic of Panama (2009–2010) and fishers in New York, USA (2009–2011). Improvement of ACTi-GPS over fixed-GPS tags was tested with the Mann–Whitney statistic by combining sample sizes across both species (P values are one-sided).

Evaluation category	Northern tamandua				fisher				improvement	
	fixed-GPS		ACTi-GPS		fixed-GPS		ACTi-GPS		%	test statistic
	(N = 11)		(N = 4)		(N = 6)		(N = 6)			
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD		
Days deployed	13.5 ^a	3.4	13.0 ^a	6.1	12.6	6.5	26.2	12.8	55.6	1.88*
GPS attempts/day	94	2.5	117	13.4	134	21.1	235	27.1	73.6	3.24***
GPS success rate (%)	29.8	14.2	49.1	11.8	45	17.3	62	13.8	61.7	2.74**
Time until successful GPS location(s)	55	5.7	46	4.7	41	2.7	20.3	7.7	38.9	-3.14***
GPS search time/attempt(s)	86	7.4	71.8	9	79.6	13.1	52.4	10.4	28.2	-3.59***
GPS location error (m)	19.2	8.3	17.9	3.6	20.9	23.5	N/A ^b	N/A ^b	12.9	-0.424
GPS success rate (%) during activity	12.7	7.4	41	12.3	20.3	7.9	54.5	10.1	219.4	4.19***

^a Thirteen of 15 tamandua tags were groomed off before the battery expired, regardless of tag type.

^b GPS location error was not tested in ACTi-GPS tags prior to deployment; no error estimate is available.

$P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***)

drawn from the full set of locations with a subsampled data set representing lower intensity fixed-GPS schedules (Fig. 2B, C) highlights events that would otherwise be under- or over-emphasized by lower intensity sampling. As the sampling interval increases (i.e., more time between successive GPS location attempts), the paths to the exploratory events (Fig. 2A, box 3) gradually disappear, including the actual events themselves, even though the site was visited twice by the fisher (Fig. 2B, C). The movement corridors are obvious in the detailed data, but become less so with the subsampled data (Fig. 2C). Simultaneously, some landscape features were overemphasized in the subsampled data, as shown by what appears to be directed movement toward a pond (box 1) in Figure 2B and C. The full location data set (Fig. 2A, box 1) suggests that this animal actually did not move within 100 m of this pond.

Similar behavioral details were captured for a northern tamandua wearing an ACTi-GPS tag, indicating rich feeding areas as dense point concentrations (boxes in Fig. 3A). With visual observations we confirmed that high GPS-point concentrations were produced by animals feeding from several locations within the same tree. This concentrated use of an area was not

apparent when location sampling intensity was typical of traditional fixed GPS schedules, as indicated by the subsampled data (Fig. 3B).

DISCUSSION

Improvements in GPS hardware technology continue to change the way we investigate ecological questions (Cagnacci et al. 2010). Our implementation of an accelerometer-informed GPS location schedule offers a significant software-based improvement in GPS performance, providing new, ecologically relevant data on animal movement and habitat use. This simple algorithm offers a partial solution to the trade-off between the longevity and sampling intensity of the tag (Burdett et al. 2007, Recio et al. 2010). The use of accelerometers as an activity sensor on animal tags is increasingly common (Wilson et al. 2008, Halsey et al. 2009), and the algorithm we developed is simple enough to run onboard most tracking devices, making our general approach broadly applicable.

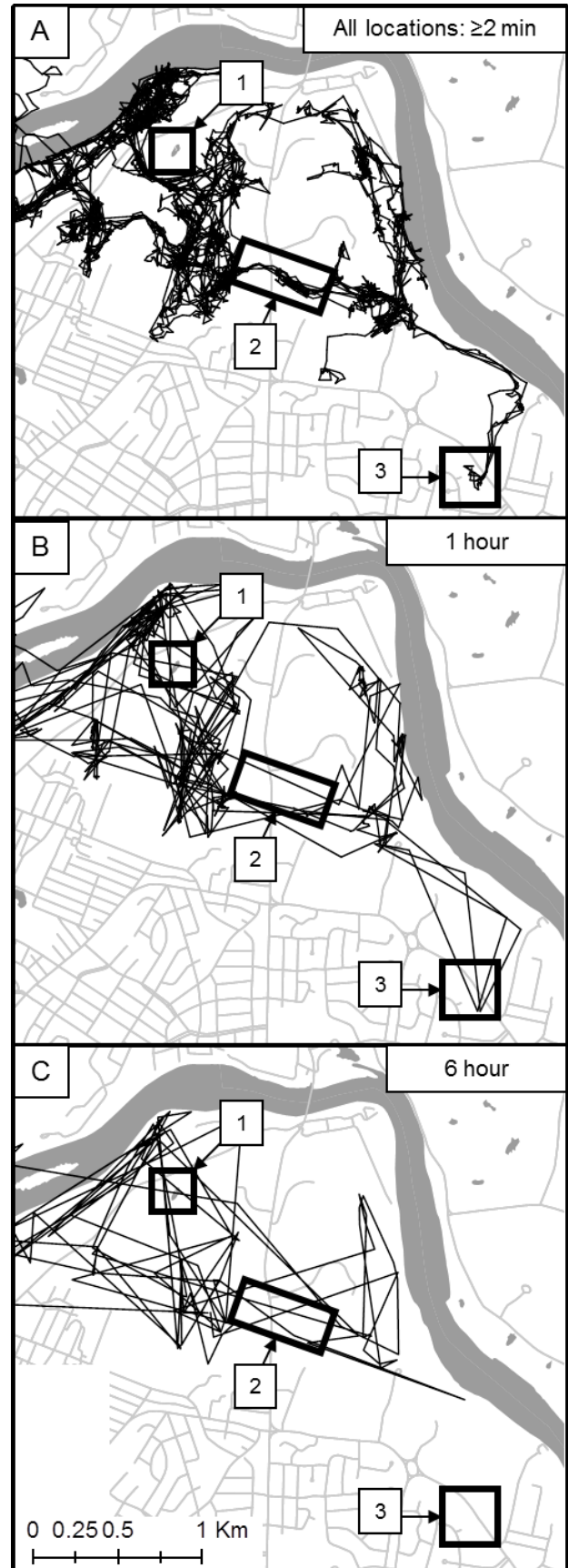
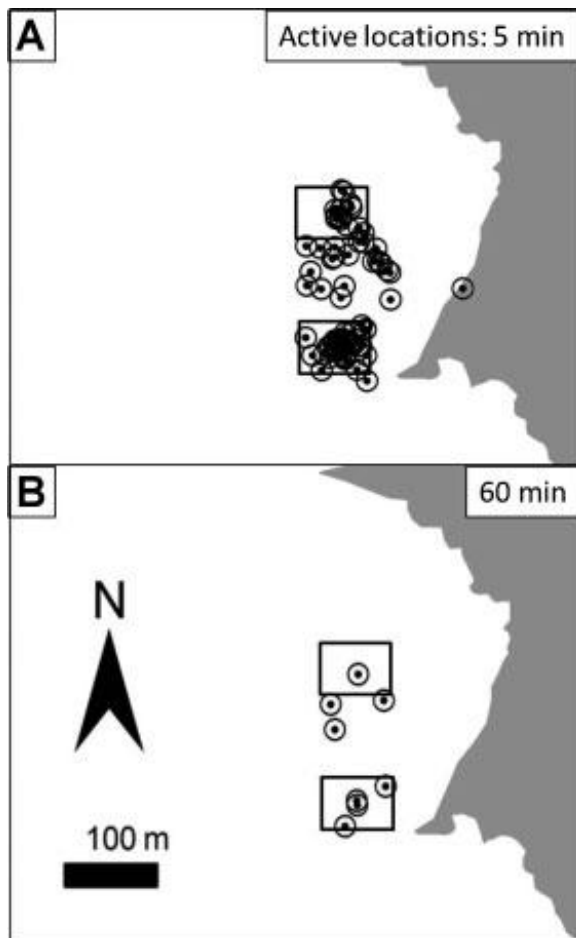
By programming the acceleration sensor to dictate the location attempt schedule of the GPS, we were able to dramatically increase both the rate and success of GPS location attempts during animal activity, while also decreasing both the time spent acquiring each location and the battery power wasted on attempts with a high probability of failure (i.e., during inactivity; Table 3). In both types of telemetry tags used in this study, each burst of tri-axial ACT measurements required only approximately 3.5 seconds and consumed 1 mA of battery current/second. In contrast, a successful GPS location attempt utilized 43 mA/second and required ≥ 20 seconds for satellite and location acquisition. Therefore, acceleration variance implemented as a trigger for adjusting the GPS schedule in ACTi-GPS tags is a low power method of reducing energy use of animal-borne tags in real time. These improvements are particularly important for species such

as the fisher, for whom high movement rates and habitats with forest canopy cover are known hindrances for consistent GPS satellite access (Moen et al. 1996, Graves and Waller 2006, Hebblewhite et al. 2007). In tropical forests, the canopy can be so thick that GPS location success rates can be exceptionally low (1–3%; Rumiz and Venegas 2006) unless the tags incorporate proprietary software, which also requires some data to be discarded (Tobler 2009). Our ACTi-GPS tags ameliorate the location success rate under tropical forest canopy (being successful in up to 64% of attempts), while providing more data per location (in the form of animal activity level). Given the high cost of GPS tracking tags in general, combined with the cost and stress of animal capture, improved tag performance increases the benefit-to-cost ratio for researchers considering GPS tracking of wildlife.

Many studies have indicated the need for greater understanding of the effects of animal behavior on GPS tag performance (Bowman et al. 2000, Mattisson et al. 2010), and GPS research is particularly scarce for small and medium-sized mammals (Recio et al. 2010). Indeed, the relationship between GPS location success and animal activity (Moen et al. 2001, Bourgoin et al. 2009) and body position (D'Eon and Delparte 2005, Graves and Waller 2006) has previously been reported for only a few species. In our study, we believe the low location sites, as well as a habit of sleeping with their backs (tags) up against tree trunks or facing the ground (as indicated by the gravitational force recorded by the ACT when animals were motionless). Although a single ACT axis was sufficient to schedule the GPS and distinguish activity from rest, the patterns of acceleration on all 3 axes enabled us to assess body orientation and the occurrence of specific behaviors, such as feeding, at each burst (Brown 2011). The potential for tri-axial ACT sensors to classify animal behavior in more detail (Shepard et al. 2010) should make it possible to better relate animal behavior to GPS performance in the future.

Figure 2 (right). High-resolution movement path (A, black lines) of a single fisher, recorded in 2010 with an accelerometer-informed (ACTi)-GPS tag near Albany, New York, USA. We also depict the movement path of the same data subsampled at either 1-hour (B) or 6-hour (C) intervals. More frequent locations recorded during activity reveal a more realistic movement path, as well as both overemphasized behaviors (indicated by pond visitation rate, box 1) and under-emphasized behaviors (indicated by an apparent movement corridor, box 2, and exploratory behavior, box 3). Roads are indicated by gray lines and water is indicated by gray fill.

Figure 3 (below). Locations of a northern tamandua on Barro Colorado Island, Panama, recorded in 2010 with an ACTi-GPS tag every 5 minutes when the animal was active (A). Boxes mark rich feeding areas as indicated by concentrated locations. Lower resolution location data (B, 1 hr) would fail to identify one of these rich feeding areas (in the top box). Total elapsed time for the locations is approximately 8 hours. Water is indicated by gray fill.



Although the ACTi-GPS tags return very detailed data, the time interval between successful locations can vary dramatically and short intervals produce locations that are autocorrelated, which may violate assumptions of some analytical methods (Worton 1989, Horne et al. 2007). A simple approach would be to use the most detailed data for appropriate analyses and inferences, and down-sample the full data set when needed for specific analyses. However, we also note that the detailed data provided by modern GPS tracking studies are also driving the development of new analytical tools, which are not restricted by assumptions of temporal independence or regular fix intervals (Fieberg et al. 2010).

MANAGEMENT IMPLICATIONS

Previous authors have questioned the practical value of the high-intensity location sampling possible with modern GPS units (Hebblewhite and Haydon 2010). In our study, high-intensity sampling provided a markedly more realistic depiction of the movement paths of both species within a short period of time. Rare and short-lived behaviors, such as the exploratory events and culvert use seen in the fisher (Fig. 2A), were only visible at high sampling rates. Common behaviors in the tamanduas (feeding bouts concentrated at a single location) are underestimated at lower sampling rates (Fig. 3B). Furthermore, intensive sampling permitted estimation of home range size for tamanduas (Brown 2011), which might not have been feasible with less frequent location attempts given that anteaters removed the glue-on tags after only 2–3 weeks, similar to other species that cannot be collared (Holland et al. 2009). Therefore, high-intensity GPS sampling becomes more valuable and may be the only option for determining habitat use by animals that are difficult to attach a tag to for longer periods of time.

As animals are faced with increasingly fragmented landscapes, managers need an adequate understanding of the “local essential resources” and how they are used by individuals (Nielsen et al. 2002). Accurately identifying both barriers to and corridors for animal movement is equally critical. For species that exist naturally at low densities and are difficult to observe, high-resolution behavioral data, even from a few individuals, can reveal essential information for conservation planning and management interventions. Global Positioning System units remain relatively expensive; therefore, every effort must be made to get the most information possible from each deployed unit. Furthermore, as scientists, we are ethically bound to minimize the stress animals endure during capture and handling, as well as the burden of carrying tracking tags. Accelerometer-informed GPS tags can lessen these burdens because they necessitate fewer and shorter deployments by providing more information for a given deployment period than a fixed-GPS tag would. By dynamically linking the location schedule to animal activity rates, accelerometer-informed GPS tags reduce the long standing trade-off between more intensive data collection and longer data collection periods.

ACKNOWLEDGEMENTS

This project was supported by the New York State Museum; the Max-Planck-Institute for Ornithology; an NSF predoctoral fellowship (D. D. Brown) and research grant (#0756920 to R. Kays), the Albany Pine Bush Preserve; the Smithsonian Tropical Research Institute; and the University of California, Davis. We thank the Smithsonian Tropical Research Institute, New York State Museum, and Autoridad Nacional del Ambiente de Panama for administrative support. D. Brown wishes to thank R. Acosta, V. Jaramillo, F. Rodriguez, S. Escobar, J. A. Ramirez Silva, and J. Thomás for assistance in the field.

Fisher activity patterns within a developed landscape

Scott LaPoint^{1,2,3} and Roland Kays^{4,5}

in preparation

¹ Max-Planck-Institute for Ornithology, Am Obstberg 1, D-78315 Radolfzell, Germany

² Department of Biology, University of Konstanz, Universitätsstraße 10, D-78464 Konstanz, Germany

³ New York State Museum, 3140 CEC, Albany, New York 12230, USA

⁴ North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, North Carolina 27601, USA

⁵ Department of Forestry and Environmental Resources, North Carolina State University, Box 8008, Raleigh, North Carolina 27695, USA

ABSTRACT

Urbanization is challenging many species to adapt their behaviors in order to survive. One mechanism for doing so is to shift the timing of one's activities. We deployed GPS-tracking collars containing accelerometers on free-ranging fishers (*Pekania pennanti*) in a developed landscape near Albany, New York, USA. Overall dynamic body acceleration data suggests that our fishers are nocturnal and have two activity peaks, one following sunset and the other prior to sunrise. We investigated whether fishers were responding to daylight or human activity (i.e., automobile traffic volume), by comparing their activity patterns on weekdays versus weekends. Traffic volume patterns differed between our urban and wild study areas and between weekdays and weekends within study area, with urban traffic volume peaks occurring earlier on weekdays than weekends. Fishers appeared to respond to this earlier traffic volume peak on weekdays by ceasing their activity earlier on weekdays than on weekends. Although preliminary, our results suggest that fishers are facilitating their survival within this urban landscape by adapting the timing of their activity to daily fluctuations in automobile traffic volumes.

INTRODUCTION

Mammals have evolved activity patterns to facilitate their survival. These patterns arise in response to biotic factors, such as food availability and mortality sources (Ashby 1972; Zielinski et al. 1983; George and Crooks 2006), and abiotic factors such as ambient temperature and light (Beier 2006; van der Merwe et al. 2011). Sunrise and sunset trigger the onset or end of activity for many species (Daan and Aschoff 1975; Halle and Stenseth 2001), however artificial lighting at night and other human activities can affect changes in the activity patterns of mammals within urban areas (Longcore and Rich 2004; Beier 2006). Our understanding of these affects is

limited, especially for carnivores, due to limitations in our ability to quantify activity in free-ranging individuals and to a lack of experimentally designed studies (Beier 2006).

The fisher (*Pekania pennanti*, formerly *Martes pennanti*) is a medium-sized (females 2.0 – 2.5 kg; males 3.5 – 5.5 kg) carnivore native to the northern forests of North America. Fishers experienced significant range contractions following the Euro-American colonization of North America and their range remains restricted within their western range (Lewis et al. 2012). However, they are expanding their eastern range, recently even colonizing previously assumed unsuitable habitats including suburban New York (LaPoint et al. 2013). Fishers are thought to be active both day and night within forested habitats (Leonard 1980; Powell 1993; Weir and Corbould 2007), yet nothing is known of their activity patterns within a developed landscape. Given the increasing anthropogenic pressures on wildlife and their habitats, a better understanding of the activity patterns of a once imperiled carnivore inhabiting a novel, developed landscape could assist conservation efforts.

Until very recently, obtaining continuous activity data on free-ranging animals has been difficult. Previous efforts to characterize fisher activity have employed anecdotal sightings, snow tracking, or fluctuations in the radio signal strength from fisher-borne very-high-frequency (VHF) radio tracking collars (Leonard 1980; Powell 1993; Weir and Corbould 2007). Although these efforts have provided valuable insight into the ecology of fishers, these insights are limited by the resolution and comparability of their data. Recent technological improvements in biotelemetry however, including the incorporation of onboard acceleration recorders (i.e., tri-axial accelerometers) into tracking collars, are improving our ability to record the activities and behaviors of free-ranging animals (Brown et al. 2012; Nathan et al. 2012; Krop-Benesch et al.

2013). Animal activity can now be recorded continuously, objectively, and remotely for long periods of time, providing unique and unparalleled insight into animal behavior.

In this study, we present daily activity patterns of free-ranging fishers. As fishers are thought to be active throughout the 24-hour period, we hypothesized that fishers within a developed landscape would avoid human activities by adapting a nocturnal activity pattern whereas fishers experiencing less human disturbance ought to be active throughout the 24-hour period. We tested this hypothesis by comparing the activity of fishers within a developed to a natural landscape. To determine whether fishers were responding to light-dark cycles or to human activity, we compared automobile traffic volume patterns on weekdays to weekends, predicting that fishers would respond to lower traffic volumes on the weekend by remaining active longer into the day. We expect our efforts to provide insight into the ecology and adaptability of a carnivore inhabiting a developed landscape.

METHODS

We recorded acceleration on free-ranging fishers within two separate study areas. One area was the suburban forest patches near Albany, New York, USA (42.765 N, -73.881 E) (herein referred to as the “urban” study area), a relatively flat (<100 m change in elevation) 350-km² matrix of residential and commercial land uses, interspersed with mixed and northern deciduous forest patches. The road density in this area is 4.77 km/km² (New York State Office of Cyber Security 2006) with a human population density of 438 persons/km² (US Census 2008). This area is highly fragmented by roads and development to where eight of our nine fishers in this area had ranges (dynamic Brownian bridge movement model utilization distribution; Kranstauber et al. 2012) that included multiple disjunct habitat patches (i.e., forest patches separated by roads,

unsuitable land cover, or other anthropogenic structures) that individuals regularly moved between (LaPoint et al. 2013). The other study area (herein referred to as the “wild” study area) was nearby (30 km) at Grafton Lakes State Park a 9.5 km² landscape of mostly contiguous forest of deciduous and coniferous tree species, with recreation trails and a few gravel roads (LaPoint et al. 2013).

Acceleration was recorded via tri-axial accelerometers onboard GPS tracking collars (e-obs GmbH; Grünwald, Germany) deployed on free-ranging fishers. The accelerometers simultaneously measure the pull of gravity (*g*) and acceleration (millivolts) due to changes in the animal’s motion along 3 orthogonal axes: forward–backward horizontal motion (X-axis), left–right horizontal motion (Y-axis), and up–down vertical movements of the body (Z-axis) (Dow et al. 2009). The data output for an accelerometer is a unit-less ratio of the voltage due to acceleration and an internal reference voltage, i.e., a reference value indicating no motion. The accelerometer was scheduled to record at 18.74 Hz in a short (3.5-sec) burst every three minutes continuously, producing 66 accelerometer measurements per burst. We calculated overall dynamic body acceleration (ODBA; Wilson et al. 2006) per accelerometer burst, by first calculating the mean accelerometer value per burst, per axis. We then subtracted this mean value from each measurement, per burst, per axis, and sum these differences per axis. Lastly, ODBA is the sum of the absolute values of the sums of each axis, per burst (see Wilson et al. 2006). Increasing activity yields increasingly higher ODBA values relative to inactivity (Shepard et al. 2010). We excluded acceleration data collected prior to the end of the first 24-hour period post-release of the tagged fisher to account for potentially atypical behaviors during the animal’s recovery.

We compared fisher activity patterns to automobile traffic patterns within our study areas. Traffic volume was recorded as counts per 15 minutes within our study area from 2008–2011 (New York State Department of Transportation 2012). We only included traffic volume data from road segments that transected or were within 200-m of a fisher’s utilization distribution. We calculated mean traffic volume per 15 minutes for weekdays (i.e., Monday – Friday) and weekends (i.e., Saturday – Sunday). We obtained sunrise and sunset data for our study areas from the Astronomical Applications Department of the US Naval Observatory (2011).

RESULTS

We recorded the activity of nine free-ranging adult fishers (6 male, 3 female) within our urban study area and two adult male fishers within our wild study area, for an average of 26 days (range: 9.2–70.4 days) during the months of December – May (Table 1). Urban and wild fishers are both mostly inactive during the day, but are active at night with two activity peaks (Figure 1 and 2). The onset and cessation of activity differs between study areas (Figure 2). Urban fishers appear to begin their activity later than fishers within the wild area, but cease their activity before fishers within the wild area, ultimately shortening their duration of activity (Figure 2).

Traffic volume patterns differ between study areas and between weekdays and weekends within both study areas (Figure 3). On weekdays in the urban study area, traffic volume peaks at 08:00 with 234 automobiles per 15 minutes, whereas weekend traffic volume peaks later at 14:00 with 177 automobiles per 15 minutes (Figure 3). The weekend traffic volume at the mean cessation of urban fisher activity is 69% less than on the weekday (weekday = 137, weekend = 43). Traffic volumes within the wild study area are overall much lower than within the urban

Table 1. Activity was recorded for eleven free-ranging fishers between December and May.

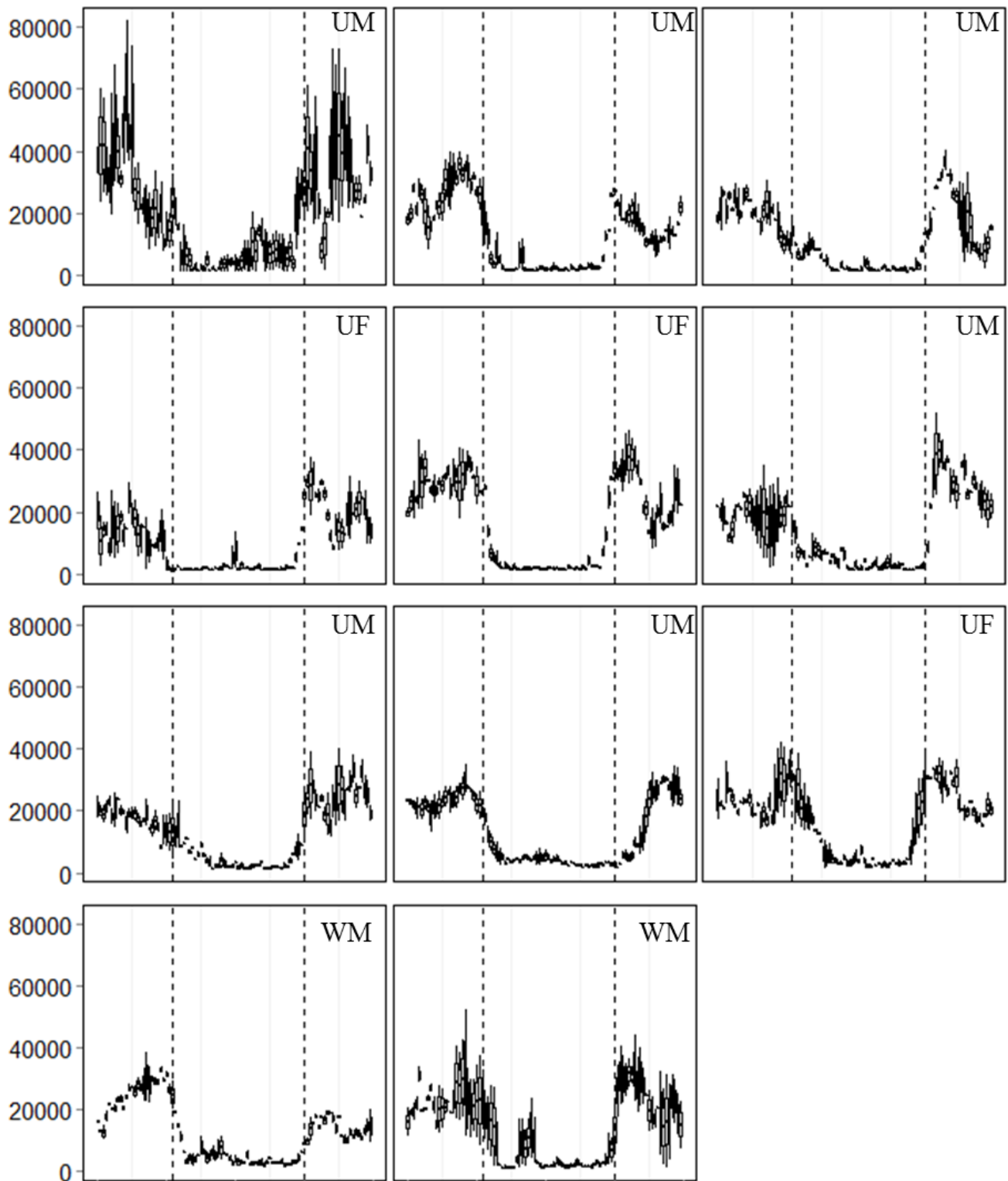
id	sex	site	deployment start	deployment end	duration
bob	male	urban	03/09/2011 14:09	03/18/2011 19:27	9.22
klause	male	urban	12/24/2010 16:15	1/11/2011 4:39	17.52
leroy	male	urban	2/11/2009 17:00	3/4/2009 12:24	20.81
lucile	female	urban	2/12/2011 15:01	3/2/2011 22:00	18.29
lupe	female	urban	12/17/2010 16:12	1/4/2011 2:45	17.44
maurice	male	urban	2/11/2011 21:48	3/7/2011 6:51	23.38
phineas	male	urban	1/20/2011 21:48	2/11/2011 2:37	21.20
potato	male	wild	3/18/2011 18:42	5/28/2011 5:13	70.44
price	male	wild	12/5/2009 14:12	12/29/2009 2:12	23.50
ricky	male	urban	2/10/2010 16:48	4/1/2010 1:20	49.36
zissou	female	urban	1/22/2011 18:24	2/6/2011 21:43	15.14

area, with similar traffic volume patterns on weekdays as on weekends (Figure 3). The weekday traffic volume peak within the wild study area is less than the weekend peak, but occurs approximately 30 minutes earlier than the urban traffic volume peak (Figure 3).

It appears that urban fishers are responding to human traffic by ceasing their activity 30 minutes earlier in the day on weekdays to avoid the automobile traffic volume peak that occurs earlier during the day on weekdays compared to weekends (Figure 4). However, the earlier weekday traffic volume peak does not appear to affect a change in the cessation of wild fisher activity (Figure 4). These fishers do however appear to delay the onset of their activity on weekends, possibly in response to longer periods of human recreational activities (Figure 4).

DISCUSSION

Figure 1. Boxplots of overall dynamic body acceleration (y-axis) per 24-hour period (x-axis) indicating the daily activity patterns of eleven free-ranging fishers. Letters indicate study area (U = urban, W = wild) and sex (F = female, M = male). Dashed vertical lines indicate sunrise (left) and sunset (right).



Automobile traffic appears to affect the onset and cessation of activity in urban fishers. Fishers in both the wild and the urban study areas were active at night with activity peaks before and after sunrise and sunset, respectively. However, by comparing activity and traffic patterns on weekdays and weekends, we were able to determine that fishers within the urban area are

Figure 2. Overall dynamic body acceleration (y-axis) per 15 minutes (x-axis) for urban (top) and wild (bottom) fishers per 24-hour period, with outliers (black dots). Dashed vertical lines indicate sunrise (left) and sunset (right).

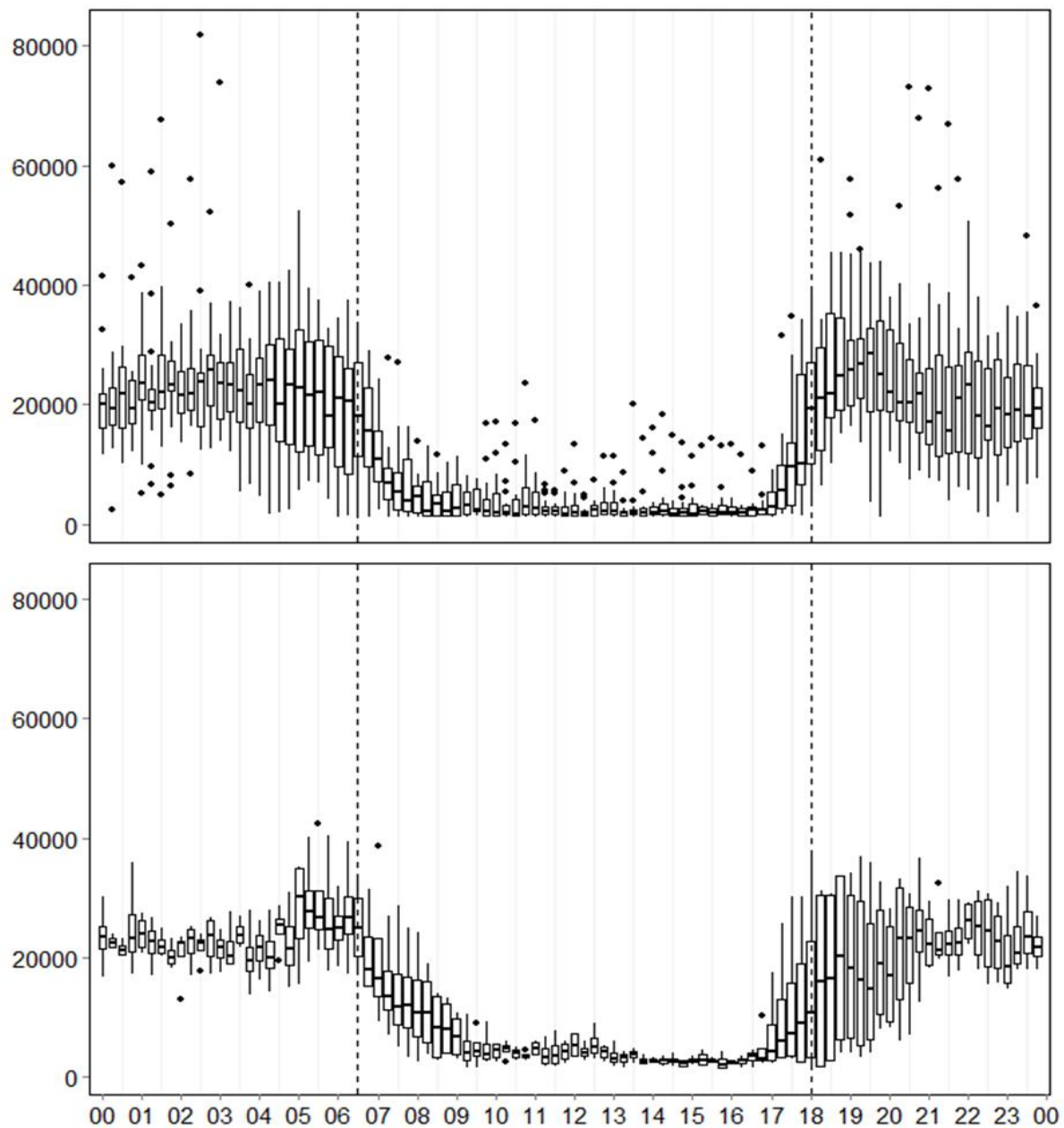
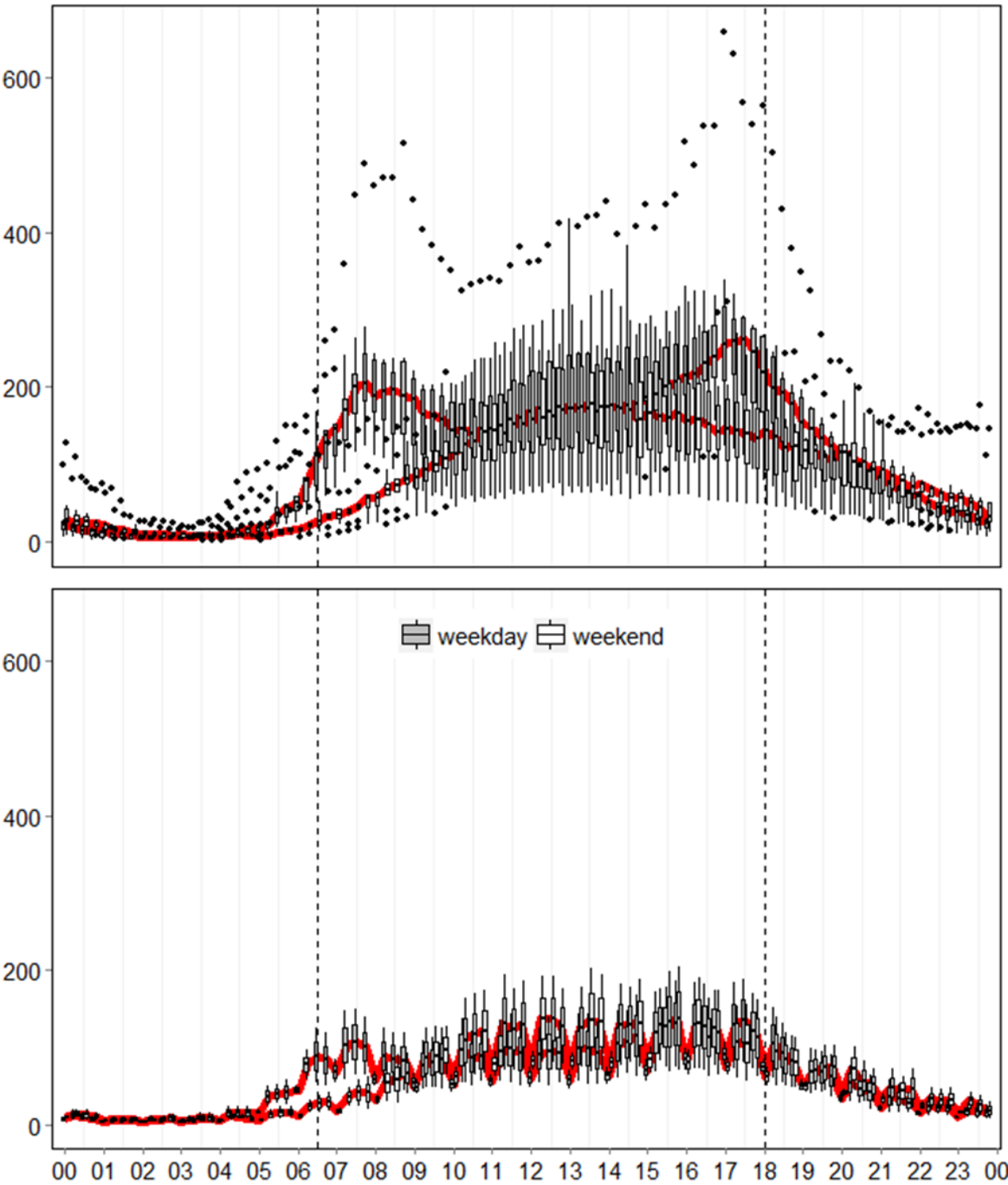


Figure 3. Median weekday (grey boxplots) and weekend (white boxplots) automobile traffic volume per 15 minute period for the urban (top) and wild (bottom) study sites. Red lines connecting medians for



responding to daylight and also automobile traffic. This is further supported as the fishers within the wild study area appear to remain active longer into the day than do urban fishers, suggesting that urban fishers cease their activities in response to increased automobile traffic rather than

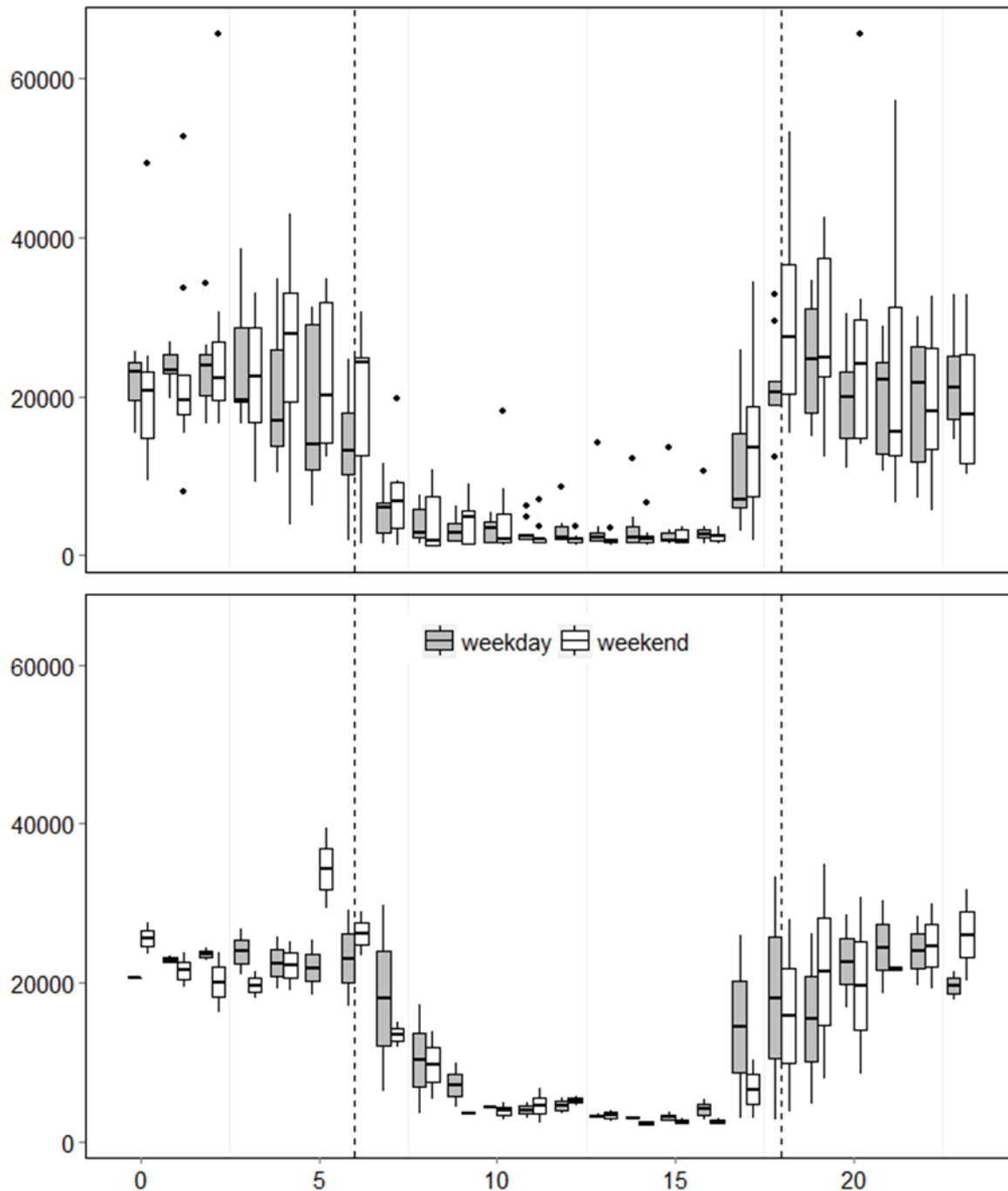
sunrise alone. These observations suggest that urban fishers are actively avoiding human activity.

The nocturnal behavior of our fishers is not well predicted by previous work nor by hypotheses on thermodynamics. Previous work suggests fishers are typically active in bouts of 2 – 5 hours, followed by extended periods of rest (Powell 1993). However the timing of these activity bouts varies across studies: nocturnal (de Vos 1952; Coulter 1966), crepuscular (Kelly 1977; Johnson 1984; Arthur and Krohn 1991; Powell 1993), or diurnal (Weir and Corbould 2007). Further, the fisher's long, slender body shape makes thermoregulation challenging (Brown and Lasiewski 1972), thus their nocturnal activities should be even more challenging given night ambient temperatures are typically lower than during the day (Weir and Corbould 2007). It is however possible that our observed fisher activity patterns are a result of the fishers hunting the two largest components of their diet within the urban study area: eastern grey squirrel (*Sciurus carolinensis*) and cottontail rabbits (*Sylvilagus floridanus*) (LaPoint, unpublished data). Fisher activity may be coincident with the crepuscular (Thompson 1977) and nocturnal (Nowak and Paradiso 1983) activities of these two prey species, thereby maximizing their encounter rates (Kamil et al. 1987). However, as the fishers within the urban and wild study areas would presumably employ similar foraging strategies and that the urban fishers demonstrated a response to automobile traffic whereas fishers within the wild study area did not, we believe that the activity patterns of our urban fishers is not a response to prey availability, but is to automobile traffic.

Energy balances for fishers are crucial due to their body shape and poor fat storage capacities (Harlow 1994), thus anthropogenic disturbances ought to be especially challenging for this species. However, our study shows that these fishers have adapted their behaviors to inhabit

an anthropogenic, developed landscape. If these fishers can avoid high traffic volumes, they may receive the additional benefits of a reduced predator community and a reduced risk of being

Figure 4. Overall dynamic body acceleration (y-axis) on weekdays (grey boxplots) and weekends (white boxplots) per hour (x-axis) for urban (top) and wild (bottom) fishers per 24-hour period, with outliers in (black dots). Dashed vertical lines indicate sunrise (left) and sunset (right).



road-killed (LaPoint, unpublished data). Understanding how fishers respond to human activities can better inform conservation efforts directed toward fishers elsewhere and carnivore species in general.

CONCLUSIONS

The activity pattern of a species is an adaptation to its environment, thus to survive within a novel environment, an individual must adapt its activity pattern accordingly. Urbanization is rapidly producing novel environments to many species across the globe, challenging species to either evolve or go extinct (Grimm et al. 2008). Advances in biotelemetry are facilitating our investigations into the activity patterns of free-ranging animals and allow us to quantify how species are adapting to the challenge of urbanization (Shochat et al. 2006). Our use of accelerometers allowed us to record high-resolution activity data on free-ranging fishers within a developed landscape and to document an apparent adaptation to human activity. Although our sample size is small, our study is novel as it offers preliminary evidence of a once rare carnivore adapting its daily activity patterns to facilitate its survival within a developed landscape. Future work should explore the variability between and within individual activity patterns and to consider development continuum rather than direct one to one comparisons. The rapidity of global urbanization and its threats to biodiversity conservation highlight the urgent need for an improved understanding of the adaptability of wildlife.

ACKNOWLEDGEMENTS

This work was supported in part by the National Science Foundation (grant 0756920 to RK), the New York State Museum, the Max-Planck-Institute for Ornithology, the North Carolina Museum

of Natural Sciences, and the National Geographic Society Waitt Grant Program (grant W157-11 to SL). We thank the Albany Pine Bush Preserve, Matthias Berger, Davide Dominoni, Neil Gifford, Grafton Lakes State Park staff, Bart Kranstauber, David Santos, and Martin Wikelski for their support and valuable input.

Animal behavior, cost-based corridor models, and real corridors

Scott LaPoint^{1,2,3}, Paul Gallery³, Martin Wikelski^{1,2}, and Roland Kays^{4,5}

Landscape Ecology (2013) doi: 10.1007/s10980-013-9910-0

¹ Max-Planck-Institute for Ornithology, Am Obstberg 1, D-78315 Radolfzell, Germany

² Department of Biology, University of Konstanz, Universitätsstraße 10, D-78464 Konstanz, Germany

³ New York State Museum, 3140 CEC, Albany, New York 12230, USA

⁴ North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, North Carolina 27601, USA

⁵ Department of Forestry and Environmental Resources, North Carolina State University, Box 8008, Raleigh, North Carolina 27695, USA

ABSTRACT

Corridors are popular conservation tools because they are thought to allow animals to safely move between habitat fragments, thereby maintaining landscape connectivity. Nonetheless, few studies show that mammals actually use corridors as predicted. Further, the assumptions underlying corridor models are rarely validated with field data. We categorized corridor use as a behavior, to identify animal-defined corridors, using movement data from fishers (*Martes pennanti*) tracked near Albany, New York, USA. We then used least-cost path analysis and circuit theory to predict fisher corridors and validated the performance of all three corridor models with data from camera traps. Six of eight fishers tracked used corridors to connect the forest patches that constitute their home ranges, however the locations of these corridors were not well predicted by the two cost-based models, which together identified only 5 of the 23 used corridors. Further, camera trap data suggest the cost-based corridor models performed poorly, often detecting fewer fishers and mammals than nearby habitat cores, whereas camera traps within animal-defined corridors recorded more passes made by fishers, carnivores, and all other non-target mammal groups. Our results suggest that (1) fishers use corridors to connect disjunct habitat fragments, (2) animal movement data can be used to identify corridors at local scales, (3) camera traps are useful tools for testing corridor model predictions, and (4) that corridor models can be improved by incorporating animal behavior data. Given the conservation importance and monetary costs of corridors, improving and validating corridor model predictions is vital.

INTRODUCTION

Conservation corridors are widely regarded as useful tools for improving landscape connectivity because they are thought to facilitate animal movement between otherwise separate but

potentially suitable habitats (Simpson 1940; Forman 1995; Rosenberg et al. 1997; Gilbert-Norton et al. 2010). Corridors are thought to facilitate dispersal (Haas 1995), maintain gene flow between populations (Mech and Hallett 2001) and, ultimately, reduce extinction risk (Brown and Kodric-Brown 1977). Surprisingly, few data show that mammals move between habitat patches via predicted corridors, perhaps prompting some ecologists to question their effectiveness and value (Simberloff et al. 1992; Hodgson et al. 2009). Given the conservation potential for wildlife corridors and the monetary costs required to implement them, both accuracy in corridor identification and appropriate methods for measuring their utility are needed (Chetkiewicz et al. 2006; Beier et al. 2008; Spear et al. 2010; Sawyer et al. 2011; Zeller et al. 2012).

Typical methods to identify corridors only indirectly consider the animal movements they are designed to facilitate (Chetkiewicz et al. 2006; Beier et al. 2008). Often, experts visually identify potential corridors (Hilty et al. 2006). More sophisticated methods such as cost-based models (e.g., least-cost mapping; Adriaensen et al. 2003 and circuit theory; McRae et al. 2008) use algorithms to analyze landscape resistance to predict corridors. This landscape resistance, or ‘cost’, is thought to represent the energetic or mortality risk for an animal to move through an area, or its unwillingness to do so. Landscape resistance is often based on habitat suitability indices or expert opinion, where high habitat suitability is interpreted as low resistance or cost (Sawyer et al. 2011; Poor et al. 2012; Zeller et al. 2012). Unfortunately, many examples of cost-based corridor model applications have weaknesses, for example the use of habitat selection information that is generalized from the literature (e.g., LaRue and Nielsen 2008; Li et al. 2010; Huck et al. 2011) (despite being locality specific and often variable across sites and thus not generalizable; Fahrig 2007) and the cost-based models themselves unrealistically assume an animal either has complete knowledge of the landscape (e.g., least cost path analysis; Adriaensen

et al. 2003) or no memory of the landscape (i.e., random walkers; e.g., McRae et al. 2008). Most importantly, despite intending to predict and facilitate animal movements, most corridor studies do not directly incorporate animal behavior into their models (Chetkiewicz et al. 2006; Beier et al. 2008; Sawyer et al. 2011; Zeller et al. 2012), and only a few have compared their model predictions with movement data (Driezen et al. 2007; Poor et al. 2012; Walpole et al. 2012).

Fortunately, animal movement data are increasingly available to both test predicted corridors and to improve the corridor models themselves (Wikelski et al. 2007; Wikelski and Kays 2012). These new data are part of the emerging field of Movement Ecology (Nathan et al. 2008), that also includes new analytical tools for identifying behaviors of free-ranging animals (Nathan et al. 2012) and for discerning animal behavior using movement data-based models (Fauchald and Tveraa 2003; Morales et al. 2004; Jonsen et al. 2005; Gurarie et al. 2009; Kranstauber et al. 2012). These movement models, coupled with improved spatial and temporal resolution of GPS-derived movement data (Brown et al. 2012), are improving our understanding of the mechanistic links between animal behavior, animal space use, and survival in dynamic environments (Morales et al. 2010; Smouse et al. 2010; Bartoń et al. 2012; Buchmann et al. 2012).

In this paper we take a movement ecological approach to delineate functional corridors and test corridor model predictions. First, we developed the “animal-defined corridor” model using high resolution GPS tracking data from fishers (*Martes pennanti*) to determine whether fishers use corridors to move between the habitat patches within their home ranges in a fragmented, suburban environment. We then used these same tracking data to build the resistance layers for two popular cost-based corridor models: least-cost path analysis (Adriaensen et al. 2003) and circuit theory (i.e., Circuitscape; McRae et al. 2008) to predict the

observed fisher corridors. Finally, we evaluated the performance of the animal-defined corridor model and tested the predictions of least-cost path analysis and circuit theory using an independent set of camera trap detection data.

METHODS

Study species and area

Fishers are medium-sized (females 2.0 – 2.5 kg; males 3.5 – 5.5 kg) carnivores native to the northern forests of North America. Fisher populations suffered dramatic declines following the Euro-American colonization of North America due to over-harvesting, habitat loss and habitat fragmentation (Powell 1993). Their range is still restricted along the western coast of the United States but they are expanding out from refugia in much of their eastern range (Lewis et al. 2012). We tracked fishers in suburban forest patches near Albany, New York, USA (42.765 N, -73.881 E), a relatively flat (<100 m change in elevation) 350 km² matrix of residential and commercial land uses, interspersed with mixed and northern deciduous forest patches. The road density in this area is 4.77 km/km² (New York State Office of Cyber Security 2006) with a human population density of 438 persons/km² (US Census 2008). Our main study area was highly fragmented by roads and development to where six of our eight fishers had home ranges (dynamic Brownian bridge movement model utilization distribution; Kranstauber et al. 2012) that included multiple disjunct habitat patches (i.e., forest patches separated by roads, unsuitable land cover, or other anthropogenic structures) that individuals regularly moved between. One study animal was tracked in nearby (30 km) Grafton Lakes State Park (9.5 km²) a mostly contiguous forested landscape dominated by deciduous and coniferous tree species, with recreation trails and a few gravel roads.

Movement data

We live-trapped fishers with covered cage traps, sedated them with a combination of ketamine hydrochloride (concentration = 200 mg/mL, dosage = 0.2 mL/kg) and xylazine hydrochloride (concentration = 300 mg/mL, dosage = 0.01 mL/kg), monitored their vital rates, and fitted them with tracking collars (E-obs GmbH; Grünwald, Germany) during the winters of 2009, 2010, and 2011. Collars contained a GPS microchip, an ultra-high frequency radio transmitter, and a tri-axial accelerometer. Prior to deployment, we estimated the location error of the GPS to be 22 m (mean) via stationary field tests (18 collars, 2071 locations). The GPS was programmed with a fixed schedule of 10 or 15 minute intervals, or a dynamic fix schedule, 24 hours per day. With the dynamic fix schedule, the GPS attempted more frequent locations (≥ 2 minutes) when a fisher moved quickly and attempted fewer fixes (every 60 minutes) when the fisher rested (see Brown et al. 2012 for details). Capture and handling protocols were approved by the Institutional Animal Care and Use Committee at the Max-Planck-Institute for Ornithology.

Cost-based corridor mapping

Cost-based approaches to corridor mapping require assigning resistance values to the landscape variables. These values should represent the cumulative costs (e.g., energetic expenditure, mortality risk, or habitat avoidance) experienced by an individual moving through the landscape (Adriaensen et al. 2003). As our intention here is to test popular cost-based corridor methods, we estimated landscape resistance values from a habitat selection analysis to replicate many of the published cost-based corridor studies (Sawyer et al. 2011). Since fishers are well documented forest specialists (Powell 1993; Lofroth et al. 2011) and roadways are significant

barriers to animal movement (Forman et al. 2003), our landscape variables included land cover (30 m resolution, 15 land cover categories; 2006 National Land Cover Dataset; Fry et al. 2011) and a road polyline layer with 7 speed categories that we rasterized to a 30 m resolution grid (New York State Office of Cyber Security 2006). Despite the influence of topography on resistance estimates, we ignored topography in our analyses as our study area experiences little change (<100 m) in elevation.

We conducted a weighted compositional analysis for fisher habitat selection (Aebischer et al. 1993; Millspaugh et al. 2006) at the home range scale (i.e., Johnson's (1980) third order of selection), per individual. We used the GPS tracking locations to estimate the 'use' of each land cover type per fisher, and used a dynamic Brownian bridge home range utilization distribution (Kranstauber et al. 2012) to estimate the 'availability' of each land cover type, per fisher. As recommended by Aebischer et al. (1993), for each fisher, if a land cover type was not used by the animal, but was available (i.e., available value was greater than zero), we replaced the unused land cover type use proportion value with a value equal to 10% of the least available land cover type proportion. We assigned a movement cost to each land cover type (per fisher) by calculating a ranking matrix of the pairwise differences of the natural log-ratios of the use to available proportions (Aebischer et al. 1993). A pairwise difference value of zero indicates random use, whereas negative values suggest the fisher avoided the land cover type and positive values suggest the fisher selected for the land cover type. These values are the basis for Aebischer et al.'s (1993) habitat rankings. We then calculated the mean of the pairwise differences per land cover type. We then standardized these pairwise difference means by first subtracting the highest mean value for a land cover type (per individual) from each land cover type value and then we divided these standardized values by the lowest standardized value to

make each land cover type relative to the least selected for (i.e., most costly). As both least-cost path analysis and Circuitscape require cost values ≥ 1 , we assigned the least costly land cover types a value of 1 (previously 0) and then multiplied the remaining values by 100. The final values range from 1 (least costly) to 100 (most costly).

Both least-cost path analysis and Circuitscape require source and destination points or areas (Adriaensen et al. 2003; McRae et al. 2008), for which we used fisher rest sites. Our fishers were highly nocturnal, typically resting at a single site throughout the day (LaPoint unpublished data). We identified these rest sites as GPS location clusters where a fisher spent >4 daytime hours during which they were minimally active, as indicated by low variability in accelerometer measures (see Brown et al. 2012). An alternative to using rest sites would have been to model corridors between habitat or home range cores. Doing so, however, requires a-priori distinguishing between habitat, periphery, and core areas, which can vary depending on the home range estimator used (Cumming and Corn  lis 2012) and can be confounded when numerous locations are recorded within frequently used corridors. Rest sites offer a simple alternative as they were numerous and well distributed across each fishers home range, they can easily be identified with animal tracking data and field investigations, and their definition is stable and straightforward across studies (Powell 1994; Kilpatrick and Rego 1994; Lofroth et al. 2010).

For each fisher separately, we predicted the locations of corridors between its rest sites with least-cost path analysis and circuit theory using the cost values from the habitat selection information for the fisher. We conducted least-cost path analysis using the Spatial Analyst toolbox within ArcMap (version 9.3 build 1770; ESRI 2008). We modeled least-cost paths between all possible combinations of rest sites, per individual. We identified possible corridors

from least-cost path analysis as cells whose least-cost path density is ≥ 2 , i.e., at least two least-cost paths overlapped within the cell, and required that these overlapping paths were each traveling in opposite directions (i.e., the path connecting a ‘source’ rest site to a ‘destination’ rest site was overlapped by another path when the designations of these rest sites was reversed). We chose least-cost path analysis over the similar least-cost corridor method (Sawyer et al. 2011) to avoid subjective accumulative cost thresholds and to force a path to/from the most isolated rest sites that least-cost corridor analysis may have determined too costly to reach (i.e., above the accumulative cost threshold). Next, for each fisher, we used the same cost layers to generate cumulative current outputs from Circuitscape (version 3.5.4; www.circuitscape.org), to predict fisher corridors between each rest site (i.e., focal nodes). Each current map is a raster with continuous grid cell values of current flow, where current values are indicative of predicted movement of random walkers. These maps are useful tools for visualizing movement bottlenecks, barriers, and connectivity across landscapes, but can be difficult to objectively interpret (Rudnick et al. 2012). We are unaware of a quantitative and objective method for delineating corridors via current maps, therefore we identified potential corridors visually from current maps, where relatively high current levels suggested funneled fisher movements. In summary, for both the least-cost path analysis and circuit theory approaches, we predicted corridors for each fisher using the same data inputs for both approaches (i.e., conducted on each fisher separately, using the same cost layers per animal, and the same source and destination points). However, the algorithms used by each approach to predict corridors from the cost layers differ. In least-cost path analysis, the cost distance (i.e., the Euclidian distance weighted by the cumulative cost of each cell traversed) is estimated between a source and a destination, from which the least costly path represents the connected cells whose summed cost-weighted distance

is the lowest (Adriaensen et al. 2003). Whereas circuit theory algorithms generate random walks originating from designated source points, with each landscape grid cell's value representing the number of walkers that reached the cell divided by the resistance of the cell. In electrical circuit theory this translates as current or the voltage (the amount of walkers) divided by the resistance (cost), thus a current cell value can indicate either low resistance or high voltage, or both.

Finally, due to the outputs for each cost model, our interpretation of each approach's results had to differ slightly since least-cost path corridors were objectively identified via overlapping paths and circuit theory corridors were identified subjectively, but with careful visual inspection of quantitative current maps. Both of these approaches are popular and current practices (Rudnick et al. 2012).

Identifying animal-defined corridors

We analyzed our high-resolution fisher tracking data to determine if fishers used corridors within their home ranges. We considered corridor use as efficient and repeated movement between two or more habitat patches within a home range (Hobbs 1992; Rosenberg et al. 1997; Hilty et al. 2006). The efficiency of movement distinguishes corridors from otherwise linear foraging habitats since corridors should primarily be used for traveling (Forman 1995; Rosenberg et al. 1997). For this analysis we interpret rapid movements as efficient movement, and define corridors as areas characterized by parallel, quick and repeated animal movement paths. We refer to these areas as animal-defined corridors. We believe our corridor definition is similar to previously used definitions. However, our definition may more explicitly incorporate corridor function (quick and repeated movements) and corridor form (parallel movements) than previously used definitions. Our method, described below, is available as the corridor function

within the move package (version 1.1; Kranstauber and Smolla 2013) for program R (version 2.15.2; R Development Core Team 2012).

We first estimated the speed and the variation in the direction traveled by an animal to define potential corridor movement behaviors empirically. For each individual we divided the entire movement path into steps representing the estimated path between successive locations, with the midpoint of each step being assigned the speed (m/min) and azimuth ($-180^\circ \leq \text{azimuth} < 180^\circ$) of the fisher moving from the previous location to the next. We identified fast movement steps as those with speeds greater than 75% of all speeds per animal (Fig. 1a). We created a circular buffer whose radius equals one-half the movement step length around each midpoint. We identified parallel movement steps by calculating a ‘pseudo-azimuth’ for each midpoint and then calculated the circular variance of these pseudo-azimuths of all midpoints falling within the buffer of each midpoint (Fig. 1b). The pseudo-azimuth is calculated for each midpoint by adding 180 to the observed azimuth, multiplying this by 2, then subtracting 360 if this value > 360 or doing nothing if this value is ≤ 360 (see Figure 2). It is important to note that the pseudo-azimuth does not preserve any directional information, but rather produces a value between 0 and 360 for the circular variance calculations. After removing steps whose pseudo-azimuth circular variance was equal to 0, (indicating that no other segment midpoints occurred within the buffer radius), we identified the movement steps whose pseudo-azimuth circular variance was within the lowest percentage quartile, indicating that they are located near other parallel movement steps. Movement steps that meet both the speed and parallel requirements are considered to exhibit corridor use behavior. These conditions allowed us to remove non-corridor use behaviors such as resting and foraging that would have slower speeds and high directional variance (either from GPS fix errors or from meandering search paths) thereby focusing on corridor use as a specific

behavior type. All other steps are considered non-corridor use behavior. After classifying all midpoints as being either corridor behavior or not, we searched for high concentrations of corridor behavior midpoints to identify animal-defined corridors. Considering only midpoints with at least two additional midpoints within their buffer, we classified a midpoint to be within a corridor if the majority of the midpoints within its buffer were also classified as corridor behavior. Finally, we delineated the boundaries of corridors using a contour interval (e.g., 20%) of a fixed kernel density estimate of corridor use behavior midpoints (Fig. 1c).

Figure 1. Schematic and description of the animal-defined corridor model using the observed track of an adult male fisher as an example.

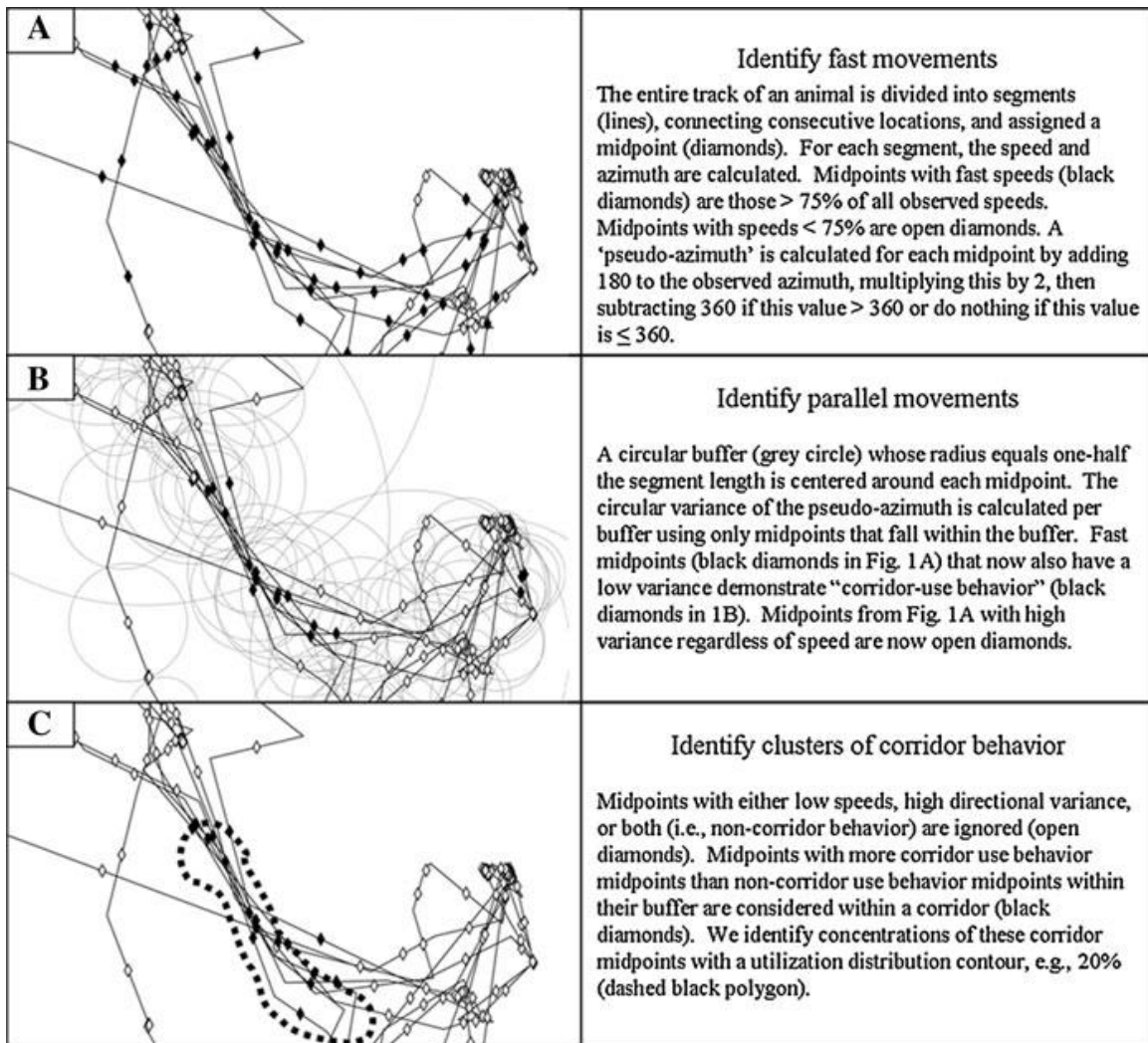
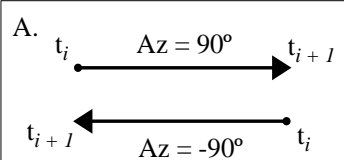
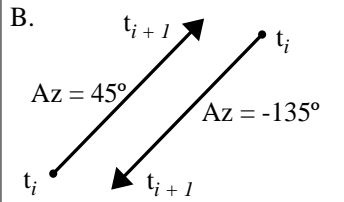
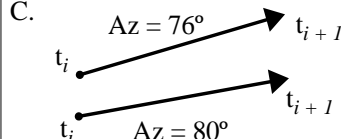


Figure 2. Schematic for calculating a step pseudo-azimuth. The azimuth of an animals step (i.e., its direction of travel from step t_i to step t_{i+1}) can have a value between $-180^\circ \leq 180^\circ$. Thus to prevent parallel steps that have opposite directions of travel from inflating the circular variance of all step azimuths within the step midpoint radius, each azimuth value is converted to a positive integer ≤ 360 . To do this we add 180 to each azimuth ("Az") and multiply this value by 2 (step 1). If the resulting value is > 360 , we subtract 360, otherwise we do nothing (step 2). The final resulting value is the 'pseudo-azimuth' (step 3). Below we provide two examples of disjunct, parallel steps, but with opposite directions of travel (A and B) and one example of two disjunct, nearly parallel steps traveling in the same direction (C).

	step 1	step 2	pseudo-azimuth
A. 	$2(90^\circ + 180^\circ)$ $2(-90^\circ + 180^\circ)$	$540^\circ > 360^\circ$ $180^\circ < 360^\circ$	180 180
B. 	$2(45^\circ + 180^\circ)$ $2(-135^\circ + 180^\circ)$	$450^\circ > 360^\circ$ $90^\circ < 360^\circ$	90 90
C. 	$2(76^\circ + 180^\circ)$ $2(80^\circ + 180^\circ)$	$512^\circ > 360^\circ$ $520^\circ > 360^\circ$	152 160

Corridor model validation

We evaluated the predictions of the three corridor models (least-cost path analysis, circuit theory, and our animal-defined corridor model) by using unbaited motion-sensitive camera traps to test if corridors predicted by each model had higher mammal detection rates than camera traps placed in nearby forest patches. We assume that cameras in true movement corridors should detect more fisher traffic than those in core areas because their narrow geometry would funnel animals near our camera. This presumes that fishers are regularly (~nightly) using corridors to move between forest fragments that make up their home range. If this between-fragment movement is rare, core area movement rates might be higher, but camera-based comparisons between predicted corridor areas would still be valid. Between September 2011 and January 2012 we

placed a camera trap at the center of each predicted corridor location and within nearby forest patches that were used by our fishers. All cameras were spaced >130 m apart, greater than the recommended minimum distance of 25 m (Kays et al. 2011), to avoid spatial autocorrelation of detections. Each camera (Reconyx RC55 or PC800, Holmen WI) was attached to a tree 0.5 m above the ground, run continuously for approximately one month, and was set to take ten pictures per trigger in rapid succession. We considered detections > 1 minute apart to be temporally independent, and analyzed movement rates for eight species groups: fishers, carnivores, carnivores excluding fishers, medium and large mammals, medium and large mammals excluding carnivores, mammals except squirrels (Sciuridae), mammals excluding carnivores and squirrels, and mammals (Table 1). We measured the detection distance for each camera set as the maximum distance it would trigger on a human walking by, and used this to test for potential habitat-related effects on detection area. We used a general linear model (Poisson distribution, including camera deployment duration and month of deployment as offset terms) to determine whether each corridor model predicted different detection rates than expected (i.e., compared to cameras within the used forest patches).

Corridor composition

We conducted a weighted compositional analysis of habitat use (Aebischer et al. 1993; Millsaugh et al. 2006) to determine whether fisher corridors and fisher home ranges are composed of statistically different land cover types. This is the same analysis we used to estimate fisher habitat selection within their home range, except we now only used the segment midpoints identified as corridor behavior for ‘use’, rather than all locations, and used a dynamic Brownian bridge movement model utilization distribution of all movement step midpoints as ‘available’ (Kranstauber et al. 2012). For this analysis, it was necessary to combine ‘use’ data

Table 1. In addition to fishers, camera trap detections of mammal species were also grouped into four categories for analyses.

Species	Mammals	Mammals excluding squirrels	Medium and large mammals	Carnivores
<i>Didelphis virginiana</i>	X	X	X	
<i>Canis latrans</i>	X	X	X	X
<i>Vulpes vulpes</i>	X	X	X	X
<i>Urocyon cinereoargenteus</i>	X	X	X	X
<i>Mephitis mephitis</i>	X	X	X	X
<i>Procyon lotor</i>	X	X	X	X
<i>Martes pennanti</i>	X	X	X	X
<i>Mustela erminea</i>	X	X	X	X
<i>Mustela frenata</i>	X	X	X	X
<i>Odocoileus virginianus</i>	X	X	X	
<i>Tamias striatus</i>	X			
<i>Sciurus carolinensis</i>	X			
<i>Tamiasciurus hudsonicus</i>	X			
<i>Glaucomys</i> sp.	X			
<i>Peromyscus</i> sp.	X	X		
<i>Sylvilagus floridanus</i>	X	X	X	

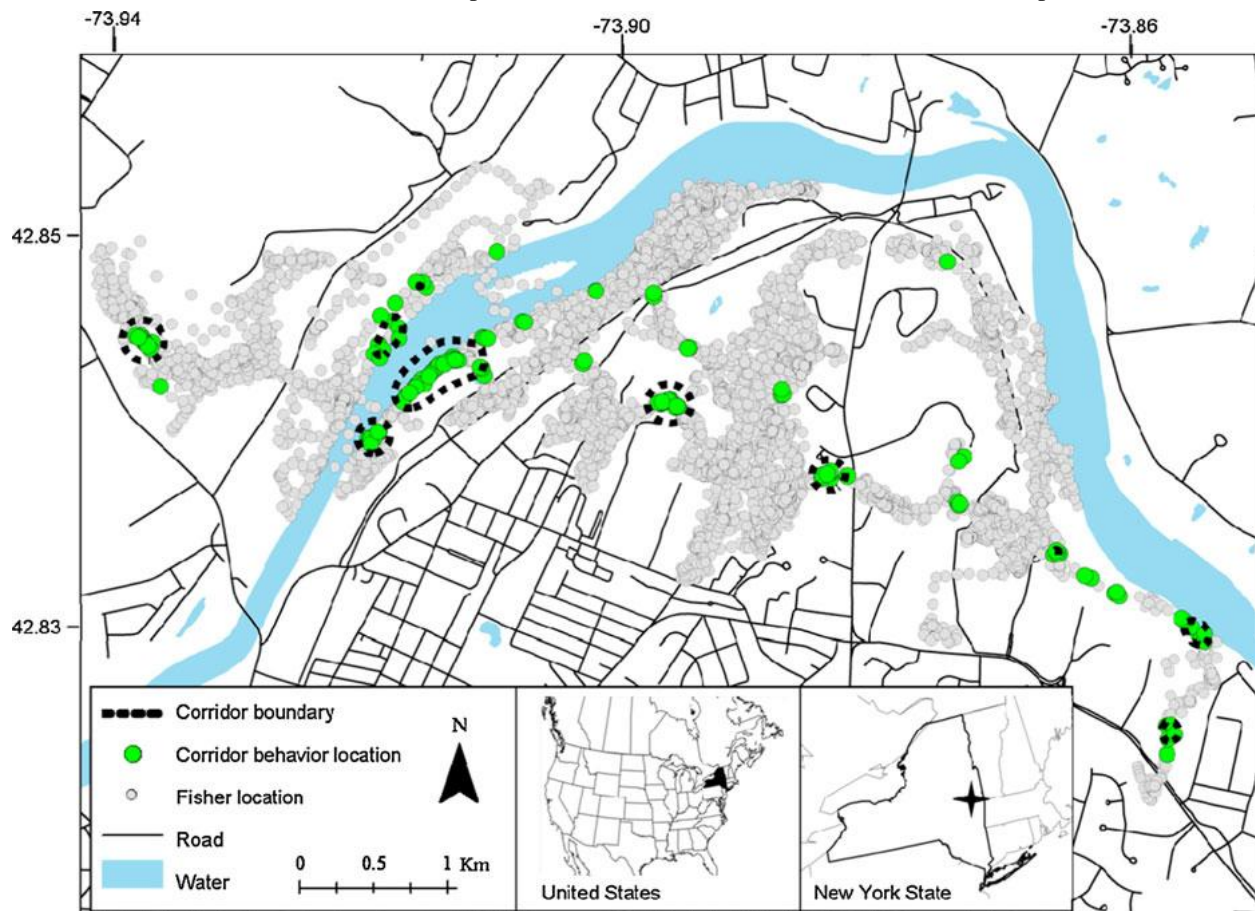
and ‘availability’ data for all individuals, by summing all corridor use behavior midpoints and all of the non-corridor use behavior midpoints for all of our fishers, as several fisher had insufficient corridor use behavior midpoints for the analysis. These analyses were run in program R (version 2.15.0; R Development Core Team 2012) using the *compana* function of the *adehabitat* package (version 0.3.5, Calenge 2006).

RESULTS

Of the 12 fishers captured and tagged, four had to be excluded from analysis (one male dispersed, one female denned during her tag deployment, and two males removed their collars early during their deployment). The remaining eight tags (5 males, 3 females) recorded for a combined 242 days (means of 38 and 18 days, males and females respectively), during winter (mid-December – end of March) producing 31,985 GPS fixes (means of 5226 and 1951 per male

and female respectively, see Figure 3 for an example). Tracking data for these animals are available at Movebank.org (DOI: 10.5441/001/1.2tp2j43g).

Figure 3. Map highlighting the results of the animal-defined corridor model for one urban male fisher. Corridor boundaries are delineated with a 20% isopleth (dashed) of a utilization distribution as an example.



A total of 5% of fisher movements met our criteria to be considered potential corridor use behavior, and 18% of these were concentrated into 23 animal-defined corridors. Based on our criteria, one female and one male did not exhibit corridor use, whereas the remaining six fishers repeatedly used between 2 and 7 corridors within their home ranges. This female used a very small home range (1.1 km²) and did not require multiple forest fragments, and the male lived in an area of continuous forest, (i.e., a single, large habitat patch). We excluded these two fishers from the corridor validation tests and the corridor composition analysis as they did not

demonstrate corridor use, thus we could not validate the animal-defined corridor model predictions nor could we quantify their corridor compositions.

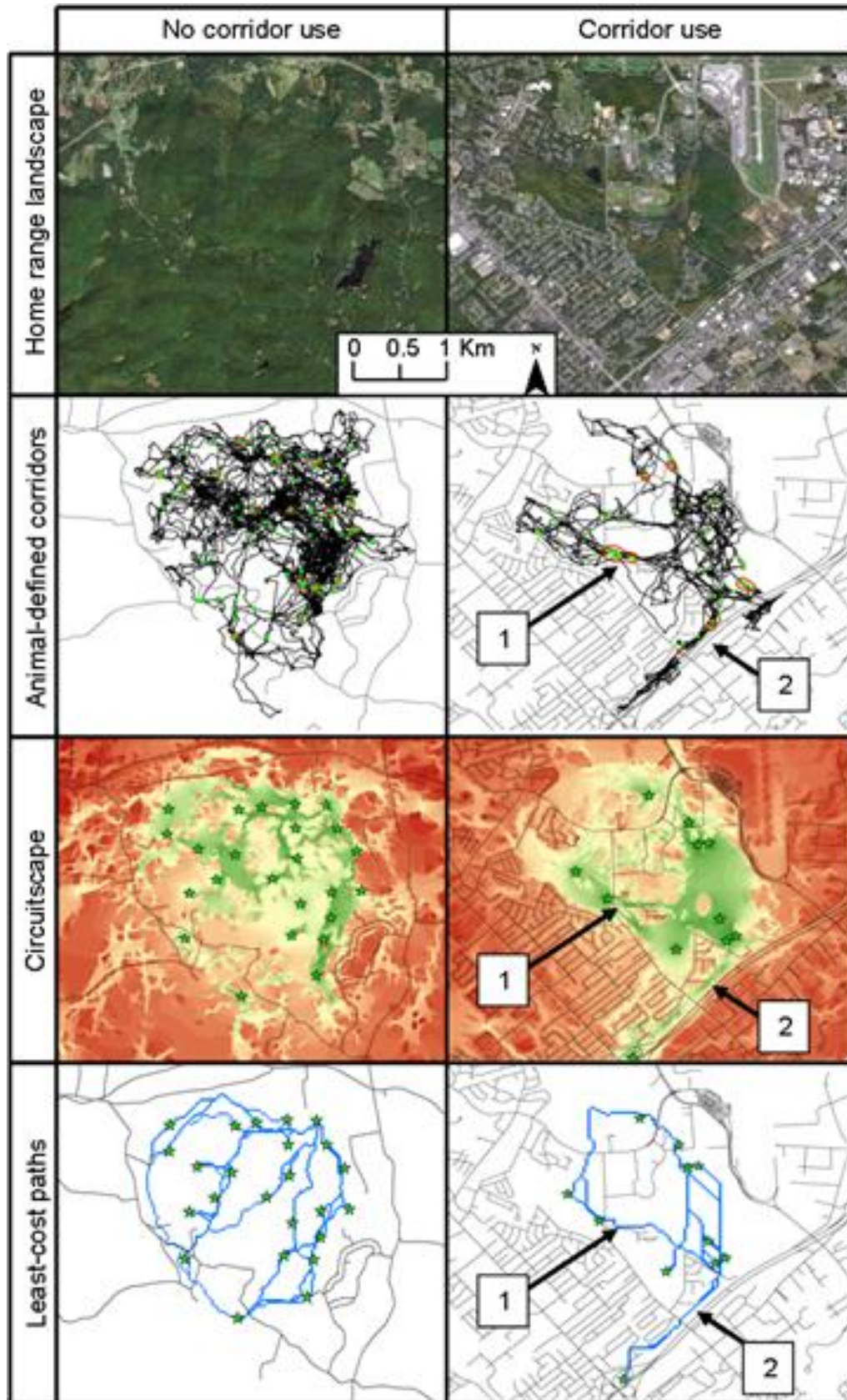
The weighted compositional analysis produced standardized pairwise log-ratio difference values between -14.9 and 8.35 (Table 2). We translated these values into ‘cost’ (i.e., land cover resistance) values per individual, that varied for the same land cover type across individuals (Table 2). Using these values, least-cost path analysis identified 17 potential corridors (1 – 6, per individual) and circuit theory identified 28 corridors (1 – 7, per individual) within the home ranges of these animals (see Figure 4 for examples). Of the 23 animal-defined corridors, only one was predicted by least-cost path analysis and only five were predicted by circuit theory. Only six of the 17 and 28 corridors predicted by least-cost path analysis and circuit theory, respectively, overlapped.

To test whether predicted corridors received higher mammal traffic than forest patches, we deployed camera traps for a total of 1909 trap nights. We were able to monitor 24 forest patch locations, but flooding, restricted access to private property, and infeasibility of some suggested corridor sites (e.g., car parking lot) limited our corridor monitoring to 40 of the 55 predicted corridor locations. Five of the monitored corridors were identified by two different corridor models and two were identified by all three corridor models, thus a single camera trap at these sites simultaneously recorded detections for multiple corridor models. The camera detection distance to a human ranged from 3.2 m to 19.1 m (mean = 10.3 m) and did not vary significantly with location type (ANOVA; F -value = 0.368, P = 0.78). Detection rates were spatially independent for each species grouping (Moran’s I ; P > 0.25). Detections of species groups, except fishers, were significantly negatively affected by the camera deployment month, with early (i.e., autumn) deployments having higher detection rates than later deployments

Table 2 The mean pairwise log-ratio differences (“pwd”; Aebischer et al. 1993) calculated for each land cover type, per individual fisher (M1–M5 and F1–F3, males and females), and the resulting cost values used to parameterize the resistance layers for the least-cost path analysis and Circuitscape corridor models.

Land cover	M1		M2		M3		M4		M5		F1		F2		F3	
	pwd	cost	pwd	cost	pwd	cost	pwd	cost	pwd	cost	pwd	cost	pwd	cost	pwd	cost
5-mile per hour road	-2.81	79.0	-6.59	84.0	-1.44	45.0	2.34	3.0	N/A	N/A	2.29	14.5	1.55	7.3	-4.38	68.2
15-mile per hour road	-4.72	92.6	3.61	19.9	-4.70	82.3	0.17	15.1	N/A	N/A	2.85	10.3	-0.40	27.5	-7.55	88.6
25-mile per hour road	-0.71	64.1	2.64	26.0	-0.45	33.8	1.67	6.7	3.15	6.9	2.06	16.2	1.82	4.5	3.01	20.6
35-mile per hour road	-0.14	60.1	3.40	21.2	0.90	18.2	1.74	6.4	N/A	N/A	2.29	14.5	1.00	13.1	5.79	2.6
45-mile per hour road	-4.07	87.9	-8.03	93.0	1.90	6.9	-12.4	85.3	-1.40	42.5	-7.23	86.8	-0.36	27.1	N/A	N/A
55-mile per hour road	-3.79	86.0	-4.37	70.0	-2.49	57.0	1.62	7.0	N/A	N/A	1.37	21.5	-3.48	59.3	N/A	N/A
65-mile per hour road	-5.78	100	-4.82	72.9	0.83	19.0	N/A	N/A	N/A	N/A	N/A	N/A	-7.42	100	-9.32	100
Barren land	-0.44	62.2	-5.75	78.7	-0.06	29.2	-6.32	51.5	N/A	N/A	N/A	N/A	N/A	N/A	-3.65	63.4
Crops	1.50	48.5	3.23	22.3	0.78	19.6	1.55	7.4	-7.56	90.5	0.91	25.0	0.99	13.1	4.16	13.1
Developed, high intensity	0.33	56.8	-8.18	94.0	-6.24	100	-0.79	20.6	N/A	N/A	-4.11	63.1	0.60	17.2	-9.16	98.9
Developed, low intensity	0.01	59.0	2.76	25.2	0.47	23.2	2.26	3.4	-4.08	63.4	0.16	30.7	0.18	21.5	3.74	15.9
Developed, med intensity	1.91	45.6	-9.14	100	-1.10	41.2	0.09	15.6	1.14	22.7	1.11	23.5	-7.41	99.9	4.63	10.1
Developed, open space	1.37	49.4	4.83	12.2	1.98	5.9	2.28	3.3	3.83	1.6	2.14	15.6	1.27	10.2	5.07	7.2
Emergent herb. wetland	8.35	1.0	-6.22	81.6	N/A	N/A	-14.9	100	-4.73	68.4	-6.01	77.6	N/A	N/A	N/A	N/A
Forest, deciduous	1.35	49.6	5.67	7.0	2.37	1.5	2.79	0.5	3.35	5.4	3.46	5.7	1.97	3.0	6.17	0.2
Forest, evergreen	3.08	37.3	6.77	1.0	2.20	3.4	2.77	0.6	3.54	3.9	4.05	1.2	1.16	11.3	-3.79	64.3
Forest, mixed	2.13	44.1	4.95	11.5	2.50	1.0	2.18	3.9	3.16	6.9	3.93	2.0	2.26	1.0	-4.99	72.1
Forested wetlands	2.26	43.1	5.71	6.7	2.07	4.8	2.87	1.0	3.81	1.8	3.93	2.1	2.09	1.7	6.20	1.0
Grassland / herbaceous	0.99	52.1	6.57	1.3	-0.34	32.5	2.42	2.5	-2.54	51.3	-3.47	58.2	N/A	N/A	N/A	N/A
Open water	-2.81	79.0	-8.40	95.4	1.15	15.5	2.00	4.9	-8.77	100	-8.97	100	1.78	4.9	4.45	11.2
Pasture	1.30	49.9	6.57	1.3	2.06	5.0	2.73	0.8	2.73	10.2	4.20	1.0	1.61	6.7	6.10	0.6
Scrub / shrub	0.43	56.1	4.18	16.3	-2.43	56.4	2.21	3.7	4.04	1.0	-5.54	73.9	0.66	16.5	-6.47	81.6

Figure 4. Maps of the home range landscape, animal-defined corridors, Circuitscape output, and least-cost paths of two male fishers. Our animal-defined corridor model suggests that the fisher within the fragmented landscape (right column) demonstrated corridor use (indicated with utilization contours around high densities of corridor behavior locations, red polygons) while the fisher within the continuous landscape (left column) did not (indicated by the lack of corridor behavior location clusters). For the fisher with no observed corridor use, both Circuitscape (red to green labeling suggests low to high flow) and least-cost path analysis (connected blue cells) still predicted corridor locations between rest sites (green stars). Both Circuitscape and least-cost path analysis did predict two of the five observed corridors for the fisher in the fragmented landscape (indicated).



(general linear model, t -values < -2.182 $P < 0.05$). For fisher detections we ran two general linear models, one with the camera deployment month as an offset and one without, but ultimately chose the more robust model for interpretation as it produced a lower AIC value.

Compared to cameras placed within forest patches, cameras within our animal-defined corridors detected higher numbers of each of our species groupings ($P < 0.05$) (Table 3). Detection rates for circuit theory cameras were significantly higher for most non-target mammal groups ($P < 0.001$), but were lower for fishers and carnivores (Table 3). Least-cost path cameras detected significantly higher rates for mammals ($P < 0.001$), but also significantly lower detection rates for mammals excluding squirrels and medium and large mammals (Table 3). Fisher detections were 64% higher at cameras within least-cost path corridors than in nearby forest patches, but this improvement was not statistically significant ($P = 0.655$), probably due to the low number of least-cost path corridors ($n = 6$) that we were able to monitor and the overall low number of detections of fishers ($n = 39$, 5 of which were detected within least-cost path corridors). A post-hoc power test with unequal observations, using an alpha of 0.05, suggests we needed to monitor three more least-cost path corridors in order to detect our observed effect size of 1.643).

Fisher corridors have a different land cover type composition than their home ranges (Figure 5). Our animal-defined corridor model suggested fisher corridors are composed of a variety (15 of 22, 68%) of the land cover types included in our analyses, with forested wetlands and deciduous forests being most prominent (Figure 5). Fisher corridors contained more forested wetlands, deciduous forests, pastures, and more 5 and 35 mile per hour roads than would be expected based on the typical fisher home range composition. Of the five most prominent corridor land cover types, only two were forests, with the remaining three being cropland,

developed open space (e.g., golf course or cemetery) and pastures (Figure 5). In contrast, all of the 22 land cover types were found in fisher home ranges, and four of the five most prominent home range land cover types were forests: deciduous forest, mixed forest, coniferous forest, pasture, and forested wetland, in decreasing order of selection (Figure 5).

DISCUSSION

Corridors are widely viewed as important tools for maintaining landscape connectivity (Gilbert-Norton et al. 2010), yet there has been little empirical evidence to test whether mammals actually move through predicted corridors. Our high-resolution tracking data show that fishers use movement corridors to connect fragmented habitats within their home ranges. The two fishers that did not show corridor-like movement behavior were also not observed moving between forest fragments, maintaining home ranges that were nearly uniformly forested with no anthropogenic barriers. This suggests that corridor use may be a behavioral adaptation by fishers to fragmented landscapes. Furthermore, using fishers as a model species, we demonstrated a repeatable approach to wildlife corridor identification that uses field data and emphasizes animal behavior, while reducing assumptions inherent to cost-based corridor models. Unfortunately, the corridors used by our study animals were generally not well predicted by the cost-based corridor models, emphasizing the need for further integration of animal behavior data into corridor models and for validating corridor model predictions with independent field data (Chetkiewicz et al. 2006; Beier et al. 2008; Sawyer et al. 2011).

Cost-based corridor models are sensitive to numerous factors including the anthropocentric categorizations of landscape variables fed into the model, their resistance

estimates, and both the spatial and temporal grain and scale of the landscape under study (Rayfield et al. 2010; Sawyer et al. 2011). Our use of tracking data to calculate land cover resistance values for these models is the recommended best practice (Beier et al. 2008;

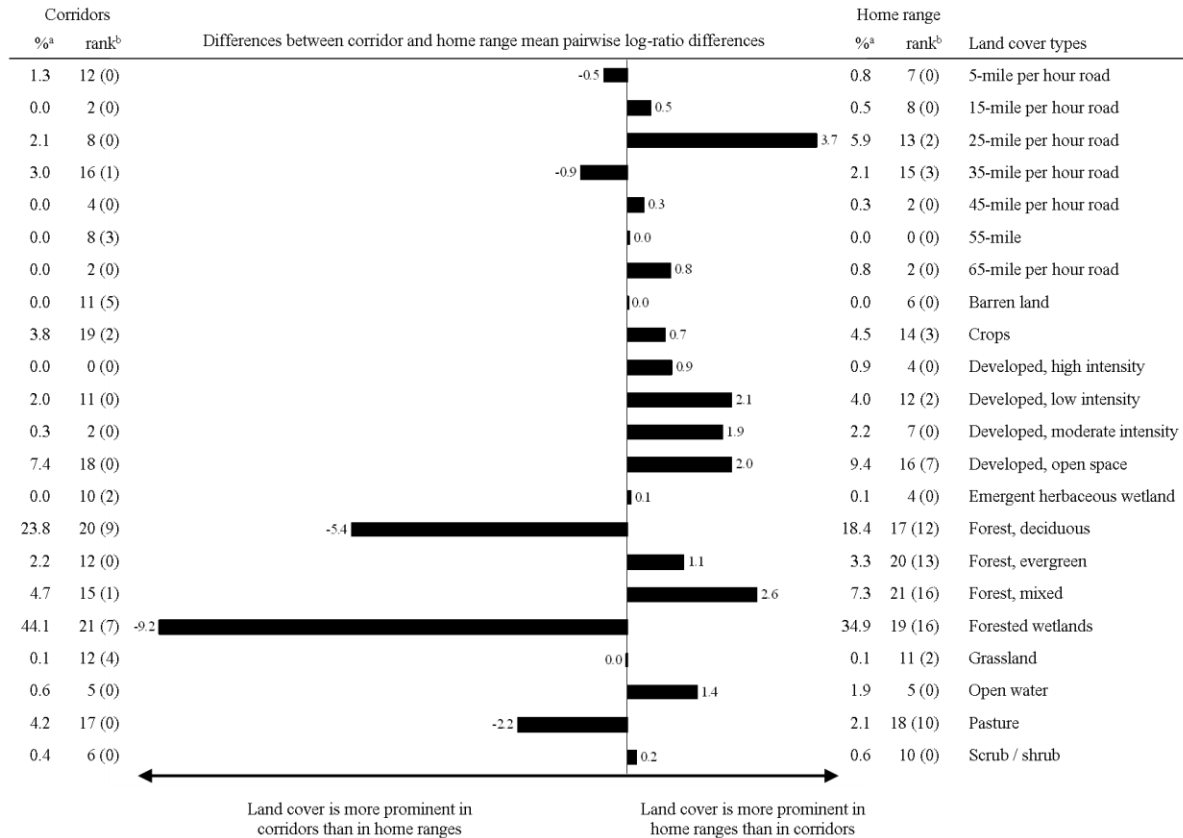
Table 3. Mean detection rates (detections/day) and mammal species richness for camera traps deployed in forest patches and corridors predicted by the three different models, with sample sizes in parentheses. Superscripts indicate significance levels (^a $P < 0.05$, ^b $P < 0.01$, ^c $P < 0.001$) for results from a general linear model comparing detection rates for each corridor model to nearby forest patches.

Species groupings	Forest patch (24)	Animal-defined corridors (17)	Circuit theory corridors (17)	Least-cost path corridors (6)
Fishers (39)	0.018	0.031 ^a	0.012	0.028
Carnivores (271)	0.139	0.185 ^c	0.094	0.122
Carnivores excluding fishers (232)	0.121	0.154 ^c	0.082	0.094
Medium and large mammals (1054)	0.475	0.587 ^c	0.622 ^c	0.431 ^b
Medium and large mammals excluding carnivores (783)	0.336	0.403 ^c	0.528 ^c	0.310 ^a
Mammals excluding squirrels (1193)	0.525	0.697 ^c	0.696 ^c	0.462 ^b
Mammals excluding squirrels and carnivores (922)	0.387	0.512 ^c	0.602 ^c	0.341 ^a
Mammals (2343)	0.776	1.379 ^c	1.327 ^c	1.857 ^c
Mammal species richness (16)	12	15	13	10

Chetkiewicz and Boyce 2009; Sawyer et al. 2011). Despite this, circuit theory predicted only 22% (5 of 23) and least-cost path analysis predicted only 4% (1 of 23) of the corridors actually used by our study animals, and further, our camera detection data suggest that locations that our interpretation of circuit theory current maps suggested were corridors received less fisher traffic than cameras within forest patches. Because of our decision to model cost-based corridors between rest sites, a few of their predicted corridors were located within a continuous forest patch. This may have reduced their camera detection rates, but this does not detract from their inability to predict the corridors used by our study animals. We believe that these differences are real and are not related to our decision to model cost-based corridors between fisher rest sites rather than between habitat cores, patches, or home range boundaries. Since fisher rest sites were numerous and located throughout the forest patches within a fisher's home range, and because the cost-based corridors are forced between all combinations of these rest sites, the cost-

based corridor models should predict corridors between these forest patches, without the need for subjective boundary delineations.

Figure 5. Land cover composition of corridors and home ranges of urban fishers demonstrating corridor use (6 of the 8 fishers studied). Horizontal bars indicate whether land cover types were more prominent within animal-defined corridors (to the left of the Y-axis) or within fisher home ranges (to the right of the Y-axis), based on the difference between the mean log-ratio pairwise differences (Aebischer et al. 1993) per land cover type for corridors and home ranges.



^a Percentage of corridor and home range total area per land cover type for fisher demonstrating corridor use.

^b The number of other land cover types that each land cover type was selected over. Higher values suggest the land cover type was increasingly selected over the other land cover types, with parentetic values indicating the number of land cover types that the row land cover type was significantly ($P < 0.001$) selected over.

We believe that the little overlap between the cost-based predictions and observed fisher corridors is due to differences between fisher's land cover selection for corridors in comparison with their home ranges (Fig. 5), which we used to build our resistance layers for cost-based models (Sawyer et al. 2011; Zeller et al. 2012). For example, four of the five most preferred

(i.e., highest ranking) fisher home range land cover types were forests, whereas only two of the five most preferred corridor land cover types were forests. The relative cost values assigned to the landscape variables and the spatial arrangement of these cost values are known to influence the results of cost-based resistance mapping (Rayfield et al. 2010). We would not suggest that corridors designed for fishers should be composed of land cover types other than those that they prefer (i.e., forests). Rather, our results suggest that corridor planners should not immediately discount these suboptimal land cover types if they are in connecting areas, and should recognize that fishers, and possibly other species, are able to utilize suboptimal cover types to connect more desirable areas. Finding that fishers select for forests is not surprising (Powell 1993; Lofroth et al. 2010). Yet, although fishers prefer forests, our data suggest that connecting separate habitat fragments is so important for suburban fishers that they are willing to use corridors composed of sub-optimal land cover types (e.g., crops, open space, and pastures). Our field observations (snow tracking and ad-hoc camera traps) also suggest that fishers made regular use of under-road tunnels and drainage pipes to cross beneath roads, including one individual who repeatedly crossed beneath a 6-lane, heavily traveled highway. Both their use of these under-road tunnels and their corridor land cover composition offer important insight into this species perception of landscape connectivity (Lima and Zollner 1996), their ability to cross gaps in forest cover (Dale et al. 1994), and have significant implications for fisher corridor modeling.

Unbaited camera traps provided a good test for within home-range movement corridors, where resident mammals should pass through movement corridors regularly. Camera traps are increasingly popular in ecology and conservation and have been used previously to monitor fishers (Kays and Slauson 2008), yet to our knowledge this work is the first to use cameras to validate corridor model predictions. We urge researchers to consider the type and frequency of

expected corridor use when designing corridor monitoring studies, including an awareness of seasonal biases in detections rates that may be attributed to increased activity, such as the high camera detection rate we observed for of sciurids preparing for winter. For example, dispersal is vitally important for biodiversity, yet confirming dispersal via corridors remains a challenge, as dispersers are less likely to pass the same camera multiple times, thus reducing their detection rates and making it difficult to distinguish them from random probability. Molecular data provide useful insight into landscape connectivity, but is best suited for measuring historic landscape connectivity (Schwartz et al. 2009) and should be used as complimentary data, particularly as recent landscape changes may require decades to be detected via population genetic methods (Spear et al. 2010).

Carefully selecting a species as a model for other local species could be a feasible alternative to more challenging multi-species corridor approaches, provided the corridor model predictions are validated with field data. Our camera trap detection data suggest that the predicted animal-defined corridors received higher traffic rates of fishers and each of the other non-target mammal species groups that we considered, suggesting that fishers are a suitable model species for the other forest dependent mammal species within our study area.

Unfortunately however, this can not be said for the cost-based corridor models tested here. It appears that circuit theory failed to predict corridors for fishers and carnivores in general and least-cost path analysis predicted more fisher traffic, but less of each of the non-target species groups except sciurids. These shortcomings may limit their utility for multi-species corridor planning. We believe that these shortcomings can be overcome by further integrating animal behavior into corridor models and recognizing corridor use as a behavior, as with our animal-defined corridor model, rather than estimating movement resistance from habitat preference

information. It is interesting to note however that each of the corridor models predicted high sciurid traffic. This may not be related to the corridor models themselves, but rather due to the sciurids increased activity during our sampling season or because predicted corridors often passed through residential areas where *S. carolinensis* (the most commonly detected species) in particular may be especially active collecting supplemental food from backyard bird feeders.

Our animal-defined corridor model was effective in identifying fisher corridors, yet it is not without its limitations. First, our model requires the capturing and monitoring of free-ranging animals, which may prove difficult for rare and/or elusive species, yet we believe that the additional information garnered from this effort (e.g., home range estimates, activity patterns, habitat selection, etc.) outweigh the required additional effort. Another shortcoming of our method is that it applies to within home range corridors and thus cannot directly predict corridors at larger scales. However, our method does objectively identify movement corridors, allowing users to avoid many of the assumptions and shortcomings of cost-based corridor models, such as potential landscape variable layer inaccuracies, proper landscape resistance parameterizations, and reduces assumptions of animal knowledge of the target landscape. Further, our results highlight the potential for animal behavior data to improve cost-based corridor models, and the need to do so. Our corridor model results can be re-incorporated into the landscape resistance estimates required for cost-based corridor modeling, thereby producing a more realistic estimate of landscape resistance to animal corridor use, rather than resistance to animal habitat selection. Finally, our animal-defined corridor model can be applied across many species and landscapes, even immediately applied to existing animal movement datasets (e.g., www.movebank.org).

Maintaining animal movements through dynamic and challenging landscapes is crucial for biodiversity (Bennett 2003; Nathan et al. 2008). Our paper confirms that animals will move

through corridors to connect fragmented habitat patches, supporting their value for conservation. We also offer two field tests of corridor model predictions: active animal tracking and passive monitoring with remote cameras. Our results suggest that cost-based models may be inaccurate if they ignore unique interactions between animal behaviors and particular landscape features. Although we are enthusiastic about the potential for corridor modeling to inform conservation decisions, we agree with Chetkiewicz et al. (2006) that more progress is needed to incorporate independent data into these models to make them more accurate and useful.

ACKNOWLEDGEMENTS

This work was supported in part by the NSF (grant 0756920 to RK), the New York State Museum, the Max-Planck-Institute for Ornithology, the North Carolina Museum of Natural Sciences, and the National Geographic Society Waitt Grant Program (grant W157-11 to SL). We thank the Albany Pine Bush Preserve, Joseph Bopp, Joseph Chase, Neil Gifford, Wolfgang Heidrich, Bart Kranstauber, Franz Kümmereth, Kevin McLean, Tristan Nuñez, Lisa Pipino, Roger Powell, Kamran Safi, Marco Smolla, and Brad Stratton for their support and valuable input. This manuscript benefited from the comments of C. Vos and two anonymous reviewers.

General discussion

CARNIVORES in the CAPITAL

Habitat fragmentation and urbanization are pushing wildlife species toward the brink of extinction (Wilcox and Murphy 1985; Saunders et al. 1991; Turner 1996; Fahrig 1997, 2003; McKinney 2002). Carnivores are highly susceptible to these threats due to their large area requirements and low population densities (Noss et al. 1996; Crooks 2002; Cardillo et al. 2005; Crooks et al. 2011). A few carnivore species however are surviving these anthropogenic forces by adapting their behaviors to best facilitate their co-existence with humans (McClennen et al. 2001; Henle et al. 2004; Prange et al. 2004; Fischer and Lindenmayer 2007; Gehrt et al. 2010; Bateman and Fleming 2012). A more complete understanding of how these species are able to do so is urgently needed.

With this dissertation I attempted to improve our understanding of how a once rare carnivore is surviving within a fragmented, urbanized landscape. Specifically, I focused on the movements, habitat use, and the timing of activity of fishers (*Pekania pennanti*) living within the most developed landscape within their geographic range. Through novel technological improvements in GPS-tracking collars and a novel model of movement-behavior, I determined that fishers within my study area actively avoid automobile traffic volume peaks by adjusting the timing and duration of their daily activities to avoid these human activity peaks. I also discovered that these individuals have lessened their habitat suitability requirements, and connect the habitat (i.e., forest) patches that constitute their territories by routinely crossing roads, (at times utilizing under-road passages and tunnels), and by making regular use of corridors. In comparison to the fishers I monitored within a nearby continuous forest landscape, the “urban” fishers clearly exhibit several behavioral adaptations that are facilitating their survival under the

constant pressures of habitat fragmentation, loss, automobile traffic, and other human disturbances.

IMPLICATIONS, CONSERVATION VALUE, and FUTURE DIRECTIONS

It was my goal and is my hope that the work presented within this dissertation will have broad implications for wildlife ecology and for conservation biology. My activity-informed, dynamic GPS-fix attempt schedule offered a solution to an often debated (Hansen and Riggs 2008; Cagnacci et al. 2010; Hebblewhite and Haydon 2010; Brown et al. 2012) logistical challenge to wildlife biologists: reducing the trade-off between data resolution and battery life. This tool has been implemented by several biotelemetry equipment manufactures and is being adopted by field biologists. I expect this technology to improve our understanding of wildlife ecology and in turn to provide better information for conservation practitioners.

In Chapter 2, I provided and rigorously tested a hypothesis that suggests fishers within the species eastern range are benefiting from a reduced mammalian predator community, i.e., a mesopredator release. The disparity in the fisher's range recovery has been debated by fisher biologists for some time, yet previous attempts to explain why fishers in the East have expanded their ranges 6-fold than fisher in the West have fallen short (Lewis et al. 2012). My efforts in Chapter 2 offer a partial explanation for this recovery disparity, but there are certainly other factors at play. I expect this work to stimulate future investigations into the phenomenon. Efforts would benefit from a range-wide collaboration of fisher biologists sharing fisher location information (e.g., telemetry data) and standardizing their field efforts. With these data in hand, range-wide analyses could be run to determine spatially explicit habitat selection requirements, for example, which could in turn be used within connectivity analyses at the landscape, regional,

eco-regional, or larger spatial scales. I have no doubt that such an effort would yield incredible insight into the species ecology providing valuable information for conservation efforts, and providing a model approach for biologists working on other species.

My investigations into fisher movement patterns yielded unique and important insights into this species behavior and ecology. From the data collected via accelerometers, I was able to show that the urban fishers are responding to human activities. By comparing automobile traffic volumes on weekdays and weekends, I was able to suggest that fishers are nocturnal and appear to cease their nightly activity earlier in the morning on weekdays, which have earlier and steeper traffic volume peaks, than on weekends. Further, it appears that these urban fishers also facilitate their survival by utilizing nearly all available forest cover, rather than requiring specific (potentially rare) forest characteristics. In the field, I observed my study animals using a variety of resting structures (e.g., back yard storage sheds, tree cavities, trash heaps, etc.) and making ready use of a potentially over-abundant prey species: eastern grey squirrels. Albeit incidental and unpublished, these observations further support conclusions on their resourcefulness. In the future, I expect the use of accelerometers to proliferate wildlife biology and ecology. Their low weight and relatively low cost make them immediately appealing. As others have already shown, the level of insight into the daily lives of free-ranging animals will yield valuable insight (Wilson et al. 2006, Wilson et al. 2008; Shepard et al. 2010).

With the fisher movement data I recorded, I was able to achieve four goals: (1) document fisher movements through a fragmented landscape, (2) develop a novel model of animal movement behavior to identify corridors, (3) replicate two popular, movement resistance-based connectivity models, and (4) validate the predictions of all three corridor models with an independent set of animal movement data. Documenting the movements of these fishers through

this landscape immediately provides valuable information on the ecology of this species which can be used by local land planners (e.g., the Nature Conservancy's Albany Pine Bush Preserve), but also by fisher biologists elsewhere working to restore this species to its former range. I have the greatest expectations however, for my efforts to identify and validate corridors. The phrase "conservation corridor" is a buzzword in conservation circles that unfortunately, in my opinion, most users do not understand. Despite their popularity, corridor model predictions and the corridors themselves are rarely validated with field data. In my work presented here, I show that it is feasible to validate model predictions. More importantly, I offer evidence that two popular approaches failed to predict animal movement corridors. I hope that my efforts in this regard encourage efforts to valid conservation corridors elsewhere. I also hope that my novel model of corridor identification is readily used and improved by future users as it is freely available as a script for program R (function "corridor" within the "move" package).

CONCLUSION

The fisher's story is a roller coaster adventure of persecution and isolation, translocation and expansion. But will their western populations recover their former range as their eastern counterparts have? My work has revealed the unexpected resourcefulness and adaptability of a once rare and once considered habitat specialist, offering encouragement for the survival of other imperiled species. I have strived to incorporate animal behavior and movement ecology directly into conservation relevant information and I believe that future conservation-orientated efforts must do the same. I believe we can do this by asking questions whose answers are given from the individual animal's point of view, an animal-defined perspective.

References

- Adrados C, Verheyden-Tixier H, Cargnelutti B, Pepin D, Janeau G (2003) GPS approach to study fine-scale site use by wild red deer during active and inactive behaviors. *Wildlife Society Bulletin* 31: 544–552
- Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of ‘least-cost’ modeling as a functional landscape model. *Landscape and Urban Planning* 64: 233–247
- Aebischer NJ, Robertson P, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325
- Arnott G, Elwood RW (2009) Assessment of fighting ability in animal contests. *Animal Behaviour* 77: 991–1004
- Arthur SM, Krohn WB, Gilbert JR (1989) Habitat use and diet of fishers. *Journal of Wildlife Management* 53: 680–688
- Ashby K (1972) Patterns of daily activity in mammals. *Mammalian Review* 1: 171–185
- Astronomical Applications Department of the US Naval Observatory (2011) Sunrise/set table for one year. Available for download at: http://aa.usno.navy.mil/data/docs/RS_OneYear.php
- Aubry KB, Raley CM (2006) Update July 2006: Ecological characteristics of fishers (*Martes pennanti*) in the Southern Oregon Cascade Range. Unpublished report, Forest Service, US Department of Agriculture, Pacific Northwest Research Station, Olympia, Washington, USA
- Bartoń KA, Hovestadt T, Phillips BL, Travis MJJ (2012) Risky movement increases the rate of range expansion. *Proceedings of the Royal Society B* 279: 1194–1202
- Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. *Journal of Zoology* 287: 1–23
- Beier P (2006) Effects of artificial night lighting on terrestrial mammals. In: Rich C, Longcore T (eds.) *Ecological consequences of artificial night lighting*. Island Press: London, pp 19–42
- Beier P, Majka DR, Spencer WD (2008) Forks in the road: choices in procedures for designing wildland linkages. *Conservation Biology* 22: 836–851
- Bennett AF (2003) *Linkages in the landscape: the role of corridors and connectivity in wildlife conservation*, 2nd edn. International Union for the Conservation of Nature, Gland, Switzerland

- Bivand R, Lewin-Koh N (2013) maptools: Tools for reading and handling spatial objects. R package version 0.8-14. <http://CRAN.R-project.org/package=maptools>
- Bivand R, Rundel C (2013) rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.2-9. <http://CRAN.R-project.org/package=rgeos>
- Blackie HM (2010) Comparative performance of three brands of lightweight Global Positioning System collars. *Journal of Wildlife Management* 74: 1911–1916
- Bograd SJ, Block BA, Costa DP, Godley BJ (2010) Biologging technologies: new tools for conservation. *Endangered Species Research* 10: 1–7
- Bourgoin G, Garel M, Dubray D, Maillard D, Gaillard JM (2009) What determines global positioning system fix success when monitoring free-ranging mouflon? *European Journal of Wildlife Research* 55: 603–613
- Bowman J, Donovan D, Rosatte RC (2006) Numerical response of fishers to synchronous prey dynamics. *Journal of Mammalogy* 87: 480–484
- Bowman JL, Kochanny CO, Demarais S, Leopold BD (2000) Evaluation of a GPS collar for white-tailed deer. *Wildlife Society Bulletin* 28: 141–145
- Brown DD (2011) Activity patterns and space use of Northern tamandua anteaters (*Tamandua mexicana*) on Barro Colorado Island, Panamá. Doctoral Thesis, University of California, Davis
- Brown DD, LaPoint S, Kays R, Heidrich W, Kümmeth F, Wikelski M (2012) Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. *Wildlife Society Bulletin* 36: 139–146
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445–449
- Brown JH, Lasieki RC (1972) Metabolism of weasels: the cost of being long and thin. *Ecology* 53: 939–943
- Brown MK, Will G (1979) Food habits of the fisher in northern New York. *New York Fish and Game Journal* 26: 87–92
- Buchmann CM, Schurr FM, Nathan R, Jeltsch F (2012) Movement upscaled – the importance of individual foraging movement for community response to habitat loss. *Ecography* 35: 436–445
- Burdett CL, Moen RA, Niemi GJ, Mech LD (2007) Defining space use and movements of Canada lynx with global positioning system telemetry. *Journal of Mammalogy* 88: 457–467

- Buskirk SW, Powell RA (1994) Habitat ecology of fishers and American martens. In:
 Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds). Martens, sables, and fishers:
 Biology and conservation. Cornell University Press: Ithaca, New York, USA.
- Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based
 radiotelemetry: a perfect storm of opportunities and challenges. Philosophical
 Transactions of the Royal Society B 365: 2157–2162
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and
 habitat use by animals. Ecological Modelling 197: 516–519
- Carbone C, Teacher A, Rowcliffe JM (2007) The costs of carnivory. PLoS Biology 5: 363–368
- Cardillo M, Mace GM, Jones KE, Bielby J, BinindaEmonds ORP, Sechrest W, Orme CDL,
 Purvis A (2005) Multiple causes of high extinction risk in large mammal species. Science
 309: 1239–1241
- Center for Biological Diversity (2008) A petition to list the Pacific fisher (*Martes pennanti*) as an
 endangered or threatened species under the California Endangered Species Act
- Channell R, Lomolino MV (2000) Trajectories to extinction: spatial dynamics of the contraction
 of geographical ranges. Journal of Biogeography 27: 169–179
- Chetkiewicz C-LB, Boyce MS (2009) Use of resource selection functions to identify
 conservation corridors. Journal of Applied Ecology 46: 1036–1047
- Chetkiewicz C-LB, St. Clair CC, Boyce MS (2006) Corridors for conservation: integrating
 pattern and process. Annual Review of Ecology and Evolution S 37: 317–342
- Clavel J, Julliard R, Devictor V (2010) Worldwide decline of specialist species: toward a global
 functional homogenization? Frontiers in Ecology and the Environment 9: 222–228
- Clem MK (1977) Food habits, weight changes and habitat selection of fisher during winter.
 Masters thesis, University of Guelph, Guelph, Ontario, Canada
- Coulter MW (1966) Ecology and management of fishers in Maine. PhD thesis, State
 University of New York College of Environmental Science and Forestry, Syracuse, New
 York, USA
- Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation.
 Conservation Biology 16: 488–502
- Crooks KR, Soulé ME (1999) Mesopredator release and avifaunal extinctions in a fragmented
 system. Nature 400: 563–566

- Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B* 366: 2642–2651
- Cumming GS, Cornélis D (2012) Quantitative comparison and selection of home range metrics for telemetry data. *Diversity and Distributions* 18: 1057–1065
- Daan S, Aschoff J (1975) Circadian rhythms of locomotor activity in captive birds and mammals: their variation with season and latitude. *Oecologia* 18: 269–316
- Dale VH, Pearson SM, Offerman HL, O'Neill RV (1994) Relating patterns of land-use change to faunal biodiversity in the Central Amazon. *Conservation Biology* 8: 1027–1036
- Dayan T, Simberloff D (1994) Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology* 75: 1063–1073
- D'Eon RG, Delparte D (2005) Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology* 42: 383–388
- deVos A (1952) Ecology and management of fisher and marten in Ontario. Technical Bulletin of the Ontario Department of Lands and Forests, Peterborough, Ontario, Canada
- Dietrich WE, Windsor DM, Dunne T (1982) Geology, Climate, and Hydrology of Barro Colorado Island. In: Leigh, E.G. Jr., Rand AS, Windsor DM (eds) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*. Smithsonian Institution Press, Washington, D.C., USA pp 21–46
- Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in Carnivora. *The American Naturalist* 167: 524–536
- Dow C, Michel KE, Love M, Brown DC (2009) Evaluation of optimal sampling interval for activity monitoring in companion dogs. *American Journal of Veterinary Research* 70: 444–448
- Drew RE, Hallett JG, Aubry KB, Cullings KW, Koepf SM, Zielinski WJ (2003) Conservation genetics of the fisher (*Martes pennanti*) based on mitochondrial DNA sequencing. *Molecular Ecology* 12: 51–62
- Driezen K, Adriaensen F, Rondini C, Doncaster CP, Matthysen E (2007) Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*) *Ecological Modelling* 209: 314–322
- Eisenberg JF (1989) Order Xenarthra (Edentata). In: Eisenberg JF (ed) *Mammals of the Neotropics Volume 1. The Northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, and French Guiana*. University of Chicago Press: Chicago, pp 51–55

- Emmons LH, Feer F (1990) Neotropical Rainforest Mammals: a field guide. University of Chicago Press: Chicago, Illinois, USA
- Environmental Systems Research Institute (2012) ArcGIS Desktop release 10.1. Redlands, California, USA
- Estes JA, Terbough J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of Planet Earth. *Science* 303: 301–306
- Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603–610
- 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
- Fauchald P, Tverra T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84: 282–288
- Fieberg J, Matthiopoulos J, Hebblewhite M, Boyce M, Frair JL (2010) Correlation and studies of habitat selection: problem, red herring, or opportunity? *Philosophical Transactions of the Royal Society B* 365: 2233–2244
- Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265–280
- Forman RTT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, New York, USA
- Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2003) Road ecology: science and solutions. Island Press: Washington, D.C., USA
- Fry J, Xian G, Jin S, Dewitz J, Homer C, Yang L, Barnes C, Herold N, Wickham J (2011) Completion of the 2006 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing* 77: 858–864
- Gabriel MW, Woods LW, Poppenga R, Sweitzer RA, Thompson C, Matthews SM, Higley JM,

- Keller SM, Purcell K, Barrett RH, Wengert GM, Sacks BN, Clifford DL (2012) Anticoagulant rodenticides on our public and community lands: spatial distribution of exposure and poisoning of a rare forest carnivore. *PLoS ONE* 7: e40163
- Gehring TM, Swihart RK (2003) Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biological Conservation* 109: 283–295
- George SL, Crooks KR (2006) Recreation and large mammal activity in an urban nature reserve. *Biological Conservation* 133: 107–117
- Gehrt SD, Riley SPD, Cypher BL (2010) Urban carnivores: ecology, conflict, and conservation. Johns Hopkins University Press: Baltimore, Maryland, USA
- Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review of corridor effectiveness. *Conservation Biology* 24: 660–668
- Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology* 10: 57–63
- Gittleman JL, Funk SM, Macdonald D, Wayne RK (2001) Carnivore Conservation. Cambridge University Press: Cambridge, UK
- Giulano WM, Litvaitis JA, Stevens CL (1989) Prey selection in relation to sexual dimorphism of fishers (*Martes pennanti*) in New Hampshire. *Journal of Mammalogy* 70: 639–641
- Golightly RT, Penland TF, Zielinski WJ, Higley JM (2006) Fisher diet in the Klamath/North Coast bioregion. Unpublished report, Department of Wildlife, Humboldt State University, Arcata, California
- Graves TA, Waller JS (2006) Understanding the causes of missed global positioning system telemetry fixes. *Journal of Wildlife Management* 70: 844–851
- Grenfell WE, Fasenfest M (1979) Winter food habits of fishers, *Martes pennanti*, in Northwestern California. *California Fish and Game* 65: 186–189
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. *Science* 319: 756–760
- Gurarie E, Andrews RD, Laidre KL (2009) A novel method for identifying behavioural changes in animal movement data. *Ecology Letters* 12: 395–408
- Haas CA (1995) Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* 9: 845–854
- Hagmeier EM (1959) A re-evaluation of the subspecies of fisher. *The Canadian Field-Naturalist*

- Hall ER (1981) *The Mammals of North America*, 2nd edn. John Wiley and Sons, New York
- Hall ER, Kelson KR (1959) *The Mammals of North America*. Ronald Press, New York, USA
- Halle S, Stenseth NC (2002) *Activity patterns in small mammals: an ecological approach*. Springer: Berlin, Germany
- Halsey LG, Green JA, Wilson RP, Frappell PB (2009) Accelerometry to estimate energy expenditure during activity: best practice with data loggers. *Physiological and Biochemical Zoology* 82: 396–404
- Hamilton WJ, Cook AH (1955) The biology and management of the fisher in New York. *New York fisher and Game Journal* 2: 13–35
- Hansen MC, Riggs RA (2008) Accuracy, precision, and observation rates of global positioning system telemetry collars. *Journal of Wildlife Management* 72: 518–526
- Harlow HJ (1994) Trade-offs associated with the size and shape of American martens. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, pp 391–403
- Harveson PM, Lopez RR, Collier BA, Silvy NJ (2007) Impacts of urbanization on Florida Key deer behavior and population dynamics. *Biological Conservation* 134: 321–331
- Heard DC, Ciarniello LM, Seip DR (2008) Grizzly bear behavior and global positioning system collar fix rates. *Journal of Wildlife Management* 72: 596–602
- Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B* 365: 2303–2312
- Hebblewhite M, Percy M, Merrill EH (2007) Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the Central Canadian Rockies. *Journal of Wildlife Management* 71: 2026–2033
- Hemerik L, Hengeveld R, Lippe E (2007) The eclipse of species ranges. *Acta Biotheoretica* 54: 255–266
- Henle K, Lindenmayer DB, Margules CR, Saunders DA, Wissel C (2004) Species survival in fragmented landscapes: where are we now? *Biodiversity and Conservation* 13: 1–8
- Hijmans RJ (2013) raster: Geographic data analysis and modeling. R package version 2.1-49. <http://CRAN.R-project.org/package=raster>

- Hilty JA, Lidicker WZ, Merenlender AM (2006) Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island Press, Washington, DC
- Hobbs RJ (1992) The role of corridors in conservation: solution or bandwagon? *Trends in Ecology and Evolution* 7: 389–392
- Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity, and conservation decision making: back to basics. *Journal of Applied Ecology* 46: 964–969
- Holland RA, Wikelski M, Kümmeth F, Bosque C (2009) The secret life of oilbirds: new insights into the movement ecology of a unique avian frugivore. *PLoS ONE* 4: e8264
- Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian bridges. *Ecology* 88: 2354–2363
- Huck M, Jędrzejewski W, Borowik T, Jędrzejewska B, Nowak S, Mysłajek RW (2011) Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. *Acta Theriologica* 56: 91–101
- Hüner EA, Peter JFB (2012) In situ caching of a large mammal carcass by a fisher, *Martes pennanti*. *Canadian Field-Naturalist* 126: 234–237
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22: 415–427
- International Union for the Conservation of Nature (2012) IUCN Red List of Threatened Species Spatial Data, version 2012.1. Available at: <http://www.iucnredlist.org> (accessed: 1 December 2012).
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71
- Johnson SA (1984) Home range, movements, and habitat use of fishers in Wisconsin. Master's thesis, University of Wisconsin, Stevens Point, Wisconsin, USA
- Johnson WE, Franklin WL (1994) Conservation implications of South American grey fox (*Dusicyon griseus*) socio-ecology in the Patagonia of southern Chile. *Vida Silvestre Neotropical* 3: 16–23
- Jones JL (1991) Habitat use of fishers in Northcentral Idaho. Master's Thesis, University of Idaho, Moscow, Idaho, USA
- Jonsen ID, Flemming JM, Myers RA (2005) Robust state-space modeling of animal movement data. *Ecology* 86: 2874–2880
- Kamil AC, Krebs JR, Pulliam HR (1987) *Foraging Behavior*. Plenum Press: London

- Kay CE (2007) Were native people keystone predators? A continuous-time analysis of wildlife observations made by Lewis and Clark in 1804–1806. *The Canadian Field-Naturalist* 121: 1–16
- Kays RW, Gompper ME, Ray JC (2008) Landscape ecology of eastern coyotes based on large-scale estimates of abundance. *Ecological Applications* 18: 1014–1027
- Kays RW, Slauson KM (2008) Remote cameras. In: Long RA, MacKay P, Zielinski WJ, Ray JC (eds) *Noninvasive methods for surveying carnivores*. Island Press, London, pp 105–134
- Kays RW, Tilak S, Kranstauber B, Jansen PA, Carbone C, Rowcliffe M, Fountain T, Eggert J, He Z (2011) Camera traps as sensor networks for monitoring animal communities. *International Journal of Research and Reviews in Wireless Sensor Networks* 1: 19–29
- Kays RW, Wilson DE (2010) *Mammals of North America*, 2nd edn. Princeton University Press, Princeton, New Jersey, USA
- Kelly GM (1977) Fisher (*Martes pennanti*) biology in the White Mountain National Forest and adjacent areas. PhD thesis, University of Massachusetts, Amherst, Massachusetts, USA
- Kilpatrick HJ, Rego PW (1994) Influence of season, sex, and site availability on fisher (*Martes pennanti*) rest-site selection in the central hardwood forest. *Canadian Journal of Zoology* 72: 1416–1419
- Kranstauber B, Kays R, LaPoint SD, Wikelski M, Safi K (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Applied Ecology* 81: 738–746
- Kranstauber B, Smolla M (2013) Move: visualizing and analyzing animal track data. <http://CRAN.R-project.org/package=move>
- Krebs J, Lofroth E, Copeland J, Banci V, Cooley D, Golden H, Magoun A, Mulders R, Shults B (2004) Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management* 68: 493–502
- Krohn WB, Arthur SM, Paragi TF (1994) Mortality and vulnerability of a heavily trapped fisher population. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, pp 137–145
- Krop-Benesch A, Berger A, Hofer H, Heurich M (2013) Long-term measurement of roe-deer (*Capreolus capreolus*) (Mammalia:Cervidae) activity using two-axis accelerometers in GPS-collars. *Italian Journal of Zoology* 80: 1–13
- Kuehn DW (1989) Winter foods of fishers during a snowshoe hare decline. *Journal of Wildlife*

- Laliberte AS, Ripple WJ (2004) Range contractions of North American carnivores and ungulates. *BioScience* 54: 123–138
- LaPoint S, Gallery P, Wikelski M, Kays R (2013) Animal behavior, cost-based corridor models, and real corridors. *Landscape Ecology*, DOI 10.1007/s10980-013-9910-0
- LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. *Ecological Modelling* 212: 372–381
- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79: 1401–1409
- Laurance WF (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* 5: 79–89
- Legendre P (2005) Species associations: the Kendall coefficient of concordance revisited. *Journal of Agricultural, Biological, and Environmental Statistics* 10: 226–245
- Leonard RD (1980) Winter activity and movements, winter diet and breeding biology of fisher in Southeast Manitoba. Master’s thesis, University of Manitoba, Winnipeg, Manitoba, Canada
- Lewis JC, Powell RA, Zielinski WJ (2012) Carnivore translocations and conservation: insights from population models and field data for fishers (*Martes pennanti*). *PLoS ONE* 7: e32726
- Li H, Li D, Li T, Qiao Q, Yang J, Zhang H (2010) Application of least-cost path model to identify a giant panda dispersal corridor network after the Wenchuan earthquake – Case study of Wolong Nature Reserve in China. *Ecological Modelling* 221: 944–952
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11: 131–135
- Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC (2009) Lower extinction risk in sleep-or-hide mammals. *The American Naturalist* 173: 264–272
- Lofroth EC, Raley CM, Higley JM, Truex RL, Yaeger JS, Lewis JC, Happe PJ, Finley LL, Naney RH, Hale LJ, Krause AL, Livingston SA, Myers AM, Brown RN (2010) Conservation of fishers (*Martes pennanti*) in South-Central British Columbia, Western Washington, Western Oregon, and California: Volume I: Conservation Assessment. USDI Bureau of Land Management, Denver, Colorado

- Logan KA, Sweanor LL (2001) Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press: Washington, DC.
- Longcore T, Rich C (2004) Ecological light pollution. *Frontiers in Ecology and the Environment* 2: 191–198
- Martin SK (1994) Feeding ecology of American martens and fishers. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, pp 297–315
- Mattisson J, Andren H, Persson J, Segerstrom P (2010) Effects of species behavior on global positioning system collar fix rates. *Journal of Wildlife Management* 74: 557–563
- McClennen N, Wigglesworth RR, Anderson SH, Wachob DG (2001) The effects of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). *American Midland Naturalist* 146: 27–36
- McKinney ML (2002) Urbanization, biodiversity, and conservation. *Bioscience* 52: 883–890
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450–454
- McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89: 2712–2724
- Mech SG, Hallett JG (2001) Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology* 15: 467–474
- Meiri S, Dayan T, Simberloff D (2005) Variability and correlations in carnivore crania and dentition. *Functional Ecology* 19: 337–343
- Meiri S, Dayan T, Simberloff D, Grenyer R (2009) Life on the edge: carnivore body size is all over the place. *Proceedings of the Royal Society B* 276: 1469–1476
- Millsbaugh JJ, Nielson RM, McDonald L, Marzluff JM, Gitzen RA, Rittenhouse CD, Hubbard MW, Sheriff SL (2006) Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70: 384–395
- Moen R, Pastor J, Cohen Y (2001) Effects of animal activity on GPS telemetry location attempts. *Alces* 37: 207–216
- Moen R, Pastor J, Cohen Y, Schwartz CC (1996) Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management* 60: 659–668
- Montgomery GG, Lubin YD (1977) Prey influences on movements of neotropical anteaters. In:

- Philips RL, Jonkel CJ (eds) Proceedings of the 1975 Predator Symposium, Montana Forest and Conservation Experiment Station. University of Montana, Missoula, pp 103–131
- Morales JM, Haydon DT, Frair J, Holsinger KE, Fryxell JM (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85: 2436–2445
- Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B* 365: 2289–2301
- Moreau M, Siebert S, Buerkert A, Schlecht E (2009) Use of a tri-axial accelerometer for automated recording and classification of goats' grazing behaviour. *Applied Animal Behaviour Science* 119: 158–170
- Moreno RS, Kays RW, Samudio R (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy* 87: 808–816
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Science USA* 105: 19052–19059
- Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM (2012) Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology* 215: 986–996
- New York State Department of Transportation (2012) Downloadable traffic volume data. Available for download at: <https://www.dot.ny.gov/divisions/engineering/technical-services/highway-data-services/hdsb>
- New York State Office of Cyber Security (2006) New York State Streets. Available for download at: <http://gis.ny.gov/gisdata/inventories/details.cfm?DSID=932>
- Nielsen SE, Boyce MS, Stenhouse GB, Munro RHM (2002) Modelling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: taking autocorrelation seriously. *Ursus* 13: 45–56
- Noss RF, Quigley HB, Hornocker MG, Merrill T, Paquet PC (1996) Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10: 949–963
- Novaro AJ (1997) *Pseudalopex culpaeus*. *Mammalian Species* 558: 1–8
- Nowak RM, Paradiso JL (1983) Walker's mammals of the world, 4th edition. The John Hopkins University Press: Baltimore, Maryland, USA

- Núñez R (1999) Hábitos alimentarios del jaguar (*Panthera onca*, Linnaeus 1758) y del puma (*Puma concolor*, Linnaeus 1771) en la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, México. Tesis de Licenciatura, Universidad Michoacana de San Nicolás de Hidalgo, Morelia
- Palacios V, Mech LD (2011) Problems with studying wolf predation on small prey in summer via global positioning system collars. *European Journal of Wildlife Research* 57: 149–156
- Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. *American Naturalist* 153: 492–508
- Pebesma EJ, Bivand RS (2005) Classes and methods for spatial data in R. *R News*, 5, 9–13. <http://cran.r-project.org/doc/Rnews/>
- Pimm SL, Askins RA (1995) Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Science* 92: 9343–9347
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20: 297–330
- Poor EE, Loucks C, Jakes A, Urban DL (2012) Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. *PLoS ONE* 7:e49390
- Powell RA (1977) Hunting behavior, ecological energetics and predator-prey community stability of the fisher (*Martes pennanti*). PhD thesis, University of Chicago, Chicago, USA
- Powell RA (1979) Ecological energetics and foraging strategies of the fisher (*Martes pennanti*). *Journal of Animal Ecology* 48: 195–212
- Powell RA (1993) The fisher: life history, ecology, and behavior. University Minnesota Press: Minneapolis, Minnesota, USA
- Powell RA (1994) Effects of scale on habitat selection and foraging behavior of fishers in winter. *Journal of Mammalogy* 75: 349–356
- Prange S, Gehrt SD, Wiggers EP (2004) Influence of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *Journal of Mammalogy* 85: 483–490
- Price SA, Gittleman JL (2007) Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. *Proceedings of the Royal Society London B* 274: 1845–1851
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. *BioScience* 59: 779–791

- Purvis A, Gittleman JL, Cowlshaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society London B* 267: 1947–1952
- R Development Core Team (2013) R: a language and environment for statistical computing, version 3.0.1. R Foundation for Statistical Computing, Vienna, Austria
- Raine RM (1987) Winter food habits and foraging behavior of fishers (*Martes pennanti*) and martens (*Martes Americana*) in Southeastern Manitoba. *Canadian Journal of Zoology* 65: 745–747
- Rayfield B, Fortin M-J, Fall A (2010) The sensitivity of least-cost habitat graphs to relative cost surface values. *Landscape Ecology* 25: 519–532
- Recio MR, Mathieu R, Maloney R, Seddon PJ (2010) First results of feral cats (*Felis catus*) monitored with GPS collars in New Zealand. *New Zealand Journal of Ecology* 34: 288–296
- Rensselaer County Bureau of Research and Information Services (2009) Rensselaer County Municipal Boundaries. Troy, New York, USA
- Ripple WJ, Wirsing AJ, Wilmsers CC, Letnic M (2013) Widespread mesopredator effects after wolf extirpation. *Biological Conservation* 160: 70–79
- Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12: 982–998
- Rosenberg DK, Noon BR, Meslow EC (1997) Biological corridors: form, function, and efficacy. *BioScience* 47: 677–687
- Roy KD (1991) Ecology of reintroduced fishers in the Cabinet Mountains of Northwest Montana. Masters thesis, University of Montana, Missoula, Montana, USA
- Rudnick DA, Ryan SJ, Beier P, Cushman SA, Dieffenbach F, Epps CW, Gerber LR, Hartter J, Jenness JS, Kintsch J, Merenlender AM, Perkl RM, Preziosi DV, Trombulak SC (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Issues in Ecology* 16: 1–20
- Rumiz DI, Venegas C (2006) Exploración de datos de radio-collares gps en pecaríes de labio blanco:¿qué podemos aprender de una muestra de n=4? *Suidform Sounding* 6: 38–44
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18–32
- Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do

- least-cost models reflect how animals use landscapes? *Journal of Applied Ecology* 48: 668–678
- Schnute JT, Boers N, Haigh R, Grandin C, Johnson G, Wessel P, Antonio F (2013) Mapping fisheries data and spatial analysis tools. R package version 2.66.53. <http://CRAN.R-project.org/package=PBSmapping>
- Schwartz MK, Copeland JP, Anderson NJ, Squires JR, Inman RM, McKelvey KS, Pilgrim KL, Waitts LP, Cushman SA (2009) Wolverine gene flow across a narrow climatic niche. *Ecology* 90: 3222–3232
- Shepard ELC, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C, Macdonald DW (2010) Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* 10: 47–60
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution* 21: 186–191
- Simberloff D, Dayan T, Jones C, Ogura G (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology* 81: 2086–2099
- Simberloff D, Farr JA, Cox J, Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6: 493–504
- Simpson GG (1940) Mammals and land bridges. *Journal of the Washington Academy of Sciences* 30: 137–163
- Smouse PE, Focardi S, Moorcroft PR, Kie JG, Forester JD, Morales JM (2010) Stochastic modeling of animal movement. *Philosophical Transactions of the Royal Society B* 365: 2201–2211
- Spear SF, Balkenhol N, Fortin M-J, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape generic studies: considerations for parameterization and analysis. *Molecular Ecology* 19: 3576–3591
- Stevens CL (1968) The food of fisher in New Hampshire. Unpublished report, New Hampshire Department of Fish and Game, Concord, New Hampshire, USA
- Stone WB, Okoniewski JC, Stedelin JR (1999) Poisoning of wildlife with anticoagulant rodenticides in New York. *Journal of Wildlife Diseases* 35: 187–193
- Swanepoel LH, Dalerum F, van Haven W (2010) Factors affecting location failure of GPS collars fitted to African leopards (*Panthera pardus*). *South African Journal of Wildlife Research* 40: 10–15

- Thompson DC (1977) Diurnal and seasonal activity of the grey squirrel (*Sciurus carolinensis*)
Canadian Journal of Zoology 55: 1185–1189
- Tobler MW (2009) New GPS technology improves fix success for large mammal collars in
dense tropical forests. Journal of Tropical Ecology 25: 217–221
- Turner IM (1996) Species loss in fragments of tropical rain forest: a review of the evidence.
Journal of Applied Ecology 33: 200–209
- United States Census (2008) American Fact Finder. Accessed March 2012
- United States Environmental Protection Agency (2010) Ecological Regions of North America,
Level 1. U.S. Environmental Protection Agency Office of Research and Development -
National Health and Environmental Effects Research Laboratory, Corvallis, Oregon, USA
- United States Geological Survey (2001) New York Land Cover Data Set. US Geological Survey,
Sioux Falls, South Dakota, USA
- van der Merwe I, Oosthuizen MK, Chimimba CT, Bennett NC (2011) Circadian rhythms of
locomotor activity in the reddish-grey musk shrew (Eulipotyphla: Soricidae) from South
Africa. Journal of Zoology 282: 124–132
- van Dijk J, Hauge K, Landa A, Anderson R, May R (2007) Evaluating scat analysis methods to
assess wolverine *Gulo gulo* diet. Wildlife Biology 13: 62–67
- Vashon J, Vashon A, Crowley S (2003) Partnership for lynx conservation in Maine: December
2001 – December 2002 unpublished field report. Maine Department of Inland Fisheries
and Wildlife
- Walpole AA, Bowman J, Murray DL, Wilson PJ (2012) Functional connectivity of lynx at their
southern range periphery in Ontario, Canada. Landscape Ecology 27: 761–773
- Weir RD, Corbould FB (2007) Ecology of fishers in the sub-boreal forests of North-central
British Columbia, final report. Unpublished report, Peace/Williston Fish and Wildlife
Compensation Program, Report No. 315, Prince George, British Columbia
- Weir RD, Harestad AS, Wright RC (2005) Winter diet of fishers in British Columbia.
Northwestern Naturalist 86: 12–19
- Wikelski M, Kays RW, Kasdin NJ, Thorup K, Smith JA, Swenson GW (2007) Going wild: what
a global small-animal tracking system could do for experimental biologists. Journal of
Experimental Biology 210: 181–186
- Wikelski M, Kays R (2012) Movebank: archive, analysis and sharing of animal movement data.
World Wide Web electronic publication. <http://www.movebank.org>

- Wilcox B A, Murphy DD (1985) Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125: 879–887
- Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* 4: 123–137
- Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* 75: 1081–1090
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168
- Yañez JL, Cardenas JC, Gezelle P, Jaksic FM (1986) Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked ranges. *Journal of Mammalogy* 67: 604–606
- Zar J (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, New Jersey
- Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. *Landscape Ecology* 27: 777–797
- Zielinski WJ, Duncan NP, Farmer EC, Truex RL, Clevenger AP, Barrett RH (1999) Diet of fishers (*Martes pennanti*) at the southernmost extent of their range. *Journal of Mammalogy* 80: 961–971
- Zielinski WJ, Spencer WD, Barrett RH (1983) Relationship between food habits and activity patterns of pine martens. *Journal of Mammalogy* 64: 387–396

Acknowledgements

I would like to thank my wife Kathy and my son Max. Her unwavering, unselfish support has been the rudder to this fisher-man's ship. Maximilian, my captain, has taught me to recognize importance. I owe them more than my love. Thanks to my parents for enduring my (at times dangerous) adventures, and for taking their first grandchild across the Atlantic: sorry...

Roland Kays deserves special thanks. For over a decade, his machete has cleared my path away from a career in resource economics toward conservation biology. He has allowed me to pursue the questions that I have most wanted to answer. I have learned much from him and expect to learn more.

I also thank Martin Wikelski for providing me with the opportunity to work with the Max-Planck-Institute. Kamran Safi and Dina Dechmann welcomed me into their groups and adopted me as one of their own. My interactions within their groups have made me a better scientist, especially: Davide, Adam, Bart, Catarina, Nawang, David, and Mariëlle. Roger Powell and Jerry Belant both provided input into my hypotheses and manuscripts. In New York, several people helped along the way, especially: Joe Bopp, Neil Gifford, and Elizabeth Wagner.

Funding from the National Science Foundation (#0756920), National Geographic Waitt Society Grant Program (#W157-11), and the Max Planck Gesellschaft facilitated this research. The New York State Museum provided logistical support for the field work portion of this dissertation. Jennifer, Elke, Maggi, and Daniel provided logistical support during my time in Germany. Thanks to the team at e-obs GmbH for building our telemetry tools and for being so willing and creative in their tag designs. Finally, thanks to the NYS Police Aviation Department for some exciting times in the air.

Lastly, thanks to the fishers. Although my time with them was often short and we never shared a spoken word, they challenged me, encouraged me to break the law, and reminded me the importance of persistence. It's been a pleasure telling their story.

Except for stipulations listed below, all ideas and data presented within this dissertation are my own, developed and collected under the supervision of Roland Kays.

Chapter 2: Mesopredator release of fishers

- I conceived the idea, performed all analyses, and wrote initial drafts of the manuscript. Condylbasal length data were measured by museum staff (as listed in the Acknowledgements section of this chapter) and Roland Kays. Roland Kays and Jerry Belant provided input on the ideas and contributed to re-writes.

Chapter 3: Accelerometer-informed GPS technology

- Roland Kays and I discussed the idea for the technology that was then developed and implemented by Franz Kümmeß and Wolfgang Heidrich. Danielle Brown and I conducted the field work, performed the analyses, and wrote the manuscript in equal efforts. Roland Kays assisted with re-writes.

Chapter 4: Fisher activity patterns within a developed landscape

- I conceived the idea, deployed the tracking collars, performed all analyses, and wrote this chapter. I discussed analyses with Davide Dominoni, Roland Kays, Bart Kranstauber, and David Santos.

Chapter 5: Animal behavior, cost-based corridor models, and real corridors

- I conceived the idea, captured and handled the study animals, deployed the tags, conducted all analyses, and wrote the initial draft of the manuscript. Paul Gallery led the camera trap deployments under the supervision of Roland Kays and myself. Bart Kranstauber, Marco Smolla, and Kamran Safi helped develop the corridor model into a function within the ‘move’ package for program R.

SCOTT D. LaPOINT

Max-Planck-Institute for Ornithology
Am Obstberg 1, 78315 Radolfzell, Germany
website: <https://sites.google.com/site/scottlapointconservation/>

Phone: 049-7732-150126
E-mail: sdlapoint@gmail.com

EDUCATION:

Dr.rer.nat in Biology, University of Konstanz (2013, Roland Kays & Martin Wikelski)
M.Sc. in Conservation Biology, State University of New York, Syracuse (2007, Mark Lomolino)
B.A. in Natural Resource Policy and Management, Paul Smith's College (2001, Justina Ray)

RESEARCH STATEMENT:

My research is focused on **carnivore movement ecology** with a strong emphasis on applied conservation. I work on questions regarding **landscape connectivity, corridors, and movement barriers** and answer these questions through empirical and modeling approaches. I have and will continue to use field-derived data collected via **biotelemetry** technology in order to tell a story from the animals point of view. I use these data to build **spatial models** of animal movements allowing me to identify areas of conservation importance. My methods emphasize the importance of **animal behavior** information within spatial models and **conservation biology**. My goal is to develop and validate a conservation orientated paradigm that builds upon individual animal-based information to meet conservation objectives.

CURRENT RESEARCH:

- **Conservation in Bhutan:** Working with the Ugyen Wangchuck Institute for Conservation and Environment of Bhutan on corridor, connectivity, and movement ecology themed projects on snow leopard, takin, and three species of otter.
- **Behavioral segmentation of movement tracks:** With Frederic Bartumeus (Centre d'Estudis Avancats de Blanes, Barcelona), I am using high temporal resolution spatial data to identify "behavior types" in free ranging fishers and to quantify behavior-specific resource selection.
- **Response of stone marten to highways:** Working with the Universidade de Aveiro to explore variable responses of individual stone marten to the presence of highways in Portugal.
- **Activity and behavior of urban fisher:** Using the data (GPS and accelerometer) collected during my dissertation to quantify the impact of automobile traffic on the circadian activity patterns of fishers, and to identify behaviorally-based habitat selection, using energy expenditure (overall dynamic body acceleration) as an indicator for suitability.

- **Identifying the matrix:** Collaborating with the Max-Planck-Institute for Ornithology and the University of Konstanz to develop an “animals perspective” method for identifying unsuitable habitat and corridors.
- **Data sharing:** I currently share the location and acceleration data of my study animals with collaborators at the Max-Planck-Institute of Ornithology, the University of Sheffield, the University of Konstanz, the Centre d'Estudis Avancats de Blanes, and the University of Illinois at Urbana-Champaign.

SKILLS:

- **Field:** live-trapping and handling of several carnivore species and small mammals, telemetry and tag/collar deployment, camera-trap study designs, track plates/boxes, snow tracking, vegetation sampling, etc.
- **Office:** Windows (chiefly), Linux, and Mac platforms, ArcGIS, program R (spatial analyses), past experience with numerous statistical programs (Minitab, Statistica, SPSS, Systat, XLstat, etc.), Windows Office, and Open Office.

GRANTS AND AWARDS RECEIVED:

- Student Travel Grant Award (2013) to attend the Wild Musteloid Conference at Oxford University, England. Amount: registration fee waiver.
- National Geographic Society Waitt Grants #W157-11 (2011) for “Animal-defined corridors: using animal movement and behavior to determine corridors.” Amount: \$9900US.
- Edna Baily Sussman Foundation (2004) for “Investigating mammalian road crossing patterns and under-road passageway use along a major highway.” Amount: \$4000US.

BOOK CHAPTERS:

Powell R.A., Gabriel M.W., Higley J.M., **LaPoint S.D.**, McCann N.P., Spencer W., Thompson C.M. (in prep.) The fisher as a model organism: the *Drosophila* for the study of wild carnivores? In: *Biology and Conservation of Wild Musteloids*. Ed: D. MacDonald.

Ascensão F., **LaPoint S.D.**, van der Ree R. (in prep.) Small mammals. In: *Ecology of Roads: A Practitioners Guide to Impacts and Mitigation*. Ed.: R. van der Ree, C. Grilo, and D. Smith.

PEER REVIEWED MANUSCRIPTS:

LaPoint S.D., Belant J.L., Kays R. (submitted) Mesopredator release explains differences in fisher (*Martes pennanti*) population range expansion. *Animal Conservation*.

Ascensão F., Grilo C., **LaPoint S.D.**, Tracey J., Clevenger A., Santos-Reis M. (in review) Road effects on marten space use and movement: combining radio-tracking data with agent-based simulation models. *Landscape and Urban Planning*.

LaPoint S.D., Gallery P., Wikelski M., Kays R. (2013) Animal behavior, cost-based corridors, and real corridors. *Landscape Ecology*. doi: 10.1007/s10980-013-9910-0

Kranstauber B., Kays R., **LaPoint S.D.**, Wikelski M., Safi K. (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Applied Ecology* 81, 738–746.

Brown D.D., **LaPoint S.D.**, Kays R.W., Heidrich W., Kummeth F., Wikelski M. (2012) Accelerometer-informed GPS telemetry: reducing the tradeoff between resolution and longevity. *Wildlife Society Bulletin* 36, 139–146.

LaPoint S.D. (2007) Mammalian road crossing patterns along a major highway within Adirondack Park of New York State, USA. Thesis. State University of New York, College of ENvironmental Science and Forestry, Syracuse, NY.

Gompper M.E., Kays R.W., Ray J.C., **LaPoint S.D.**, Bogan D.A., Cryan J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildlife Society Bulletin* 34, 1142–1151.

LaPoint S.D., Kays R.W., Ray J.C. (2003) Animals crossing the Northway: are existing culverts useful? *Adirondack Journal of Environmental Studies* Spring/Summer, 11-17.

PUBLIC OUTREACH:

- Wilson, J. (2013) “New ideas for improving corridor models”, Article, www.conservationcorridor.org, 31 July.
- Johnson, J. (2012) “Dynamic GPS Fine-Tunes Tracking”, Article, *The Wildlife Professional*, Winter.
- Zapletal, M. (2012) “Fisher-Man”, Article, www.practiceconservation.com, 16 July.
- Kays, R. (2011) “Albany’s urban weasels”, Article series, *New York Times Scientist at Work* series, January – May.
- LaPoint, S.D. (2011) “Ecology and behavior of urban fishers”, Talk, Saratoga County Fur Trappers association.
- LaPoint, S.D. (2011) “The fisher: our old neighbor is back”, Talk, Save the Pine Bush.
- LaPoint, S.D. (2011) “Our old neighbor the fisher is back”, Talk, Thatcher Park Nature Center.
- Gallery, P. (2010) “Fishing”, Article, www.thinkinglikeamountain.wordpress.com, 19 February.
- Foss, S. (2009) “State Museum researchers on trail of urbanized fishers: GPS system tracks animals in Pine Bush”, Article, *The Daily Gazette*, 9 March.
- All Over Albany (2009) “Your new neighbor, the fisher”, Article, www.alloveralbany.com, 13 February.

TEACHING EXPERIENCE:

- Guest lecture for the Vertiefungskurs of the University of Konstanz, Spring 2013.
- Field advisor for two undergraduate senior honors theses.
- Teaching assistant for 4 different courses for 3 years during my thesis.

RECENT (post-2010) CONFERENCE PRESENTATIONS:

LaPoint, S.D., Wikelski M., Kays, R. Re-wilding suburbia: ecology and behavior of fisher in a semi-urban landscape. Poster presented at the Wild Musteloid Conference, Oxford, England, March 2013.

LaPoint S.D., Wikelski M., Kays R. What can the animals tell us about landscape connectivity? Using animal movement data to identify corridors. Invited talk at the Ugyen Wangchuck Institute for Conservation and Environment, Bumthang, Bhutan, August 2012.

LaPoint S.D., Gallery P., Wikelski M., Kays R. Animal-defined corridors: using animal movement data to identify functional wildlife corridors. Poster presented at the Biodiversity Asia 2nd Asia Regional Conference of the Society for Conservation Biology, Bangalore, India, August 2012. Awarded "**Best Poster Presentation**".

LaPoint S.D., Kays R.W., Wikelski M., Powell R.A. Movement patterns and corridor use of fisher (*Martes pennanti*) within a developed landscape. Talk presented at the 85th Annual Conference of the German Society of Mammalogy, Luxembourg City, Luxembourg, September 2011.

LaPoint S.D., Kays R.W., Wikelski M., Powell R.A. Fisher (*Martes pennanti*) movement patterns and corridor use across an urban gradient. Talk presented at the VIth European Congress of Mammalogy, Paris, France, July 2011.

LaPoint S.D. & Kays R.W. Behavior and ecology of fisher (*Martes pennanti*) inhabiting an urban ecosystem. Talk presented at the American Society of Mammalogists meeting, Portland, Oregon, June 2011.

LaPoint S.D. & Kays R.W. Ecological and behavioral adaptations for survival in urban fisher (*Martes pennanti*). Talk presented at the Urban Wildlife Management and Planning Conference, Austin, Texas, May 2011.

LaPoint S.D. The fisher: our old neighbor is back! Invited talk for the Catskill Institute for the Environment, Sullivan, New York, April 2011.

Kays R.W., Chase J., Licht L., **LaPoint S.D.** Camera trap surveys comparing the diversity and abundance of wildlife in suburban and wild forests. Talk presented at the Northeast Natural History Conference, Albany, New York, April 2011.

LaPoint S.D. & Kays R.W. Ecological and behavioral adaptations in urban fisher (*Martes pennanti*). Talk presented at the Northeast Natural History Conference, Albany, New York, April 2011.

PROFESSIONAL MEMBERSHIPS:

- American Society of Mammalogists
- Society for Conservation Biology
- The Wildlife Society

REFERENCES:

Roland Kays (Academic advisor)
Director, Biodiversity and Earth Observation Lab,
North Carolina Museum of Natural Sciences,
11 West Jones St., Raleigh, North Carolina, 27601 USA
roland.kays@naturalsciences.org

Martin Wikelski (PhD advisor)
Director, Max-Planck-Institute for Ornithology
Am Obstberg 1, 78315 Radolzell, Germany
martin@orn.mpg.de

Mark Lomolino (M.Sc. advisor)
Professor, State University of New York College of Environmental Science and Forestry
1 Forestry Drive, Syracuse, New York, 13210 USA
island@esf.edu

PERSONAL:

Birth: 18 January 1980 in Argyle, New York, USA
Married with 1 son.

Publications produced during this dissertation

Manuscripts:

Brown D.D., **LaPoint S.D.**, Kays R.W., Heidrich W., Kümmeth F., Wikelski M. (2012) Accelerometer-informed GPS telemetry: reducing the tradeoff between resolution and longevity. *Wildlife Society Bulletin* 36, 139–146.

Kranstauber B., Kays R., **LaPoint S.D.**, Wikelski M., Safi K. (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Applied Ecology* 81, 738–746.

LaPoint S.D., Gallery P., Wikelski M., Kays R. (2013) Animal behavior, cost-based corridors, and real corridors. *Landscape Ecology*. doi: 10.1007/s10980-013-9910-0

Ascensão F., Grilo C., **LaPoint S.D.**, Tracey J., Clevenger A., Santos-Reis M. (in review) Road effects on marten space use and movement: combining radio-tracking data with agent-based simulation models. *Landscape and Urban Planning*.

LaPoint S.D., Belant J.L., Kays R. (submitted) Mesopredator release explains differences in fisher (*Pekania pennanti*) population range expansion. *Animal Conservation*.

Works in preparation:

LaPoint S.D., Kays R. Behavioral avoidance of traffic volume by fishers (*Martes pennant*) within a semi-urban landscape.

Powell R.A., Gabriel M.W., Higley J.M., **LaPoint S.D.**, McCann N.P., Spencer W., Thompson C.M. The fisher as a model organism: the *Drosophila* for the study of wild carnivores? In: *Biology and Conservation of Wild Musteloids*. Ed: D. MacDonald.

Ascensão F., **LaPoint S.D.**, van der Ree R. Small mammals. In: *Ecology of Roads: A Practitioners Guide to Impacts and Mitigation*. Ed.: R. van der Ree, C. Grilo, and D. Smith.

Declaration

Hereby I declare in lieu of oath:

I produced the submitted thesis without illegitimate help of others and without use of sources other than mentioned. Data and concepts that were directly or indirectly taken from sources are correctly cited. Further individuals, particularly ghost-writer, did not participate in the production of this thesis. This thesis or a similar version was not submitted to any other examination authority worldwide.

Sincerely,

Scott Daniel LaPoint

Date