COPING WITH CHANGE AND CHANGING TO COPE: ESTIMATING THE EFFECTS OF ANTHROPOGENIC LAND USE CHANGE FROM ANIMAL MOVEMENT

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Summary

In many regions of the world, wildlife is threatened by anthropogenic habitat loss through degradation, fragmentation and land use change. If they are to survive, individuals have to cope with this challenge by adapting their behavior and how they use the changing environment. To facilitate the survival of species in this struggle, it is of pivotal importance to understand how individuals use suboptimal conditions, and connect habitats in fragmented landscapes. The long-term observation of animals with high spatial and temporal accuracy has become possible through the advances in remote animal tracking. Data collected with modern tracking devices allow us to infer movement, energy expenditure, and habitat use, enabling us to describe behavior in an integrative way and help us to get a better understanding of how animals interact with their environment. In this thesis, I wanted to investigate how land use change affects the movement behavior of several carnivore species and how these changes in the landscape can be redeemed most effectively by identifying key restoration areas.

First, I wanted to assess how animals spend their energy across space and time as this can reveal how animals interact with the environment, and give insight into how changes in the environment affects their energy budgets. I investigated the effects of anthropogenic land use change on how and where animals spend their energy by constructing energetic landscapes of fishers (*Pekania pennanti*) within their home ranges. I derived a proxy for individual energy expenditure from accelerometers, and coupled the estimates to the individuals' movements. My results show that fishers have

a highly structured energy landscape which can only be partially explained by correlates of the environment and space use, revealing an unexpected complexity in space use of animals. However, I show that energy expenditure derived from acceleration data lacks a clear behavioral correspondence, which could mask different behaviors with similar signatures. Overcoming these limitations would improve the interpretation of energy expenditure in relation to the environment.

Second, I wanted to investigate the use of corridors, another possible strategy of coping with altered landscapes. The existence of wildlife corridors influences the connectivity of a landscape, thereby increasing the ability of individuals to cope with fragmented habitat. But despite their importance for facilitating animal movement between habitat fragments, they are notoriously difficult to identify. Common approaches use measures of habitat suitability, rather than estimating corridors directly from movement data. I tested whether such habitat suitability measures relate to wildlife corridors by identifying corridors of four large carnivore species using only movement characteristics. While most of the tracked individuals showed corridor behavior, I could not find a direct link between corridors and habitat suitability, or defining environmental characteristics. These results lead me to speculate that studies that identify corridors using a cost-based model derived from habitat suitability may place corridors in the wrong places, at least at an individual based level.

Last, I wanted to investigate how to efficiently restore the quality of the environment. Once a pristine habitat is degraded, the restoration into its original state is a resource intensive and lengthy process. This makes it crucial to find efficient procedures providing the best trade-off between area and resources invested, and the increase of suitable habitat for a species. Since the degradation of a landscape usually affects many species at the same time, it is also necessary to focus restoration initiatives on more than a single species, a fact that is still often neglected. By focusing on the shared areas of the unsuitable habitat of four large carnivore species, I developed a prioritization process that identifies key areas for which restoration would affect multiple species simultaneously. I contrasted the results from this process with a classic single species approach. My results showed that the multi-species approach increased the area of suitable habitat for all species despite differing habitat preferences. In contrast to this, the single-species approach identified areas for restoration that benefited only the focal species. While my approach in this study is theoretical and does not account for the feasibility of restoration, it could be used as a starting point to select the areas that would provide most benefit if restored. An additional feasibility analysis taking into account political and social aspects could then highlight where restoration might have a significant impact, and should thus be prioritized.

In conclusion, throughout this thesis I attempted to provide insight into the complex relationships between animals and their environment. This will help to interpret the behavior of wild-ranging animals as sensors of nature to better understand the changing rhythms of the planet.

Zusammenfassung

In vielen Regionen der Welt bedrohen anthropogene Umweltveränderungen wildlebende Tiere, indem sie den Lebensraum zerstören. Beispielsweise durch Fragmentierung und Landnutzung. Um zu überleben, müssen einzelne Tiere diese Herausforderung meistern, indem sie ihr Verhalten und den Nutzen der sich verändernden Umwelt entsprechend anpassen.

Um Arten unter solchen Umständen das Überleben zu erleichtern, ist es von entscheidender Bedeutung, dass man versteht wie Individuen subopitmale Bedingungen nutzen und wie sie ihre Habitate in zersplitterten Landschaften verbinden. Die Langzeitbeobachtung von Tieren mit einer hohen räumlichen und zeitlichen Präzision wurde durch Fortschritte in der Fernortung von Tieren möglich. Daten, die mit modernen Ortungsgeräten gesammelt wurden, erlauben uns Bewegungen, Energieverbrauch und Habitatnutzung der Tiere zu erschließen. Das ermöglicht uns, das Verhalten integrativ zu beschreiben und hilft dabei besser zu verstehen, wie Tiere mit ihrer Umwelt interagieren. In dieser Dissertation untersuchte ich, wie Landnutzungsveränderungen das Bewegungsverhalten von mehreren Raubtierarten beeinflusst und wie diese Veränderungen in der Landschaft am effektivsten wieder ausgeglichen werden können, indem die Hauptrenaturierungsgebiete identifiziert werden.

Als Erstes wollte ich feststellen, wie Tiere ihre Energie in Raum und Zeit verbrauchen, da dadurch aufgedeckt werden kann, wie die Tiere mit der Umwelt interagieren und man Einblicke bekommt, wie Veränderungen in der Umwelt ihren Energiehaushalt beeinflussen. Ich untersuchte die Einflüsse der anthropogenen Landnutzungsveränderungen auf den Energieverbrauch von Tieren, genauer gesagt wie und in welchem Bereich die Tiere ihre Energie verbrauchen, indem ich energetische Landschaftsbilder von Fischermardern (*Pekania pennanti*) in ihrem Lebensraum konstruierte. Von Beschleunigungsmessern leitete ich eine Näherung für den individuellen Energieverbrauch ab und bezog diese Schätzungen auf die individuellen Bewegungen. Meine Ergebnisse zeigen, dass Fischermarder ein hochstrukturiertes energetisches Landschaftsbild haben, das nur teilweise durch Zusammenhänge mit der Umwelt und der räumlichen Lebensraumnutzung erklärt werden kann. Dies deckt eine unerwartete Komplexität in der räumlichen Lebensraumnutzung von Tieren auf. Jedoch zeige ich hiermit, dass der Energieverbrauch, der durch Beschleunigungsdaten abgeleitet wird, noch klare Defizite aufweist, wenn es darum geht das Verhalten der Tiere mit einzubeziehen. Hierbei könnten also verschiedene Verhaltensweisen gleich charakterisiert werden. Das Überwinden dieser Einschränkungen würde das Interpretieren vom Energieverbrauch in Relation zur Umwelt verbessern.

Als Zweites wollte ich die Nutzung von Korridoren untersuchen. Korridore stellen eine andere mögliche Strategie dar, wenn es darum geht als Tier mit Veränderungen in der Umwelt zurechtzukommen. Die Existenz von Wildtierkorridoren beeinflusst die Konnektivität einer Landschaft, wodurch es Individuen erleichtert wird mit fragmentierten Habitaten zurechtzukommen. Aber trotz, dass sie bei Tierbewegungen zwischen einzelnen Habitatgebieten eine wichtige Rolle spielen, sind Korridore bekanntlich schwer zu identifizieren. Gängige Ansätze nutzen eher Messungen von Habitattauglichkeit, als dass sie Korridore direkt von den Bewegungsdaten errechnen.

Ich untersuchte, ob solche Habitattauglichkeitsmessungen zu Wildtierkorridoren zugeordnet werden können, indem ich die Korridore von vier Raubtierarten nur durch die Nutzung von Bewegungseigenschaften identifizierte. Während die meisten georteten Individuen Korridorverhalten zeigten, konnte ich weder eine direkte Verbindung zwischen Korridoren und Habitattauglichkeit finden, noch Umwelteigentschaften charakterisieren. Diese Ergebnisse ließen mich annehmen, dass Studien, die Korridore identifizieren indem sie kostenbezogenen Modelle nutzen, die auf Habitattauglichkeit abgeleitet werden, zumindest auf Individuen-basierter Ebene die Korridore an falsche Stellen setzen.

Als Letztes wollte ich untersuchen, wie man die Qualität der Umwelt effizient wiederherstellen kann. Sobald ein naturbelassenes Habitat zerstört wurde, kostet die Wiederherstellung in seinen ursprünglichen Zustand viele Ressourcen und ist ein langwieriger Prozess. Daher ist das Finden von effizienten Vorgehensweisen, die das beste Mittelmaß zwischen genutzten Flächen und eingesetzten Ressourcen und dem Erhöhen der Habitatstauglichkeit für eine Art finden, von besonderer Wichtigkeit. Da die Zerstörung einer Landschaft normalerweise viele Arten auf einmal beeinflusst, ist es zu dem nötig, dass man Wiederherstellungsmaßnahmen von mehr als einer Art mit einbezieht. Dies wird immer noch häufig vernachlässigt. Indem ich mich auf die gemeinsam genutzten ungeeigneten Gebiete von vier Raubtierarten konzentrierte, habe ich einen Priorisierungsprozess entwickelt, der die Schlüsselgebiete, in denen die Wiederherstellung mehrere Arten beeinflussen würde, gleichzeitig identifiziert. Ich habe diese Ergebnisse mit einem klassischen Einzelarten-Ansatz verglichen. Meine Ergebnisse zeigten, dass der Mehrarten-Ansatz die Fläche von tauglichem Habitat für alle Arten vergrößerte, obwohl unterschiedliche Habitatpräferenzen vorlagen. Im

Gegensatz dazu, identifizierte der Einzelarten-Ansatz Flächen zur Wiederherstellung, die nur die jeweils fokussierte Art begünstigten. Trotz, dass mein Ansatz in dieser Studie theoretisch ist und nicht die Durchführbarkeit der Wiederherstellung mit einbezieht, könnte man ihn dennoch als einen Startpunkt um die Gebiete auszusuchen nutzen, in denen man den größten Vorteil erzielen könnte, wenn sie renaturiert würden. Eine zusätzliche Durchführbarkeitsanalyse, die politische und soziale Aspekte mit einbezieht, könnte dann zeigen, wo die Renaturierung einen signifikanten Einfluss haben kann und daher priorisiert werden sollte.

Zusammenfassend lässt sich sagen, dass ich mit der gesamten Dissertation Einblicke in die komplexen Beziehungen zwischen Tieren und deren Umwelt geben wollte. Dies wird beim Interpretieren vom Verhalten wildlebender Tiere helfen, welche die Botschafter der Natur sind und dazu beitragen, die wechselnden Rhythmen unseres Planeten besser zu verstehen.

General Introduction

Changes in land use have dramatically altered global biodiversity patterns (Schipper et al. 2008). In the last 300 years we have lost ~24% of our forests, ~45% of grasslands and ~71% of shrublands, but croplands and pastures increased by 400-500% worldwide (Goldewijk 2001). Consequently croplands and pastures are now one of the largest terrestrial biomes on the planet and occupy 40% of the land surface (Foley et al. 2005). For example it has been estimated that only 0.2% of Central European deciduous forests remain in a relatively natural state and no pristine forests appear to remain in the Mediterranean region (Bengtsson et al. 2000). These changes in land use have variable effects on the landscape composition, and this has downstream effects on the type and quality of the habitat available to resident species.

Anthropogenic land use causes fragmentation, degradation and loss of habitat for many species (Foley et al. 2005). These ongoing changes in the habitat have variable effects on the affected species. For those species sensitive to disturbance, it has severe consequences. The acceleration in landscape change has already had a high impact on nature and caused the extinction of 5-20% of the species in different groups of organisms (Chapin et al. 2000). These current extinction rates are 100-1000 times larger than pre-human rates (Pimm et al. 1995). Those species that are less sensitive to disturbance can adjust their behavior and use of the environment to survive in often suboptimal conditions. Some species have learned to take advantage of the urban areas by exploiting anthropogenic food sources and shelter (Bateman & Fleming 2012). Other species have modified the characteristics of their acoustic signals to reduce masking by noise (Barber et al. 2010) or shifted their daily cycles (LaPoint 2013). Studies have also shown, for example, that individuals living in more fragmented habitats experienced greater physiological stress, and showed differences in behavior and in home range size, when compared to those living in a less fragmented habitat (Riley et al. 2003; Martínez-Mota et al. 2007; Poessel et al. 2014).

One way of getting a better understanding of the effects of the environment on animals is investigating their movement behavior. The movement path of an animal not only depends on its internal state, motion and navigation capacity, but also on a broad range of external factors including the physical environment (Nathan et al. 2008). The movement paths animals choose will largely depend on the spatial configuration of the environment. Environmental conditions are often dynamic and animals have move to fulfill their different needs. Traditional tracking methods allowed us to measure relatively spatially inaccurate and sparse data that could be used to test general patterns of animals space use. The current advances in technology, however, provides the opportunity to track animals at a nearly continuously rate to observe how animals move through their environment with high detail. Now we have the possibility to obtain detailed information on the movement of animals throughout time, under changing environmental conditions and different biological stages. These movement data in combination with remote sensing data can give us fine scale habitat selection and help us better identify the impacts of fragmentation or barriers, where wildlife corridors are located, which areas are important to preserve or restore, or suitable for reintroductions. Understanding the relationship between the animals and their environment, which habitats they prefer and why, is crucial to understand how species will adapt to changing environments, and also give us the opportunity to use the animals as passive sensors of the changes in the environment (Kays et al. 2015; Wilmers et al. 2015).

In my PhD theses I wanted to improve the understanding through movement behavior of the effects of land use change on wildlife at three different levels:

i) the consequences that the alteration and degradation of the environment has on the energy expenditure of individual animals (Chapter 1),

ii) how animals may adjust their movement behavior to cope with the fragmentation in their habitat (Chapter 2),

iii) and finally how we can take actions in the most efficient way to restore the quality of the environment (Chapter 3).

To answer all these questions I used movement data of different North American carnivore species. Carnivores are potentially highly vulnerable to fragmentation and habitat loss as they require large home ranges, exist in low numbers and are often persecuted by humans (Woodroffe & Ginsberg 1998). This makes them an ideal study model to investigate the effect of land use changes.

In my first chapter I tested the feasibility of reconstructing the energy landscape of free-ranging animals along a gradient of urbanization. An improved understanding of animal energy expenditure may allow us to describe how individual space use patterns are affected by changes within the environment. I derived overall dynamic body acceleration (ODBA) as a proxy for individual energy expenditure from accelerometers attached to free-ranging fishers (*Pekania pennanti,* Erxleben 1777) in a mixed urban habitat in Albany, New York (USA). I associated these data with GPS locations to estimate the spatial distribution of energy expenditure to produce a more comprehensive view of the energy landscape from the perspective of the animal. Several studies have taken advantage of the combination of GPS with acceleration data and ODBA to get a better understanding of how animals optimize energetically costly behaviors. All these studies aimed to understand how different species optimize their feeding strategy, in terms of energy expenditure, given the environment they were exposed to, by adjusting their behavior. I wanted to understand where animals spend their energy in space, without focusing on one specific behavior or environmental characteristic, as this might provide information on how the animal is interacting, in a more generic way, with the environment it encounters. My results showed that the ODBA of fishers was highly structured in space; however, I was not able to predict it using the environmental data I selected. These results suggest an unexpected complexity in the space use of animals that was only captured partially by individual utilization distribution and habitat suitability estimates.

In my second chapter I attempted to identify wildlife corridors by relying exclusively on the movement characteristics of 60 individuals of four large carnivore species in northern Michigan (USA): black bears (*Ursus americanus* Pallas, 1780), bobcats (*Lynx rufus* (Schreber, 1777)), coyotes (*Canis latrans* Say, 1823), and wolves (*Canis lupus* Linnaeus, 1758). Although the wildlife corridor concept is intrinsically linked to animal movement, in most studies they are identified by only using habitat suitability measures. The corridors identified using these methods are mostly swaths of habitat with higher suitability embedded in a matrix of habitat with lower suitability. As these methods do not treat the corridors as independent units, it is possible that the intrinsic characteristics of habitat that determine corridors are neglected. Therefore I wanted to identify corridors independently of environmental features, and avoid the theoretical assumption of a relationship between corridors and habitat suitability. And test whether corridors have an environmental composition that consistently differs from the environmental composition of the home range. I found that most of the tracked individuals used corridors within their home ranges and that several corridors were used simultaneously by individuals of the same species, but also by individuals of different species. However I could not confirm a direct link between habitat suitability and corridors, nor could I find defining environmental characteristics spatially identifying known corridors.

In my third chapter I aimed to establish a modeling and prioritization procedure in identifying areas for restoration in the landscape for multiple species simultaneously. Although the degradation of the landscape usually affects multiple species simultaneously, often only single focal species are being considered in restoration initiatives. Often the decisions of where and how to restore an area are based on expert opinion, existing generally a lack of a systematic prioritization in the decision making process. The difficulty of an approach that considers a community of species, is that habitat quality assessments is predominantly conceptually centered around single species. Given the difficulty of restoring a shared site that is unsuitable for one species, but may be suitable for another species, one solution could be to direct restoration efforts to those areas that are equally unsuitable for all species under consideration. Using the same carnivore data as in Chapter 2, I contrasted a multi-species restoration modeling approach considering only common unsuitable areas, with a classic single species restoration model, to test if this approach would be more effective increasing habitat suitability in a balanced fashion thus avoiding inadvertent negative effects on communities by single species restoration. My results showed that even though the different species had dissimilar habitat preferences, with the multi-species approach the area of habitat suitability increased for all of them. Whereas with the single species approach the area of suitable habitat only increased for the focal species and remained unchanged for all others.

Acceleration data reveal highly individually structured energetic landscapes in free-ranging fishers *(Pekania pennanti)*

Scharf, A. K., S. LaPoint, M. Wikelski & K. Safi (2016) Acceleration Data Reveal Highly Individually Structured Energetic Landscapes in Free-Ranging Fishers (*Pekania pennanti*). PLOS ONE 11(2):e0145732.

ABSTRACT

Investigating animal energy expenditure across space and time may provide more detailed insight into how animals interact with their environment. This insight should improve our understanding of how changes in the environment affect animal energy budgets and is particularly relevant for animals living near or within human altered environments where habitat change can occur rapidly. We modeled fisher (*Pekania pennanti*) energy expenditure within their home ranges and investigated the potential environmental and spatial drivers of the predicted spatial patterns. As a proxy for energy expenditure we used overall dynamic body acceleration (ODBA) that we quantified from tri-axial accelerometer data during the active phases of 12 individuals. We used a generalized additive model (GAM) to investigate the spatial distribution of ODBA by associating the acceleration data to the animals' GPS-recorded locations. We related the spatial patterns of ODBA to the utilization distributions and habitat suitability estimates across individuals. The ODBA of fishers appears highly structured in space and was related to individual utilization distribution and habitat suitability estimates. However, we were not able to predict ODBA using the environmental data we selected. Our results suggest an unexpected complexity in the space use of animals that was only captured partially by re-location data-based concepts of home range and habitat suitability. We suggest future studies recognize the limits of ODBA that arise from the fact that acceleration is often collected at much finer spatio-temporal scales than the environmental data and that ODBA lacks a behavioral correspondence. Overcoming these limits would improve the interpretation of energy expenditure in relation to the environment.

INTRODUCTION

Habitat change, and ultimately loss, is an ongoing process and the main threat to biodiversity globally (Schipper et al. 2008). Habitat changes affect animals at an individual level (Debinski & Holt 2000; Fischer & Lindenmayer 2007). Studies on different mammal species have shown, for example, that individuals living in more fragmented habitats experienced greater physiological stress, and showed differences in behavior and in home range size, when compared to those living in a less fragmented habitat (Riley et al. 2003; Martínez-Mota et al. 2007; Poessel et al. 2014). Changes in the environment, may force animals to adjust their movement behavior. This, in turn, can strongly affect their energy expenditure (Shepard et al. 2013).

An improved understanding of animal energy expenditure would allow researchers to describe how individual space use patterns are affected by changes within the environment. In general, animals should strive to minimize energy expenditure. Studies on pallid sturgeons (*Scaphirhynchus albus; (McElroy et al. 2012)*, savannah elephants (*Loxodonta africana; (Wall et al. 2006)* and humans (Rees 2004) for example show that, when calculating the energetic cost of moving through the landscape in relation to a specific environmental variable (drag for pallid sturgeons, and slope for savannah elephants and humans), the selected pathways corresponded to the route that required the least energy expenditure. Although these studies focused on specific behaviors and considered only one environmental variable, they consistently reveal spatially influenced variation in energetic costs of the behavior in question.

Accelerometers provide biologists with a unique opportunity to collect detailed information on the activities of animals, yielding information on their behavior and indirectly, energy expenditure. From the data collected by the accelerometers, the overall dynamic body acceleration (ODBA) can be calculated as a proxy for individual energy expenditure (Wilson et al. 2006). ODBA is based on motion, does not contain any behavioral information *per se*, and is strongly correlated with metabolic costs (Halsey et al. 2009; Williams et al. 2014). These data, if associated with GPS locations, allow researchers to estimate the spatial distribution of energy expenditure producing a more comprehensive view of the energy landscape from the perspective of the animal (Gleiss et al. 2011; Wilson et al. 2012). Up to now, several studies have taken advantage of the combination of GPS with acceleration data and ODBA to get a better understanding of how animals optimize energetically costly behaviors. For example, ODBA was used to understand how green turtles (*Chelonia mydas; Okuyama et al. 2014)*, imperial shag (*Phalacrocorax atriceps; Shepard et al. 2009)* and imperial cormorants (*Phalacrocorax atriceps;* Wilson et al. 2012) optimize their energy expenditure during foraging dives. Amélineau et al. (2014) investigated how northern gannets (*Morus bassanus*) optimize their foraging events under different wind conditions. Williams et al. (2014) used GPS and acceleration data to reveal how pumas (*Puma concolor*) optimize their energy expenditure during hunting events. These studies all aimed to understand how different species optimize their feeding strategy, in terms of energy expenditure, given the environment they were exposed to, by adjusting their behavior.

Understanding where animals spend their energy in space, without focusing on one specific behavior or environmental characteristic, might provide information on how the animal is interacting, in a more generic way, with the environment it encounters. Therefore, we tested the feasibility of reconstruction of the energy landscape of free-ranging animals along a gradient of urbanization. We used ODBA and

GPS-recorded location data from 12 fishers (*Pekania pennanti*), a medium-sized forest-dependent carnivore, to investigate the spatial allocation of energy when the animals were active. We expected that (1) animals spend energy non-randomly in space, which at a landscape level is related to (2) their utilization distribution, i.e., their time spent in a given area. As utilization distributions capture the amount of time spent in a given area, which in turn is at least partly related to how quick animals move through space, we hypothesized that animals spend comparably less energy in the core areas of their utilization distributions. The non-random distribution of energy expenditure hypothesized to correlate with utilization distribution is ultimately mediated through non-random use of the environment, hence (3) we also expected a relationship between energy expenditure and environmental characteristics. Given the expected negative relationship between time spent in an area, expressed in the utilization distribution probability, and the energy expenditure mediated through environmental factors, we therefore also (4) hypothesized that the amount of energy expended in an area and that area's habitat suitability should correlate. Finally, we expected that (5) resources as well as the distribution of utilization distribution core areas should have a patchier distribution with increasing urbanization and affect the movement behavior and energy expenditure of the fishers. Higher proportions of urban area within an animals home range should translate into a more heterogeneous spatial pattern of energy expenditure. We expect this as some activities could be restricted to particular patches that are spatially more restricted than in an area with a more homogeneous landscape. By combining the acceleration data with spatial information, we aim to directly translate habitat properties as assessed by remote sensing, such as resource composition or availability, into energetic costs for naturally behaving animals and thus obtain better insight into the animals' interaction with its environment.

MATERIAL & METHODS

(a) Study area and tracking data

Twelve fishers were tracked near Albany (New York, USA) during 2009 - 2011 (Figure 1.1, Table 1.1). Nine of these individuals were tracked in suburban forest patches. This 350 km² area is composed of residential and commercial land interspersed with forest patches. It is relatively flat (< 100 m change in elevation) with a road density of 4.77 km/km² (New York State Office of Cyber Security 2006) and a human population density of 438 persons/km² (United States Census Bureau 2008). The remaining three individuals were tracked in a nearby area (Grafton Lakes State Park, 9.5 km^2), a mostly contiguous forest containing recreation trails and a few gravel roads (see LaPoint et al. 2013 for details). Capture and handling protocols are described in LaPoint et al. (2013).

Fishers were fitted with tracking collars equipped with GPS and tri-axial accelerometers (E-obs GmbH; Grünwald, Germany). The collars recorded a GPS-location every 10 minutes for five individuals and every 15 minutes for one individual. The GPS collars of the remaining six individuals, were programmed with a dynamic sampling (Brown et al. 2012), taking GPS fixes every two minutes when the animal was highly active (e.g., running), every 10 minutes at moderate activity, and every 60 minutes during low activity (e.g., resting) (Table A.1). We regularized the location data for the individuals with dynamic sampling to compensate for different sampling schedules and to obtain an unbiased quantification of activity levels. To do this we

Table 1.1. General information of the tracked individuals

Individuals	Sex	% of home range with urban area	Deployment duration in days (time period tracked)	Number of GPS fixes used in analysis
F01	m	0.3	71 (17.03. – 29.05.2011)	3714
F02	m	3.5	24 (04. – 29.12.2009)	708
F03	f	4.0	28 (13.08. – 14.09.2009)	443
F04	m	13.3	49 (09.02. – 02.04.2010)	2669
F05	f	15.6	18 (16.12.2010 – 05.01.2011)	913
F06	f	16.5	16 (21.01. – 08.02.2011)	423
F07	m	27.9	18 (23.12.2010 – 12.01.2011)	684
F08	f	35.7	19 (11.02. – 04.03.2011)	765
F09	m	36.3	20 (11.02. – 05.03.2009)	655
F10	m	43.0	22 (19.01 – 12.02.2011)	737
F11	m	49.9	10 (08. – 18.03.2011)	617
F12	m	50.9	24 (10.02. – 08.03.2011)	1253

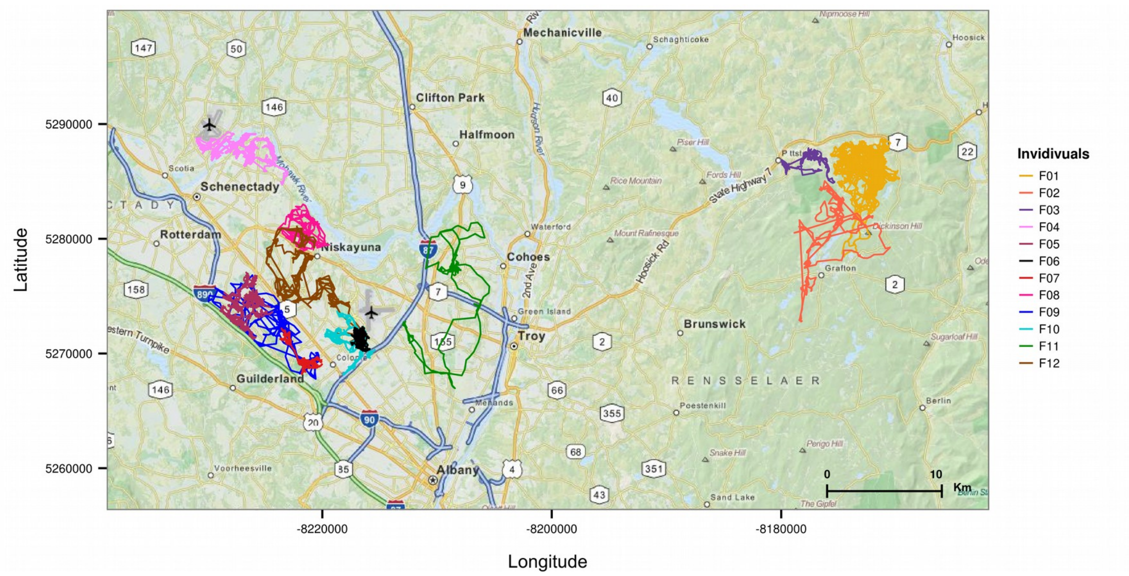

Figure. 1.1. Tracks of the individuals included in this study.

created locations with the same coordinates every 10 minutes during inactive periods. Similarly, we subsampled the locations by a minimum of 10 minutes when the fisher had been active and the collar collected locations every two minutes. The accelerometer data were recorded at 18.74Hz in a 3.5-second burst every 3 minutes, obtaining for every burst 54 accelerometer measurements. We associated each acceleration burst to the location closest in time (median time gap between the acceleration burst and the GPS fix was 1.2 seconds and the maximum time gap was 60 seconds).

(b) ODBA calculation

To transform the raw accelerometer data into m/s², we applied the equation provided by the manufacturer of the collars:

$$a_i = (n_i - n_{i,zerog}) \cdot c_i \cdot g$$

where a_i is the acceleration of axis *i* in m/s^2; *i* is the axis x, y or z; n_i is one digital sample of raw data for axis *i*; $n_{i,zerog}$ is the raw value for zero acceleration for axis *i*; c_i is the slope for axis *i* and *g* is the magnitude of observed gravitational acceleration caused by the earth (9.81 m/s^2). The default value for the slope for accelerometers configured with high sensitivity was 0.001, and for those configured with low sensitivity was 0.00269 as indicated by the manufacturer. The default value for zero acceleration was 2048.

We quantified the mean ODBA per burst as in Wilson et al. (2006), using the following equation:

$$ODBA_j = \frac{\sum_{i=1}^{n} \left(|x_i - \bar{x}| + |y_i - \bar{y}| + |z_i - \bar{z}| \right)}{n}$$

Here, ODBA is calculated for burst *j*. A burst consists of *n* samples in each of the three axes (x, y and z). x_i represents i[th] component and $\bar{x}$ the mean of all *n* samples of the x-axis of burst *j* (same for axis y and z). Due to the different sensitivity settings of the accelerometers (Table A.1), we had to standardize the ODBA values for cross comparability between individuals. We standardized the ODBA to range between 0 and 1 within each individual as follows:

$$ODBA'_i = \frac{ODBA_i - min(ODBA)}{max(ODBA) - min(ODBA)}$$

(c) Landscape data

Land cover data was obtained from the National Land Cover Database 2011 (Jin et al. 2013) at 30 m resolution. We visually compared the land cover map to the Google Earth satellite images closest in time to the tracking periods of each individual, to account for potential land cover changes that may have occurred since the creation of the land cover data set. We reclassified the original land cover types (see NLCD 2011; Jin et al. 2013) into developed low, developed high, and the natural land use categories deciduous forest, evergreen forest, mixed forest, shrub, grassland, crop, woody wetland, herbaceous wetland, barren, and open water. For each 30 m grid cell of the land cover map, we also calculated the distance to the forest edge and estimated the proportion of urban area and landscape heterogeneity within a 240 m radius circle (Table A.2). We chose this radius as possible distance of perception based on our experience in the field while approaching these individuals for data downloads, where we would observe them move away from us when the distances were less than 240 m. We also included the distance to roads from each grid cell (United States Census Bureau 2011). We quantified the proportion of urban area within each individual's home range (i.e., the 95% of the utilization distribution; see details in *(d) Statistical analyses* below). As urban areas we included those areas that were classified as developed in the land cover map in addition to roads (Table A.2).

(d) Statistical analysis

As the tracked fishers were highly nocturnal, we identified resting bouts as time periods with low activity levels lasting for more than 4 hours during the day, indicated by low variability in the accelerometer measures (LaPoint et al. 2013) and excluded them from our analyses. We also excluded resting periods that met these criteria but extended into the night. Additionally, we excluded the first 48 hours of data collection after collaring to avoid possible effects of capture and handling. Thus, for all subsequent analyses (energy landscape models, utilization distribution, and habitat suitability models) we used only the active data set and, where applicable, regularized location data.

To model ODBA as a function of space and time for each individual, we used generalized additive models (GAM; Woods 2006), since we were expecting potentially complex and non-linear spatio-temporal patterns. We fitted the spatial position as an explanatory thin plate regression spline smooth term consisting of the latitude and longitude (of where each burst was collected) to the cubic root of each single ODBA burst. The cubic root transformed the residuals of the model to meet the Gaussian distribution assumption. We set the number of knots, the k value of the smooth term, to 100. For all GAMs we allowed the model to add an extra penalty to each term added and thus, as part of the model fitting, allow to remove terms completely from the model. The distribution family was chosen to be Gaussian and the smooth terms were estimated based on the restricted maximum likelihood, “REML”. To incorporate the temporal pattern in energy expenditure we included the time of the day at which each burst was collected in seconds as a cyclic penalized cubic regression spline smooth term. For this smooth term we set k to 10. The residuals were checked for Gaussian normal distribution and for the absence of auto-correlation to meet the assumptions of the GAM. The models were calculated with the R package *mgcv* (Woods 2006).

We estimated the proportion of time spent within the different areas of an individual’s home range, the individual utilization distribution (UD), using the dynamic Brownian bridge movement model (Kranstauber et al. 2012) with the R package *move* (Kranstauber & Smolla 2014). To test whether the predicted energy landscape was correlated with the utilization distribution, we modeled ODBA as a function of spatial position, time and UD for all individuals using a generalized additive mixed model (GAMM; Woods 2006). We extracted the UD value for each location where each ODBA burst was collected and included it as an explanatory variable together with longitude and latitude and time of day as smooth terms as in the previous GAMs. We included individuals as a random factor.

To evaluate the influence of the environment on the spatial distribution of energy expenditure, we added land cover as a categorical variable, distance to forest edge, landscape heterogeneity, proportion of urban area and distance to roads, all as continuous values, to the previous purely spatio-temporal explicit models, and searched for a minimum adequate model for each individual separately. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to rank the models of each individual, selecting models with a delta AICc value lower than 4 (Table A.3), as these are the models that have considerably greater empirical support (Burnham & Anderson 2002). We used weighted model averaging on this subset of best models and calculated a prediction of the energy landscape for each individual. The AICc, the weighted model averaging and the prediction were calculated with the R package *MuMIn* (Barton 2018).

We calculated habitat suitability using a step selection function (Fortin et al. 2005; Thurfjell et al. 2014). This function compares the environmental attributes of an observed step (based on two consecutive GPS locations) with a number of random steps that have the same starting point. We generated the random steps from a multivariate normal distribution, using the function *rmvnorm* of the R package *mvtnorm* (Genz et al. 2014), maintaining the variance/covariance structure of speed and turning angle of the empirical track of each individual. We used 5 random steps per observed step, converting speed to step length by multiplying the random speed by the time between fixes of the corresponding observed step. To analyze the habitat preferences, we compared the environmental characteristics of the end points of each observed step with its corresponding random steps, by means of a conditional logistic regression model using the *mclogit* function of the R package *mclogit* (Elff 2014). The environmental variables included in the model were land cover, distance to forest edge, landscape heterogeneity, proportion of urban area and distance to roads (Table A.2). As the likelihood of realizing a specific option is a function of step length and relative turning angle, we also included these two measurements as variables in the model. We built one model per individual, based on 75% of the observed locations, and calculated the predicted habitat suitability. For the predictions, we kept distance and relative turning angle constant, selecting a random pair of values from the previously mentioned multivariate normal distribution. We used the previously excluded 25% of the observed locations to assess the performance of the model predictions by comparing them with random points selected from the obtained maps (for details see Appendix A.1). To test whether the predicted energy landscape was correlated with the habitat suitability, we modeled ODBA as a function of spatial position, time and habitat suitability for all individuals using a GAMM. We extracted the habitat suitability value for each location where each ODBA burst was collected and included it as an explanatory variable together with longitude and latitude and time of day as smooth terms as in the previous GAMs. We included individual as a random factor.

As a measure of heterogeneity in the predicted energy landscape, we used the obtained adjusted R^2 of the spatio-temporal models. As spatio-temporal non-randomness increases, the spatial and temporal explanatory variables in the GAMs can capture more of the pattern. Therefore the adjusted R^2 of the models would increase with increasing non-randomness in the distribution of ODBA, i.e. increasing heterogeneity in the energy landscape. To investigate whether urbanization and energy expenditure were correlated we calculated the Pearson's correlation coefficient between the adjusted R^2 of the spatio-temporal GAMs and the degree of urbanization each individual experienced. We used the adjusted R^2 as an unbiased estimator which only increases when the addition of explanatory variables improves R^2 more than expected by chance taking into account the number of additional variables and in case of the smooth terms the number of knots used in the additive models (Oksanen et al. 2018). We also directly tested whether urbanization resulted in more heterogeneity in predicted energy expenditure in the landscape by calculating the spatial variance of the predicted values from the spatio-temporal GAMs, and correlated the predicted values with the degree of urbanization.

In addition, we identified the areas with the most extreme predicted ODBA values. We did this by identifying the hot spots of the lowest (ODBA valleys) and highest (ODBA peaks) energy expenditure for each individual. We defined them as the areas with the lowest 5% and highest 5% of predicted ODBA values respectively. We compared the environmental composition and the time spent in the ODBA valleys versus peaks. For each hot spot type we calculated its area (m^2), extracted the time spent in it from the UD, and its environmental composition. To compare the time spent between hot spots, we built a linear model where the spent time was the response variable and the type of hot spot, area and individuals were the explanatory variables. As the amount of time spent in a hot spot will depend on its size, we included area in the model and individuals to account for potential differences between them. To compare the environmental composition of the two types of hot spots, we applied a compositional analysis using the function *adonis* from the R package *vegan* (Oksanen et al. 2018). The environmental variables including land cover, distance to forest edge, landscape heterogeneity, proportion of urban area and distance to roads (Table A.2) were the response variable, and type of hot spot and area were the explanatory variables. We included individuals as strata and set the number of permutations to 999.

To investigate if other movement-related behaviors changed along the urbanization gradient, we calculated the number of active bouts per day, the duration of these active bouts and the cumulative distance traveled per day for each individual. We defined "day" as the period of time from sunset to sunset (of the following day). We calculated the bouts of activity from the acceleration data, being each bout a continuous period where the animal was active. Then, we correlated each of these three measurements with the degree of urbanization. We conducted all analysis with R 3.1.0 (R Core Team 2017).

RESULTS

Our analysis revealed a non-random spatial structure of energy expenditure (Figure 1.2, Figure A.1). The mean ± SD value of adjusted R^2 for the models only including the longitude and latitude was 0.35 ± 0.09 (Table 1.2). For most individuals the time of day did not have a large effect on the distribution of energy, as the adjusted R^2 of the spatio-temporal models increased only marginally (mean ± SD = 0.37 ± 0.08, Table 1.2).

The time spent in an area (UD, Figure A.2) had a significant negative influence (estimate ± SE = -20.05 ± 0.5, t-value = -40.03, p<0.001, DF = 13627, adjusted R^2 = 0.10) on the energy expenditure. This result was supported by the analyses of the time spent in ODBA valleys versus peaks, where we found that fishers spent 0.015 ± 0.002 (estimate ± SE, t-value = 7.26, p<0.001, $F_{13,360}$ = 9.0, Figure 1.3) times more time in ODBA valleys than in peaks.

The mean ± SD adjusted R^2 across models after inclusion of environmental variables and subsequent model selection was 0.37 ± 0.08 (Table 1.2), showing only small increases compared to the first model. Distance to forest edge, percentage of urban area, and distance to roads were retained in the models of all 12 individuals. The remaining environmental variables were retained in variable combinations for each individual (Table 1.3). The importance, size effect, and sign of the environmental

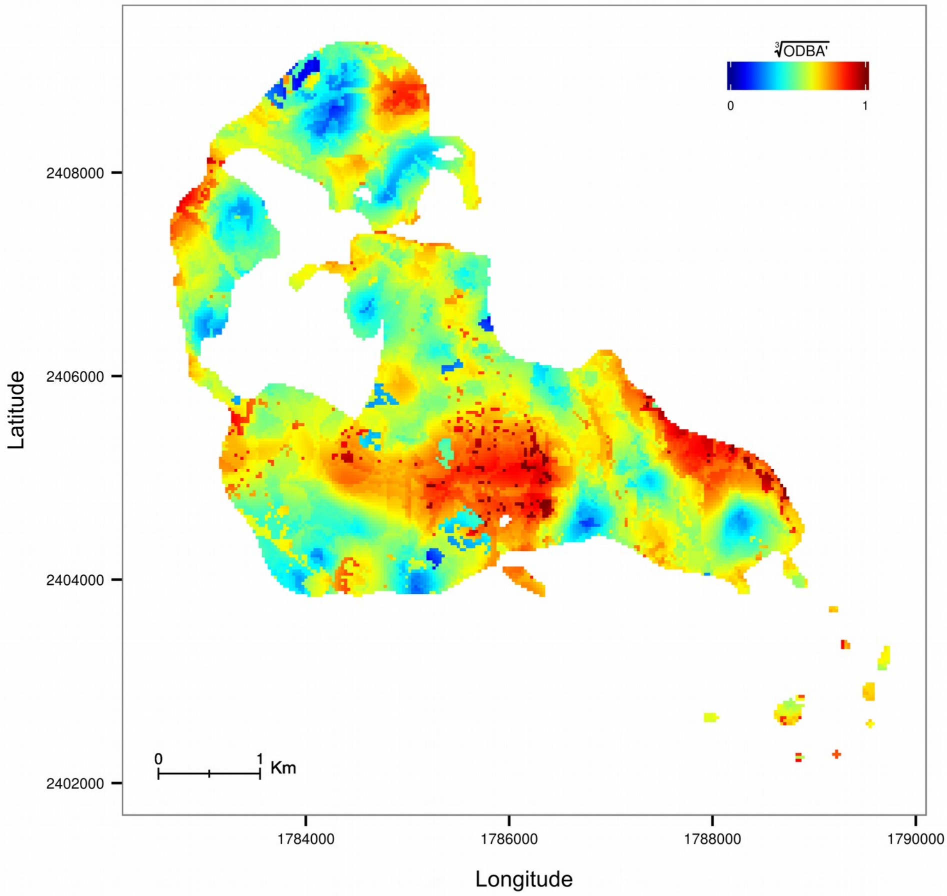

Figure 1.2. Predicted energy landscape for individual F12. The prediction is made from the averaged set of best models including spatial position, time of day and environmental variables. The area of the map corresponds to the home range of this individual (95%UD).

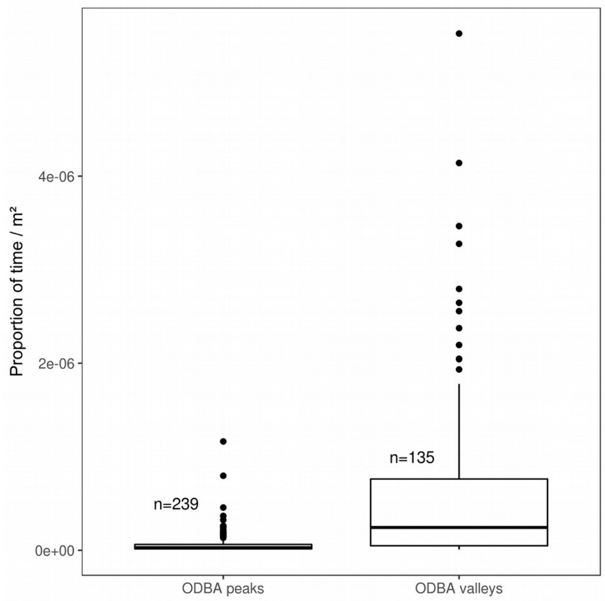

Figure 1.3. Comparison of time/m^2 spent in ODBA valleys and ODBA peaks across all individuals. The y-axis represents the proportion of time spent in each hot spot divided by its area. *n* is the total number of each type of hot spot.

Table 1.2. Generalized additive models (GAM) results, of the model including only spatial position, the model including the spatial position and time of day, and the model including also the environmental variables.

Individuals	Adj. R^2 of spatial model	Adj. R^2 of spatio - temporal model	Adj. R^2 of spatio - temporal and environment model	Variance of the predicted values of the spatio - temporal model
F01	0.23	0.26	0.26	0.05
F02	0.47	0.47	0.47	0.77
F03	0.41	0.43	0.43	0.01
F04	0.26	0.31	0.32	0.05
F05	0.38	0.40	0.42	0.06
F06	0.26	0.30	0.30	0.01
F07	0.33	0.35	0.36	0.12
F08	0.46	0.46	0.46	0.07
F09	0.42	0.44	0.44	0.08
F10	0.23	0.25	0.25	0.04
F11	0.34	0.36	0.37	0.03
F12	0.38	0.38	0.40	0.10

variables varied across individuals (Table 1.3), yet did not show a consistent pattern related to the urbanization gradient.

The habitat suitability models performed well (Figure A.3). The mean ± SD habitat suitability of the observed locations across individuals was 0.51 ± 0.27 and significantly higher than the average of 0.28 ± 0.26 from the randomly selected points (Appendix A.1 for details). We found a negative influence of the habitat suitability (estimate ± SE = -0.12 ± 0.01, t-value = -16.2, $p<0.001$, DF = 13627, adjusted R^2 = 0.05) on the energy expenditure. These results were supported by the differences we found between the ODBA valley and peaks in environmental composition ($F_{1,371}$ = 11.97, $p<0.001$).

The individual fishers had variable proportions of urban area within their home ranges, resulting in a gradient that spanned from 0.3 to 51% (Table 1.1). Contrary to our expectations, however, the heterogeneity in the energy landscape was not related to the urbanization gradient. The correlation between the adjusted R^2 of the models and the percentage of urban area in the home range was very low ($r = -0.006$, DF = 10, $p = 0.98$). In addition, the differences in the variance of the predicted values of the energy landscape between individuals (Table 1.2) were not correlated with the percentage of urban area in the home range ($r = -0.28$, DF = 10, $p = 0.38$).

Individual variation in total daily distance traveled, and the duration and number of activity bouts per day was high. We found a low, but positive relationship between the total distance traveled (slope ± SE = 0.033 ± 0.012, t-value = 2.828, DF = 291, $p<0.01$) and the degree of urbanization (Figure 1.4). We also found a low, but significant, relationship between the degree of urbanization and the number of active

Table 1.3. Contribution of the environmental variables included in the GAMs

Environmental variables	Number of models in which present	Size effect range
Distance to the forest edge	12	-0.1825 - 0.0263
Proportion of urban area	12	-0.0807 - 0.0220
Distance to roads	12	-0.4607 - 0.0935
Landscape heterogeneity	11	-0.1694 - 0.1871
Land cover *	5	
Developed low		-0.2838 - 0.3695
Deciduous forest		-0.4166 - 0.8625
Coniferous forest		-0.5265 - 0.1197
Mixed forest		-0.3887 - 0.4793
Shrub		-0.0162 - 0.1270
Crop		-0.3362 - 0.2367
Woody wetland		-0.3952 - 1.0853
Herbaceous wetland		-0.0126 (only present in one model)
Grassland		0.0027 (only present in one model)

* Land cover is included as a factor in the model, all land cover types are compared to the land cover type "Developed high"

bouts per day (slope ± SE = 0.012 ± 0.004, t-value= 2.791, DF = 343, $p < 0.01$) and the duration of these active bouts (slope ± SE = -0.651 ± 0.162, t-value= -4.009, DF = 1341, $p < 0.001$; Figure 1.4).

DISCUSSION

The fishers we studied spent energy in a spatially structured manner during their active period, that did not depend on the time of day. It seems that fishers tended to spend the same amount of energy in a given area independent of the time of the day, which points to some environmental structuring of energy use. However, our environmental variables, including natural and human related variables, could not explain energy expenditure all too well. As we expected, the amount of time spent in a given area was negatively related with how much energy they spent there. Following this expectation we found that the time spent in the ODBA valleys was significantly longer than in the ODBA peaks. This is intuitive, as an animal moving fast and therefore spending high amounts of energy will implicitly spend less time in that same area. Although the relationship between utilization distribution and energy expenditure was significant, the model only explained a small proportion of the variance in the data.

According to our expectation, composition of the environment should influence activity and therefore shape individual energetic landscapes (Mosser et al. 2014). However, we were unable to identify the environmental characteristics that defined individual energy landscapes. Nevertheless, we did find a relation between habitat suitability and energy expenditure across all individuals. They spent less energy in areas with higher habitat suitability. We also found that the environmental composition of the

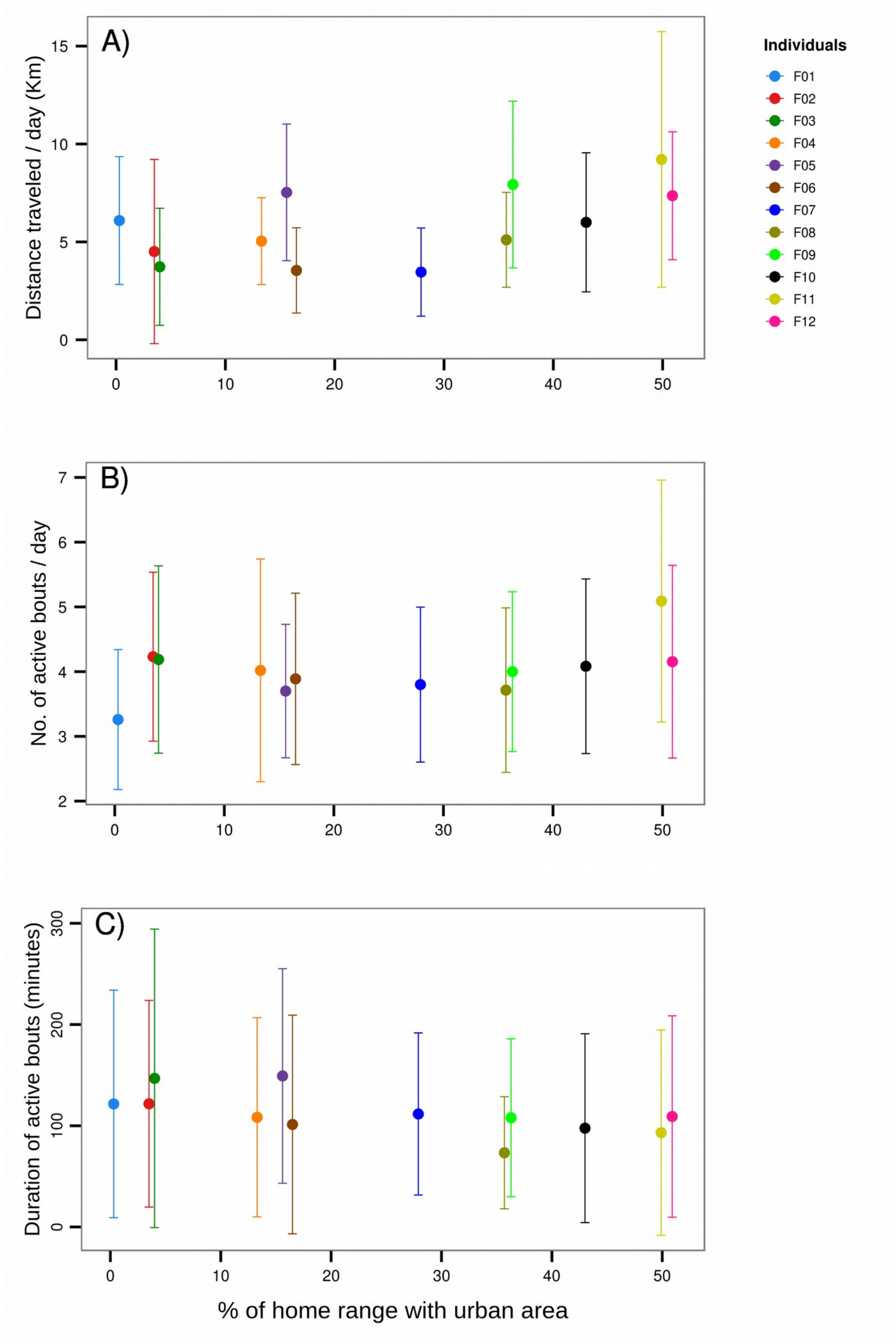

Figure 1.4. Activity measurements per individual along the urbanization gradient. (A) Cumulative distance traveled per day (mean±SD). (B) Number of active bouts per day (mean±SD). (C) Duration of active bouts (mean±SD).

ODBA valleys and peaks was significantly different. Although the habitat suitability could only explain a very small part of the variance in energy expenditure across individuals, these results indicate that the environment did influence how much energy these fishers were spending in a given place. Fishers are forest specialists (Powell 1993) and our simple classification based on remote sensing seems not to incorporate the heterogeneity of forest environments. Smaller scale variation in forest composition and micro-climate likely have important impacts on the behavior of fishers (Weir & Harestad 2003), but these could not be measured in this study. Accelerometer-derived data might provide more insight into how animals respond to these subtle nuances, yet there is a large mismatch in the scales at which acceleration data and environmental data are typically collected. If the changes in behavior occur at very fine temporal and spatial scales, the available remotely-sensed environmental data may be insufficient to allow us to detect them.

Contrary to our prediction, neither the total amount of explained variance in the observed energy expenditure, nor the total amount of predicted variance in the energy landscape were explained by the amount of urbanization. We found high inter-individual variation in activity measurements such as duration and number of daily bouts of activity, as well as the cumulative distance traveled per day. Although these measurements were only weakly correlated with the degree of urbanization, individuals with more urban area in their home ranges seem to have slightly shorter activity bouts that are then compensated by a higher number of bouts per day. There also seems to be a slight increase in total distance traveled per day as the percentage of urban area within the home range increased. Despite these results hinting towards some effect of the urbanization on the activity budget, this was not reflected in differences of spatial distribution of energy expenditure. Overall, our results indicate that, if present, the effect of urbanization on the energy landscape are subtle. Either fishers were not as negatively affected by urbanization as one might expect or the effects were not reflected appropriately by ODBA.

One limitation of using ODBA is that it lacks a behavioral context. Although specific behaviors have been identified from tri-axial accelerometers (Shepard et al. 2008; Grünewälder et al. 2012; Wilson et al. 2013; Wang 2014), doing so remains challenging, in particular teasing apart distinct behaviors that may have similar acceleration characteristics (e.g., hunting or escaping). For a more complete view of the energetic landscape we would need a full cost-benefit comparison, requiring more information, ideally from identified behaviors with known energetic costs.

The survival of animals largely depends on the balance between energy acquisition and expenditure (Brown et al. 2004). Understanding where, when, and how much energy animals spend, is key to understanding the interactions of species and individuals with their environment. Our work revealed a spatial structure of energy expenditure and suggests that close examination of environmental details are necessary to understand how the landscape structures energy expenditure. Future efforts should strive to identify the additional factors that underlie the non-random structure that we observed. This may require new data at spatial and temporal resolutions that more clearly match the perspectives of the study animals. Disentangling the causal relationships from which the patterns we observed emerged will improve our understanding of how environmental changes affect animal energy expenditure and behavior, potentially aiding efforts to mitigate the causes and consequences of habitat alteration.

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Habitat suitability does not capture the essence of animal-defined corridors

Scarf, A.K., J.L. Beland, D.E. Jr Beyer, M. Wikelski & K. Safi (*in press.*) Habitat Suitability does not capture the essence of Animal-Defined Corridors. Movement Ecology.

ABSTRACT

Increases in landscape connectivity can improve a species' ability to cope with habitat fragmentation and degradation. Wildlife corridors increase landscape connectivity and it is therefore important to identify and maintain them. Currently, corridors are mostly identified using methods that rely on generic habitat suitability measures. One important and widely held assumption is that corridors represent swaths of suitable habitat connecting larger patches of suitable habitat in an otherwise unsuitable environment. Using high-resolution GPS data of four large carnivore species, we identified corridors based on animal movement behavior within each individual's home range and quantified the spatial overlap of these corridors. We thus tested whether corridors were in fact spatial bottle necks in habitat suitability surrounded by unsuitable habitat, and if they could be characterized by their coarse-scale environmental composition. We found that most individuals used corridors within their home ranges and that several corridors were used simultaneously by individuals of the same species, but also by individuals of different species. When we compared the predicted habitat suitability of corridors and their immediate surrounding area we found, however, no differences. We could not find a direct correspondence between corridors chosen and used by wildlife on the one hand, and a priori habitat suitability measurements on the other hand. This leads us to speculate that identifying corridors relying on typically-used habitat suitability methods alone may misplace corridors at the level of space use within an individual's home range. We suggest future studies to rely more on movement data to directly identify wildlife corridors based on the observed behavior of the animals.

INTRODUCTION

Changes in land use are affecting many species worldwide through fragmentation and loss of their habitats (Schipper et al. 2008; Tucker et al. 2018). Consequently, the affected animals live in an environment where patches of high quality habitat are scattered throughout the landscape. The connectivity between these resulting resource patches depends on the degree to which the landscape facilitates or impedes movement between them (Taylor et al. 2006). Greater landscape connectivity increases an individual's ability to cope with many changes in the environment (Heller & Zavaleta 2009; Vasudev et al. 2015). One way to increase and maintain landscape connectivity is through wildlife corridors (LaPoint et al. 2013). It is therefore important to identify corridors and facilitate their use (Gilbert-Norton et al. 2010).

Although the corridor concept is intrinsically linked to animal movement (LaPoint et al. 2013; Clark et al. 2015; Abrahms et al. 2016; Panzacchi et al. 2016), currently wildlife corridors are generally identified at the population level, relying on habitat suitability measures only. Most studies aim to identify wildlife corridors without a priori knowledge about what a corridor actually is and where they are. The general assumption underlying the prediction of possible corridor locations is that there is a constant habitat preference during all life stages and across behaviors of animal species, although it is known not to be necessarily true (Fattebert et al. 2015). The most widely used method for corridor identification is through an estimation of landscape resistance to movement (Sawyer et al. 2011). In these landscape resistance models the permeability of the landscape to movement is determined by using the inverse of the habitat suitability as a resistance surface. Some studies have included movement data in their habitat models (Abrahms et al. 2016; Panzacchi et al. 2016), but ultimately they all identify corridors based on habitat properties. The corridors identified through landscape resistance models, tend to be mostly swaths of habitat with higher suitability embedded in a matrix of habitat with lower suitability (Beier et al. 2008). As these methods do not treat the corridors as independent units, it is possible that characteristics of habitat that determine corridors above and beyond habitat suitability are neglected. These same methods have been used to identify corridors across different scales, e.g. connecting areas 100-1000 km apart (e.g. LaRue & Nielsen 2008; Rabinowitz & Zeller 2010; Dutta et al. 2016), or at smaller scales connecting areas 10-50 km apart (e.g. Poor et al. 2012; Abrahms et al. 2016; Panzacchi et al. 2016). Although it could be reasonable to assume ecologically that the factors driving corridor use are the same across scales, they could be scale dependent (Rettie & Messier 2000). Within home range corridor use happens at a third-order selection (*senu Johnson 1980)*, which will be constrained by the second-order selection for the home range placement in the landscape. If the second-order selection is strong, one might expect the third-order selection to be random, hence the movement corridors are independent from habitat suitability, and more movement driven. On the contrary, if second-order selection is rather weak, one might expect a stronger third-order selection, and movement corridors are more habitat driven. LaPoint et al. (2013) developed an algorithm to identify wildlife corridors solely based on movement, identifying those areas where the animals show quick and parallel movement behavior. In this study they analyzed the corridor behavior of one species (*Pekania pennanti*) and detected, using camera traps, that these areas were also used more often than random by other species within the study area. To understand where corridors occur, and what shapes them, we need to understand the drivers of this corridor behavior.

We identify corridors within home ranges of 60 individuals of four large carnivore species, relying exclusively on their movement characteristics. Thus, we identify corridors independently of environmental features, to investigate the theoretical assumption of a relationship between corridors and habitat suitability. Corridors are mostly identified at a larger scale, aiming to connect populations and communities (Rabinowitz & Zeller 2010), but individuals not only rely on corridors during migration, seasonal home range shifts (Poor et al. 2012) or during dispersal (LaRue & Nielsen 2008), but also within their home ranges, especially when living in fragmented landscapes. Corridors are important at all scales, and few studies (LaPoint et al. 2013; Abrahms et al. 2016) have evaluated corridors at the individual home range level. We predict that individuals with home ranges containing more heterogeneous landscape use corridors more often, as a greater heterogeneity of the landscape could imply greater patchiness of suitable habitat to be connected through corridors within their home ranges. We test whether the corridors within home ranges too are swaths of suitable habitat surrounded by less favorable habitat as shown for corridors at larger scales. Finally, we test whether corridors have an environmental composition that consistently differs from the environmental composition of the home range, which in turn would give us a better understanding of potential drivers shaping corridors at a home range level and enable us to better predict them spatially.

MATERIALS & METHODS

(a) Study area

The study area covered about 2800 km^2 within Delta and Menominee counties in the Upper Peninsula of Michigan, USA (45°35'0.00"N, 87°23'0.00"W, Figure 2.1). The main land cover types of the study area included woody wetlands (44%) (e.g., black spruce *Picea mariana*, green ash *Fraxinus pennsylvanica*, northern white cedar *Thuja occidentalis*, speckled alder *Alnus incana*), deciduous forest (17%) (e.g., sugar maple *Acer saccharum*, quaking aspen *Populus tremuloides*), and agriculture (12%) (i.e., row crops and pastures). The remaining 27% of the study site included conifer forest, mixed forest, urban areas, roads, herbaceous wetlands, shrub, and open water (NLCD 2011; Jin et al. 2013). Land covers with direct human influence (agriculture, urban areas and roads), represented 18% of the study area. The area is relatively flat, with an elevation range of 170 to 310 m.a.s.l. and mean road density of 1.2 km/km^2.

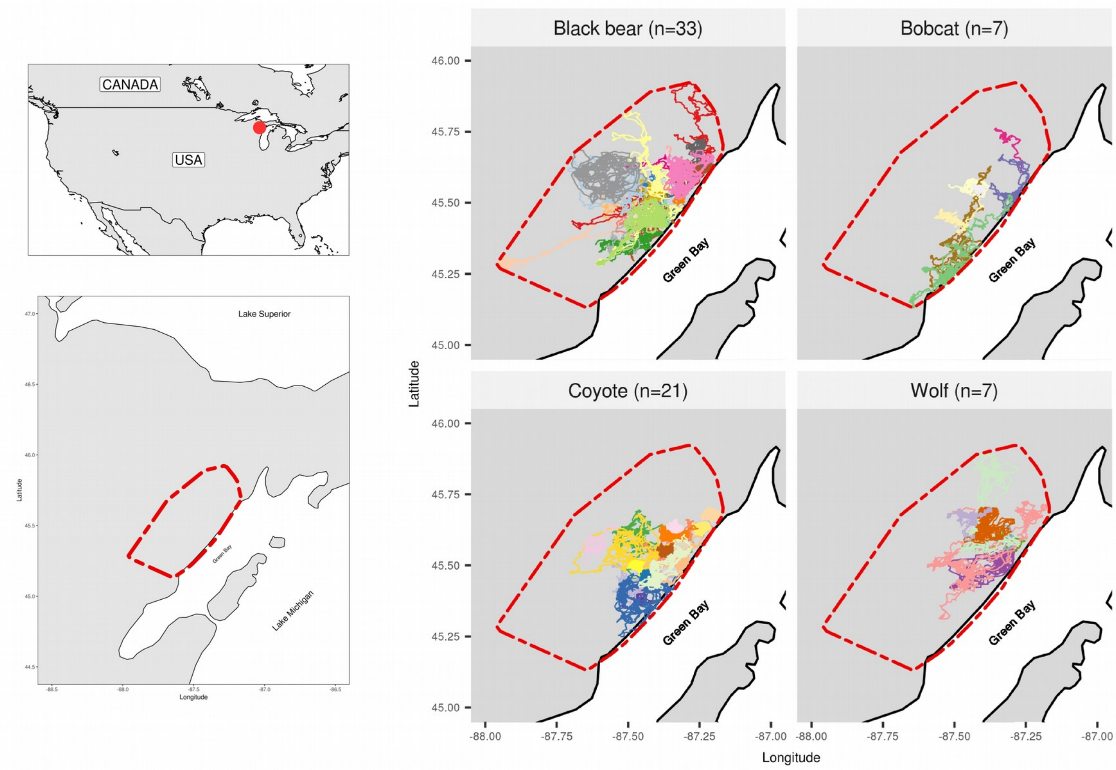

Figure 2.1. **Study site**. Red polygons represent the 100% MCP (minimum convex polygon) containing all individuals of all species. Left panel: colored lines represent the tracks of the different individuals. "n" represents the number of tracks.

(b) Tracking data

During March-August 2009-2011 we captured and immobilized 25 black bears (*Ursus americanus*), 7 bobcats (*Lynx rufus*), 21 coyotes (*Canis latrans*) and 7 wolves (*Canis lupus*) (Table 2.1). We fitted all individuals with Lotek GPS collars (model 7000MU for black bears and 7000SU for bobcats, coyote and wolves; Lotek Wireless, Newmarket, Ontario, Canada), programmed to obtain a location every 15 minutes between the 1 May and 30 September. We located black bears collared the previous year in their winter dens, immobilized them and replaced their GPS collars. The collars fitted to bobcats, coyote and wolves included drop-off mechanism to release collars 30 weeks after deployment. Location data from all collars could be downloaded remotely. For the data analyses in this study we used GPS locations recorded from 1 May - 30 September 2009-2011. If individuals were trapped during this time window, we removed the first 5 days of tracking data collected after collaring to avoid possible effects of capture and handling on movements and habitat selection analysis. For the 8 black bears that were monitored over consecutive years, we analyzed data from each year separately. For each individual we calculated the range distribution, as the 100% minimum convex polygon, which represents the broad space required by the animal, i.e. the home range. We also calculated the occurrence distribution, which estimates where the animal was located during the observation period (Fleming et al. 2015). We calculated the occurrence distributions with the dynamic Brownian bridge movement model (Kranstauber et al. 2012) with the R package *move* (Kranstauber & Smolla 2016) (Figure B.1).

Table 2.1. Summary of individuals and tracks included in study.

Species	Number of individuals	Sex		Life stage		Number of days tracked* (mean±SD)	Number of locations* (mean±SD)
		Female	Male	Adult	Juvenile		
Black bear	25 (+8)#	10 (3)#	14 (5)#	20 (8)#	5	82 ± 37	7431 ± 3511
Bobcat	7	1	6	5	2	87 ± 44	8166 ± 4090
Coyote	21	11	10	19	2	101 ± 29	9435 ± 2762
Wolf	7	5	2	7	0	105 ± 26	9504 ± 2298

*Only the data used in the analysis of this study is included (i.e. within the time window of interest ,1st May - 30th September)
Number of individuals that were tracked in consecutive years for which tracks of different years were analyzed separately.

(c) Ethical statement and trapping procedure

Ethics of all capture and handling procedures were approved by the Mississippi State University Institutional Animal Care and Use Committee (#09-004). Also, animal capture and handling procedures followed guidelines established by the American Veterinary Medical Association and the American Society of Mammalogists (Sikes et al. 2011). Details of capture and handling procedures are described in Stillfried and colleagues (Stillfried et al. 2015; black bears), Svoboda and colleagues (Svoboda et al. 2013; bobcats), Etter & Belant (Etter & Belant 2011; coyotes) and Petroelje and colleagues (Petroelje et al. 2013; wolves).

(d) Environmental data

We obtained land cover data from the 2011 National Land Cover Database (Jin et al. 2013) at 30 m resolution, and complemented this map with data for highways, secondary roads (United States Census Bureau 2011), rivers and lakes (United States Geological Survey 2016). We rasterized highways, secondary roads, rivers and lakes at the resolution of the land cover data (30 x 30 m). Though most roads and rivers are not 30 m wide, our GPS collars had a position error of about 20 m and we considered this resolution adequate for our analysis. We reclassified the pixels in the original land cover layer corresponding to highways, secondary roads, rivers and lakes (Table B.1). Finally we reclassified land cover data into 7 land cover classes (human development, open cover, evergreen forest, mixed forest, deciduous forest and woody wetland), and calculated for each 30 m grid cell the percentage of each land cover type within a 30 m radius around it. We also calculated the distance from the centroid of each grid cell to water, highways and secondary roads. We excluded those areas classified as lakes for analyses of habitat suitability. We did not include topography, as the study area had low topographic relief.

(e) Corridors

We used the *corridor* function in the R package *move* (Kranstauber & Smolla 2016) to locate the animal defined corridors as described by LaPoint et al. (2013). We used the function's default settings, selecting the upper 25% of the speeds (speedProp=0.75), and lower 25% of the circular variances of the pseudo-azimuths of the segments midpoints, measurement used to identify the near parallel segments (circProp=0.25). This method identifies wildlife corridors relying solely on characteristics of animal movement behavior, classifying the locations of a track into corridor and non-corridor. We calculated for each individual the occurrence distribution of the locations classified as corridors. We defined each contiguous area of the 95% occurrence distribution as a corridor polygon. We identified those corridor polygons composed of only three or less consecutive locations as "outlier" corridors, and reclassified these locations as non-corridor (Figure B.2). After reclassifying the outliers, we calculated two separate occurrence distributions per individual, one for the corridor locations, and one for the non-corridor locations. From the obtained occurrence distribution for the corridor locations, we defined each contiguous area of the 95% occurrence distribution as a corridor polygon, and calculated the maximum length and average width of these polygons with the R library *lakemorpho* (Hollister 2016). To test whether the areas around the corridors had lower habitat suitability, we identified the area immediately surrounding each corridor polygon (Figure B.1 & B.3), with a different width for each species. The width corresponded to the species average step length between locations identified with corridor behavior (black bear: 300 m; bobcat: 200 m; coyote: 400 m; wolf: 600 m).

Once corridors were identified, we investigated if the same corridor was used by the same individual in different years, by individuals of the same species in the same year and in different years, and by individuals of different species in the same and different years. We did this by calculating the degree of spatial overlap of all corridor polygons. We superimposed all the corridor polygons and calculated the percentage of overlap for each of the overlapping polygons. We counted each overlapping pair once, always the one with the highest percentage of overlap.

(f) Landscape heterogeneity

We used the Hill numbers diversity index to measure landscape heterogeneity (Jost 2006). The Hill numbers, a modified Shannon Index, takes into account that the number of land cover types present in each home range is different. This enabled us to compare the diversity indices derived from home ranges with different number of land cover types. We extracted for each individual the number of pixels of each land cover type (Table B.1) within its home range. We used these frequencies to calculate the

Shannon Index for each individual home range using the function *diversity* of the R package *vegan* (Oksanen et al. 2018). The Hill numbers index is obtained by calculating the exponential of the Shannon Index. The higher the Hill numbers index, the higher the diversity in land cover types within the individuals' home range, which indicates a higher heterogeneity of the landscape. We also calculated the Hill numbers index of the corridor polygons and the 95% occurrence distribution of the non-corridor locations of each individual, to test if there were differences in landscape heterogeneity among the home range and the occurrence distribution, i.e., where the animal was observed, differentiating between corridors and non-corridors. We compared the diversity indices of these three areas by means of three pairwise t-tests per species.

We considered two variables as indicators of intensity in corridor use. First, we considered the number of corridor segments identified within an individuals' track, second, we accounted for the number of corridor polygons present in the home range. To investigate if the landscape heterogeneity was determining the intensity in corridor use, we fit one generalized linear model (GLM) with a Poisson distribution, where the number of corridor segments per individual was our dependent variable, and the Hill numbers index, the home range size (m^2) and the number of days the individual was tracked were included as explanatory variables. And we fit another GLM with number of corridor polygons as a dependent variable, and the same explanatory variables as in the previous model. We fitted both models for each species separately, because the sample sizes were very different between species. We also calculated the Pearson's correlation coefficient between the number of corridor segments and the number of corridor polygons per species.

(g) Habitat suitability

We calculated habitat suitability using a step selection function (SSF, Fortin et al. 2005). This function compares the environmental attributes of an observed step (based on two consecutive GPS locations) with a number of random steps that have the same starting point. As observed steps we included those steps with a time lag of approx. 15 min, excluding steps with missing fixes. We generated the random steps from a multivariate normal distribution, using the function *rmvnorm* of the R package *mvtnorm* (Genz et al. 2014), maintaining the variance/covariance structure of speed and turning angle of the empirical track of each individual. The variance/covariance structure of speed and turning angles used to create these random steps was based on the steps without missed fixes. We used 5 random steps per observed step, converting speed to step length by multiplying the random speed by the time between fixes of the corresponding observed step. To model habitat suitability, we compared the environmental characteristics of the end points of each observed step with its 5 corresponding random steps in a binary conditional logistic regression model using the *clogit* function of the R package *survival* (Therneau 2015). The explanatory variables included the proportion within a 30 m radius of human cover, open cover, evergreen forest, mixed forest, deciduous forest and woody wetland, distance to roads, and distance to water. We also included step length and relative turning angle as explanatory variables in the model as the likelihood of realizing a specific option is a function of these two measurements. This accommodates persistence in movement and the relationship between speed and turning angle. When animals move, they will be likely to maintain both their direction of movement and speed as well as a certain relationship between the two metrics. When moving fast (i.e. cover larger distances per time unit) they will be moving with low tuning angles, while when turning resulting in a high turning angles, they usually do so while moving slowly (i.e. covering shorter distances per time unit).

We built a series of SSF models to investigate the habitat suitability and the environmental composition of the home ranges and the corridors. We built one model per individual which contained all locations (*full SSF model*) and calculated the habitat suitability prediction within its home range. Each *full SSF model* per individual was based on 75% of the randomly selected observed locations. We used the remaining 25% of the locations for posterior cross-validation. For each individual we calculated the predicted habitat suitability. For each prediction, we kept distance and relative turning angle constant, selecting a random pair of values from the observed locations. To make the results comparable, we rescaled the predicted values between 0 and 1. We rescaled the data using the normalization formula $X' = (X_i - X_{min}) / (X_{max} - X_{min})$, where X' is the rescaled and X_i the original value. To evaluate the model performance we extracted the predicted value for the 25% excluded observed locations, and also for the same number of random locations selected from the individual's home range. We repeated this a 100 times. With a Kolmogorov-Smirnov test we compared the distribution of the predictive values of the observed locations with each set of random locations. We used the predictions from the *full SSF models*, to compared the predicted habitat suitability values between corridor and non-corridor locations, to test if there were differences between them. For this we extracted the habitat suitability value for each location, calculated the mean ± SD for the corridor locations and non-corridor locations per individual and compared these two values by means of a t-test. We also compared the predicted habitat suitability of each corridor polygon with its immediate surrounding area to investigate if the corridors were surrounded by habitat of lower suitability. For this we extracted the mean ± SD habitat suitability values of the corridor polygons and of their immediate surrounding area, and compared these values using a paired t-test.

We built another SSF model per individual this time only including corridor locations (*corridor SSF model)* to find out if corridors could be predicted in space at the individual level. We calculated the prediction of this model and assessed how well it predicted the corridor locations compared to random points sampled from the individuals home range. Each *corridor SSF model* per individual was based only on corridor locations. For the calculation of random steps of the *corridor SSF model*, we used the variance/covariance structure of speed and turning angle of the non-corridor steps. We calculated the difference between the mean predictive value of corridor locations and the mean predictive value of random locations sampled in the individual's home range, to test how well the *corridor SSF model* could predict corridors. For each individual we sampled the same number of random locations as they had corridor locations, and calculated the difference between the means of the model predictions. We repeated this procedure 100 times to obtain a better estimate of the mean differences of model prediction for random versus corridor locations for each individual.

Finally we wanted to test whether the underlying environmental characteristics of corridors and non-corridors differed. One possible simple approach would be to develop a model for each group of locations, and assess the models' ability to predict the environmental composition of the other group. However for our tracked individuals on average (± SD) only 0.51 ± 0.35% of the total locations were identified as corridors. Notably, any observed difference could be due to differences in sample size rather than reflecting a true difference in the underlying environmental characteristics between these two groups of locations. Therefore, we built for each individual 1000 SSF models including in each of them a random subset of non-corridor locations (*non-corridor SSF model*). Each random subset contained the same number of non-corridor locations as corridor locations of the individual. We evaluated the ability of the *corridor SSF model* and the *non-corridor SSF models* to predict the corridor locations and assessed if the prediction ability differed between these two models. For this we calculated the mean prediction value of the corridor locations for each of the 1000 *non-corridor SSF models* and for the *corridor SSF model*. We then assessed whether the mean predicted value of the *corridor SSF model* was within the distribution of predicted values of the *non-corridor SSF models*. All calculations were done in R 3.3.1 (R Core Team 2016).

RESULTS

(a) Corridor identification and intensity of corridor use

All tracked individuals (Table 2.1), except for one black bear, one bobcat and one coyote, showed corridor usage (Figure 2.2). The number of corridors each individual presented was highly variable across all individuals of all species. We found an average of 42 ± 34 (mean ± SD) corridor segments (black bear: 48 ± 38, bobcat: 22 ± 20, coyote: 31 ± 16, wolf: 70 ± 41) and of 11 ± 8 corridor polygons across all individuals (black bear: 13 ± 10, bobcat: 7 ± 5, coyote: 8 ± 5, wolf: 13 ± 7). The number of corridor segments were highly positively correlated with corridor polygons (in black bears: $r = 0.967$, $DF = 31$, $p > 0.001$, bobcats: $r = 0.918$, $DF = 5$, $p = 0.003$, and coyotes: $r = 0.773$, $DF = 19$, $p > 0.001$). In wolves the correlation was also positive, but not significant ($r = 0.669$, $DF = 5$, $p = 0.099$). With increasing home range size and days of

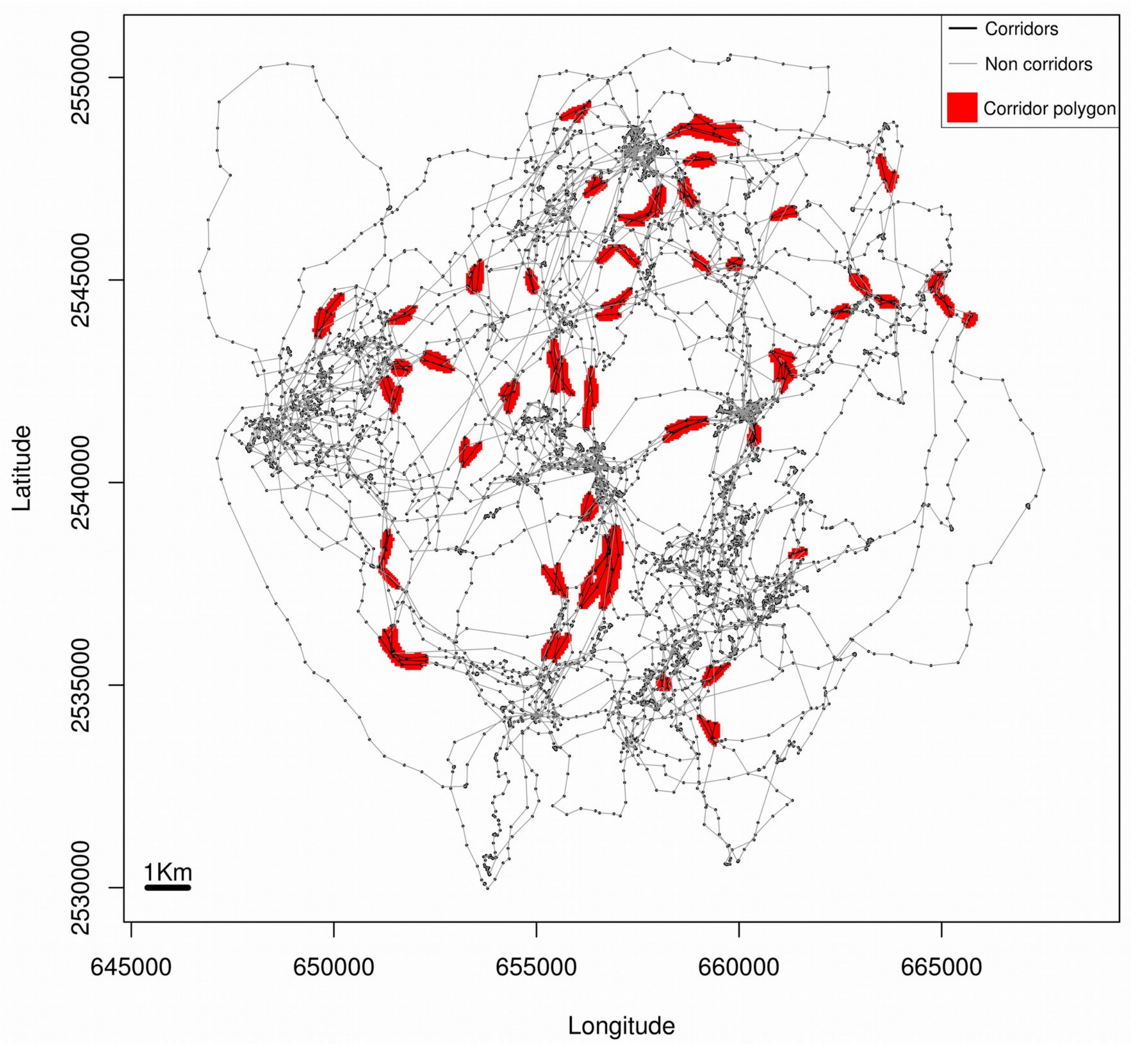

Figure 2.2. **Corridor segments and polygons** (Example of one black bear individual tracked 130 days in 2011)

tracking the number of corridor segments identified increased in black bears, coyotes and wolves, but decreased for bobcats. We found that with increasing landscape heterogeneity the number of corridor segments increased for black bears and decreased for wolves. For bobcats and coyotes we did not find a significant relationship between the number of corridor segments and landscape heterogeneity. We found similar relationships between the number of corridor polygons and home range size, number of days tracked and landscape heterogeneity (Table 2.2).

Table 2.2. Results of generalized linear models explaining intensity of corridor use.

		Corridor segments		Corridor polygons	
Species	**Variable**	**ß (p-value)**	**Deviance explained**	**ß (p-value)**	**Deviance explained**
Black bear	Landscape heterogeneity (Hill numbers)	0.1168 (**)	69.83	0.1172 (ns)	77.83
	Home range size (m^2)	0.0014 (***)		0.0014 (***)	
	Number of days tracked	0.0150 (***)		0.0156 (***)	
	Intercept	1.5912 (***)		0.2156 (ns)	
Bobcat	Landscape heterogeneity (Hill numbers)	-0.0347 (ns)	84.07	-0.0159 (ns)	71.74
	Home range size (m^2)	-0.0020 (**)		-0.0003 (ns)	
	Number of days tracked	0.0241 (***)		0.0165 (***)	
	Intercept	1.1553 (*)		0.4291 (ns)	
Coyote	Landscape heterogeneity (Hill numbers)	0.0470 (ns)	24.87	0.0571 (ns)	44.08
	Home range size (m^2)	0.0017 (***)		0.0029 (***)	
	Number of days tracked	0.0060 (***)		0.0017 (ns)	
	Intercept	2.3062 (***)		1.1291 (*)	
Wolf	Landscape heterogeneity (Hill numbers)	-0.5444 (***)	49.80	-0.3981 (*)	83.32
	Home range size (m^2)	0.0012 (***)		0.0017 (***)	
	Number of days tracked	0.0037 (ns)		-0.0019 (ns)	
	Intercept	6.5771 (***)		4.4767 (***)	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' 1

Corridors varied in size across species; the shortest (148 x 79 m) was from a bobcat and the narrowest (174 x 51 m) from a black bear, while the longest (7878 x 941 m) and widest (3189 x 1572 m) corridors were from wolves. Wolves had on average (± SD) the longest corridors (1385 ± 998 m) and bobcats the shortest (372 ± 157 m). Black bears and coyotes had a similar mean corridor size of 727 ± 406 m and 792 ± 424 m, respectively. The mean aspect ratio of the corridors for all species was similar with a mean (± SD) of 2.8 ± 1.1 (range = 1.2-10.9).

We found corridors to be used by the same individual over several years, and also

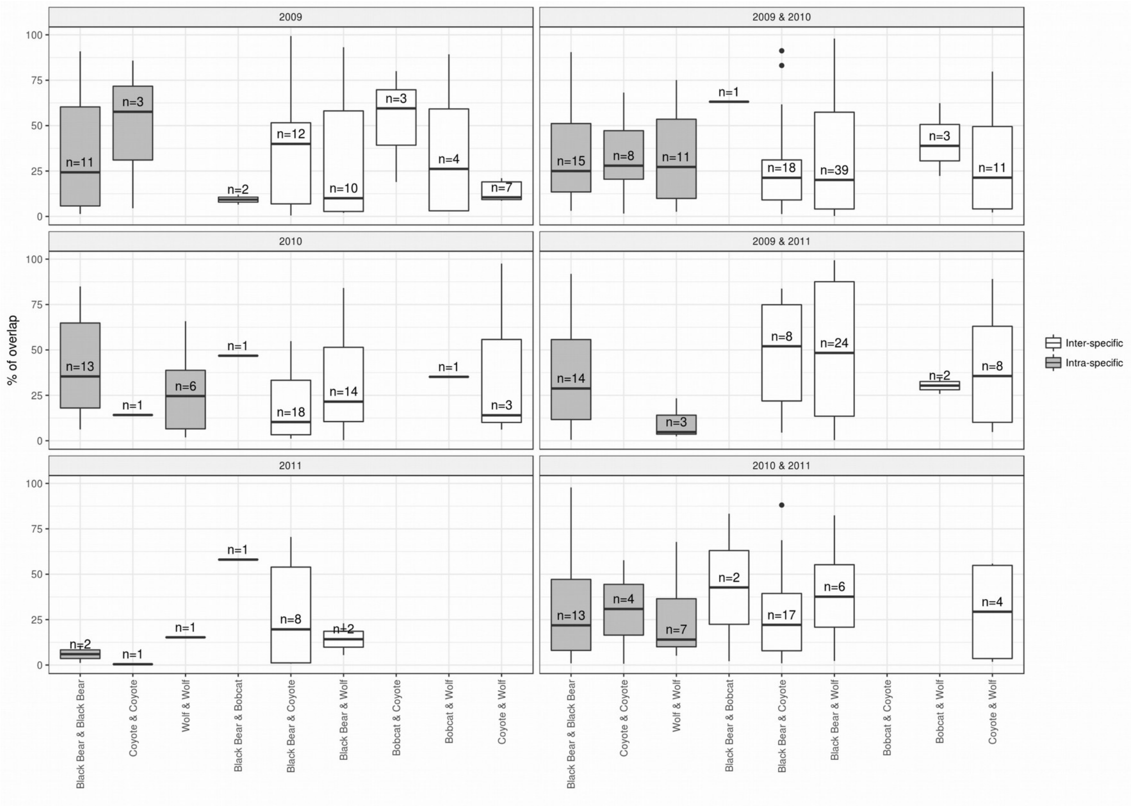

Figure 2.3. Overlap of corridors. Percentage of overlap of corridors within species and among species within the same year and among years. Each overlapping pair is counted once, always the one with the highest percentage of overlap. "n" represents the number of overlapping pairs of corridors. Overlap between corridors used by the same individual over several years are excluded, and represented separately in Figure B.4.

corridors used by several individuals of the same or different species. Black bears showed the highest number of corridors shared intra-specifically, but they also had the highest overlap with all other species, especially coyotes and wolves. In contrast, bobcats did not share corridors intra-specifically, and their corridors only occasionally overlapped with those of other species (Figure 2.3, Figure B.4). We found all possible combinations of overlapping corridors including a black bear that used several of the same corridors during the 2 consecutive years (Figure 2.4A), overlapping corridors of individuals of the same species tracked during the same (Figure 2.4B), or different years (Figure 2.4C), and overlapping corridors of individuals of different species tracked in the same year (Figure 2.4D).

(b) Habitat suitability within and around corridors

The *full SSF model* performed well in predicting overall habitat suitability (Figure B.5). The distribution of the predicted values of habitat suitability of the locations left out for validation, differed from the distribution of randomly sampled locations from the

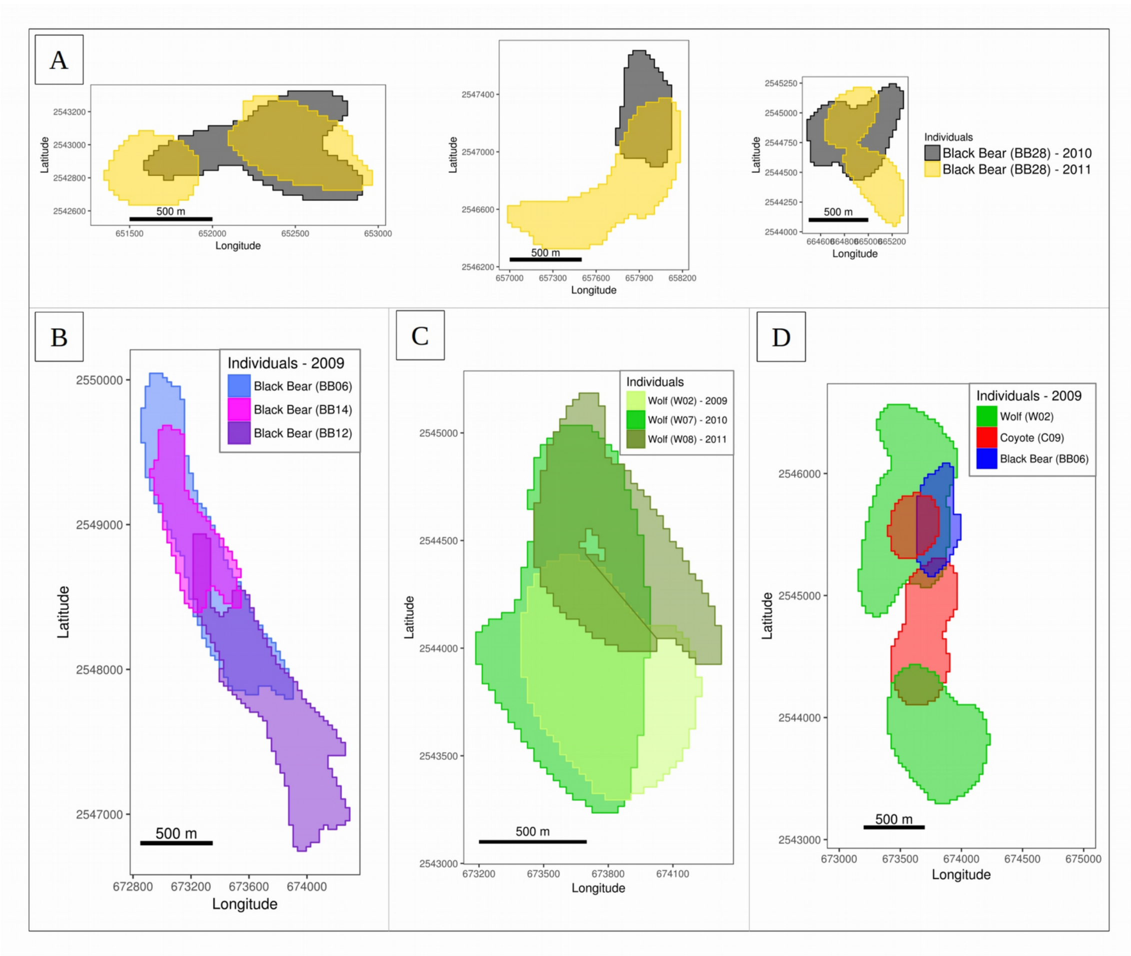

Figure 2.4. Examples of overlaying corridors. (A) Corridors of 2 different years of the same black bear. (B) Corridors of 3 black bears overlapping in the same year. (C) Corridors of 3 wolves overlapping in different years. (D) Corridors of 3 individuals of 3 species overlapping in the same year.

prediction map for all individuals (Kolmogorov-Smirnov tests; black bear: D = 0.30 ± 0.12, $p < 0.001$; bobcat: D = 0.25 ± 0.10, $p < 0.001$; coyote: D = 0.28 ± 0.10, $p < 0.001$; wolf: D = 0.32 ± 0.18, $p < 0.001$; D = mean ± SD). Habitat suitability was lower in corridors than in non-corridors for the vast majority of individuals across all species (black bear: 91%, bobcat: 86%, coyote: 95%, wolf: 100%). Although for 75% of these individuals this difference was significant, the difference between the values was very small, 0.05 ± 0.03 (mean ± SD across all individuals and species, Table B.2). Interestingly, we did not find a significant difference between habitat suitability within the corridor polygon and its immediate surrounding area (Table B.3).

(c) Environmental composition of corridors

For black bears, bobcats and wolves the landscape heterogeneity within the corridor and non-corridor areas was lower than within the entire home range. For wolves this difference was not significant. We did not find any differences in landscape heterogeneity for coyotes (Figure 2.5). When comparing the landscape heterogeneity between corridor and non-corridor areas we did not find any differences in any of the species (Figure 2.5).

The *corridor SSF models* which we built to predict corridors in space had a poor performance. Although for most individuals these models were able to predict the corridor locations better than random locations drawn from their home range (Figure B.6), the differences between the predictive values of the corridor and the random locations were very small, 0.037 ± 0.031 (mean ± SD across all tracks with corridor behavior (n= 67)). We also found that the underlying environmental characteristics between corridors and non-corridors was not distinguishable for most individuals. Only in 12% of the individuals on average (black bears: 15%, bobcats: 17%, coyotes: 10%, wolves: 0%), the predictions of corridor locations from the *corridor SSF model* were better than 95% of the values obtained from the *non-corridor SSF models* (Figure B.7).

DISCUSSION

We found that corridors identified solely by the movement behavior of the individuals within a home range, were virtually indistinguishable from the surrounding areas using typical landscape metrics previously employed in corridor studies. Our

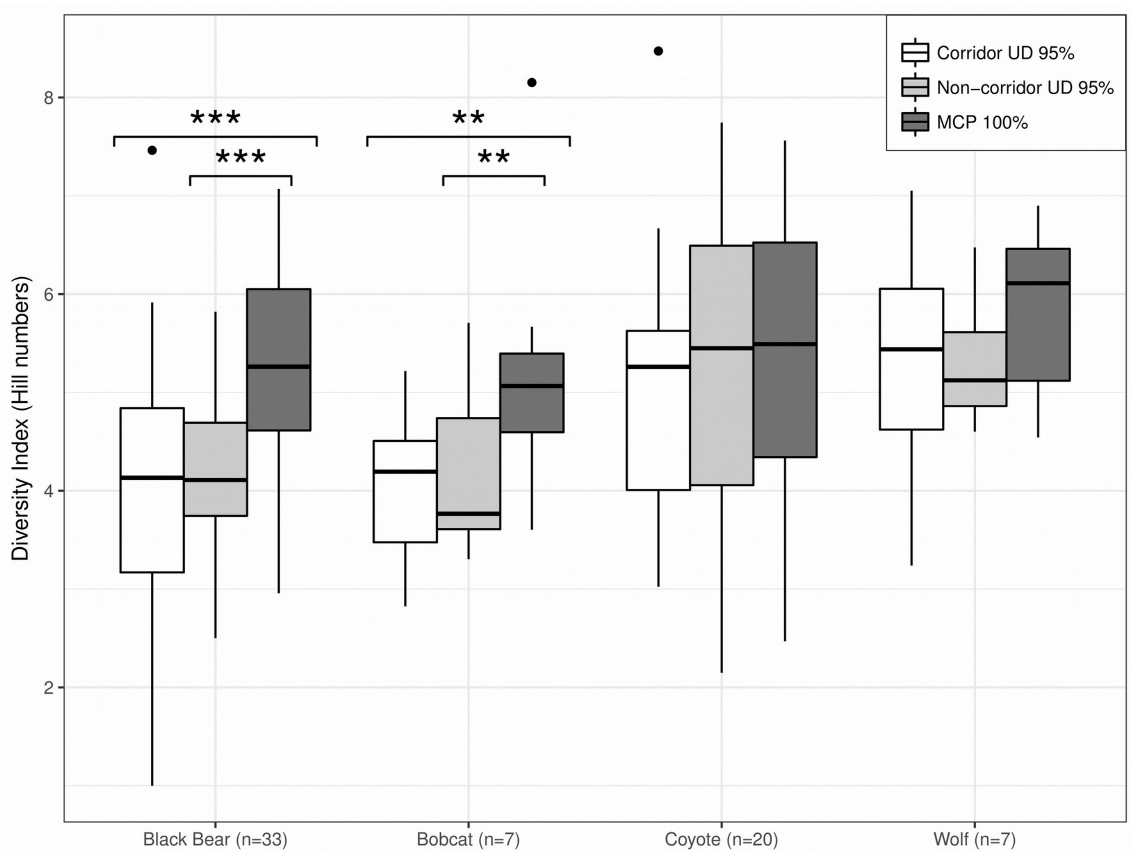

Figure 2.5. Landscape heterogeneity comparison in home range, non-corridor occurrence distribution and corridor occurrence distribution. *** : p- value < 0.001. All other pairs did not show a significant difference. "n" represents the number of individuals included in the analysis.

corridor models predicted corridor locations marginally better than random points. As the corridor models were based on locations that also correspond to a behavioral state of traveling, they probably predict areas suitable not only for corridors, but for all directed movements (Abrahms et al. 2016). Additionally, the sample size of relocations used to build the corridor models was quite small, which could have influenced the model performance.

We observed a high degree of variation in the number of corridors used by individuals tracked in our study. This variation was partly explained by the duration of the tracking period. The longer an individual was tracked increased the chances of recording revisits to the same areas and thus detecting corridor behavior. Beyond tracking duration, however, landscape heterogeneity could not completely explain the remaining variation. We expected a greater heterogeneity of the landscape to imply greater patchiness of the habitat, which seemed not necessarily to be the case. LaPoint et al. (2013) found a difference in corridor use between fishers (*Pekania pennanti*) occupying home ranges with different levels of landscape heterogeneity. In their study fishers located in a heterogeneous suburban area showed corridor usage, whereas those inhabiting a homogeneous forested area did not use corridors. The landscape heterogeneity among the tracked individuals in our study may have been less extreme than in previous studies, wherefore we might not have been finding a clear relationship between the variation in intensity of corridor use and the landscape heterogeneity.

The areas identified as corridors in most individuals across all species had lower habitat suitability values than the areas identified as non-corridors. However, the small differences detected can hardly be considered biologically relevant. The variability of habitat suitability was both within corridor and non-corridor location an order of magnitude higher than the difference between these 2 groups of locations. The corridors also did not contain habitat with higher suitability than the adjacent areas surrounding them. These findings clearly fail to support the general theoretical assumption of corridors being defined as relatively suitable habitat surrounded by less suitable habitat (e.g. McRae et al. 2008; Beier et al. 2008; Sawyer et al. 2011) providing the basis for a resistance landscape. Nevertheless, we cannot exclude the possibility that the choice of the size of the immediate surrounding area of the corridor might have been too large. By including areas that should have been considered non-corridors, we might have missed potential differences. The size of the area delineating a corridor likely depends on many factors. For example, it could depend on the perception distance of the species, the characteristics of the landscape or the length of the corridor and there may not be a means to define corridors generally. We chose an average step length distance as the width of the immediate surrounding area, because in the multiple times they used the corridor, theoretically they could have, at any time, taken a step outside of the corridor instead of continuing straight ahead. We assumed this directed movement shaping the corridor to be an "avoidance" behavior to the surrounding area of the corridor.

Where corridors come to be placed in the landscape is probably a consequence of many factors. Their placement could depend on environmental features that are not detected with existing remote sensing technology or our analysis, such as the permeability of the landscape (e.g. vegetation density of the forest understory). Individuals likely select their travel paths where the composition of the vegetation provides the least physical resistance to movement. It is possible that land cover itself is not the most important factor, but the geometry of the patch itself or that of the neighboring patches. Furthermore, the spatial location of corridors in the landscape can be also “learned” and inherited and thereby have become landscape features themselves. Individuals of the same pack or family group may “learn” a given path from the other members of the group, and reuse this path, e.g. a convenient place to cross a road or river (Strandburg-Peshkin et al. 2017). Our results demonstrate spatial overlap of corridors from multiple individuals of the same and different species. Although these findings are anecdotal, as only a very small portion of the animals present in the study area were captured and tagged, they also represent minimum estimates of corridor use by multiple individuals. Often a diversity of species are recorded along corridors identified for one individual (e.g. LaPoint et al. 2013). This result supports the idea that a particular feature of those areas rather than the environmental conditions pertaining to specific species’ ecology triggered individuals to exhibit corridor behavior. This finding suggests that identifying corridors used by multiple species simultaneously would ultimately enhance conservation efforts.

We found that at a level of home range movement, animals did use corridors. Our results however suggest that corridors were not directly linked to habitat suitability, and we thus could not identify landscape attributes characterizing them. These results open up the question a as to whether studies that identify corridors using a cost-based model relying on general habitat suitability may place corridors in the wrong places, at least at an individual level within home ranges. The areas where animals of various species chose to establish their corridors, were not the same areas we would have suggested using models relying on habitat suitability models and the set of generally available remote sensing information (LaPoint et al. 2013). We suggest future studies to rely more on movement data when attempting to identify wildlife corridors.

CONCLUSIONS

Surprisingly, most individuals used corridors within their home ranges. Several corridors were used simultaneously by individuals of the same species, but some were also shared between different species. This gives an indication that there probably is something in the environment that triggers the corridor behavior. However, we found no direct link between corridors and habitat suitability, or defining environmental characteristics identifying actual corridors. We also found no difference between predicted habitat suitability of corridors and their immediate surrounding area. This leads us to speculate that identifying corridors relying on the habitat suitability methods only, may misplace corridors at the level of space use within an individual's home range. We suggest future studies when possible to rely more on movement data than on habitat suitability measures to identify wildlife corridors based on empirical evidence.

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Multi-species habitat restoration models are more than the sum of the parts

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ABSTRACT

Restoring degraded landscapes is expensive and time consuming. Hence, efficiency is a crucial aspect in improving degraded landscapes. Although degradation of landscapes usually affects many species, restoration initiatives often are focused on single species because habitat quality assessment is predominantly conceptually centered around single species. One solution to the challenge of restoration at community level could be to direct restoration specifically to areas of low suitability for multiple species simultaneously to avoid antagonistic actions by altering habitat that is unsuitable for one species, but may be still suitable for another. We used a large data set of four large carnivore species that were tracked simultaneously in the same area to develop habitat suitability predictions and investigate theoretically the possible benefit of such a restoration approach. There was an increase of total area with highly suitable habitat for all species when modifying the values of the environmental variables of areas with low habitat suitability for all species (multi-species approach). When modifying the values of the environmental variables of areas with low suitability for each species separately (single-species approach), the area with highly suitable habitat increased for the focal species, but had no positive nor negative effect on the other species. Despite the dissimilar habitat preferences of the four carnivore species, the multiple-species approach was able to improve the habitat for all species simultaneously. Our results highlight the utility of focusing on the common unsuitable habitats of a community when planning restoration actions. A multi-species approach can avoid inadvertent antagonistic effects on communities, or at least ensure spatial prioritization of areas with beneficial collateral effects, increasing the effectiveness of the invested resources.

INTRODUCTION

Habitat degradation, fragmentation and loss are major threats to biodiversity worldwide (Schipper et al. 2008). Restoration of degraded landscape aims to improve overall habitat quality and strategically increase connectivity among fragments of suitable habitat (Young 2000). Restoration, however, is a costly and time intensive process, necessitating a maximization of effectiveness (Holl et al. 2003; Noss et al. 2009). The most defining steps in any restoration effort are site selection and the types of actions selected for altering the landscape to fulfill restoration goals. Currently, there are different approaches to restoration. One approach aims to restore an ecosystem back to its pristine conditions, with emphasis usually on the vegetation (Wilson et al. 2011), though some also aim to restore elements that maintain ecosystem processes (Licht et al. 2010). Other approaches focus on restoring the vegetation for a specific species (Heer et al. 2013), or restoring an animal species in an area where it was extirpated (Carroll et al. 2003). Each of these approaches have limitations; for example, how far should we go back in time to consider an ecosystem pristine (Choi 2007)? Or, what are the consequences for other species if we change the environment taking in consideration only one particular species (Lindenmayer et al. 2002)? Likewise, if we reintroduce an animal species to a previously occupied ecosystem, is the system, in its possibly altered condition, still able to support this species (Carroll et al. 2003)? Here, we refer to restoration as the process of modifying a landscape to increase its habitat suitability for a given species.

Although landscape degradation usually affects multiple species simultaneously, often only single focal species are considered in restoration initiatives. In addition, there are different approaches used to determine which of the areas under consideration should be prioritized for restoration (Holl et al. 2003; Noss et al. 2009; McBride et al. 2010). Often these decisions are based on expert opinion, taking into consideration the ecology and the environmental features of the habitat, and also socio-political and economic aspects such as land ownership or property value (Holl et al. 2003). Sometimes, a focal species is chosen based on its suitability to act as an "umbrella" species, based on the idea that improving habitat for this species will have a positive effect on the other species in the community (Branton & Richardson 2014). However, there is often a lack of a systematic procedure in the decision making process of selecting sites to restore (Noss et al. 2009; McBride et al. 2010). The difficulty of an approach that considers a community of species, is that habitat quality assessments are predominantly centered around single species. Considering that improving habitat for one species could result in degradation for another, one solution could be to direct restoration to those areas that are unsuitable for all species under consideration. Thus, restoration initiatives could be designed to generate beneficial effects for a wider range of species and avoid the potential adverse effects of a single species restoration approach.

Here, we used a large data set of four carnivore species which were tracked simultaneously in time and space. We chose this data set as it is suitable to test our hypothesis that restoration efforts will be more economical and effective ecologically if habitat needs of multiple species are simultaneously considered. These four species have stable populations occurring in a partially-altered landscape without need of immediate conservation action or restoration. The associated data, however, provides a rare and unique opportunity to investigate quantitatively the suitability of different procedures in identifying areas for restoration in an empirical and realistic setting for these species. We established a modeling and prioritization procedure to identify areas for restoration that will benefit multiple species simultaneously. We contrast our multi-species restoration approach with the more traditional single-species approach. We hypothesized that restoring common unsuitable areas for multiple species simultaneously will (1) prioritize different areas for restoration than if each species was considered separately, and (2) be more effective by increasing habitat suitability in a balanced fashion, avoiding inadvertent negative (antagonistic) effects on communities by single species restoration. In this study we tested only the theoretical feasibility of restoring common unsuitable areas of multiple species, and did not consider the feasibility of implementing the changes in the environment, as this would be a second step and case specific for further studies to examine.

MATERIAL & METHODS

(a) Study area

The study area covered about 2800 km^2 within Delta and Menominee counties in the Upper Peninsula of Michigan, USA (45°35'0.00"N, 87°23'0.00"W). The main cover types on the study area included woody wetlands (44%) (e.g., black spruce *Picea mariana*, green ash *Fraxinus pennsylvanica*, northern white cedar *Thuja occidentalis*, speckled alder *Alnus incana*), deciduous forest (17%) (e.g., sugar maple *Acer saccharum*, quaking aspen *Populus tremuloides*), and agriculture (12%) (i.e., row crops and pastures). The remaining 27% of the study site included conifer forest, mixed forest, urban areas, roads, herbaceous wetlands, shrub, and open water (NLCD 2011; Jin et al. 2013). Land covers with direct human influence (agriculture, urban areas and roads), represented 18% of the study area. It was relatively flat, with an elevation range from 170 to 310 m.a.s.l. and the mean road density was 1.2 km/km^2.

(b) Tracking data

During March-August 2009 - 2011 we captured and immobilized 25 black bears (*Ursus americanus*), 7 bobcats (*Lynx rufus*), 21 coyotes (*Canis latrans*) and 7 wolves (*Canis lupus*) (Table C.1). We fitted all individuals with Lotek GPS collars (model 7000MU for black bears and 7000SU for bobcats, coyote and wolves; Lotek Wireless, Newmarket, Ontario, Canada), programmed to obtain a location every 15 minutes between the 1 May and 30 September. We located black bears collared the previous year in their winter dens, immobilized them and replaced their GPS collars. The collars fitted to bobcats, coyote and wolves included drop-off mechanism to release collars 30 weeks after deployment. The data of all collars could be downloaded remotely. For the data analysis in this study we used the GPS fixes recorded within the time window from 1 May - 30 September 2009 - 2011. If individuals were trapped during this time window, we removed the first 5 days of tracking data collected after collaring to avoid possible effects of capture and handling on movements and habitat selection analysis.

(c) Ethical statement and trapping procedure

Ethics of all capture and handling procedures were approved by the Mississippi State University Institutional Animal Care and Use Committee (#09-004). Also, animal capture and handling procedures followed guidelines established by the American Veterinary Medical Association and the American Society of Mammalogists (Sikes et al. 2011). Details of capture and handling procedures are described in Stillfried et al.

(2015; black bears), Svoboda et al. (2013; bobcats), Etter & Belant (2011; coyotes) and Petroelje et al. (2013; wolves).

(d) Environmental data

We obtained land cover data from the 2011 National Land Cover Database (Jin et al. 2013) at 30 m resolution, and complemented this map with data for highways, secondary roads (United States Census Bureau 2011), rivers and lakes (United States Geological Survey 2016). We rasterized highways, secondary roads, rivers and lakes at the resolution of the land cover data (30 x 30 m). Though most roads and rivers are not

Table 3.1. Environmental variables

Variables	Description	Source
Land Cover	Water, developed open, developed low, developed medium, developed high, barren, deciduous forest, evergreen forest, mixed forest, shrub, grassland, pasture, crops, woody wetland, herbaceous wetland, rivers, lakes, highways and secondary roads	NLCD11 Classes* Rivers§; Lakes$ Highways# Secondary roads#
% Human cover	% of land covers with human presence (urban areas and roads) within a 30 m radius circle from each 30m grid cell	NLCD11 Classes: 21,22,23,24,27* Highways# Secondary roads#
% Open cover	% of grasslands, shrubs, crops, barren within a 30 m radius circle from each 30m grid cell	NLCD11 Classes: 31,52,71,81,82,95*
% Evergreen forest	% of evergreen forest within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 42*
% Mixed forest	% of mixed forest within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 43*
% Deciduous forest	% of deciduous forest within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 41*
% Woody wetland	% of woody wetland within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 90*
Distance to highways (m)	Distance from each grid cell to highways	Highways#
Distance to secondary roads (m)	Distance from each grid cell to secondary roads	Secondary roads#
Distance to water (m)	Distance from each grid cell to rivers and lakes	NLCD11 Class: 11* Rivers§; Lakes$

* Classes correspond to the classification of the National Land Cover Database 2011 legend (NLCD 2011; Jin et al. 2013).
# Classification of highways and secondary roads as provided by the United States Census Bureau (United States Census Bureau 2011).
§ Rivers correspond to the NHDFlowline layer with the feature type "stream/river" according to the NHD classification (United States Geological Survey 2016).
$ Lakes correspond to the NHDWaterbody layer, excluding the feature type swamp/marsh (United States Geological Survey 2016).

30 m wide, our GPS collars had a position error of about 20 m and we considered this resolution adequate for our analysis. We reclassified the pixels in the original land cover layer corresponding to highways, secondary roads, rivers and lakes (Table 3.1). Finally we reclassified land cover data into 7 land cover classes (human development, open cover, evergreen forest, mixed forest, deciduous forest and woody wetland), and calculated for each 30 m grid cell the percentage of each land cover type within a 30 m radius around it. We also calculated the distance from the centroid of each grid cell to water, highways and secondary roads. We excluded those areas classified as lakes for analyses of habitat suitability. We did not include topography, as the study area had low topographic relief.

(e) Habitat suitability

We calculated habitat suitability using a step selection function (SSF, Fortin et al. 2005). This function compares the environmental attributes of an observed step (based on two consecutive GPS locations) with random steps that have the same starting point. We included steps with a time lag of about 60 min, based on visual inspection of the variogram (Fleming et al. 2014) which we displayed using the R package *ctmm* (Fleming & Calabrese 2016). The step selection functions assume that successive steps have uncorrelated speeds. This condition can be identified in the variogram at the time interval where the variogram starts to become linear after an initial concave phase. Steps with missing fixes, i.e. with time lags larger than 60 min, were excluded. We generated 100 random steps per each observed step. We sampled these random locations based on parametric distributions for turning angle (uniform) and step lengths (exponential with parameter λ equals twice the sample mean of observed step lengths).

To model the habitat suitability for each species, we compared the environmental characteristics of the end points of each observed step with its 100 corresponding random steps, in a binary mixed conditional logistic regression model using the *Ts.estim* function of the R package *TwoStepCLogit* (Craiu et al. 2016). The explanatory variables differentiating random and realized steps included percentage within a 30 m radius of human development, open cover, evergreen forest, mixed forest, deciduous forest and woody wetland, distance to highways, distance to secondary roads, and distance to water. We also included step length in meters and the cosine of the relative turning angle calculated in radians as explanatory variables. In the *group* term of the function we included the names of the individuals included in the model. We built one model per species, based on 75% of the randomly selected observed steps of each individual. We used the remaining 25% of the steps for posterior cross-validation. For each species we then calculated the predicted habitat suitability. For each prediction, we used a distance and relative turning angle of zero. To make the results comparable, we rescaled the predicted values between 0 and 1. We rescaled the data using the normalization formula $X' = (X_i - X_{min)} / (X_{max} - X_{min})$, where X' is the rescaled and X_i the original value. To evaluate model performance we extracted the predicted values for the 25% excluded steps, and also for the same number of randomly selected locations within the study area (100% minimum convex polygon of all individuals of all species). We repeated this 100 times and compared the distribution of the predicted values of the cross-validation locations with the random locations, to investigate if these two distributions differed in median, variability or shape with a Kolmogorov-Smirnov test.

(f) Multi-species restoration

For our theoretical exercise we aimed to identify a maximum of 5% of the study area (140 km^2) to restore for all 4 carnivore species simultaneously. In real case scenarios the size of the selected area will depend on case specific factors. We used the traditional default threshold of 0.5 to divide the predicted habitat suitability in suitable and unsuitable (Franklin 2010). We then identified those areas where the models predicted unsuitable habitat for all four species and calculated the geometric mean of the predicted values for these areas. We selected the pixels with the highest geometric mean values in a decreasing order prioritizing the top 5% (140km^2) for restoration. We prioritized for restoration those areas with the highest suitability values because highly degraded areas of very low suitability, may not be recoverable (Miller & Hobbs 2007) or require too much effort and money to restore. Our aim was to identify the change necessary in the environmental conditions of these areas to make them more similar to the conditions of the suitable areas. For this we compared the distribution of each environmental variable in the areas to be restored with the same number of pixels randomly sampled from the areas where the habitat was suitable for all four species simultaneously. We compared the distributions for each variable with a Kolmogorov-Smirnov test, and selected those that differed. We then calculated the factor of increase/decrease between the two areas based on the mean value of the areas to be restored and the mean value of sampled common suitable areas of each environmental variable. To assess the potential effect in the change in habitat suitability after a restoration we multiplied the selected environmental variables in the areas to be restored by their corresponding factor. Thus, we calculated a new prediction of habitat suitability based on the previously calculated step selection functions per species for the areas to be restored and compared the habitat suitability values of the areas to be restored of the models before and after modifying the environment.

(g) Single species restoration

For the single species restoration modeling we followed the same procedure as in the previous section, but for each species separately. For each species we selected the pixels with the top 5% of the unsuitable area (140 km^2). For each species, we also calculated the factor of increase/decrease between the mean values of the variables selected in the two areas (to restore and suitable), and multiplied these environmental variables by their corresponding factor following the same procedure as described above. We then used this new set of environmental variables to estimate habitat suitability of the focal species for the areas to be restored. To estimate how these single species restorations approaches would affect the other carnivore species, we calculated the change in the habitat suitability due to restoration in the habitat of the other three species. All calculations were done in R version 3.3.1 (R Core Team 2016).

RESULTS

The step selection functions performed well in predicting habitat use of each of the four species (Figure C.1). The results of the Kolmogorov-Smirnov test indicated that the distribution of habitat suitability values of the true locations was greater than the values of random points (Black bear: $D = 0.26 \pm 0.02$, $p < 0.001$; Bobcat: $D = 0.37 \pm 0.02$, $p < 0.001$; Coyote: $D = 0.35 \pm 0.02$, $p < 0.001$; Wolf: $D = 0.18 \pm 0.02$, $p < 0.001$;

(mean ± SD)). Overlaying the habitat suitability predictions of the four species revealed that 14% (390 km^2) of the study area was unsuitable for all species simultaneously. When considering only suitable habitat, there was an overlap of only 9.6% (270 km^2) of the study area between all four species (Figure 3.1). The areas selected to restore in the multi-species approach differed from those selected for each species using the single-species approach (Figure 3.2). The areas selected for restoration for black bears, bobcats and wolves had minimal overlap with the areas selected in the multi-species approach (black bears: 0.7%, bobcats: 1.6%, wolves: 0.9%). The overlap with areas selected for restoration for coyotes was larger (64.7%).

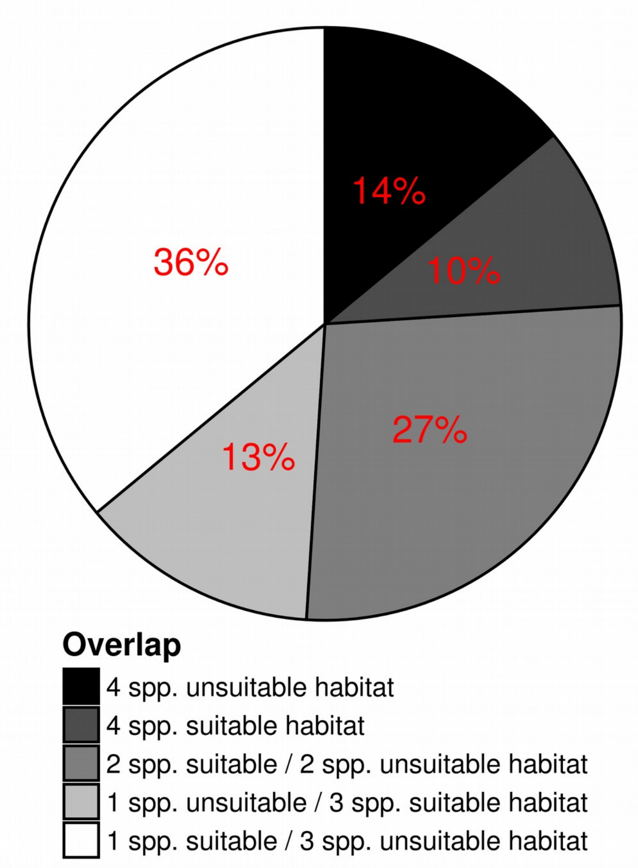

Figure 3.1. Percentage of area overlapping with suitable and/or unsuitable habitat between different number of species.

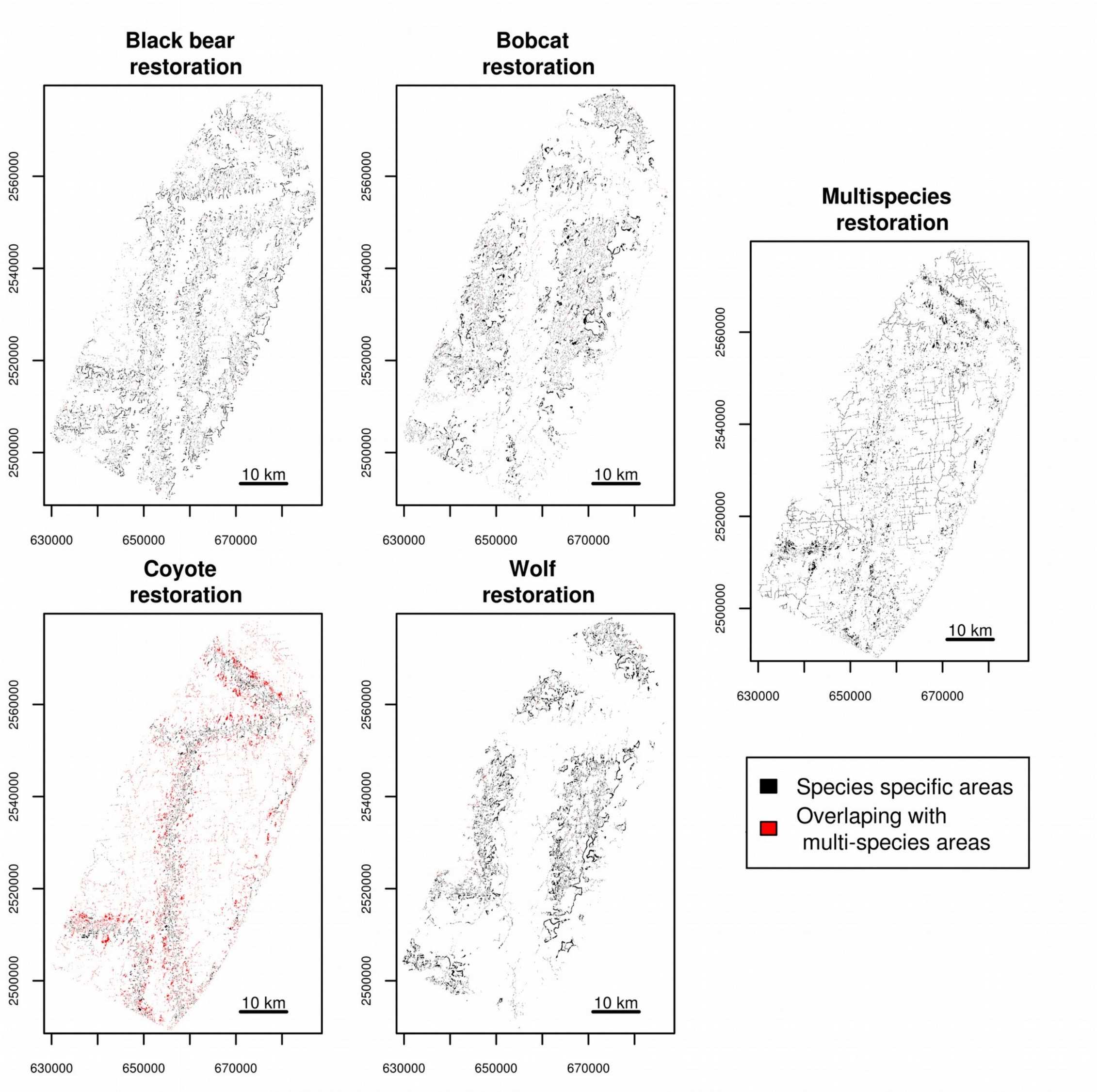

Figure 3.2. Areas selected for restoration for the multi-species and each single species approach. In all cases the selected area corresponds to 140 km^2 (155973 pixels). Areas in red in the single species approaches correspond to areas that also were selected in the multi-species approach.

In the **multi-species restoration** the values of habitat suitability each species contributed to the selected area for restoration differed; consequently, some selected areas contained lower habitat suitability values for some species than for others (Figure 3.3A). All comparisons of the distributions of each environmental variable between the areas to restore and the suitable areas differed ($p < 0.01$) The low p-values indicate that the two distributions differed in median, variability or shape. Given our high number of points contributing to the distributions, small differences were significant. Therefore, we only selected those variables that presented a statistic D-value larger than 0.1 (Table C.2). By modifying the environmental variables (Table 3.2) we obtained a large variation in the degree of change in habitat suitability values, but were overall able to improve average habitat suitability values for all four species 12 % (Black bear: 9.4 ± 15.6%; Bobcat: 15.1 ± 14.3%; Coyote: 9.1 ± 16.4%; Wolf: 15.2 ± 11.4% (mean increase ± SD); Figure C.2). We aimed to increase the total area with suitable habitat by 5%, and with this approach the area of suitable habitat across all species increased on average (±SD) 1.9 ± 0.36 % (Black bear: 1.7%, Bobcat: 2.1%, Coyote: 2.3%, Wolf: 1.5%; Table 3.3). Although the habitat suitability value increased for most pixels, some did not exceed the 0.5 threshold and consequently we did not reach the target 5% increase in suitable habitat area (Figure C.2).

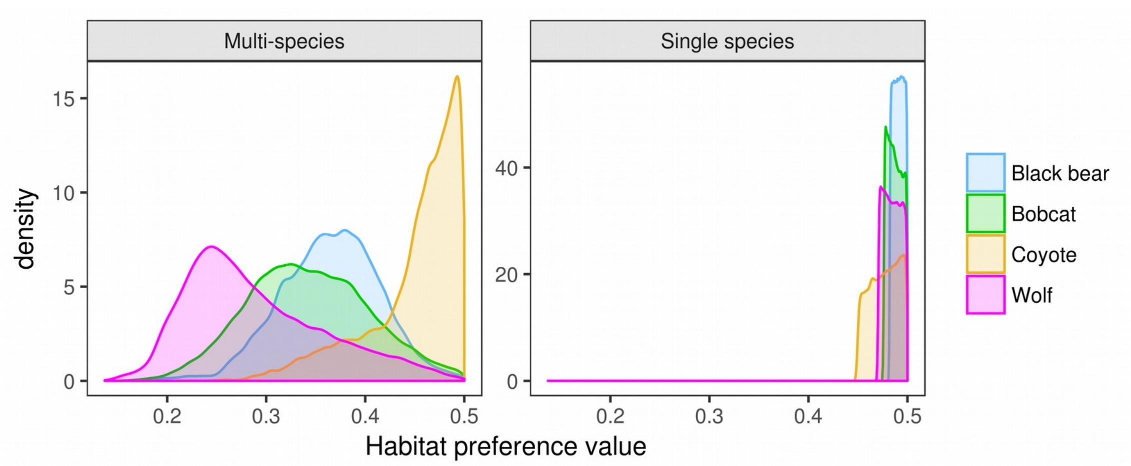

Figure 3.3. Contribution per species of habitat suitability values of the pixels to restore. (A) Multi-species approach. (B) Single-species approach.

Table 3.2. Factor of change of the environmental variables used in each restoration approach. The values of the environmental variables in the selected areas were multiplied by these numbers "to be restored".

Variables	Multi-species restoration	Restoration for black bears	Restoration for bobcats	Restoration for coyotes	Restoration for wolfs
Distance highways	2.639	1.676	1.252	2.099	1.311
Distance second roads	2.121	1.525		1.742	1.290
Distance water	0.902		0.660	1.303	
% woody wetland in 30m	4.600	1.198		3.951	
% deciduous forest in 30m	0.234			0.316	
% human cover 30m	0.042			0.099	
% open cover in 30m				1.866	
% mixed forest in 30m				0.453	
% evergreen forest in 30m					

In the **single species restoration** the values of habitat suitability in the selected areas to restore the focal species exceeded 0.45, much higher than in the multi-species approach (Figure 3.3B). When we overlapped the selected areas for restoration for each species, there were no pixels shared by all four species. In 0.07 % of the area three species overlapped, but 94.5% were only selected for one species (Figure 3.4). If we intended to restore 5% of the study area for each species, but selected the areas based on single species approaches, we would have to restore nearly 4 times more area (532 km^2) than needed to restore 5% of the study site for each species using the multi-species approach (140 km^2).

The environmental variables modified in the restoration exercise for each species differed. In this case we also only selected those that presented a D statistic higher than 0.1 (Table C.2). In most cases the variables had the same direction of change but of different magnitude, and no antagonistic effects were expected. The exception was

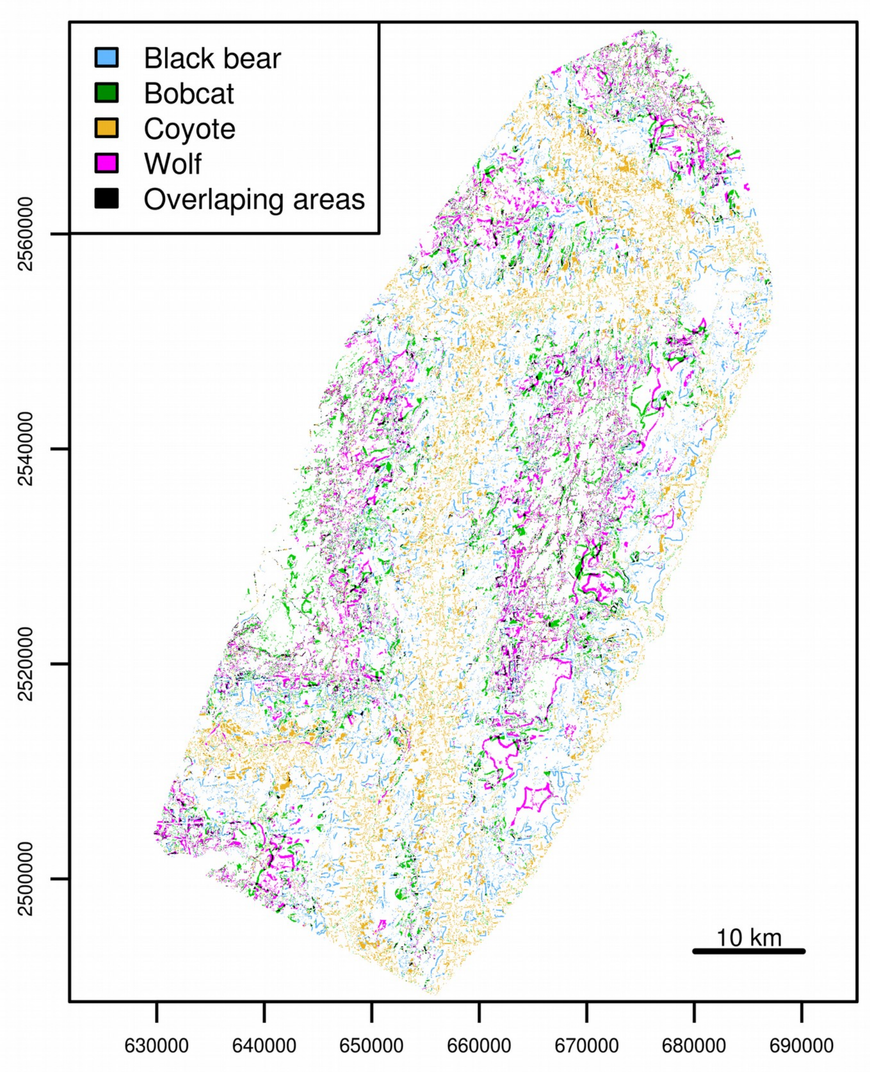

Figure 3.4. Areas selected for restoration for each of the single specie approaches. "Overlapping areas" refer to selected areas that overlap for 2 or 3 species.

distance to water, where the restoration for bobcats suggested decreasing distance to water, whereas in the coyotes, areas for restoration should be further from water (Table 3.2). The selected areas to restore for each focal species had a lower increase in habitat suitability values after restoration than in the multi-species approach (Black bear: 11.4 ± 4.3%, Bobcat: 4.9 ± 2.3%, Coyote: 2.1 ± 9.4%, Wolf: 9.2 ± 1.8%). For the non-focal species in each case, the mean increase in habitat suitability values was small (mean ±

SD = 3.6 ± 4.5%); in some cases the average outcome was an overall decrease in habitat suitability (Figure C.2, Table C.3). For the focal species (except coyotes) the area of suitable habitat increased close to the aim of 5%, therefore more than with the multi-species approach, but for the non-focal species, this increase was always less than 1% (Figure 3.5).

DISCUSSION

Despite different habitat preferences among species, the multi-species approach identified candidate areas for restoration into suitable habitat for all species simultaneously. With the single species approach, the increase in net area to restore into suitable habitat was higher for the focal species, but minimally affected non-focal species. With the multi-species approach, however, all species benefited from a single concentrated action, although the overall increase in area of suitable habitat per species was lower than with each single species approach.

Table 3.3. **Percentage of suitable habitat in the study area, before and after restoration**. The number in brackets is the percentage of increase in area of suitable habitat after restoration.

			After restoration				
				Focal species			
		Before restoration	Multi-species	Black bear	Bobcat	Coyote	Wolf
Affected species	**Black bear**	46.1	47.8 (+1.7)	51.1 (+5)	46.2 (+0.1)	46.4 (+0.3)	46.6 (+0.5)
	Bobcat	18.2	20.3 (+2.1)	18.2 (+0)	22.9 (+4.7)	19.0 (+0.8)	19.1 (+0.9)
	Coyote	85.8	88.1 (+2.3)	85.8 (+0)	85.8 (+0)	87.2 (+1.4)	85.9 (+0.1)
	Wolf	18.5	20.0 (+1.5)	19.0 (+0.5)	19.5 (+1)	18.8 (+0.3)	23.5 (+5)

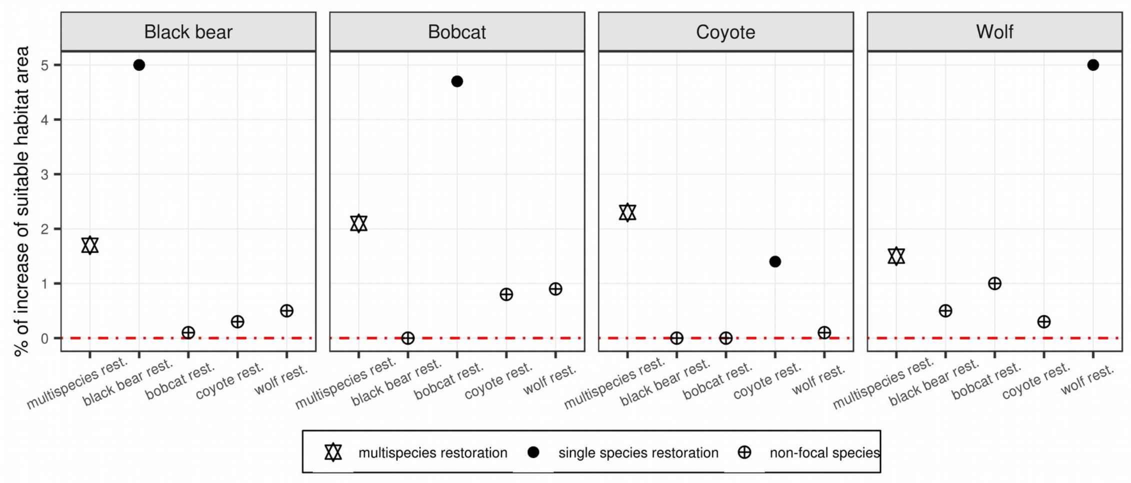

Figure 3.5. **Increase of area with suitable habitat in the study area after each restoration approach.** The labels on the x-axis refer to: "multi-species rest.": multi-species restoration approach; "black bear rest., bobcat rest., coyote rest., wolf rest.": the focal species in the single species restoration approach. The red dotted line is the reference to the area of suitable habitat that was available before restoration. The values of the percentage of suitable habitat in the study area can be found in Table 3.

In our study site we found that the four species shared more unsuitable than suitable habitat. If we compared the area of overlapping unsuitable habitat of at least three species to the area of shared suitable habitat, the difference was even larger (Figure 3.1). Though the characteristics that make an area unsuitable for a species are specific to that species, as they likely are for suitable habitat, the species in our study appeared most similar in the habitats they least preferred. This finding suggests that there may be specific habitat characteristics making areas unsuitable for multiple species.

Focusing on the shared unsuitable habitat of a species community has several advantages. As we demonstrated, focusing on these areas as candidate sites can improve habitat quality simultaneously for all species while avoiding decreasing the quality of the habitat for any species of interest. As the species community in this study belonged to the same taxonomic order (Carnivora), it would be interesting to investigate if multi-species approaches also have positive results when applied to communities with species of different taxonomic groups, and if species not included in the model also benefit from this action. The restoration of moderately unsuitable compared to highly unsuitable habitats are likely to require less time and resources, since restoration involves complex ecological processes that need time to develop (Ricketts 2001; Eycott et al. 2012). In addition, restoring moderately unsuitable habitat, which often is found adjacent to existing suitable habitat, can increase the overall suitable area available to the animals. Although we did not quantify these effects, our approach should lead to maximizing restoration with a decrease in fragmentation and increase in connectivity.

The areas selected for each species using a single species approach overlapped only marginally (Figure 3.4). If the aim is to restore the habitat for all four species, using a species-by-species implementation, similar restoration outcomes would require a nearly four times larger area than using the multi-species restoration approach. In the species community we focused on here, we only found one environmental variable that would have caused antagonistic effects. In this case, changing this environmental feature for one species to increase habitat suitability would have simultaneously decreased suitability for other species in that area.

Our approach can also inform how future modifications of the landscape will affect habitat suitability for species. In both approaches (multi-species and single species; but note the exception of bobcats), one of the common restoration actions was to increase distance to highways and secondary roads. What this also indicates that for all these species, building new roads will directly decrease habitat suitability for a whole community. We intentionally took a theoretical approach not taking into account the feasibility of actual conservation practices. Our approach could, however, generally be used as a first step to select areas that would provide the greatest benefit to the target community if restored; with site feasibility that incorporates ecological, political, economic, and societal aspects guiding the next round of selection of sites.

CONCLUSIONS

Focusing on multiple species simultaneously is already common in conservation actions, restoration plans would largely benefit if they adopted similar strategies (Holl et al. 2003). Our results support the utility of focusing on common unsuitable habitat of a community of species when planning restoration actions. Considering the complexity of restoration for an entire community can reduce the inadvertent negative effects of single species restoration, increasing the effectiveness and efficacy of invested resources.

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General Discussion

In my dissertation I attempted to give insight into the complex relationships that animals have with their environment, namely I wanted to improve our understanding on how animals cope with changes in the environment by changing their movement behavior. Advances in tracking technology provide us the possibility to use wild ranging animals as sensors of nature (Kays et al. 2015; Wilmers et al. 2015). We have to get a better understanding of the relationship between animals and their environment to fully interpret these animal-borne sensors. Data collected with modern tracking devices allow us to infer movement, energy expenditure, and habitat use, enabling us to describe behavior in an integrative way and help us to get a better understanding of how animals interact with their environment.

I was able to show a highly structured energetic landscape of free-ranging fishers (Chapter 1) by using their activity measure through high resolution GPS data associated with tri-axial accelerometer data. The predicted amount of energy spent in a given area could be partially explained by the amount of time spent in that area and its predicted habitat suitability, however, a large part of the variance in energy expenditure remained unexplained. Although I expected the environmental composition to have influence of the activity (Mosser et al. 2014) and therefore shape individual energetic landscape, I could not find a clear relation between the environmental characteristics and the energy expenditure in the individuals included in my study. One difficulty in finding this relationship could be due to a mismatch in spatial and temporal resolution of the tracking and remote sensing data. The behavioral changes may happen at temporal and spatial scales that are too fine to accurately match to subtle environmental changes that may not be detectable using commonly available remote sensing data. Additionally, the use of ODBA (overall dynamic body acceleration) as a proxy for energy expenditure has limitations as it lacks behavioral context. The information of different behaviors (e.g. hunting or escaping) that may occur in different environments may be masked as they potentially have similar ODBA signatures. Overcoming the limitations of remote sensing data by using drones to map the environment of the study site, and assigning ODBA signatures to specific behavior in captive individuals (Williams et al. 2014) will improve the interpretation of energy expenditure in relation to the environment. This can make substantial improvements in understanding the consequences of habitat alteration on animal movement.

I identified wildlife corridors through the movement behavior of individuals of four large carnivore species (black bear, bobcat, coyote and wolf) (Chapter 2). Interestingly I did not find a direct link between these corridors and the habitat suitability nor strong distinctive environmental conditions that characterized them. Corridors are often thought of as swaths of relatively suitable habitat surrounded by less suitable habitat, but this is probably scale dependent. For corridors connecting populations or communities over large distances (e.g. Rabinowitz & Zeller 2010), this may be true, but at smaller scales (e.g. within home ranges in fragmented habitats) where corridors are located may have different explanations. The location of corridors could depend on environmental features that were not picked up by the currently available remote sensing data or our analysis. The permeability of the landscape (e.g. vegetation density) or the geometry of the patch or neighboring patches would be obvious to the animals moving through the landscape but could be obscured by remote sensing data. Another possibility could be that the repeated routes taken are pathways that have been learned from other members of the group (e.g. convenient place to cross a road or river), that are landscape features in themselves. This leads us to speculate that studies that identify corridors using a cost based model relying on the general habitat suitability may place corridors in the wrong places, at least at an individual based level.

I was able to establish a modeling and prioritization procedure to identify areas for restoration that will benefit multiple species simultaneously by taking advantage of a large data set of four large carnivore species where all tracked individuals were exposed to the same environment at the same time (Chapter 3). Even though each species had different habitat preferences, I was able to predict improvement for the habitat for all species simultaneously by focusing on their common unsuitable areas. With a single species approach, habitat suitability improved for the focal species and did not benefit the other species. Modifying the environment for a focal species always comes with the risk that, although for one species the habitat is increasing in suitability, for others the modification may decrease the habitat suitability. By focusing on the common unsuitable areas of a group of species we can apply restoration measures without being too concerned to decrease the quality of the habitat for any of the species of interest. My approach in this study is theoretical, without accounting for the feasibility of the changes. But this approach could be used as a staring point to select the areas that would provide most benefit if restored, and thereafter accounting for feasibility, and taking into account political and social aspects, a further selection could be done.

Overall, I have been able to show that by focusing on the movement of individuals we are able to more accurately predict how they will use landscapes in general but also how they will react to specific modifications of their environment. In the past, the relationship between animals and their environment was often based on scarce data points of individual locations. Now, individual tracking potentially can give more detailed and more useful information for population-level conservation issues as tracking allows the animals to tell us what they prefer. Advances in tracking technology drive devices smaller and less invasive, and incorporate more diverse sensors to monitor details of behavior and physiology. Animals can now be tracked at high resolution for their entire life span and provide us with fascinating new insights into wildlife and changes in the environment. All the gain of knowledge and improved understanding of animal movement in their natural environment, together with sensors measuring their internal state and immediate surroundings, can provide alternatives and complement existing management strategies making them more effective (Wilson et al. 2015; Allen & Singh 2016). With systems like the ICARUS Initiative (http://icarusinitiative.org), we will be able to get near to live information of high numbers of tagged animals around the world that will help us better understand the changing rhythms of the planet and it could even be used to predict upcoming natural disasters (Wikelski et al. 2014).

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Author contributions

CHAPTER 1. Acceleration data reveal highly individually structured energetic landscapes in free-ranging fishers *(Pekania pennanti)*

Anne K. Scharf: conceived and designed the study, performed all analyses and wrote the manuscript.

Scott LaPoint: provided the data, contributed to the design of the study and to finalizing the manuscript.

Martin Wikelski: contributed to the design of the study and provided valuable feedback on the manuscript.

Kamran Safi: helped to design and conceive the study, and contributed to finalizing the manuscript.

CHAPTER 2. Habitat suitability models fail to identify corridors in four carnivore species

Anne K. Scharf: conceived and designed the study, performed all analyses and wrote the manuscript.

Jerrold L. Belant: provided the data and provided valuable feedback on the manuscript.

Dean E. Beyer, Jr.: provided the data

Martin Wikelski: contributed to conceive the study and provided valuable feedback on the manuscript.

Kamran Safi: helped to design and conceive the study, and contributed to finalizing the manuscript.

CHAPTER 3. Multi-species habitat restoration models are more than the sum of the parts

Anne K. Scharf: conceived and designed the study, performed all analyses and wrote the manuscript.

Jerrold L. Belant: provided the data

Dean E. Beyer, Jr.: provided the data

Martin Wikelski: contributed to conceive the study

Kamran Safi: helped to design and conceive the study, and contributed to finalizing the manuscript.

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A. Supplementary material of Chapter 1

APPENDIX A1. Habitat suitability model performance assessment

For each individual we did not include in the model 25% randomly selected observed locations. For these observed locations we extracted the corresponding habitat suitability value from the obtained model. We also extracted, a 100 times, randomly the same number of points as locations excluded from each predicted map within the individuals home range (95%UD). With a Kolmogorov-Smirnov test we compared the distribution of habitat suitability values from the observed locations with those from the random points extracted. For all individuals the two distributions were significantly different (Table A1.1).

Table A1.1. Results form the Kolmogorov-Smirnov tests

Individuals	D	p-value
F1	0.11	<0.001
F2	0.26	<0.001
F3	0.22	<0.001
F4	0.28	<0.001
F5	0.17	<0.001
F6	0.23	<0.001
F7	0.16	<0.001
F8	0.37	<0.001
F9	0.32	<0.001
F10	0.32	<0.001
F11	0.58	<0.001
F12	0.40	<0.001

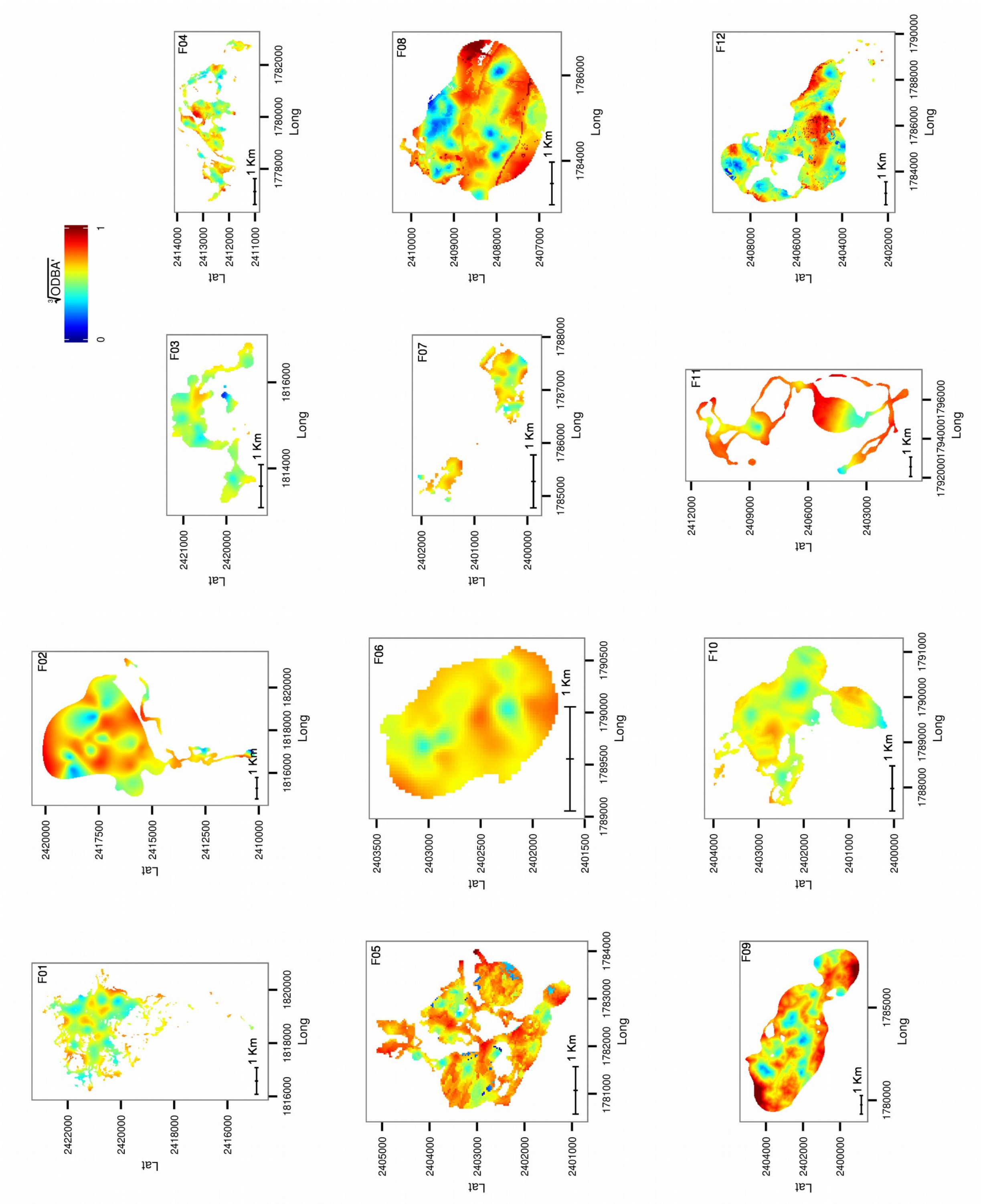


Figure A.1. Predicted energy landscape for all individuals. The prediction is made from the averaged set of best models, per individual, including spatial position, time of day and environmental variables. The areas of the maps correspond to the home ranges of the individuals (95%UD).

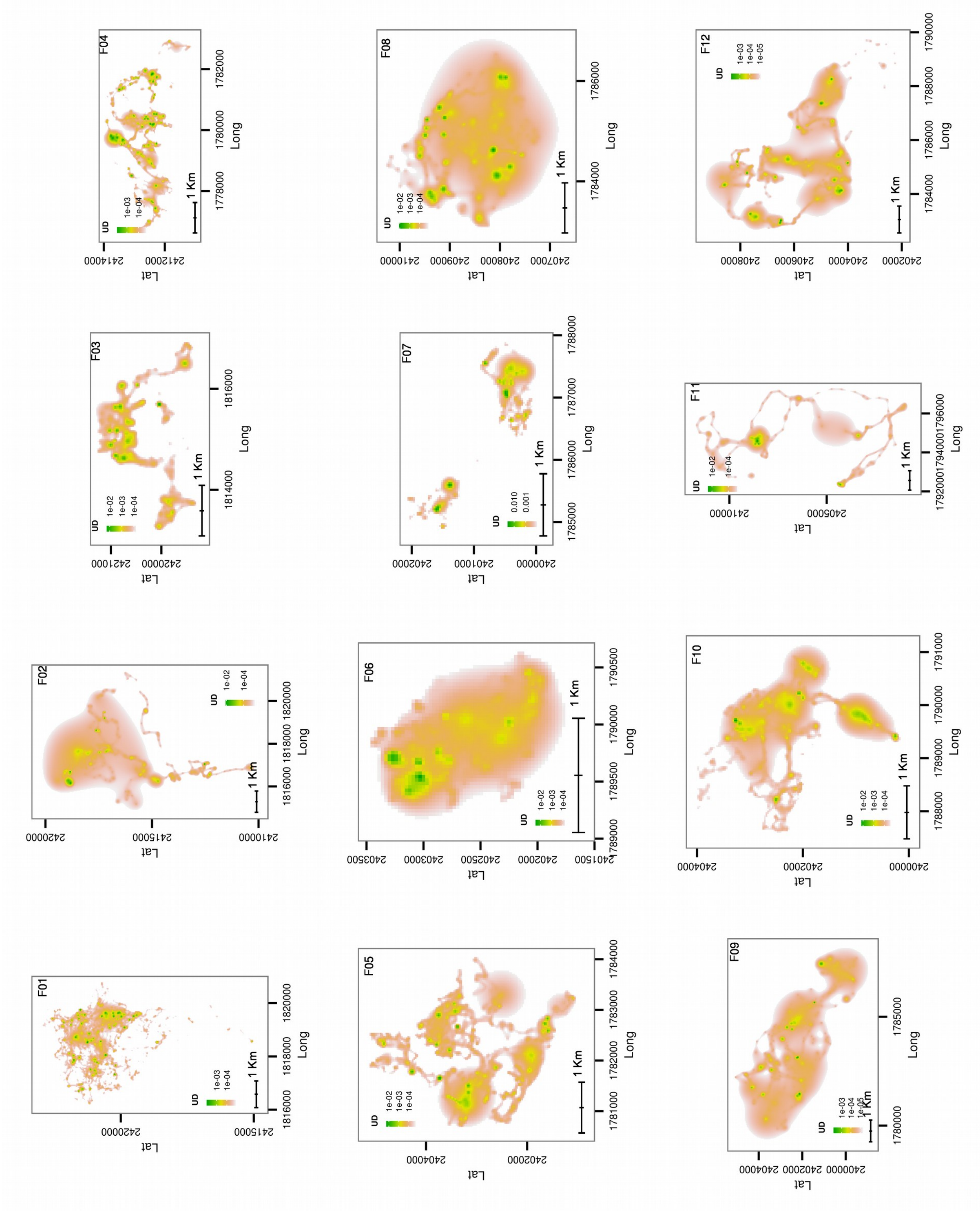


Figure A.2. Utilization distribution (UD) of each individual. The color scale represents the relative proportion of time spent in each cell. The areas of the maps correspond to the home ranges of the individuals (95%UD).

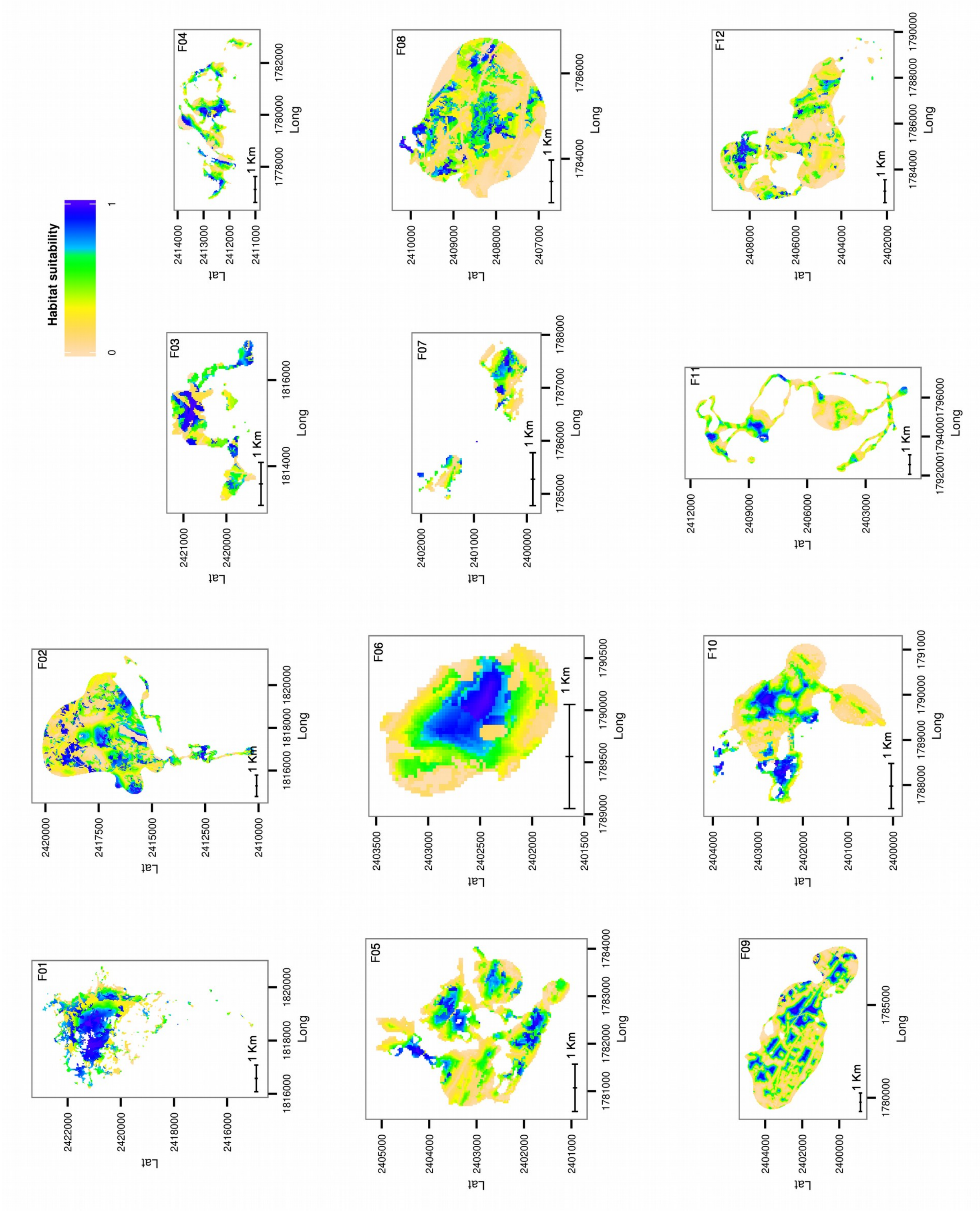


Figure A.3. Habitat suitability maps of all individuals. The areas of the maps correspond to the home ranges of the individuals (95%UD).

Table A.1. Supplementary information of the tracked individuals

Individuals	Total number of points collected	GPS fix rate	Accelerometer settings
F01	17600	Dynamic sampling*	High sensitivity
F02	1077	10 min	High sensitivity
F03	874	10 min	High sensitivity
F04	10429	Dynamic sampling*	High sensitivity
F05	3444	Dynamic sampling*	High sensitivity
F06	1541	Dynamic sampling*	High sensitivity
F07	2824	Dynamic sampling*	High sensitivity
F08	1349	10 min	Low sensitivity
F09	919	15 min	High sensitivity
F10	2616	Dynamic sampling*	High sensitivity
F11	748	10 min	Low sensitivity
F12	1638	10 min	Low sensitivity

*GPS fixes every two minutes when the animal was highly active (e.g., running), every 10 minutes at moderate activity, and every 60 minutes during low activity (e.g., resting) (Brown et al. 2012)

Table A.2. Environmental variables included in the analyses

Variable	Description
Land cover:	
- developed low	Developed open space and developed low intensity*
- developed high	Developed medium intensity and developed high intensity*
- deciduous forest	Deciduous forest*
- evergreen forest	Evergreen forest*
- mixed forest	Mixed forest*
- shrub	Shrub/scrub*
- grassland	Grassland/herbaceous*
- crop	Pasture/ hay and cultivated crops*
- woody wetland	Woody wetland*
- herbaceous wetland	Emergent Herbaceous Wetlands*
- barren	Barren land*
- open water	Open water*
Distance to the forest edge (m)	Distance to deciduous,evergreen and mixed forest*. Positive values from inside the forest, and negative values form outside of the forest
Proportion of urban area (%)	% of developed high, medium and low intensity* within a 240 m radius circle from each 30m grid cell
Landscape heterogeneity	Number of different land cover types within a 240 m radius circle from each 30m grid cell
Distance to roads (m)	Distance from each grid cell to highways and paved roads[#]

*Classes correspond to the classification of the National Land Cover Database 2011 legend (Jin et al. 2011, NLCD11)
[#]Classification as provided by the United State Census Bureau (2011)

Table A3. AICc values of GAMs including environmental variables. For each individual all possible combinations of the environmental variables were tested. Within each individual, the models are sorted by increasing ΔAIC values. In this table only the models with a ΔAIC smaller than 4 are shown.

Intercept	Dist. Forest edge	Dist. Roads	Land cover	Proportion developed	Landscape heterogeneity	s(Space)	s(Time of day)	AICc	ΔAIC	Indiv.
0.51553277	*NA*	*NA*	*NA*	*NA*	-0.0168413891	+	+	-1715.2139	0.000000000	F1
0.51553069	*NA*	*NA*	*NA*	0.000000000	-0.0168408305	+	+	-1715.2074	0.006522108	F1
0.48359502	*NA*	4.777449e-05	*NA*	*NA*	-0.0162818549	+	+	-1714.4327	0.781264177	F1
0.48360045	*NA*	4.776292e-05	*NA*	0.000000000	-0.0162813735	+	+	-1714.4263	0.787677786	F1
0.53503361	*NA*	*NA*	+	*NA*	-0.0188670597	+	+	-1714.1481	1.065837483	F1
0.53503362	*NA*	*NA*	+	0.000000000	-0.0188662115	+	+	-1714.1407	1.073215573	F1
0.51729367	-3.410885e-06	*NA*	*NA*	*NA*	-0.0169310722	+	+	-1713.8841	1.329842608	F1
0.51728584	-3.399514e-06	*NA*	*NA*	0.000000000	-0.0169302459	+	+	-1713.8777	1.336238271	F1
0.48912749	-2.339468e-05	5.734013e-05	*NA*	*NA*	-0.0167445104	+	+	-1713.3885	1.825436075	F1
0.48912884	-2.337667e-05	5.732112e-05	*NA*	0.000000000	-0.0167437071	+	+	-1713.3821	1.831812276	F1
0.52450587	*NA*	1.823139e-05	+	*NA*	-0.0186535811	+	+	-1713.0764	2.137561531	F1
0.52451131	*NA*	1.822200e-05	+	0.000000000	-0.0186528313	+	+	-1713.0692	2.144764222	F1
0.53908472	-9.758053e-06	*NA*	+	*NA*	-0.0191209465	+	+	-1712.9761	2.237844810	F1
0.53907741	-9.740387e-06	*NA*	+	0.000000000	-0.0191196812	+	+	-1712.9687	2.245186403	F1
0.52802537	-1.889631e-05	2.572692e-05	+	*NA*	-0.0190417051	+	+	-1712.0826	3.131350291	F1
0.52802632	-1.887222e-05	2.570804e-05	+	0.000000000	-0.0190405012	+	+	-1712.0753	3.138637201	F1
0.45284235	*NA*	*NA*	*NA*	*NA*	*NA*	+	+	-1711.4561	3.757850744	F1
0.45284235	*NA*	*NA*	*NA*	0.000000000	*NA*	+	+	-1711.4495	3.764401244	F1
0.40090757	*NA*	8.310711e-05	*NA*	*NA*	*NA*	+	+	-1711.2602	3.953732210	F1
0.40091526	*NA*	8.309480e-05	*NA*	0.000000000	*NA*	+	+	-1711.2537	3.960195554	F1
0.49248800	*NA*	*NA*	*NA*	*NA*	*NA*	+	+	-356.0058	0.000000000	F2
0.49248800	*NA*	*NA*	*NA*	0.000000000	*NA*	+	+	-355.9330	0.072719813	F2
0.49289646	*NA*	-1.030512e-06	*NA*	*NA*	*NA*	+	+	-355.3288	0.676915316	F2
0.49283171	*NA*	-8.671629e-07	*NA*	0.000000000	*NA*	+	+	-355.2579	0.747890747	F2
0.48203118	6.280356e-05	*NA*	*NA*	*NA*	*NA*	+	+	-354.9700	1.035756697	F2
0.48202675	6.283014e-05	*NA*	*NA*	0.000000000	*NA*	+	+	-354.8980	1.107782947	F2
0.49189161	7.230696e-05	-2.886912e-05	*NA*	*NA*	*NA*	+	+	-354.5034	1.502386811	F2
0.49182549	7.227270e-05	-2.868790e-05	*NA*	0.000000000	*NA*	+	+	-354.4334	1.572331458	F2
0.49905033	*NA*	*NA*	*NA*	*NA*	-0.0015564940	+	+	-354.2701	1.735680153	F2
0.49907143	*NA*	*NA*	*NA*	0.000000000	-0.0015614986	+	+	-354.1983	1.807477651	F2
0.50171857	*NA*	-5.764143e-06	*NA*	*NA*	-0.0016474591	+	+	-353.5803	2.425491185	F2
0.50166289	*NA*	-5.605048e-06	*NA*	0.000000000	-0.0016492113	+	+	-353.5105	2.495290149	F2
0.47707743	6.734442e-05	*NA*	*NA*	*NA*	0.0009956334	+	+	-353.1154	2.890325830	F2
0.47708251	6.736213e-05	*NA*	*NA*	0.000000000	0.0009937285	+	+	-353.0450	2.960740709	F2
0.48790312	7.551523e-05	-2.818828e-05	*NA*	*NA*	0.0007553064	+	+	-352.6212	3.384518415	F2
0.48783958	7.547904e-05	-2.800800e-05	*NA*	0.000000000	0.0007548597	+	+	-352.5529	3.452900041	F2
0.49377385	*NA*	*NA*	*NA*	*NA*	*NA*	+	+	-330.0687	0.000000000	F3
0.49377385	*NA*	*NA*	*NA*	0.000000000	*NA*	+	+	-329.9572	0.111497165	F3
0.48232160	*NA*	*NA*	*NA*	*NA*	0.0017794976	+	+	-328.6224	1.446367096	F3
0.48281114	*NA*	*NA*	*NA*	0.000000000	0.0017034310	+	+	-328.4925	1.576174837	F3
0.50566968	-3.010230e-04	*NA*	*NA*	*NA*	*NA*	+	+	-327.8575	2.211208316	F3
0.50569272	-3.016059e-04	*NA*	*NA*	0.000000000	*NA*	+	+	-327.7398	2.328945690	F3
0.45348035	*NA*	1.425371e-04	*NA*	*NA*	*NA*	+	+	-327.5178	2.550927393	F3
0.45306283	*NA*	1.440141e-04	*NA*	0.000000000	*NA*	+	+	-327.3872	2.681550938	F3
0.49275233	-3.006511e-04	*NA*	*NA*	*NA*	0.0020048672	+	+	-326.4926	3.576093429	F3
0.43273135	*NA*	1.461145e-04	*NA*	*NA*	0.0030669267	+	+	-326.4468	3.621885071	F3
0.49325119	-3.012041e-04	*NA*	*NA*	0.000000000	0.0019307480	+	+	-326.3578	3.710951580	F3
0.43277753	*NA*	1.474299e-04	*NA*	0.000000000	0.0030019745	+	+	-326.3050	3.763699793	F3
0.39005716	-6.181833e-04	*NA*	+	*NA*	0.0127404134	+	+	-1016.2407	0.000000000	F4
0.39047359	-6.186046e-04	-2.387918e-06	+	*NA*	0.0127577191	+	+	-1015.1909	1.049746562	F4
0.39017211	-6.227061e-04	*NA*	+	-0.138788455	0.0126856015	+	+	-1015.0519	1.188814353	F4
0.39133631	-6.230746e-04	-4.977568e-06	+	-0.141453158	0.0126874030	+	+	-1013.9725	2.268134672	F4
0.28738749	-3.954497e-04	*NA*	+	*NA*	-0.0365019473	+	+	-363.8175	0.000000000	F5

Intercept	Dist. Forest edge	Dist. Roads	Land cover	Proportion developed	Landscape heterogeneity	s(Space)	s(Time of day)	AICc	ΔAIC	Indiv.
0.28718229	-3.926321e-04	NA	+	-2.978949450	-0.0364552028	+	+	-362.3850	1.432522192	F5
0.26646501	NA	NA	+	NA	-0.0322884776	+	+	-362.0176	1.799877933	F5
0.26639697	NA	NA	+	-3.387832627	-0.0322838333	+	+	-360.7394	3.078058302	F5
0.32613455	-3.501629e-04	-1.728894e-04	+	NA	-0.0376815000	+	+	-360.5721	3.245391700	F5
0.53573599	NA	2.264863e-04	NA	NA	NA	+	+	-291.2640	0.00000000	F6
0.54053281	NA	2.204332e-04	NA	-0.225809767	NA	+	+	-290.8624	0.40152922	F6
0.59074183	NA	NA	NA	NA	NA	+	+	-290.4113	0.85263178	F6
0.59590496	NA	NA	NA	-0.350459334	NA	+	+	-290.3574	0.90655227	F6
0.53583439	-2.862122e-05	2.363337e-04	NA	NA	NA	+	+	-290.0278	1.23612518	F6
0.54050216	-2.726377e-05	2.303237e-04	NA	-0.225776849	NA	+	+	-289.6068	1.65715607	F6
0.59195872	-1.398752e-05	NA	NA	NA	NA	+	+	-289.2447	2.01922231	F6
0.59728392	-1.526501e-05	NA	NA	-0.353916779	NA	+	+	-289.1482	2.11571007	F6
0.69677993	NA	-6.962629e-04	NA	-2.964730404	NA	+	+	-535.3741	0.00000000	F7
0.68647971	1.402339e-04	-6.904601e-04	NA	-3.082125469	NA	+	+	-535.2072	0.16688200	F7
0.73055593	NA	-7.126672e-04	NA	-2.970593616	-0.0051961168	+	+	-534.1199	1.25417851	F7
0.72124807	1.437931e-04	-7.066894e-04	NA	-3.089925372	-0.0054116653	+	+	-533.9198	1.45430938	F7
0.68664110	NA	-6.654918e-04	NA	NA	NA	+	+	-532.9676	2.40646388	F7
0.67905986	1.050934e-04	-6.623630e-04	NA	NA	NA	+	+	-532.7395	2.63459704	F7
0.72152279	NA	-6.815654e-04	NA	NA	-0.0053980575	+	+	-531.6416	3.73252080	F7
0.66974506	NA	NA	+	NA	NA	+	+	-179.9039	0.00000000	F8
0.66977373	NA	NA	+	0.000000000	NA	+	+	-179.8510	0.05286103	F8
0.66453342	2.481802e-04	NA	+	NA	NA	+	+	-179.1405	0.76342113	F8
0.66456868	2.480809e-04	NA	+	0.000000000	NA	+	+	-179.0891	0.81482224	F8
0.71889371	NA	-2.736610e-04	+	NA	NA	+	+	-178.4594	1.44449089	F8
0.39159425	NA	NA	NA	NA	NA	+	+	-178.4186	1.48527180	F8
0.71895795	NA	-2.738455e-04	+	0.000000000	NA	+	+	-178.4076	1.49632858	F8
0.39159425	NA	NA	NA	0.000000000	NA	+	+	-178.3071	1.59684989	F8
0.74669368	4.993309e-04	-4.852330e-04	+	NA	NA	+	+	-178.1025	1.80138368	F8
0.72612542	NA	NA	+	NA	-0.0073330583	+	+	-178.0659	1.83803418	F8
0.74676376	4.993259e-04	-4.853813e-04	+	0.000000000	NA	+	+	-178.0490	1.85488524	F8
0.72620540	NA	NA	+	0.000000000	-0.0073394542	+	+	-178.0137	1.89022478	F8
0.45627525	NA	-3.324385e-04	NA	NA	NA	+	+	-177.5056	2.39830751	F8
0.45630945	NA	-3.326143e-04	NA	0.000000000	NA	+	+	-177.4070	2.49688125	F8
0.70092653	2.220060e-04	NA	+	NA	-0.0046661906	+	+	-177.2238	2.68006583	F8
0.70101088	2.218654e-04	NA	+	0.000000000	-0.0046724202	+	+	-177.1724	2.73148655	F8
0.39068621	NA	NA	NA	NA	0.0001431974	+	+	-176.5172	3.38667587	F8
0.40064957	-1.490782e-04	NA	NA	NA	NA	+	+	-176.5000	3.40392866	F8
0.80149417	NA	-3.063919e-04	+	NA	-0.0099696524	+	+	-176.4700	3.43393036	F8
0.80164923	NA	-3.066144e-04	+	0.000000000	-0.0099801242	+	+	-176.4169	3.48703487	F8
0.39073782	NA	NA	NA	0.000000000	0.0001350580	+	+	-176.4041	3.49978227	F8
0.40065637	-1.491900e-04	NA	NA	0.000000000	NA	+	+	-176.3768	3.52712267	F8
0.79399473	4.693683e-04	-4.917590e-04	+	NA	-0.0059187725	+	+	-176.1528	3.75110993	F8
0.79412912	4.693160e-04	-4.919170e-04	+	0.000000000	-0.0059266519	+	+	-176.0997	3.80422955	F8
0.45610494	-2.058964e-06	-3.309204e-04	NA	NA	NA	+	+	-176.0111	3.89282357	F8
0.45613846	-2.073602e-06	-3.310881e-04	NA	0.000000000	NA	+	+	-175.9114	3.99251650	F8
0.49582597	-5.556896e-04	NA	NA	NA	NA	+	+	-172.0894	0.00000000	F9
0.53986938	-5.961111e-04	NA	NA	NA	-0.0071771559	+	+	-170.2452	1.84418559	F9
0.54996567	-4.976312e-04	-2.771063e-04	NA	NA	NA	+	+	-169.8915	2.19784310	F9
0.50215794	-5.665291e-04	NA	NA	-0.325621126	NA	+	+	-168.9017	3.18763074	F9
0.59957034	-5.417400e-04	-2.815552e-04	NA	NA	-0.0079383899	+	+	-168.0730	4.01635596	F9
0.62551041	NA	-4.539630e-04	NA	NA	NA	+	+	-433.7438	0.00000000	F10
0.63063908	NA	-4.593714e-04	NA	NA	-0.0007632462	+	+	-432.2543	1.48952605	F10
0.61425762	NA	-4.407719e-04	NA	0.181135169	NA	+	+	-432.0142	1.72954079	F10
0.62410602	-2.130360e-04	-3.831129e-04	NA	NA	NA	+	+	-431.7195	2.02428231	F10
0.61743645	NA	-4.446750e-04	NA	0.179597066	-0.0004433790	+	+	-430.5759	3.16791917	F10
0.61610271	-1.958731e-04	-3.800040e-04	NA	0.132864001	NA	+	+	-430.2730	3.47077158	F10
0.64077577	-2.200138e-04	-3.957285e-04	NA	NA	-0.0025647971	+	+	-429.9650	3.77877214	F10

Intercept	Dist. Forest edge	Dist. Roads	Land cover	Proportion developed	Landscape heterogeneity	s(Space)	s(Time of day)	AICc	ΔAIC	Indiv.
0.37447853	*NA*	*NA*	*NA*	*NA*	0.0187873591	+	+	-160.8217	0.00000000	F11
0.46747139	*NA*	*NA*	*NA*	*NA*	*NA*	+	+	-160.2879	0.53384267	F11
0.37348906	*NA*	*NA*	*NA*	0.383157836	0.0187480617	+	+	-160.1996	0.62215738	F11
0.46626990	*NA*	*NA*	*NA*	0.388822889	*NA*	+	+	-159.7585	1.06322325	F11
0.40580580	-2.473261e-04	*NA*	*NA*	*NA*	0.0162747424	+	+	-158.4484	2.37331699	F11
0.49099957	-3.080466e-04	*NA*	*NA*	*NA*	*NA*	+	+	-157.8774	2.94431138	F11
0.40458063	-2.466527e-04	*NA*	*NA*	0.382415594	0.0162731355	+	+	-157.8052	3.01649818	F11
0.47402513	*NA*	-3.887832e-04	*NA*	*NA*	0.0182786774	+	+	-157.5016	3.32013350	F11
0.48972784	-3.069124e-04	*NA*	*NA*	0.383517737	*NA*	+	+	-157.2917	3.53007672	F11
0.56659392	*NA*	-3.971727e-04	*NA*	*NA*	*NA*	+	+	-157.2660	3.55576368	F11
0.51887994	-2.883929e-04	*NA*	+	*NA*	0.0279665524	+	+	-539.3394	0.00000000	F12
0.50893533	-2.972261e-04	*NA*	+	-0.912479939	0.0284812892	+	+	-537.8103	1.52907268	F12
0.53783006	-2.588108e-04	-8.832322e-05	+	*NA*	0.0267753179	+	+	-537.4385	1.90096230	F12
0.52836996	-2.666986e-04	-9.195519e-05	+	-0.940249892	0.0272591453	+	+	-535.9759	3.36353334	F12
0.52977837	*NA*	*NA*	+	*NA*	0.0287165145	+	+	-535.8267	3.51272277	F12

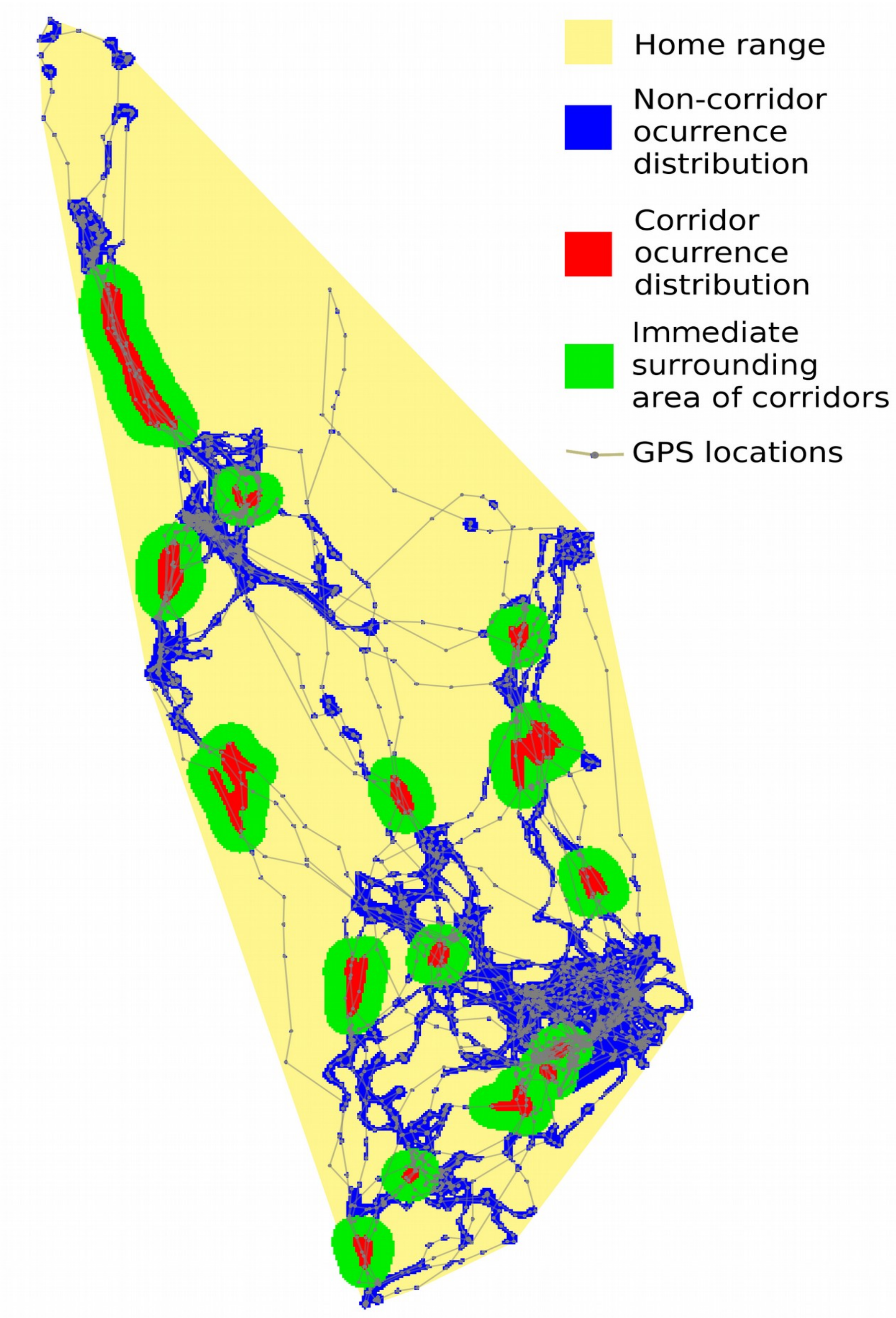


Figure B.1. Example of a brown bear's (BB06, tracked 79 days in 2009) home range, occurrence distributions (for corridor and non-corridor locations) and the immediate surrounding areas of the corridors.

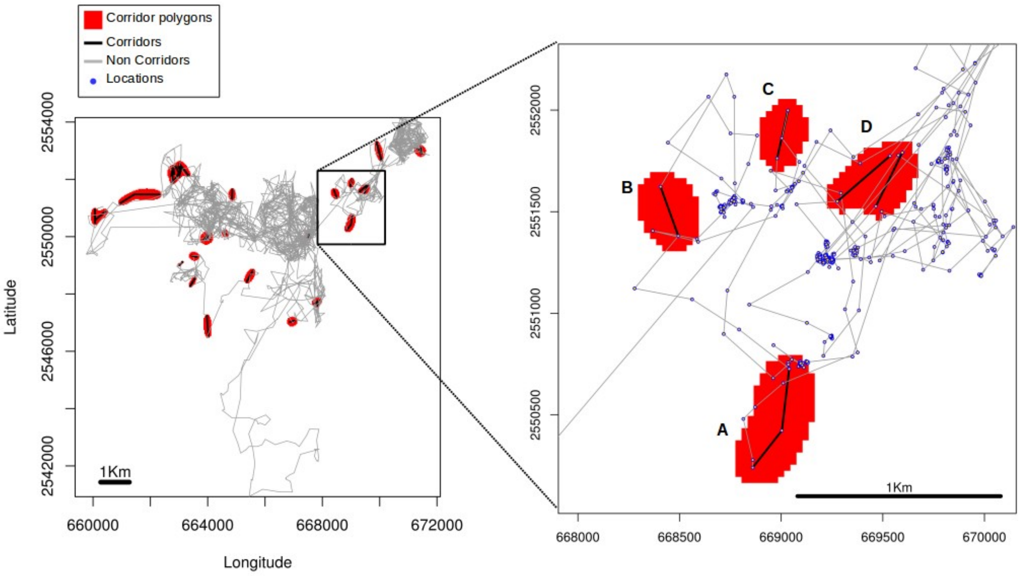


Figure B.2. Corridor outliers calculation. Left panel: track of one wolf (W01), with all corridors identified by the *corridor* function of the *move* R package. Right panel: detail of one section of the track. Corridors A, B and C are considered as outliers. Corridor D would be accepted as corridor.

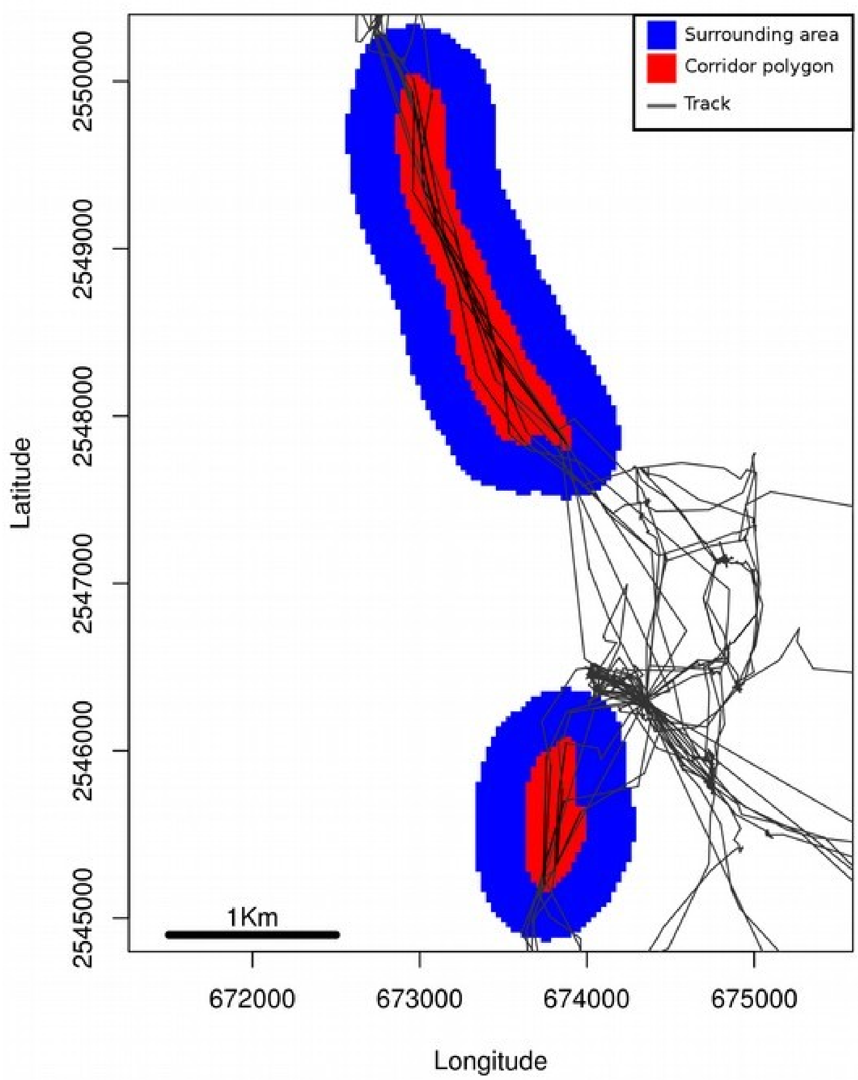


Figure B.3. Detail of corridor polygons and their immediate surrounding areas.

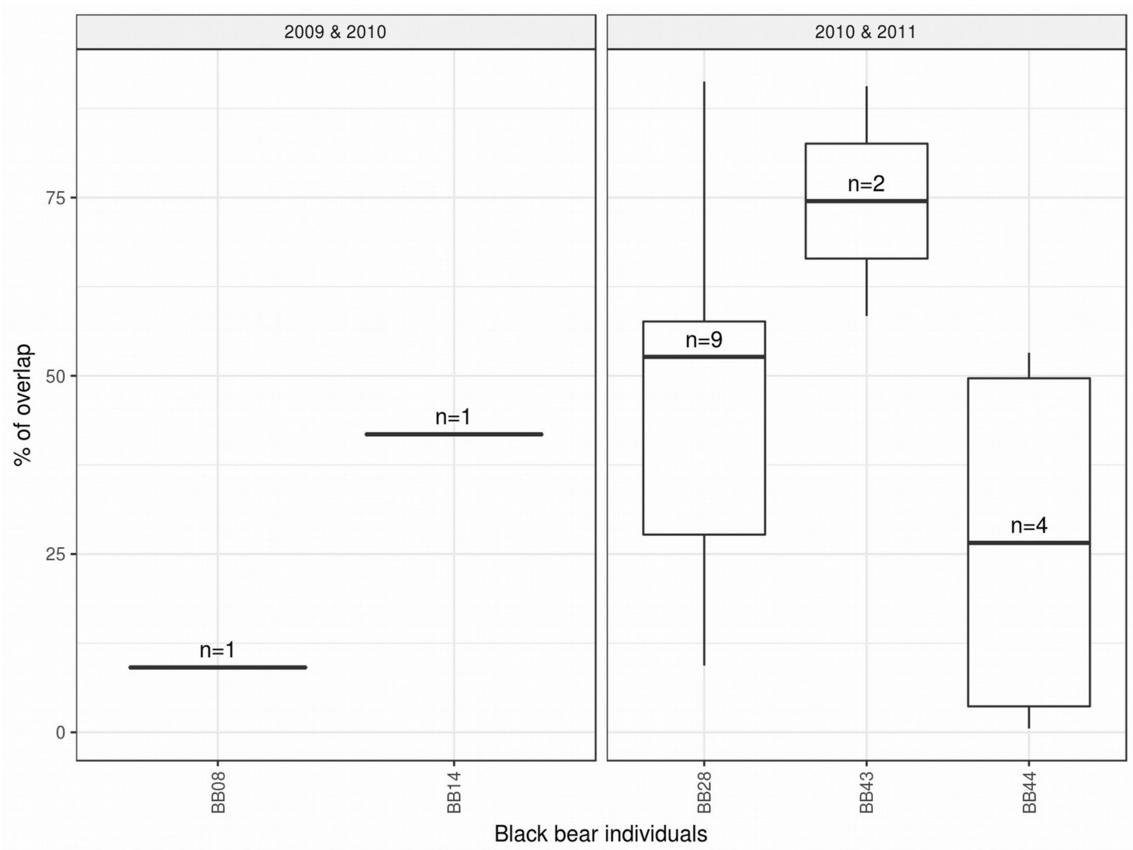


Figure B.4. Overlap of corridors of the same individual. Percentage of overlap of corridors within one black bear tracked over several years. Each overlapping pair is counted once, always the one with the highest percentage of overlap. "n" represents the number of overlapping pairs of corridors.

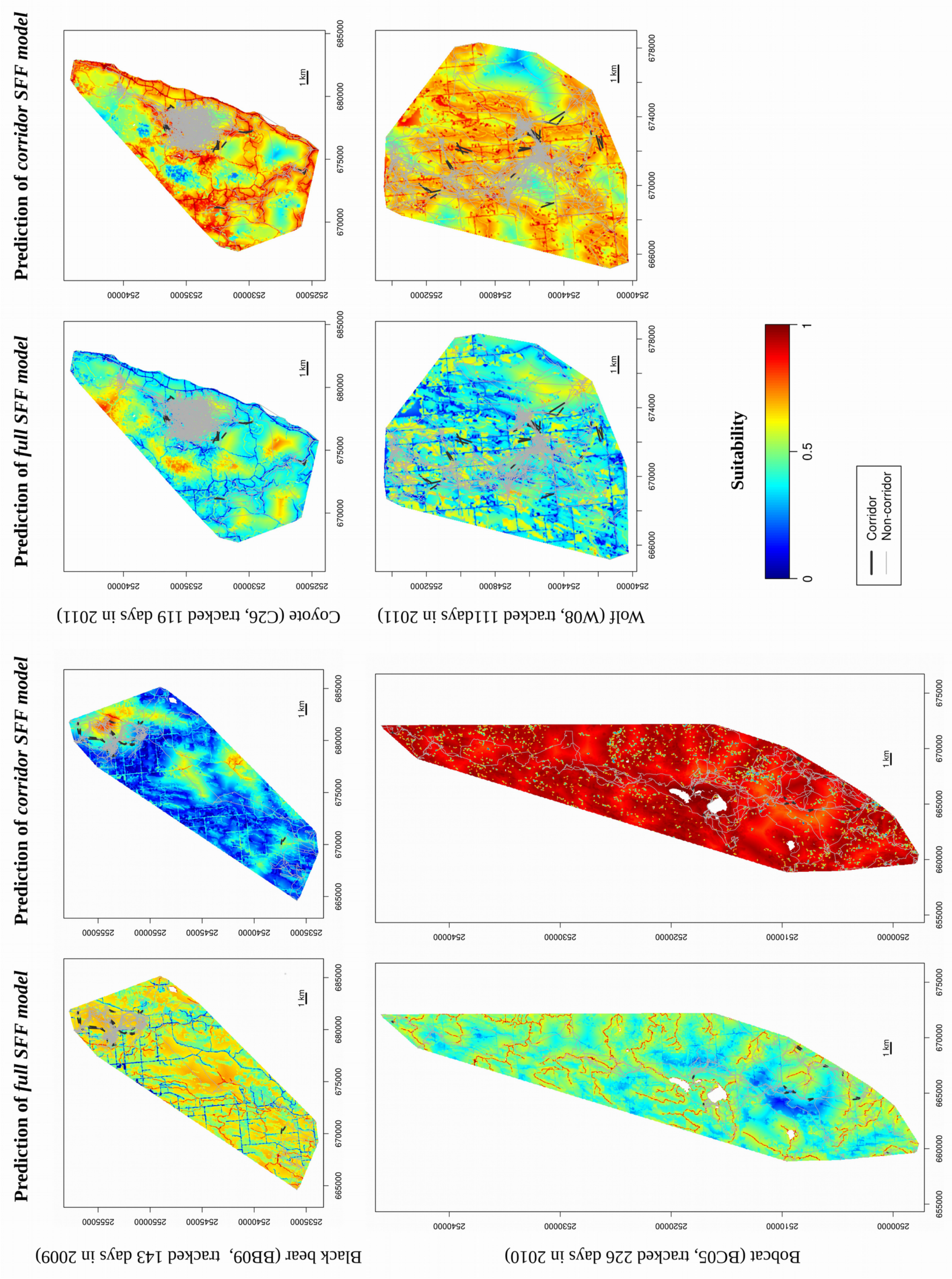


Figure B.5. Example of *full SSF model* and *corridor SSF model* predictions for one black bear, bobcat, coyote and wolf. Prediction area corresponds to the individuals' home range.

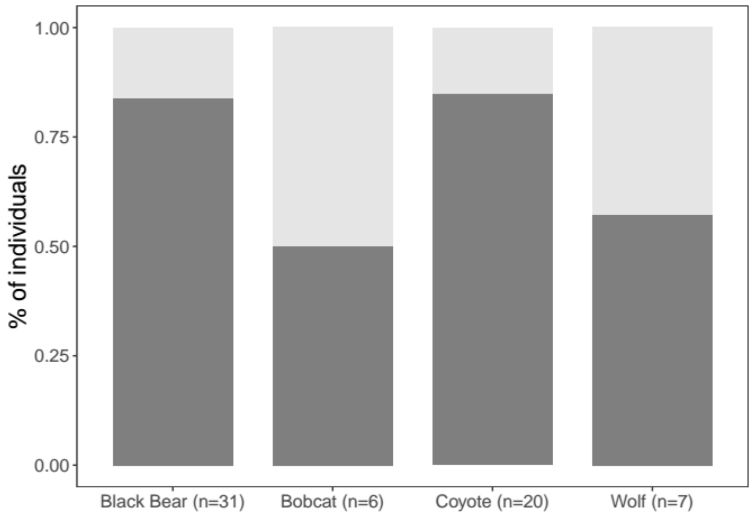
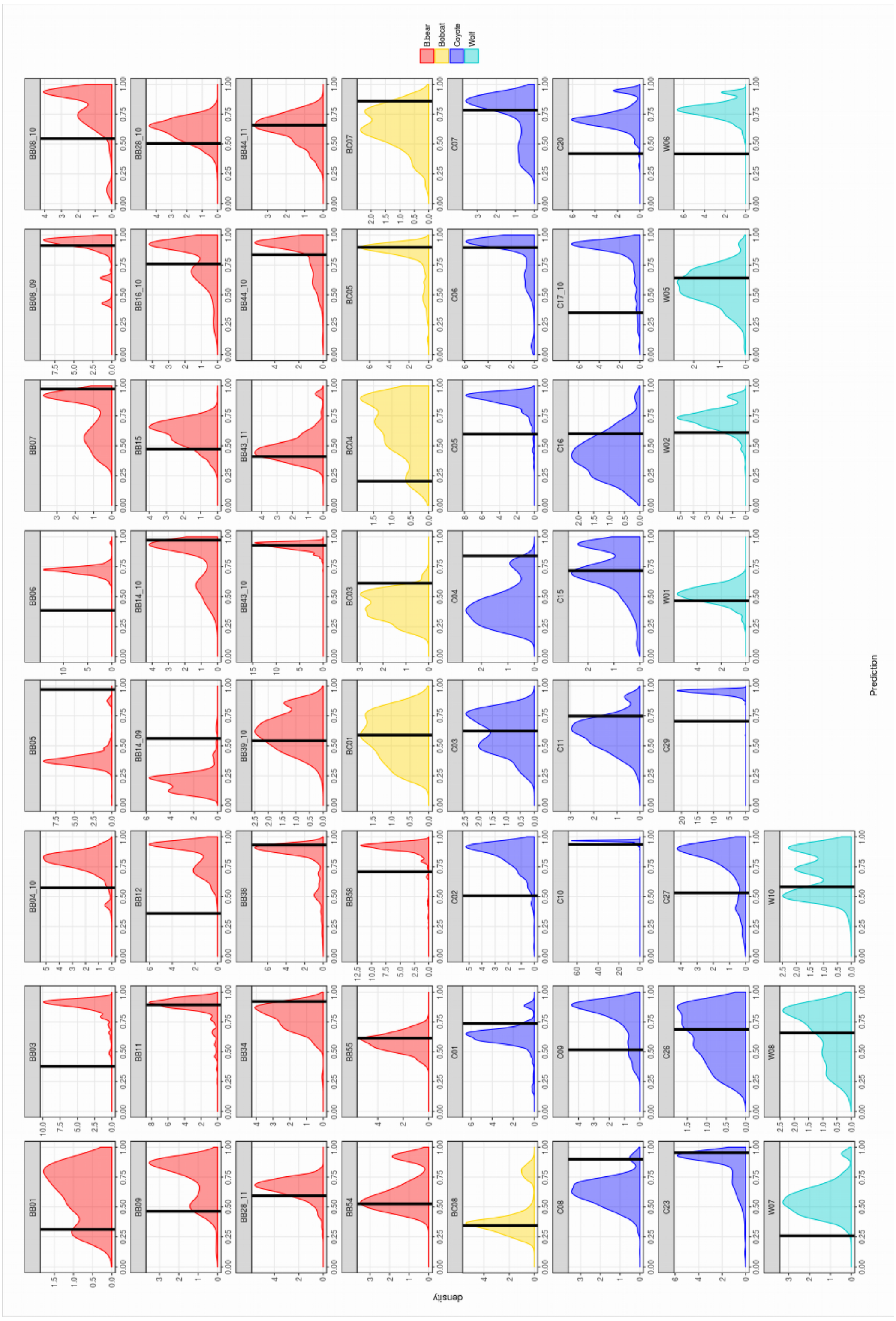


Figure B.6. Prediction success of *corridor SSF models*. Dark gray: individuals where corridor locations had higher prediction value than random locations. Light gray: individuals where random locations had higher prediction value than corridor locations.



Additional file 10. Comparison between prediction of corridor locations by the *corridor SSF model* and the *non-corridor SSF models.* The black line represents mean prediction value of the *corridor SSF model*, and the colored area represents the distribution of the mean predictions of the 1000 repetitions of the *non-corridor SSF models.* When the line is to the right of the largest peak of the distribution of the predictions of the *non-corridor SSF models*, the *corridor SSF model* could predict better the corridor locations (e.g. BB05, BC07, etc). In all other cases the *non-corridor SSF model* could predict the corridor locations as good or better than the *corridor SSF model*. Red: black bears; yellow: bobcats; dark blue: coyotes; light blue: wolves.

Table B.1. Environmental variables used

Variables	Description	Source
Land Cover	Water, developed open, developed low, developed medium, developed high, barren, deciduous forest, evergreen forest, mixed forest, shrub, grassland, pasture, crops, woody wetland, herbaceous wetland, rivers, lakes and roads	NLCD11 Classes* Rivers§; Lakes$ Roads#
% Human cover	% of land covers with human presence (urban areas and roads) within a 30 m radius circle from each 30m grid cell	NLCD11 Classes: 21,22,23,24,27* Roads#
% Open cover	% of grasslands, shrubs, crops, barren within a 30 m radius circle from each 30m grid cell	NLCD11 Classes: 31,52,71,81,82,95*
% Evergreen forest	% of evergreen forest within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 42*
% Mixed forest	% of mixed forest within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 43*
% Deciduous forest	% of deciduous forest within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 41*
% Woody wetland	% of woody wetland within a 30 m radius circle from each 30m grid cell	NLCD11 Class: 90*
Distance to roads (m)	Distance from each grid cell to roads	Roads#
Distance to water (m)	Distance from each grid cell to rivers and lakes	NLCD11 Class: 11* Rivers§; Lakes$

* Classes correspond to the classification of the National Land Cover Database 2011 legend (Jin et al. 2013 & NLCD11)
# Classification as provided by the United States Census Bureau (US Census Bureau).
§ Rivers correspond to the NHDFlowline layer with the feature type "stream/river" according to the NHD classification (USGS)
$ Lakes correspond to the NHDWaterbody layer, excluding the feature type swamp/marsh (USGS)

Table B.2. T-test results of the comparison between the habitat suitability value (HS) of corridor vs non-corridor locations from the *full SSF model.* Negative value of "t" implies that the corridor locations had lower habitat suitability than the non-corridor locations.

Species	Individuals	t	p-value	DF	HS corridor (mean±sd)	HS non-corridor (mean±sd)
black bear	BB01	-0.075	0.9399	3559	0.45 ± 0.17	0.45 ± 0.14
black bear	BB03	-1.789	0.0737	7850	0.85 ± 0.08	0.87 ± 0.1
black bear	BB04_09	-4.870	<0.001	8528	0.25 ± 0.1	0.28 ± 0.08
black bear	BB04_10	-4.584	<0.001	2575	0.33 ± 0.09	0.41 ± 0.09
black bear	BB05	-3.463	<0.001	7093	0.42 ± 0.13	0.48 ± 0.14
black bear	BB06	-5.011	<0.001	6713	0.72 ± 0.09	0.76 ± 0.1
black bear	BB07	-7.286	<0.001	5368	0.27 ± 0.11	0.36 ± 0.12
black bear	BB08_09	-4.480	<0.001	7120	0.72 ± 0.07	0.78 ± 0.08
black bear	BB08_10	-5.708	<0.001	13243	0.51 ± 0.1	0.57 ± 0.11
black bear	BB08_11	-2.972	0.003	2455	0.7 ± 0.13	0.77 ± 0.08
black bear	BB09	-8.811	<0.001	6828	0.58 ± 0.1	0.64 ± 0.07
black bear	BB10	-1.090	0.2756	2039	0.72 ± 0.1	0.73 ± 0.06
black bear	BB11	-2.693	0.0071	5801	0.39 ± 0.13	0.44 ± 0.12
black bear	BB12	-2.881	0.004	6029	0.7 ± 0.1	0.73 ± 0.11
black bear	BB14_09	-13.520	<0.001	4914	0.79 ± 0.05	0.92 ± 0.07
black bear	BB14_10	-3.203	0.0014	13059	0.65 ± 0.15	0.7 ± 0.15
black bear	BB15	-5.663	<0.001	10446	0.34 ± 0.11	0.41 ± 0.16
black bear	BB16_10	-9.809	<0.001	13384	0.49 ± 0.1	0.56 ± 0.07
black bear	BB16_11	-0.675	0.5001	1157	0.58 ± 0.13	0.59 ± 0.06
black bear	BB28_10	-7.836	<0.001	13093	0.42 ± 0.14	0.48 ± 0.12
black bear	BB28_11	-14.209	<0.001	12010	0.31 ± 0.13	0.41 ± 0.12
black bear	BB34	0.131	0.8954	7935	0.55 ± 0.07	0.55 ± 0.07
black bear	BB38	-1.073	0.2834	8105	0.51 ± 0.07	0.52 ± 0.08
black bear	BB39_10	-4.945	<0.001	7973	0.36 ± 0.11	0.44 ± 0.12
black bear	BB39_11	-1.450	0.1473	1648	0.23 ± 0.01	0.31 ± 0.12
black bear	BB41	0.138	0.8899	3758	0.51 ± 0.05	0.5 ± 0.08
black bear	BB43_10	-2.116	0.0343	6283	0.45 ± 0.12	0.49 ± 0.12
black bear	BB43_11	-5.518	<0.001	10549	0.52 ± 0.1	0.57 ± 0.1
black bear	BB44_10	-5.098	<0.001	7848	0.34 ± 0.1	0.39 ± 0.1
black bear	BB44_11	-3.425	<0.001	9980	0.35 ± 0.1	0.38 ± 0.09
black bear	BB54	-8.601	<0.001	9224	0.42 ± 0.11	0.47 ± 0.07
black bear	BB55	1.113	0.2658	9547	0.41 ± 0.11	0.4 ± 0.11
black bear	BB58	-0.514	0.6069	6399	0.45 ± 0.08	0.45 ± 0.09
bobcat	BC01	-2.062	0.0392	6574	0.62 ± 0.13	0.67 ± 0.11
bobcat	BC03	-1.492	0.1357	2268	0.37 ± 0.14	0.42 ± 0.13
bobcat	BC04	0.880	0.3789	9034	0.83 ± 0.09	0.82 ± 0.08
bobcat	BC05	-3.237	0.0012	11307	0.48 ± 0.13	0.54 ± 0.14
bobcat	BC06	-1.541	0.1233	3556	0.57 ± 0.04	0.63 ± 0.08
bobcat	BC07	-4.065	<0.001	10894	0.4 ± 0.13	0.49 ± 0.11
bobcat	BC08	-5.623	<0.001	12683	0.67 ± 0.1	0.72 ± 0.09

Species	Individuals	t	p-value	DF	HS corridor (mean±sd)	HS non-corridor (mean±sd)
coyote	C01	-3.373	<0.001	6610	0.56 ± 0.1	0.62 ± 0.11
coyote	C02	-3.579	<0.001	6613	0.56 ± 0.12	0.62 ± 0.09
coyote	C03	-0.939	0.3479	834	0.26 ± 0.12	0.3 ± 0.14
coyote	C04	-3.253	0.0011	8804	0.4 ± 0.13	0.5 ± 0.15
coyote	C05	-2.097	0.0361	8778	0.32 ± 0.12	0.39 ± 0.17
coyote	C06	0.868	0.3853	8631	0.75 ± 0.1	0.74 ± 0.11
coyote	C07	-6.141	<0.001	8512	0.3 ± 0.1	0.42 ± 0.13
coyote	C08	-9.011	<0.001	7874	0.44 ± 0.13	0.55 ± 0.12
coyote	C09	-7.182	<0.001	6788	0.47 ± 0.12	0.57 ± 0.1
coyote	C10	-4.264	<0.001	10613	0.62 ± 0.1	0.67 ± 0.11
coyote	C11	-7.113	<0.001	11073	0.76 ± 0.1	0.81 ± 0.07
coyote	C15	-6.727	<0.001	11791	0.49 ± 0.09	0.55 ± 0.09
coyote	C16	-4.347	<0.001	11102	0.63 ± 0.11	0.68 ± 0.1
coyote	C17_10	-5.536	<0.001	9714	0.41 ± 0.08	0.48 ± 0.1
coyote	C20	-10.774	<0.001	9477	0.73 ± 0.11	0.8 ± 0.07
coyote	C23	-6.118	<0.001	10846	0.61 ± 0.07	0.66 ± 0.06
coyote	C24	-5.534	<0.001	14242	0.4 ± 0.11	0.49 ± 0.11
coyote	C26	-5.568	<0.001	10450	0.36 ± 0.08	0.45 ± 0.1
coyote	C27	-5.203	<0.001	12009	0.63 ± 0.1	0.69 ± 0.07
coyote	C29	-5.210	<0.001	10509	0.43 ± 0.08	0.49 ± 0.09
wolf	W01	-21.002	<0.001	6310	0.55 ± 0.09	0.7 ± 0.11
wolf	W02	-5.123	<0.001	6497	0.44 ± 0.11	0.49 ± 0.08
wolf	W05	-5.735	<0.001	11850	0.42 ± 0.09	0.46 ± 0.08
wolf	W06	-9.216	<0.001	11305	0.24 ± 0.07	0.33 ± 0.12
wolf	W07	-1.553	0.1204	11072	0.41 ± 0.08	0.42 ± 0.09
wolf	W08	-4.157	<0.001	9802	0.4 ± 0.1	0.45 ± 0.11
wolf	W10	-1.755	0.0794	8878	0.46 ± 0.07	0.47 ± 0.06

Table B.3. Paired t -test results of the comparison between the mean habitat suitability value of the corridor polygon and its immediate surrounding area from the *full SSF model.* Negative value of “t” and “mean of differences” imply that the corridor polygon had lower habitat suitability than the immediate surrounding area.

Species	Individuals	t	p-value	DF	mean of differences
black bear	BB01	0.727	0.500	5	0.0042
black bear	BB03	0.548	0.603	6	0.0078
black bear	BB04_09	-0.887	0.389	15	-0.0063
black bear	BB04_10	-1.795	0.147	4	-0.0303
black bear	BB05	1.756	0.113	9	0.0165
black bear	BB06	0.400	0.695	14	0.0048
black bear	BB07	-0.446	0.664	11	-0.0067
black bear	BB08_09	-0.198	0.850	6	-0.0011
black bear	BB08_10	-0.227	0.824	12	-0.0037
black bear	BB08_11	0.398	0.729	2	0.0159
black bear	BB09	-1.494	0.159	13	-0.0135
black bear	BB10	0.851	0.457	3	0.0152
black bear	BB11	0.990	0.368	5	0.0162
black bear	BB12	0.851	0.412	12	0.0063
black bear	BB14_09	-1.751	0.178	3	-0.0304
black bear	BB14_10	0.563	0.583	13	0.0149
black bear	BB15	0.956	0.347	29	0.0085
black bear	BB16_10	-2.584	0.021	15	-0.0125
black bear	BB28_10	1.939	0.059	41	0.0148
black bear	BB28_11	1.534	0.133	40	0.0126
black bear	BB34	1.932	0.085	9	0.0167
black bear	BB38	-0.746	0.475	9	-0.0061
black bear	BB39_10	-0.399	0.700	8	-0.0051
black bear	BB43_10	0.529	0.616	6	0.0054
black bear	BB43_11	-0.929	0.363	22	-0.0071
black bear	BB44_10	-0.091	0.929	17	-0.0006
black bear	BB44_11	1.974	0.063	19	0.0126
black bear	BB54	-1.684	0.110	17	-0.0204
black bear	BB55	1.214	0.240	18	0.0074
black bear	BB58	1.882	0.102	7	0.0215
bobcat	BC01	1.011	0.387	3	0.0258
bobcat	BC03	-6.260	0.025	2	-0.0362
bobcat	BC04	0.559	0.590	9	0.0054
bobcat	BC05	-0.071	0.945	11	-0.0009
bobcat	BC07	-1.107	0.330	4	-0.0360
bobcat	BC08	0.041	0.968	12	0.0003
coyote	C01	0.301	0.774	6	0.0057
coyote	C02	-1.911	0.129	4	-0.0363
coyote	C03	-0.816	0.564	1	-0.0279

Species	Individuals	t	p-value	DF	mean of differences
coyote	C04	0.346	0.762	2	0.0133
coyote	C05	0.452	0.670	5	0.0057
coyote	C06	-1.073	0.315	8	-0.0107
coyote	C07	1.118	0.314	5	0.0172
coyote	C08	-0.266	0.794	16	-0.0026
coyote	C09	-0.972	0.376	5	-0.0120
coyote	C10	-0.421	0.702	3	-0.0125
coyote	C11	0.721	0.481	16	0.0076
coyote	C15	0.513	0.615	16	0.0057
coyote	C16	0.793	0.445	11	0.0085
coyote	C17_10	1.205	0.256	10	0.0176
coyote	C20	0.112	0.915	5	0.0016
coyote	C23	-0.686	0.542	3	-0.0115
coyote	C24	0.073	0.948	2	0.0011
coyote	C26	-5.398	0.003	5	-0.0193
coyote	C27	-0.912	0.429	3	-0.0187
coyote	C29	0.226	0.827	9	0.0024
wolf	W01	-0.668	0.512	20	-0.0049
wolf	W02	-0.554	0.595	8	-0.0088
wolf	W05	-0.186	0.854	22	-0.0020
wolf	W06	-0.793	0.448	9	-0.0107
wolf	W07	-0.756	0.469	9	-0.0070
wolf	W08	0.177	0.863	10	0.0026
wolf	W10	2.951	0.032	5	0.0388

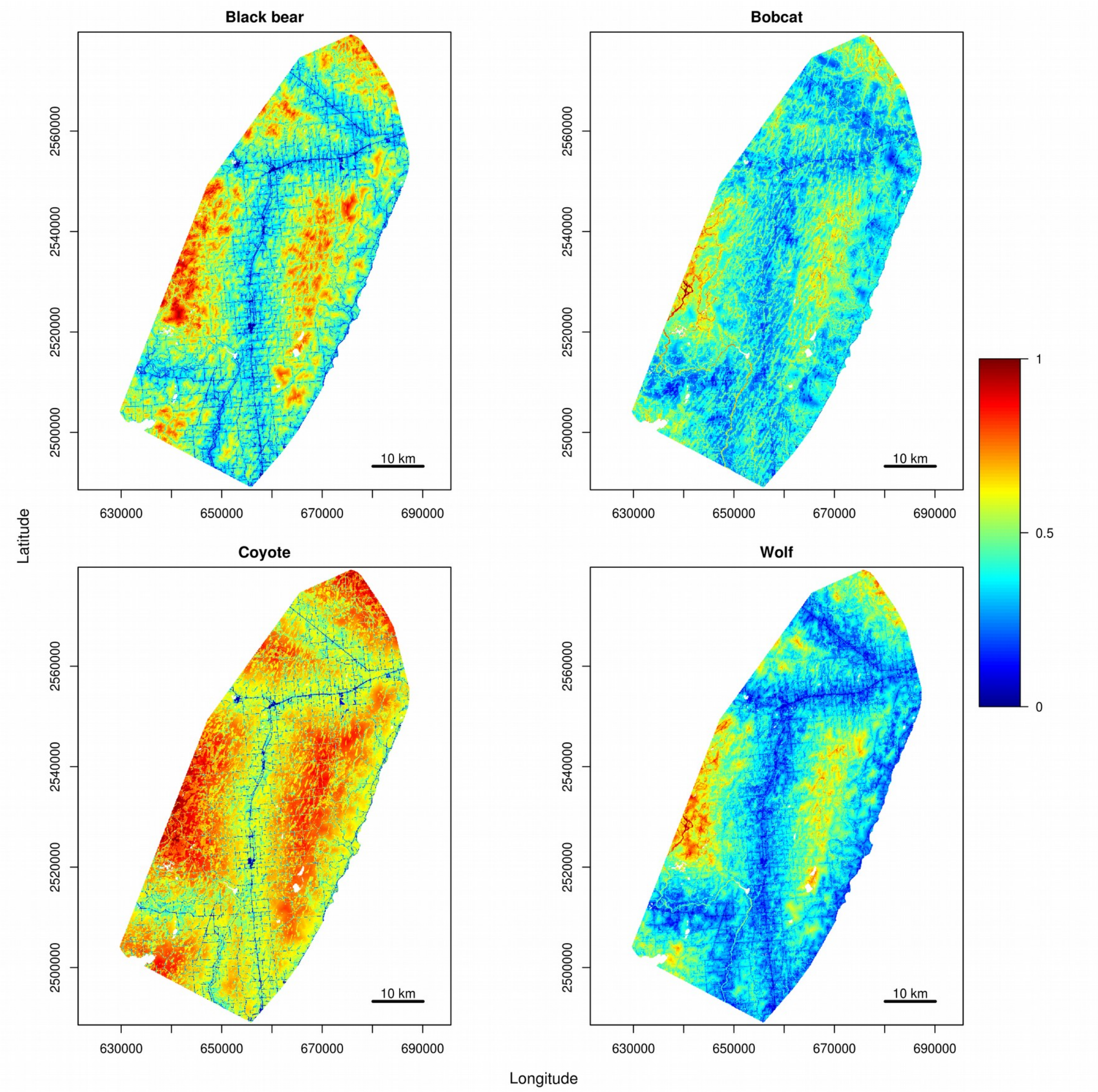


Figure C.1. Predicted habitat suitability for each species previous to any restoration action.

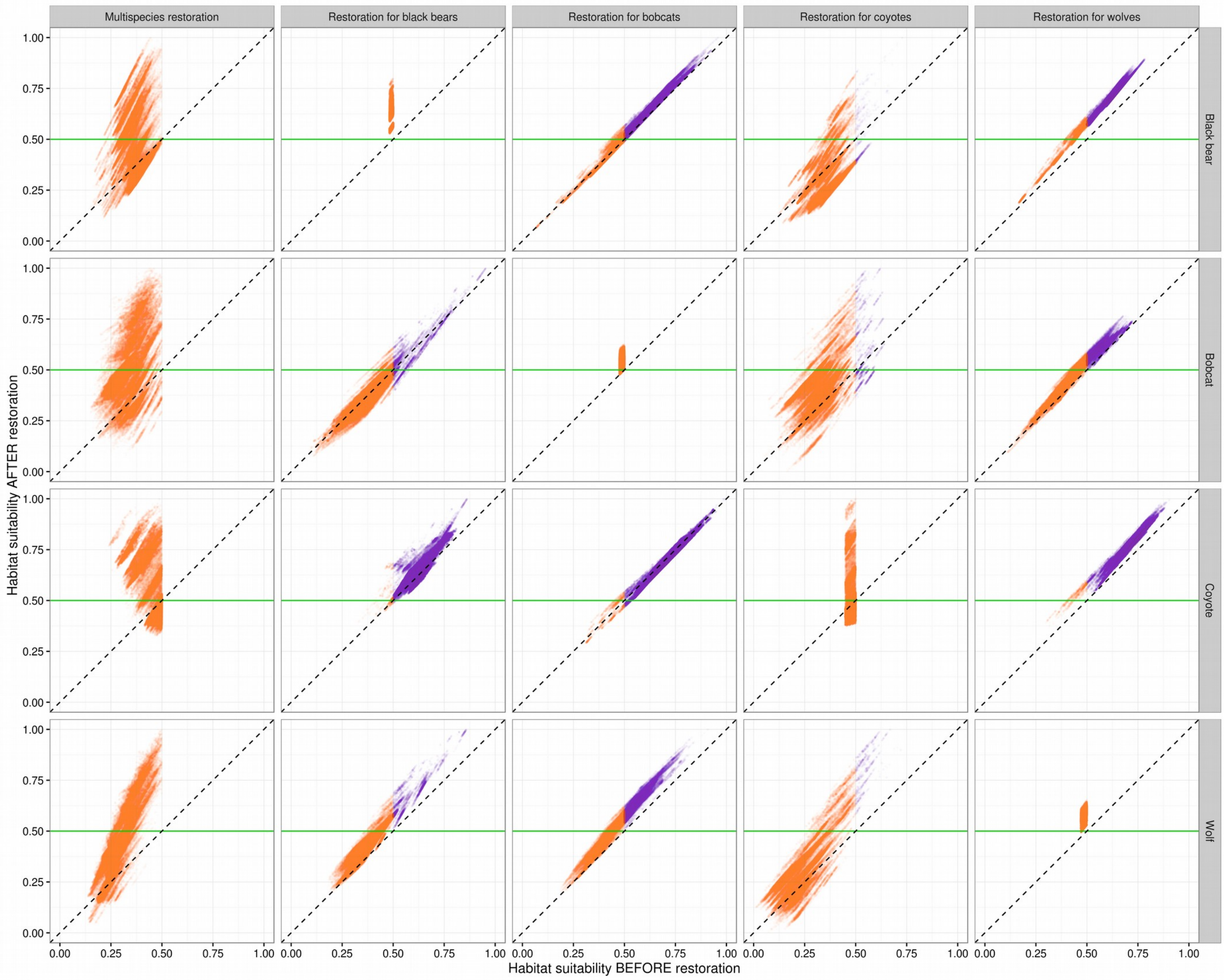


Figure C.2. Representation of the habitat suitability values of all pixels involved in the different restoration approaches. The number of points in each plot is 155973, this is the number of pixels that represents 5% of the study area. The orange points were unsuitable before restoration, the purple points were suitable before restoration. All points above the green line were suitable after restoration, those below, remained unsuitable. The points under the diagonal dashed line decreased in habitat suitability after restoration, those above increased. The density of the color (orange or purple) corresponds to the density of overlapping points.

Table C.1. Summary of individuals included in study

Species	Number of individuals	Sex		Life stage		Number of days tracked* (mean±SD)	Number of locations* (mean±SD)
		Female	Male	Adult	Juvenile		
Black bear	25 (+8)#	10 (3)#	14 (5)#	20 (8)#	5	82 ± 37	1759 ± 945
Bobcat	7	1	6	5	2	87 ± 44	2041 ± 1022
Coyote	21	11	10	19	2	101 ± 29	2265 ± 816
Wolf	7	5	2	7	0	105 ± 26	2359 ± 562

*Only the data used in the analysis of this study is included (i.e. within the time window of interest (1st May - 30th September) and 60 min time lag)
Number of individuals that were tracked in consecutive years, and accounted for as separate individuals in the analysis.

Table C.2. Factor of change and D value of the Kolmogorov-Smirnov test of the variables used in each restoration approach. The variables are sorted by the D statistic for each restoration approach.

Multi-species restoration

	D	Factor of change	Used for restoration
Distance highways	0.765***	2.639	x
% woody wetland in 30m	0.607***	4.600	x
% human cover 30m	0.510***	0.042	x
% deciduous forest in 30m	0.435***	0.234	x
Distance second roads	0.426***	2.121	x
Distance water	0.100***	0.902	x
% open cover in 30m	0.066***	0.740	
% mixed forest in 30m	0.063***	0.678	
% evergreen forest in 30m	0.022***	1.829	

Restoration for black bear

	D	Factor of change	Used for restoration
Distance highways	0.351***	1.676	x
Distance second roads	0.218***	1.525	x
% woody wetland in 30m	0.117***	1.198	x
% open cover in 30m	0.068***	0.644	
Distance water	0.055***	1.112	
% deciduous forest in 30m	0.030***	0.914	
% human cover 30m	0.030***	0.371	
% evergreen forest in 30m	0.021***	0.710	
% mixed forest in 30m	0.017***	0.845	

Restoration for bobcat

	D	Factor of change	Used for restoration
Distance highways	0.262***	1.252	x
Distance water	0.203***	0.660	x
% deciduous forest in 30m	0.065***	0.601	
% woody wetland in 30m	0.053***	0.975	
% open cover in 30m	0.042***	0.545	
Distance second roads	0.029***	0.957	
% human cover 30m	0.018***	0.650	
% evergreen forest in 30m	0.012**	0.808	
% mixed forest in 30m	0.012**	0.948	

Restoration for coyote

	D	Factor of change	Used for restoration
Distance highways	0.439***	2.099	x
% woody wetland in 30m	0.400***	3.951	x
% deciduous forest in 30m	0.397***	0.316	x
% human cover 30m	0.330***	0.099	x
Distance second roads	0.269***	1.742	x
Distance water	0.136***	1.303	x
% mixed forest in 30m	0.123***	0.453	x
% open cover in 30m	0.112***	1.866	x
% evergreen forest in 30m	0.025***	1.488	

Restoration for wolf

	D	Factor of change	Used for restoration
Distance highways	0.385***	1.311	x
Distance second roads	0.123***	1.290	x
Distance water	0.088***	0.823	
% human cover 30m	0.026***	0.567	
% woody wetland in 30m	0.023***	1.034	
% mixed forest in 30m	0.020***	0.757	
% open cover in 30m	0.019***	0.921	
% deciduous forest in 30m	0.015***	0.952	
% evergreen forest in 30m	0.011**	0.824	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns ' 1

Table C.3. Mean difference between the habitat suitability values after and before restoration. Positive values indicate an increase of habitat suitability values after restoration, negative values indicate a decrease of habitat suitability values after restoration

Habitat restored for	Species affected	Change of habitat suitability values before and after restoration (mean ± SD)
Multi-species	Black bear	0.094 ± 0.156
Multi-species	Bobcat	0.151 ± 0.143
Multi-species	Coyote	0.091 ± 0.164
Multi-species	Wolf	0.152 ± 0.114
Black bear	Black bear	0.114 ± 0.043
Black bear	Bobcat	- 0.016 ± 0.035
Black bear	Coyote	0.014 ± 0.035
Black bear	Wolf	0.044 ± 0.035
Bobcat	Black bear	0.014 ± 0.017
Bobcat	Bobcat	0.049 ± 0.023
Bobcat	Coyote	- 0.013 ± 0.015
Bobcat	Wolf	0.057 ± 0.027
Coyote	Black bear	- 0.053 ± 0.087
Coyote	Bobcat	0.087 ± 0.098
Coyote	Coyote	0.021 ± 0.094
Coyote	Wolf	0.063 ± 0.081
Wolf	Black bear	0.083 ± 0.016
Wolf	Bobcat	0.040 ± 0.019
Wolf	Coyote	0.060 ± 0.016
Wolf	Wolf	0.092 ± 0.018

List of publications

Scharf, A.K., J.L. Beland, D.E. Jr Beyer, M. Wikelski & K. Safi (*in press*.) Habitat Suitability does not capture the essence of Animal-Defined Corridors. Movement Ecology.

Scharf, A.K., N. Fernández. (2018) Up-scaling local-habitat models for large-scale conservation: Assessing suitable areas for the brown bear comeback in Europe. Diversity and Distributions, 00:1–10.

Cooper, D.M., A.J. Dugmore, B.M. Gittings, **A.K. Scharf,** A. Wilting & A.C. Kitchener (2016) Predicted Pleistocene - Holocene range shifts of the tiger (*Panthera tigris*). Diversity and Distributions, 22(11): 1199-1211.

Bautista, C., J. Naves, E. Revilla, N. Fernández, J. Albrecht, **A.K. Scharf,** R. Rigg, A.A. Karamanlidis, K. Jerina, D. Huber, S. Palazón, R. Kont, P. Ciucci, C. Grodd, A. Dutsov, J. Seijas, P.I. Quenette, A. Olszańska, M. Shkvyria, M. Adamec, J. Ozolins, M. Jonozvic & N. Selva (2016) Patterns and correlates of claims for brown bear damages on a continental scale. Journal of Applied Ecology

Abedi-Lartey, M., D.K.N. Dechmann, M. Wikelski, **A.K. Scharf** & J. Fahr (2016) Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. Global Ecology and Conservation, 7: 12-24

Scharf, A.K., S. LaPoint, M. Wikelski & K. Safi (2016) Acceleration Data Reveal Highly Individually Structured Energetic Landscapes in Free-Ranging Fishers (*Pekania pennanti*). PLOS ONE 11(2):e0145732.

Wilting, A., A. Courtiol, P. Christiansen, J. Niedballa, **A.K. Scharf,** L. Orlando, N. Balkenhol, H. Hofer, S. Kramer-Schadt, J. Fickel & A.C. Kitchener (2015) Planning tiger recovery: Understanding intraspecific variation for effective conservation. Science Advances, 1(5), e1400175.

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Ossa G, S.Kramer-Schadt, A.J. Peel, **A.K. Scharf** & C.C. Voigt (2012) The Movement Ecology of the Straw-Colored Fruit Bat, *Eidolon helvum*, in Sub-Saharan Africa Assessed by Stable Isotope Ratios. PLOS ONE 7(9): e45729

IN PREPARATION

Scharf, A.K., J.L. Beland, D.E. Jr Beyer, M. Wikelski & K. Safi (*in prep.*) Multi-species habitat restoration models are more than the sum of the parts

O'Mara, M.T., **A.K. Scharf**, J. Fahr, M. Abedi-Lartey, M. Wikelski, D.K.N. Dechmann, K. Safi (*in prep.*) Dynamic body acceleration in straw-coloured fruit bats is constant across wind conditions and airspeeds.