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Increasing ecological realism in conservation network design: a case study in Belize and an evaluation of global satellite telemetry for connectivity research

submitted by

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"Everyone talks about leaving a better planet for our children... we should not forget to leave better children to our planet."

Anonymous

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Abstract

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Human-caused fragmentation and loss of natural habitat are among the world's major challenges today. In combination with climate change, these processes contribute to soaring local and global extinction of many plant and animal species. Specifically, habitat loss and fragmentation disrupt contiguous natural areas, leading to low population sizes and geographic, demographic, and genetic isolation of populations. To avoid increased risk of extinction, conservation networks are created to preserve connectivity between the remaining patches of natural habitat. Oftentimes, conservation networks are clusters of protected areas connected through corridors or stepping-stone linkages. In applied conservation these networks have largely been based on expert-opinion. In landscape ecological research, more systematic modelling approaches are being developed to identify, evaluate, and optimise networks. These models aim to increase ecological realism in network design in order to avoid misguided management actions. However, increasing the ecological complexity in models requires more detailed ecological data, which is not always available in conservation settings. In this dissertation, I investigate the challenges and opportunities that arise when aiming for conservation network design based on models that use increasingly detailed ecological information.

I used remotely-sensed landscape data and species detection data in Belize to model potential connectivity for white-lipped peccaries *Tayassu pecari*. This species is an endangered forest ungulate and acts as an umbrella species due to its large area requirements and relatively short dispersal distance. I included data on protected area effectiveness to determine habitat suitability, and estimated connections between high-suitability areas.

I found that the model contributed to and augmented the current conservation network design by identifying alternative corridor routes and areas that were particularly important for connectivity conservation.

Additionally, I deployed a satellite telemetry collar on a white-lipped peccary in southern Belize to obtain more detailed ecological data to parametrise the connectivity model. However, I found that data collection for the species was challenging, presumably due to the effects of forest cover and terrain ruggedness. I also observed that the success of GPS fixes was lowered by animal activity. The resulting data did not allow for connectivity modelling, but yielded an average home-range size estimate and relatively slow movement rates compared to other estimates for the species, and confirmed the species' preference for forested habitats.

Lastly, I conducted a global evaluation of satellite telemetry performance in wildlife research. I used a standardised questionnaire to avoid the bias towards successful implementations that is suspected to be present in the literature. I gathered information from over 3,000 telemetry units deployed on 63 species over 143 study areas, aiming to gain insight into the relative influence of the environment, topography, species characteristics, and unit specifications on the success of fix acquisition, data transfer and unit failure rate. I found that, in an average project, fix acquisition was relatively high but nonetheless only just satisfied researchers' expectations. Species and unit characteristics were more important predictors of success rates than environmental factors. Data transfer rates were generally high, with satellite-based data transfer performing slightly worse. However, close to half of the deployments failed prematurely, and half of these suffered a technical malfunction.

Understanding and modelling functional connectivity with increasing ecological realism is necessary for effective conservation network design. Network design based on moderately data-demanding models seems to be an achievable objective for current applied connectivity conservation initiatives. However, despite considerable developments in technology and analysis methods, modelling with high levels of ecological detail is still challenged by technological shortcomings and limited availability of detailed data. Ultimately, effective conservation network design depends on the continued collaboration between the modelling, empirical, and applied domains of connectivity conservation.

Zusammenfassung

Der Verlust und die Fragmentierung natürlicher Habitate bedingt durch anthropgene Störungen stellen weltweit eine große Herausforderung dar. In Kombination mit dem Klimawandel tragen diese Prozesse zum Verlust der lokaler und globaler Artenvielfalt bei. Im speziellen zerschneidet die Fragmentierung zusammenhängende Naturräume, was zu einer verringerten Größe, sowie zu geographischer, demographischer und auch genetischer Isolation von Populationen führen kann. Naturschutznetzwerke wurden dafür eingerichtet um die Konnektivität zwischen den verbleibenden Habitaten aufrecht zu halten und das Aussterberisiko zu minimieren. Diese Naturschutznetzwerke setzen sich oft sowohl aus Naturschutzgebieten als auch aus Korridoren und Trittsteine zusammen. In der Praxis basiert die Ausweisung solche Netzwerke häufig auf Expertenwissen. In die Landschaftsökologie werden neue Modelanätze erforscht, um solche Schutznetzwerke besser zu identifizieren, zu bewerten und zu optimieren. Diese Modelle zielen darauf ab, ökologische Prozesse in ihrer Komplexität besser abbilden zu können, um unzureichende Schutzmaßnamen zu vermeiden. Solche Modelle benötigen allerdings sehr detaillierte ökologische Daten, die im Naturschutz nich immer zur verfügung stehen oder nur schwer zu erheben sind. Im Rahmen meiner Doktorarbeit wurde die Planung und Ausweisung solcher Netzwerke, die Herausforderungen und Anwendungsmöglichkeiten neuer Modelle mit zumehmendem Informationsgehalt näher betrachtet.

Dafür wurden sowohl Fernerkundungsdaten als auch Vorkommensnachweise von Weißlippenpekaris *Tayassu pecari* verwendet, um die potenzielle Konnektivität innerhalb des Staates Belize zu modellieren. Dieser bedrohte waldlebende Paarhufer stelt eine Schirmart für den Naturschutz dar, da sie auf große zusammenhängende Habitate angewiesen

ist und sich nur über kurze Distanzen ausbreitet. Für die Studie wurden Daten über die Effektivität ausgewiesener Schutzgebiete verwendet, um die Habitateignung sowie die Konnektivität besonders geeigneter Lebensräume zu bestimmen. Es konnte dabei festgestellt werden, dass das neue Model zur Ausweitung des bereits bestehenden Schutznetzwerks beitrug, indem es alternatieve Korridore und neue wichtigen Flächen für den Lebensraumverbund identifizierte.

Desweiteren wurde ein Pekari im südlichen Belize mit einem GPS-Sender ausgestattet, um detailliertere Daten über die Lebensraumnutzung zu erhalten und anschließend das Model bezüglich der Konnektivität besser parameterisieren zu können. Allerdings konnte dabei festgestellt werden, dass die Erhebung solcher Daten durch die Bewaldung als auch durch die Beschaffenheit des Terrains erheblich negativ beeinflusst wurde. Darüber hinaus konnte beobachtet werden, dass die erfolgreiche Übertragung der GPS-Lokalisierungen stark von der Aktivität des Tieres abhängig war. Daher konnten die Ergebnisse zwar nicht direkt für die Modellierung der Konnektivität verwendet werden, aber die Streifsgebietsgröße konnte berechnet werden. Die geschätzte Streifsgebietgröße, die relativ geringe Bewegungsraten sowie die Präferenz bewaldeter Gebiete waren vergleichbar mit den Ergebnissen anderer Studien für diese Tierart.

Abschließend wurde eine weltweite Bewertung der Leistungsfähigkeit von GPS-Telemetrie im Rahmen der Wildtierforschung durchgeführt. Dabei wurde auf eine standardisierten Fragebogen zurückgegriffen, um auch die Probleme bei nicht erfolgreichen Forschungsvorhaben berücksichtigen zu können. Es konnten Informationen von über 3.000 Telemetriesendern gesammelt werden, die für 63 verschiedene Tierarten in über 143 Untersuchungsgebieten eingesetzt wurden. Das Ziel war Einblicke über die Einflusse der Umwelt, Topographie, sowie bestimmter Arteigenschaften und der Beschaffenheit der Sendereinheit auf die erfolgreiche Datenerhebung, sowie deren erfolgreiche Übertragung oder Gründe für den Ausfall des Senders zu erheben. Es konnte festgestellt werden, dass es im Durchschnitt für das jeweilige Projekt, einen relativ hohen Anteil erfolgreich aufgezeichnete Positionen gab, dieser entsprach allerdings nicht immer den Erwartungen der Forscher. Außerdem waren artabhängige und senderspezifische Eigenschaften häufiger ausschlaggebend für die erfolgreiche Erhebung der Daten, als Umweltfaktoren. Die Übertragungsraten waren generell sehr hoch, aber bei der satellitengestützten Übertragung fehleranfälliger. Bei nahezu der Hälfte aller Anwendungen versagten die Sender bereits frühzeitig, was in der Hälfte dieser Fälle auf technisches Versagen zurückzuführen war.

Die Modellierung der funktionellen Landschaftskonnektivität mit Einbindung ökologischer Erkentnisse ist für eine effektive Ausweisung von Naturschutznetzwerke unumgänglich. Die Ergebnisse dieser Studie zeigten, dass bereits eine geringfügige Erhöhung der verfügbaren Daten zu einer besseren Planungsgrundlage für Naturschutznetzwerken führen. Trotz

des erheblichen technologischen Fortschritts und neuen Auswertungsansätzen, ist die ökologische Detailschärfe der Modelle immer noch stark durch technische Defizite und die Verfügbarkeit ausreichender Daten eingeschränkt. Schlussendlich ist die effektive Planung von Naturschutznetzwerke auf die Zusammenarbeit verschiedener Fachgebiete angewiesen, die die empirische Erhebung der Daten sowie deren Analyse, Modellierung und praktischen Umsetzung vereint.

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Abbreviations

AIC	Akaike Information Criterion
AICc	Akaike Information Criterion, adjusted for small sample size
ASTER	Advanced Spaceborne Thermal Emission and Reflection Radiometer
AVHRR	Advanced Very High Resolution Radiometer
BERDS	Biodiversity and Environmental Resource Data System of Belize
BM	Brownian Motion model
BNR	Bladen Nature Reserve
Cat.	Category
CI	Confidence Interval
DOP	Dilution of Precision
EVI	Enhanced Vegetation Index
FONASO	Forests and Nature for Society
GAMLSS	Generalised Additive Models for Location, Scale and Shape
GLONASS	Global Navigation Satellite System
GPS	Global Positioning System
GSM	Global System for Mobile communications
HDOP	Horizontal Dilution of Precision
IUCN	International Union for the Conservation of Nature
KDE	Kernel Density Estimate
LiDAR	Light Detection and Ranging
MCP	Minimum Convex Polygon
MODIS	Moderate-resolution Imaging Spectroradiometer
NDVI	Normalised Difference Vegetation Index
NGO	Non-Governmental Organisation
NOAA	National Oceanic and Atmospheric Administration

OU	Ornstein-Uhlenbeck motion model
OUF	Ornstein-Uhlenbeck motion model, with foraging included
PA	Protected Area
PAEF	Protected Area Effectiveness
PC	Probability of Connectivity, a landscape connectivity metric
PCM	Potential Connectivity Model
PDOP	Positional Dilution of Precision
PG	Punta Gorda, Toledo, Belize
QFP	Quick Fix Pseudoranging
SIDS	Small Island Developing State
SRTM	Shuttle Radar Topography Mission
SVF	Semi-Variance Function
UHF	Ultra High Frequency
UK	United Kingdom
UN	United Nations
USA	United States of America
VHF	Very High Frequency
Ya'axché	Ya'axché Conservation Trust

For Anna Hofman, Trevonney Rushelle Luna,
William Hofman Macedo Caixeiro, and Ulrike Smet

The future is theirs, but we decide
what environment it will take place in . . .

Chapter 1

Introduction

The current and ongoing level of biodiversity loss is challenging the resilience of global ecosystems (Ceballos *et al.*, 2015). An important driver of biodiversity loss is the conversion of natural habitat to accommodate the needs of the ever-increasing human population (Venter *et al.*, 2016). This conversion has at least two major effects on the natural landscape. Firstly, due to the overall loss of natural habitat, the remaining habitat provides less living space for other species forming part of the Earth's ecosystems. The effects of habitat loss on species diversity, abundance and persistence are not always consistent across species. For example, habitat generalists tend to be less affected by habitat loss than specialists as they are more tolerant to landscape changes. Nonetheless, a consistent effect of decreasing population size with decreasing habitat availability has been found after taking into account these species-specific uses of the landscape (Betts *et al.*, 2014). Secondly, as habitat loss increases, the disruptions in previously contiguous habitat increasingly reduce fragment size, induce edge effects within fragments and increase isolation of the fragments, a process referred to as habitat fragmentation (Bennett, 2004; DeFries *et al.*, 2005; Fahrig, 2003). Edge effects include the degradation of previously intact habitat due to impacts originating from neighbouring land uses, leading to less undisturbed core habitat as compared to fringe habitat (Baskent & Jordan, 1995). Increased isolation of habitat fragments can prevent recolonisation and genetic exchange between populations. Fragmentation is usually defined as a landscape-scale process (Fahrig, 2003). Species are expected to be affected most by fragmentation in landscapes with intermediate levels of habitat available, because the habitat configuration is most variable within such landscapes (Villard & Metzger, 2014).

These effects of habitat fragmentation often lead to population declines and to geographic, demographic and genetic isolation, rendering populations vulnerable to extinction (i.e. extinction vortex; Gilpin & Soulé, 1986). The effects are further exacerbated

by the predicted shifts of entire ecosystems due to climate change (Parmesan *et al.*, 2003): loss of contiguous natural habitat will force species to move large distances across human-modified landscapes in order to keep track of climatological changes, potentially disrupting dispersal and other ecosystem processes such as nutrient cycles, seed dispersal, pollination, and predation (Schloss *et al.*, 2012).

1.1   Connectivity

Over the last few decades, the increasing levels of habitat fragmentation and the resulting isolation has prompted interest in studying and preserving the connectivity between remaining patches of natural habitat (Bennett, 2003; Correa Ayram *et al.*, 2015; Crooks & Sanjayan, 2006b). In applied conservation settings, preserving connectivity is usually accomplished through the establishment of conservation networks, i.e. "coherent system[s] of natural and/or semi-natural landscape elements that [are] configured and managed with the objective of maintaining or restoring ecological functions as a means to conserve biodiversity while also providing appropriate opportunities for the sustainable use of natural resources"(Bennett, 2004, p.6). In practice, such conservation networks are often composed of a combination of protected areas on one hand, and linkages connecting them on the other hand (Beier *et al.*, 2008, 2011; Bennett, 2003, 2004). Usually, these linkages are designed as linear habitat corridors or a series of habitat patches that act as stepping stones between protected areas. Expert judgement is commonly used to evaluate the physical landscape characteristics and the extent to which they allow or obstruct wildlife movement, such as vegetation type and cover, topography, and intensity or proximity of human disturbance (Benedict & Drohan, 2004; Brodie *et al.*, 2014; Hoctor *et al.*, 2000; Jones *et al.*, 2007; Wangchuk, 2007; Wikramanayake *et al.*, 2004; Zeller *et al.*, 2011). Land tenure, agricultural potential or planned infrastructural developments are sometimes taken into account as well, acknowledging the fact that short-term socio-economic considerations often supersede ecological factors such as park size, fragmentation and connectivity, despite these being fundamentally important in the long term (UNEP-WCMC & IUCN, 2016). More recently, conservationists have also been able to take advantage of the progress made in landscape ecological modelling to inform the design of conservation networks. Simultaneous with the development of applied conservation networks, landscape ecologists started to focus on habitat fragmentation and, and developed models and metrics to represent and measure observed fragmentation effects on landscape connectivity (Taylor *et al.*, 1993; Tischendorf & Fahrig, 2000).

In a landscape ecological context, connectivity broadly means facilitation of movement through the landscape, whereby the moving agents can be wind or soil, animals, plants

or propagules, or even ecological interactions (Crooks & Sanjayan, 2006a). However, the science behind landscape connectivity is more complex than that, because habitat conversion and climate change disrupt connectivity at multiple spatial and temporal scales (Bennett, 2004). Habitat conversion and climate change influence species of all sizes and characteristics, disrupt ecosystem processes on local (e.g. pollination) to global (e.g. carbon sequestration) scales, and influence behaviour and evolutionary pathways over time spans of weeks to millennia (e.g. speciation). It is evident that, in order to study and understand the consequences of habitat conversion and climate change on landscape connectivity, this complexity needs simplification by zooming in on a well-defined area, for a limited number of species and over a limited time span. Hence, within landscape ecology, representing the reality with simplified models is a preferred way of gaining insight in the connectivity of a landscape.

1.1.1 Increasing ecological realism

With the inclusion of increasingly detailed biological data, the complexity of these simplified models increases and improves the representation of the biological reality behind them (Fagan & Calabrese, 2006). For example, in connectivity modelling, a distinction is made between structural and functional components of landscape connectivity (Taylor *et al.*, 2006). Early developments in landscape connectivity research focused mostly on structural connectivity. The structural connectivity of a landscape is determined solely by the spatial characteristics of landscape elements (nature, size, shape and orientation), and disregards the way different species perceive and use the landscape. In contrast, functional connectivity depends not only on the spatial configuration of landscape elements, but also on the extent to which different landscape elements allow movement through the landscape for a particular species (Taylor *et al.*, 2006). Functional landscape connectivity has been defined as "the degree to which the landscape facilitates or impedes movement among resource patches"(Taylor *et al.*, 1993, p.571). With (1997) described it as the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure. The distinction between structural and functional connectivity is not a trivial one. For some species, structural connectivity is a good approximation of functional connectivity (Fattebert *et al.*, 2015), but a structurally connected landscape is not necessarily functionally connected for a particular species. Conversely, the landscape can be functionally connected for a particular species through a permeable matrix even though patches of species' habitat are not structurally connected. The addition of more detailed, species-specific, biological data renders the functional connectivity models more complex, as they take into account more of the intricacies of real-world biological systems. They

are therefore considered more ecologically representative than structural connectivity models (Taylor *et al.*, 2006; Tischendorf & Fahrig, 2000).

Increasing the ecological realism of these models is ultimately important because, rather than relying on crude models or exclusively on expert judgement, designing conservation networks based on more realistic connectivity models avoids misguided land management decisions (Abrahms *et al.*, 2016). Indeed, it is one of the driving forces behind the developments in landscape ecology (Crooks & Sanjayan, 2006b).

1.2 The modelling process

Since functional connectivity is species-specific, estimating it requires the selection of one or more target species; a delicate process in its own right (Andelman & Fagan, 2000; Breckheimer *et al.*, 2014). Chosen target species should ideally represent a range of species with similar habitat requirements and dispersal capabilities, and thus function as umbrella species (Brodie *et al.*, 2014). Indeed, a set of target species are ideally considered, representing different priority habitats in the landscape (Sanderson *et al.*, 2002).

Once target species are selected, the functional connectivity modelling process involves several steps (see Figure 1.1; Spear *et al.*, 2016; Zeller *et al.*, 2012). First, experts and literature are consulted, and data on species and landscape characteristics gathered. The availability and resolution of the movement and landscape data is what eventually limits the quality and realism of the connectivity model. Second, a resistance model is created by assigning resistance values to landscape elements reflecting their influence on successful movement. Resistance values are assigned either based on expert opinion, or by estimation through resource selection functions that combine the landscape and species data. Subsequently, one (or more) of many corridor estimation tools is used to delineate corridors of low resistance in the digital landscape between known populations of the study species, patches of suitable habitat, or protected areas. This linkage delineation is usually accompanied by a more numerical evaluation of the overall landscape connectivity by means of one or more of a wide range of connectivity metrics. The resulting connectivity measurements are then statistically validated either by collecting additional field data or by comparing them to genetic structure within the area for the species.
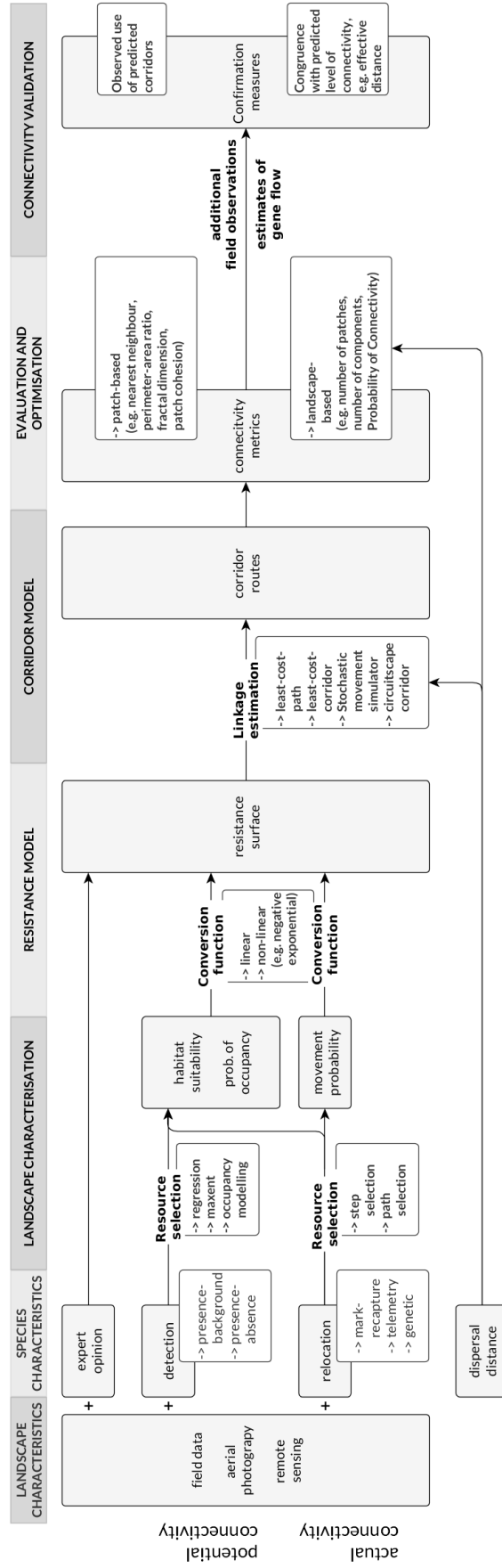
FIGURE 1.1: General overview of the connectivity modelling process. Landscape and species data are combined to produce a digital landscape characterisation that represents the resistance posed by the landscape to movement of the species. Low resistance corridors are identified and evaluated and optimised by calculating connectivity metrics. Additional field observations or estimates of gene flow are used to validate the corridors.

1.2.1 Incorporating species-specific data

In this process, incorporating species-specific movement parameters (e.g. habitat preferences) is most often done during the habitat characterisation steps leading up to the resistance model. The particular type of species-specific data used in this step is important because it eventually determines the type of connectivity measured. Below, I will touch upon the most common data types used. Zeller *et al.* (2012) provide a more in-depth overview of possible data types and approaches to calculate resistance values.

Expert opinion

In many studies, data on the dispersal range of the species and the resistance of landscape elements are provided by consulting expert opinion on the species in the area (Correa Ayram *et al.*, 2015; Sawyer *et al.*, 2011). However, this data type has been criticised for being subjective and reducing the repeatability and defensibility of the research (Chetkiewicz & Boyce, 2009; Rayfield *et al.*, 2010; Sawyer *et al.*, 2011). Furthermore, expert opinion based resistance estimates have been found not to improve resistance estimates obtained using other data types (Seoane *et al.*, 2005). A second data type, empirically gathered biological data, usually leads to more robust and repeatable resistance value assignments than expert opinion. Depending on the type of empirical data used, functional connectivity itself can be split up further into 'potential' and 'actual' connectivity (Fagan & Calabrese, 2006; Rödder *et al.*, 2016).

Detection data: potential connectivity

Potential connectivity estimates are based on species detection data (i.e. static biological point data originating from museum specimens, monitoring grids, camera trap observations, etc.). In combination with landscape data, detection data can provide objective information on the species' preference for certain landscape elements. Landscape data are often obtained from remotely-sensed datasets, and include variables such as land cover, weather variables (e.g. rainfall, insolation), topographic variables (e.g. elevation, slope and aspect), and measures of proximity to the nearest landscape feature of interest (e.g. water source, human settlement, etc.). Species detection data usually come either as presence-absence data or presence-only data. In presence-absence data, the absence of a species is confirmed due to repeated site visits that enable the inference of detectability at different sites. With confirmed presence and absence points, site occupancy is modelled by comparing the predictor values at presence versus absence sites yielding an estimate of the probability of occupancy throughout the landscape

(MacKenzie *et al.*, 2006). Presence-absence models are considered more accurate than presence-only approaches for a number of reasons, *inter alia* because they do not assume constant detection probability across the landscape (Yackulic *et al.*, 2013). However, for many species of conservation concern and/or in remote areas, the effort and resources required to obtain such data inhibit the occupancy modelling approach (Guillera-Arroita *et al.*, 2015). Because presence-only data can be gathered in a variety of ways, they are often easier to compile from many different sources across larger areas. Presence-only data are often used to model habitat suitability for a species using regression or machine learning approaches, whereby the predictor variables at presence sites are compared to a set of background points randomly sampled throughout the landscape (sometimes called pseudo-absence points). MaxEnt 3.3.3. (Phillips *et al.*, 2006) is a well-tested species distribution modelling tool based on machine learning principles that is often used for this purpose (Franklin, 2010). I applied this tool in Chapter 2 of this dissertation.

The resulting landscape characterisation (i.e. probability of occupancy or habitat suitability) is usually translated into a resistance model of the landscape, whereby a higher probability of occupancy or habitat suitability indicates lower resistance (Correa Ayram *et al.*, 2015). This conversion is often accomplished linearly by inverting the habitat suitability, assuming that habitat preferences observed from the detection data represent the preferences the species exhibits e.g. while dispersing. However, detection data can represent a range of movements by the species, and habitat preferences may differ among them. Due to the relative rarity of dispersal or migratory movements, detection data most likely represent daily forage and home-range movements, rather than seasonal and migratory movements, dispersal movements or range expansion. However, an important ecological process in connectivity studies is dispersal; a process that happens outside the home-range, and for which species' habitat preferences can be considerably different from those observed in home-range and foraging movements (Abrahms *et al.*, 2016). For example, many species are likely to traverse sub-optimal habitat when dispersing to new areas (Mateo-Sánchez *et al.*, 2015; Trainor *et al.*, 2013). This means that a habitat suitability or probability of occupancy surface based on detection data could underestimate the suitability (and overestimate resistance) of landscape elements for facilitating dispersal movement. Recent studies have found that the conversion between the suitability and the resistance is instead better represented by a negative exponential relationship (Keeley *et al.*, 2016; Mateo-Sánchez *et al.*, 2015). The negative exponential conversion lowers the resistance values of sub-optimal suitability values and reflects the willingness of many species to cross such landscape elements during dispersal movements (Keeley *et al.*, 2016). This approach increases the validity of potential connectivity estimates. However, the approach still uses point-based observations that lack crucial information on actual movement and its underlying ecological process. Precisely because they do not

contain explicit information on actual behaviour, detection data have been questioned as a basis for estimating landscape resistance for movement-based processes (Spear *et al.*, 2016). Estimating connectivity from such resistance models could result in misguided conclusions regarding landscape connectivity (Mateo-Sánchez *et al.*, 2015).

Relocation data: actual connectivity

In contrast, 'actual' functional connectivity estimates circumvent this problem by basing the resistance surface on movements observed in individual animals, i.e. relocation data. Capture-recapture studies (representing e.g. home-range movements), genetic studies (representing dispersal movement with successful reproduction) or telemetry studies (continuous movement paths) are sources of such data (Fagan & Calabrese, 2006; Taylor *et al.*, 2006). Due to their frequent sampling frequency, telemetry data usually contain highly detailed information on the characteristics of movement paths through the modelled landscape. A path can be described as a combination of subsequent steps, each with their properties (e.g. step length, turning angles, boundary behaviour or travel speed in different landscape elements). Hence, the basic analysis unit becomes the observed movement steps or paths. Step and path selection functions are the most commonly used methods to derive habitat preferences that can be translated into resistance models (Benz *et al.*, 2016; Zeller *et al.*, 2016). Step selection functions are a type of resource selection function that, for each step in the animal's movement path, estimates the relative probability of selecting a resource unit versus alternative possible resource units within the same step length (Manly *et al.*, 2002; Thurfjell *et al.*, 2014; Zeller *et al.*, 2016). Step selection functions are modelled in a conditional regression framework that pairs up the landscape variables measured along the observed steps with those along a number of randomly generated steps from the same start point. The regression models are then used to predict relative probability of movement through different parts of the landscape. Path selection functions are analogous to step selection function, but make use of multiple subsequent steps for a similar 'used' vs 'available' approach (Zeller *et al.*, 2016). One advantage of using movement paths is that it reduces the unwanted statistical effects of temporal and spatial autocorrelation that are inherent in step selection approaches (Cushman, 2010). Another advantage of using movement paths is that they can be separated into movement associated with different behavioural states (dispersing, migrating, foraging, resting). These behavioural states are identified using algorithms to clip paths and cluster path segments with similar characteristics (Edelhoff *et al.*, 2016). This allows for state-specific resistance surfaces to be constructed, thereby ensuring that estimated connectivity models represent the correct ecological process considered in the study (Abrahms *et al.*, 2016; Zeller *et al.*, 2016). Actual functional connectivity

is the most ecologically relevant modelling approach in landscape ecology to date, as it contains the highest amount of movement information (Benz *et al.*, 2016; Calabrese & Fagan, 2004; Spear *et al.*, 2016; Zeller *et al.*, 2012). However, it is also the most novel and most challenging way of modelling connectivity: data analysis methods are still in early development (Thurfjell *et al.*, 2014).

1.2.2 Estimating connectivity

Once the resistance model has been developed, connections between populations, suitable habitat or protected areas can be estimated, usually using one of two commonly used approaches: least-cost and electrical circuit theory (Lechner *et al.*, 2015; Rudnick *et al.*, 2012; Spear *et al.*, 2016). The least-cost method draws a single line or corridor between a pair of patches that minimises the cumulative resistance between them (also called the 'effective distance' — Adriaensen *et al.*, 2003), whereas electric circuit theory estimates the pairwise resistance while allowing for the resistance to be split over multiple pathways instead of a single least-cost path or corridor (McRae & Beier, 2007). Both of these methods will delineate a connection between every pair of patches, regardless of whether the Euclidean or effective distance between them can be biologically covered by the study species. The species' maximum dispersal distance can be used as a threshold value to cut off modelled connections to a plausible distance. This step incorporates further species-specific data in the connectivity estimates (see Figure 1.1 on p.5).

1.2.3 Evaluating and optimising connectivity

Landscape ecology has produced a multitude of metrics to quantify, assess, and optimise modelled connectivity between patches and for the entire landscape (Calabrese & Fagan, 2004). Because patch-based metrics (e.g. patch size, shape and isolation) do not allow for landscape-level inference (Fahrig, 2003), they have been largely replaced by more recent connectivity metrics involving calculations of the pairwise distances between network patches, the amount of habitat in the landscape, and/or the spatial contagion of habitat patches. In contrast to connectivity measures on the patch level, these metrics have the advantage that they are not tied to a limited area extent. That is, they allow for upscaling conservation actions from local, to landscape, regional and even continental scales (Bennett *et al.*, 2006; Santini *et al.*, 2016). This is advantageous in the context of the expected effects across spatial scales as a consequence of global changes, but does require careful consideration of spatial and temporal resolutions of source data (see sections 1.3 and 1.4). These metrics are based on a diverse array of approaches, and have been reviewed on several occasions (Calabrese & Fagan, 2004; Kindlmann & Burel,

2008; Magle *et al.*, 2008; Tischendorf & Fahrig, 2000). Nevertheless, their properties, behaviour and adequacy for use in conservation network planning have not often been evaluated and no general consensus on preferred methods has emerged (Saura & Pascual-Hortal, 2007). Because graph-theoretic approaches provide a good trade-off between a reasonably detailed picture of landscape connectivity at larger scales and relatively low data requirements (Calabrese & Fagan, 2004), I briefly describe the use of the Probability of Connectivity metric (Pascual-Hortal & Saura, 2006; Saura & Pascual-Hortal, 2007). This metric is an implementation of a graph theoretic connectivity evaluation that I used in Chapter 2 of this dissertation.

Probability of Connectivity

Graphs in graph theory are a mathematical representation of interlinked entities. The entities are called 'nodes', whereas the links between them are referred to as 'edges' (Bunn *et al.*, 2000; Minor & Urban, 2008). In graph-theoretic connectivity assessments, the conservation network is the graph, whereby the nodes of the graph are represented by the known populations or suitable habitat patches in the network, and the graph edges by the estimated connections between them. Nodes can be characterised by habitat quality, patch size, or a combination of both, while the edges are usually characterised by a probabilistic model of the least-cost or resistance values of the connections (Dale & Fortin, 2010; Murphy *et al.*, 2016; Saura & Pascual-Hortal, 2007). The Probability of Connectivity index considers the connectivity within the network to be determined by both the edge and node characteristics, and thus the index essentially summarises the quality and the quantity of reachable available habitat in the entire landscape in a single value (Saura & Pascual-Hortal, 2007). Additionally, by removing each element of the corridor network one at a time and recording the relative change in the Probability of Connectivity, one can evaluate the importance of different patches in the network (see Chapter 2; Bodin & Saura, 2010). The relative change in Probability of Connectivity (dPC) is evaluated in three fractions, each of which specifies changes in a different role of the removed patch in the network: dPC_{intra} represents the removed element's contribution in habitat area and quality, dPC_{flux} represents its contribution to the flux of dispersing organisms, and $dPC_{connector}$ the extent to which it acts as a connecting element (Bodin & Saura, 2010). Hence, these metrics allow a quantitative assessment of the specific role of core patches in the network. These properties, among other strengths, make the index a prime candidate for use in applied connectivity conservation settings.

1.2.4 Towards application in connectivity conservation

Several analytical tools have been developed in recent years that aim to streamline the process of functional connectivity estimation and make the approaches described above accessible for application in connectivity conservation. For example, Linkage mapper (McRae & Kavanagh, 2011) is a an open-source tool that maps linkages between core areas, starting from user-defined core area maps and resistance surfaces. It calculates least-cost corridors between each pair of core areas and compiles them together in a single corridor map. It is implemented as a toolbox in the commonly used Geographic Information System ArcGIS (ESRI, 2015). It also has added modules for detection of barriers, connectivity bottlenecks, and climate gradient linkages. Chapter 2 uses this tool for corridor delineation. The Linkage Mapper toolbox is housed under the same umbrella as Circuitscape (McRae *et al.*, 2008), another open-source tool that uses circuit theory and random-walk algorithms (Doyle & Snell, 1984) to model landscape connectivity. It is often used in landscape genetic studies and to identify bottlenecks in corridor designs. A graph-theoretic example is the Conefor2.6 software (Saura & Torné, 2009, 2012), also used in Chapter 2. This stand-alone software package makes several graph-theoretic connectivity indices available, including the Probability of Connectivity index that quantifies the importance of habitat areas and links for the maintenance or improvement of landscape connectivity. These packages, and a range of others, are listed on the website http://conservationcorridor.org, which provides a concise and well-structured overview of the different tools available to conservationists and land managers for connectivity assessment and corridor design. Some tools include a full overview of the process of conservation linkage design, from engaging stakeholders and identifying barriers to choosing the appropriate modelling tools and incorporating results in decision making (e.g. http://corridordesign.org or http://www.landscope.org/focus/connectivity/).

Given the more recent developments in satellite telemetry, available software packages that handle movement data originating from telemetry are not developed to the same extent, but many R (R Development Core Team, 2015) add-on packages have been developed as that cover both basic and advanced analysis tools, such as `adehabitat` (Calenge, 2006), `move` (Kranstauber *et al.*, 2012), `T-LoCoH` (Lyons *et al.*, 2013), `crawl` (Johnson *et al.*, 2008), `rhr` (Signer & Balkenhol, 2015), and `moveHMM` (Michelot *et al.*, 2017), among others.

Hence, a broad range of opportunities exist for using more ecologically realistic models in conservation network design. However, the level of ecological detail and the application of these tools to address specific connectivity questions for land management purposes depends on the availability of sufficiently fine-scale resolution data on species-specific

movement and landscape elements. In the next sections, a brief overview of both data types is provided.

1.3 Landscape data through remote sensing

The rapid increase of connectivity modelling efforts has been made possible largely due to the increasing amount of remotely-sensed data becoming available parallel to the technological developments in satellite telemetry. Since the 1970s, satellite-based remote sensing data has been gathered across a wide range of spatial and temporal scales (Neumann *et al.*, 2015). As with satellite telemetry, the underlying ecological process studied determines the scale and type of remotely-sensed data to be used. Currently available remote sensing technology inherently involves a trade-off between infrequently gathered data of fine spatial resolutions (e.g. land cover), and more frequently gathered data on much coarser spatial resolutions (Neumann *et al.*, 2015). It is important for the landscape information to match fine-scale information originating from satellite telemetry used in order to avoid inaccuracies in the resistance surface (Simpkins *et al.*, 2017). Hence the fine-scale infrequent data is arguably the most useful in connectivity studies, although a combination of the two types is often used. In aerial applications, remotely-sensed data that is both fine-scale and high-frequency, e.g. on atmospheric conditions, can be of crucial importance to understand movement patterns (Bohrer *et al.*, 2012; Klaassen *et al.*, 2011).

1.3.1 Remote sensing and connectivity assessments

Frequently used fine-scale remote sensing data in connectivity studies include Landsat imagery or aerial photography (Neumann *et al.*, 2015). These are used to determine the size, shape and orientation of landscape elements, including anthropogenic infrastructure. Gathering details on the specific nature of these elements (e.g. level of forest degradation or type of infrastructure) has recently become possible through the development of Light Detection and Ranging (LiDAR—http://oceanservice.noaa.gov/facts/lidar.html) and hyperspectral remote sensing (Kays *et al.*, 2015). Digital elevation models derived from primarily the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) or the Shuttle Radar Topography Mission (STRM) provide additional fine-scale information on topographic characteristics of the landscape such as altitude, aspect and slope. Coarse-scale data are usually gathered much more frequent. For example, measures of primary productivity (e.g. Normalised Difference Vegetation Index [NDVI] or Enhanced Vegetation Index [EVI]) are available on 8–16 day intervals. Data on fire regimes and climate and weather indices are provided by the Advanced Very High

Resolution Radiometer (AVHRR) of the National Oceanic and Atmospheric Administration (NOAA), by the Moderate-resolution Imaging Spectroradiometer (MODIS) or by monthly WorldClim data. Many of these datasets and their derived indices are freely available and relatively straightforward to obtain at reasonable temporal resolution for many regions of the globe (Neumann *et al.*, 2015). Additionally, animal movement databases (e.g. Movebank) have started to make several remote sensing datasets and indices available as direct annotation to movement paths (Kays *et al.*, 2015).

It is acknowledged that the spatial and temporal resolutions and accuracy of remotely-sensed datasets vary (Neumann *et al.*, 2015). For example, the minimum mapping unit (i.e. the smallest observable feature that can be mapped) is around 1–5 m^2 for images from the finest scale data (Quickbird and Worldview, which are only in part freely available), but goes up to 3,600 m^2 for Landsat and 250,000 m^2 for MODIS data, which is much coarser than most movement data gathered using satellite telemetry. Simpkins *et al.* (2017) found that the grain (i.e. the area represented by a single grid cell) had a large overall effect on accuracy of connectivity estimates. In addition, low accuracy of the remotely-sensed data can impact the validity of animal movement and habitat use models for connectivity. Both of these issues are ideally taken into account when using remote sensing for estimating habitat selection in connectivity studies, regardless of whether static or time-series species-specific data are used.

1.4 Obtaining movement data

Species-specific movement information is often more difficult to obtain in the quality and quantity needed for fruitful application in connectivity estimates (Gitzen *et al.*, 2013). Direct observation of movements may be possible for species that generally move short distances such as insects or breeding birds (Wilson & Thomas, 2002). They tend to represent behaviour restricted to limited spatial and temporal scales, usually within the home-range of the animal. However, increasing the biological realism of landscape connectivity estimates requires identifying the behavioural decisions and habitat preferences specific to migration or dispersal. These processes tend to occur on large scales that inhibit direct observation. Moreover, while migration is a recurring event and can potentially be observed multiple times in a single individual, dispersal events in many species are relatively rare and difficult to observe. Often capturing individual animals, sometimes repeatedly, to mark them, obtain genetic samples or fit them with telemetry units is required to obtain information on these events. Mark-recapture and genetic samples provide evidence that an individual has moved from one location to the next, indicating that it was able to cross the landscape in between these points. However,

obtained locations do not capture information on the actual route taken to cover the distance between them. Wildlife telemetry provides this possibility by enabling the tracking of individuals' movement paths at increasingly detailed resolution.

1.4.1 Satellite telemetry

Wildlife telemetry is a research technique that has been used since the 1960s by equipping a collar with a Very High Frequency (VHF) tag (Cochran & Lord, 1963). These traditional VHF telemetry tags emit pulses that allow researchers to get bearings of the direction in which the tag is located in the field using an antenna and receiver. Triangulation of multiple subsequent bearings from different points in the landscape provides the approximate location of the tag (Nams, 2006). This technique has provided significant advances in the study of animal movements and their interaction with the environment (Thomas *et al.*, 2011). Satellite telemetry is an extension of the traditional VHF telemetry that incorporates an automated satellite sensor device on the unit, in addition to the usual VHF tag. The satellite tag uses either Doppler shifts of Argos satellite radio signals or a combination of signals from satellites in the Global Positioning System (GPS) to determine the location of the unit on the globe (Rodgers *et al.*, 1996; Thomas *et al.*, 2011). The unit automatically attempts to obtain a location according to a programmed schedule and stores the result of each attempt on an in-built memory device. Subsequently, the data is transferred to the user either through physically connecting the unit to a computer after recovering the unit from the field or by using a remote download option. Commonly used remote download options are via Ultra High Frequency (UHF), the mobile telephone (GSM) network or communication satellites such as Argos, Iridium, or GlobalStar (Tomkiewicz *et al.*, 2010, see also Chapter 4). Satellite telemetry enables the acquisition of location data at unprecedented spatial and temporal scales, and has opened up an extensive range of options for remotely tracking movement (Kays *et al.*, 2015). The frequent transfer of data even enables monitoring of movements in near real-time, which provides many useful applications in the field. For example, in Kenya wildlife managers managed to curb crop raiding behaviour in an elephant as the telemetry collar informed them when the animal was nearing the fields (Wall *et al.*, 2014). Current sensors can determine the location of a unit as frequent as every second (Li *et al.*, 2015) and can have a spatial error of typically less than 5–10m (Kays *et al.*, 2015; Wilmers *et al.*, 2015). Units can be equipped with automated drop-off mechanisms, removing the need for recapturing the animal. These characteristics allow researchers to get detailed information about the behaviour and the movement decisions made by the animal while moving through the landscape. Hence the technique has become very popular for answering many research questions dealing with concepts such

as dispersal and corridor use, migration, foraging behaviour, physiological performance, habitat selection, ecosystem services (e.g. seed dispersal) and social interactions (Kays *et al.*, 2015; Wilmers *et al.*, 2015). The number of publications using satellite telemetry has increased steadily over the last decades (see Figure 4.1 on page 55).

1.4.2 Spatial and temporal scales

In connectivity assessments, movement data originating from satellite telemetry are mostly used for the parametrisation of resistance surfaces. As mentioned in the previous section, dispersal or migration are the relevant ecological processes in most connectivity assessments, and hence movement data representing these processes are preferable. Generally, a resource selection function is applied to the movement steps in order to identify habitat selection probabilities, which are then rescaled as resistance values (Keeley *et al.*, 2016; Zeller *et al.*, 2012). In these statistical models, the temporal scale of the data (i.e. the fix acquisition interval of the telemetry unit, or fix frequency) is of paramount importance because it determines at which spatial scale the responses of the study species to the environment are detected (Zeller *et al.*, 2016). Thurfjell *et al.* (2014) give an example where a movement path with a 15 minute resolution showed that the study animal avoids crossing a road, whereas the 60 minute resolution suggested that the animal crosses the road twice. If the research goal is to identify the barrier effect of roads for connectivity, the temporal resolution clearly needs to be matched to the scale at which the response of the animal to landscape elements is expected.

Dispersal or migration usually act over relatively large scales, but are in fact a sequence of many smaller scale behavioural choices, and thus still require short fix intervals, dependent of the species' locomotory capacity (Neumann *et al.*, 2015; Richard & Armstrong, 2010). However, the time needed to detect dispersal events can be long and maintaining a high fix frequency requires large batteries. Hence, a compromise needs to be found between fix frequency and battery life, i.e. the time the unit is expected to collect and transmit data. Telemetry units for large animals can be equipped with a sizeable battery and could potentially handle relatively short fix acquisition intervals for longer periods of time. In studies on smaller animals this trade-off is more pertinent and researchers tend to choose battery life over fine-scale resolution data (Matthews *et al.*, 2013). Solutions to increase battery life have been developed. For example, in studies where insolation is abundant, units with solar panels have been deployed that can charge the battery in the field (Patton *et al.*, 1973; Thomas *et al.*, 2011). Energy yield is usually limited because the size of the unit limits the size and capacity of the solar panels, but the units' weight can be reduced and its life time extended. Additionally, multiple fix acquisition schedules can be programmed to save battery. Fix schedules can be programmed such

that fewer fix attempts are made during the time the animal is expected to be inactive. Alternatively, fix frequency can be made dependent on the activity sensors attached to the units. This way, one can apply a higher fix frequency schedule when the animal is moving and a lower frequency schedule when the animal is resting (Brown *et al.*, 2012). Similarly, multiple fix schedules can be programmed in order to sample at a different frequency whenever an animal crosses a 'virtual fence'. A virtual fence is a line drawn in the landscape model that separates a specific part of the study area from the rest of it, e.g. residential areas from forested areas. This technique is also called geofencing (Wall *et al.*, 2014). The latter feature holds particular promise for dispersal studies. For example, with 2-way communication being possible in more recent telemetry units, fix schedules can be adjusted remotely. This opens up the possibility to first identify an individual's home-range using a high fix frequency and subsequently use the home-range boundary as a virtual fence within which the fix frequency can be kept low until the animal leaves its home-range. Once it crosses the virtual fence, the fix frequency can be increased to obtain high detail movement patterns during exploratory trips or dispersal events.

1.4.3 Endless possibilities?

Satellite telemetry opens a broad range of exciting options for studying animals and their movements. However, the technique does have its own limitations and not everything is possible. For example, given the potential impact of telemetry units on the behaviour and survival chances of tracked animals, the size of the units is an important factor in their design. Thanks to considerable progress in unit size reductions in recent years (Kays *et al.*, 2015), current units without remote data transfer options (or with a single remote download at the end of the study period) weight as little as 1–10g. But they only have the energy budget for a limited amount of fix attempts. In longer studies where a high number of fix attempts needs to be transferred remotely, the simplest units start from around 250g. This means that 70% of bird species and 65% of mammal species cannot be tracked while on the move due to the weight of the units (Kays *et al.*, 2015). This makes studies of dispersal particularly difficult, because without periodical data transfer, tracking where dispersing individuals go is challenging.

Furthermore, as shown in Chapters 3 and 4, environmental factors, species behaviour and characteristics, and unit specifications and orientation often negatively affect the success with which units manage to obtain locations, as well as the precision of these locations. Challenges with either the retrieval of the unit from the field or the download connection between the unit and the receiver can cause data not to be transferred from the unit to the user. Additionally, the units are frequently used in harsh environmental

conditions resulting in the electronics or the mechanics of the units to malfunction, further increasing the risk of data loss or unit loss. Even though methods exist to deal with missing data (Frair *et al.*, 2010; Laver *et al.*, 2015; Nielson *et al.*, 2009), as little as 10% missing data can distort resource selection estimates (Nielson *et al.*, 2009).

In summary, satellite telemetry provides the most detailed information on the movement decisions of an individual in the landscape and is arguably the best available method for the acquisition of data for the purpose of actual connectivity analyses. Nonetheless, it faces restrictions due to the rare occurrence of dispersal events and the general limitations of satellite communication due to environmental and study species characteristics.

1.5 Structure

In this dissertation, I investigate the possibilities to increase ecological realism in conservation network design by including species-specific information under limited data availabilities, and by evaluating satellite telemetry as a technique to provide detailed movement information for connectivity models. Specifically, I combine fine-scale landscape data with species-specific detection data to delineate a conservation network based on potential connectivity estimates in Belize, Central America. For this, I use the white-lipped peccary *Tayassu pecari* as an umbrella species. White-lipped peccaries are a gregarious ungulate that roam in large herds though Neotropical rainforests (Sowls, 1997). Additionally, I investigate the performance of satellite telemetry as one of the most important tools for the collection of detailed species-specific movement information (Correa Ayram *et al.*, 2015).

In Chapter 2, I give background on the existing conservation network in Belize, outline why *T. pecari* is a suitable umbrella species, and estimate 'potential' functional connectivity corridors using a compiled presence-only data set and an extended version of the Potential Connectivity Model (Rödder *et al.*, 2016). Potential Connectivity Models use a habitat suitability model and fragmentation threshold to model connectivity. Chapter 2 extends the model by adding a graph-theoretic evaluation of the identified core areas and corridors. Furthermore, instead of estimating corridors between protected areas, the protected areas are incorporated in the habitat suitability model and connectivity is estimated between areas of suitable habitat instead of protected areas.

In Chapter 3, I explore possibilities of satellite telemetry for obtaining movement data of white-lipped peccaries in Belize. I obtained two satellite telemetry collars to track the movement of two pairs of individuals consecutively in different parts of Belize. The

observed movement information would be used to create a resistance surface for estimating 'actual' functional connectivity for the species in Belize. However, one of the collars failed before it was deployed due to technical issues, while the trapping success to deploy the second collar was so low that it could only be deployed once within the time frame of this dissertation work. The chapter describes the relatively low success rates of the collar in the field and the resulting low temporal and spatial resolution of the data. It discusses the challenges of using satellite telemetry for white-lipped peccaries in Belize, but also shows that the low resolution data was still useful for obtaining preliminary impressions of home-range and movement patterns.

Motivated by the experiences from Chapter 3, Chapter 4 reports on a worldwide evaluation of the success of satellite telemetry units in terrestrial wildlife research. By modelling the relative importance of some of the limiting factors of satellite telemetry in wildlife research, the chapter investigates whether certain conditions can be identified that need to be fulfilled in order successfully obtain fine-scale movement data.

In Chapter 5 I give an overview of my findings and conclude with evaluating the current integration of detailed biological information in connectivity modelling used for conservation network design.

Chapter 2

Enhancing conservation network design with graph–theory and a measure of protected area effectiveness: refining wildlife corridors in Belize, Central America

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Abstract

Maintaining connectivity between remaining natural areas has become increasingly important to ameliorate the effects of habitat loss and fragmentation. Typically, corridor networks are based on structural connectivity (i.e. habitat structure) and designed to connect protected areas. Here, we refine a typically designed corridor network in Belize by estimating potential functional connectivity for white-lipped peccaries *Tayassu pecari* between systematically identified core patches. We use a modified habitat suitability analysis, accounting for protected area effectiveness, as a starting point for least-cost corridor estimates, and evaluate the network using graph theory. The habitat suitability model is used for both delineating highly suitable core areas and predicting the most suitable movement corridors between them. To evaluate the importance of network elements, we measure their relative contribution to overall landscape connectivity according to graph–theoretical indices. We found that forest productivity and protected area status were important predictors of habitat suitability for white-lipped peccaries (contributing 28.6 and 21% to the model prediction, respectively), along with core forest area (15.8%) and terrain ruggedness (15.4%). Our corridor analyses indicated potentially weak links in the existing network and suggested alternative, ecologically relevant locations for connectivity–enhancing measures, as well as areas that are particularly important for overall landscape connectivity. With this study, we provide a framework to improve the scientific rigour, ecological meaningfulness and conservation relevance of applied corridor network design.

2.1 Introduction

Landscape connectivity is fundamental to maintaining or improving ecologically resilient landscapes undergoing environmental change (Crooks & Sanjayan, 2006a). Consequently, conservation networks are established, consisting of natural core areas that are connected through conservation corridors.

The design of conservation networks typically identifies corridors between protected areas (PAs) that are informed by expert opinion. This approach has a number of limitations. For example, boundaries of PAs are often used as start and end points for delineating corridors (Belote *et al.*, 2016; Brodie *et al.*, 2014; Zeller *et al.*, 2011), but some PAs may not hold suitable habitat for the species of conservation concern; and using solely PAs as nodes could exclude potentially suitable areas that are not protected (Beier *et al.*, 2011). Moreover, PAs are usually located in sections of the landscape that are not particularly suitable for human activities and are therefore biased towards certain

environmental characteristics, e.g. poor soil habitat types or steep topography (Joppa & Pfaff, 2009). Finally, some PAs provide more protection than others depending on their level of management and the time they have been under protection (Geldmann *et al.*, 2013). Thus, a better approach for defining core areas would be to use a combination of empirically–derived habitat suitability and actual protection status (Beier *et al.*, 2011).

A second limitation is that corridor routes connecting core areas are typically based on structural connectivity of the landscape, which only takes into account the spatial configuration of habitat. It is widely agreed in landscape ecology that estimates of functional connectivity are ecologically more meaningful (Crooks & Sanjayan, 2006b; Magle *et al.*, 2008). Functional connectivity considers species characteristics as well as landscape structure and is thus a property of the species–landscape interaction (Calabrese & Fagan, 2004; Taylor *et al.*, 2006; Tischendorf & Fahrig, 2000). Using functional connectivity could improve the ecological relevance of the corridor network design, but is rarely used in conservation applications.

Third, regardless of how core areas and corridors are defined, few conservation network designs provide quantitative assessments of the relative importance of each corridor or patch for maintaining or improving landscape–wide connectivity, although these are needed for prioritization in practical planning (Galpern *et al.*, 2011). In landscape ecology, quantitative methods—e.g. based on graph–theoretic approaches—have been used for this purpose, where the core areas represent 'nodes' and the corridors represent 'edges' or 'links' (Fall *et al.*, 2007; Urban & Keitt, 2001).

Here, we address the above limitations of corridor network design by incorporating PA effectiveness in corridor estimates between core habitat patches and quantitatively evaluating these estimates using graph–theoretic indices. Specifically, we show how to create Potential Connectivity Models (PCMs— Rödder *et al.*, 2016) that a) use species–specific habitat suitability and protected area effectiveness to define nodes (as opposed to using PA outlines), b) focus on functional connectivity for delineating corridors, and how to extend the PCMs by c) applying graph–theory to quantify the relative importance of network elements for overall landscape connectivity. We illustrate the framework by refining an existing corridor network in Belize, Central America, for an umbrella species, the white-lipped peccary *Tayassu pecari*. The existing network has largely been designed based on expert opinion, using PAs as nodes and structural connectivity to delineate corridors. Our framework combines well–established methods for objectively identifying nodes and corridors with recent developments in graph–theoretic connectivity indices to evaluate their relative importance for maintaining or improving connectivity. The framework aims to improve the repeatability, ecological meaningfulness and conservation relevance of typical corridor network design.

2.2 Methods

2.2.1 Study area & species

Belize is a small country south of Mexico with over 60% forest cover and 36% of the its terrestrial surface area protected to various extent (Meerman & Roger-Wilson, 2005; Young, 2008, see Figure 2.1). The majority of the forest is contained within two major blocks: La Selva Maya and Maya Mountains (Figure 2.1a). La Selva Maya is the second largest contiguous tropical forest in the Americas after the Amazon and spans Guatemala, Mexico and Belize (Briggs *et al.*, 2013; Radachowsky *et al.*, 2012). The Maya Mountains are a mountain range bordering the south-eastern edge of La Selva Maya that are becoming increasingly isolated due to increasing industrial and small scale development (Briggs *et al.*, 2013). Belize also hosts connections between these inland forests and the forests on the Caribbean coast (Figure 2.1b). All connections are part of the Mesoamerican Biological Corridor (Sabido & Gutiérrez, 2003; Wildtracks, 2013), but are negatively affected by habitat destruction and fragmentation (Briggs *et al.*, 2013; Meerman & Roger-Wilson, 2005). Within Belize, a current set of corridors has been suggested between blocks of PAs (Meerman, 2000; Petracca, 2010; Wildtracks, 2013), which are used as reference throughout the study (Figure 2.1b). The delineation of these corridors has been based primarily on structural connectivity. In this study we refine the existing corridor network by predicting functional connectivity, using the white-lipped peccary as an umbrella species (Breckheimer *et al.*, 2014). The white-lipped peccary (Vulnerable— IUCN, 2012) is a gregarious ungulate that usually travels in herds (sounders) of up to 300 individuals (Keuroghlian *et al.*, 2013; Sowls, 1997). It is an important forest ecosystem engineer (Beck *et al.*, 2010; Silman *et al.*, 2003) and is a prey species for puma *Puma concolor* and jaguar *Panthera onca* (Foster *et al.*, 2010; Mayer & Wetzel, 1987). It inhabits highly productive primary and secondary forest mosaics close to water and away from human impacted areas (Keuroghlian & Eaton, 2008b; Reyna-Hurtado *et al.*, 2009a). Home ranges expand and contract seasonally according to food availability (Altrichter *et al.*, 2001; de Almeida Jácomo *et al.*, 2013; Keuroghlian & Eaton, 2008a). We chose this species because it has large space requirements and limited propensity for actual long-distance dispersal (see section 2.4), making it particularly sensitive to changes in landscape connectivity. Furthermore, in Bolivia Coppolillo *et al.* (2004) identified the species as the most important 'landscape species' (i.e. a species out of a suite whose conservation would benefit the entire landscape, Sanderson *et al.*, 2002) based on more than 10 objective criteria. Altrichter *et al.* (2012) likened the species in terms of conservation importance in Latin America, to bison *Bison bison* in North America and elephants *Laxodonta africana* in Africa.
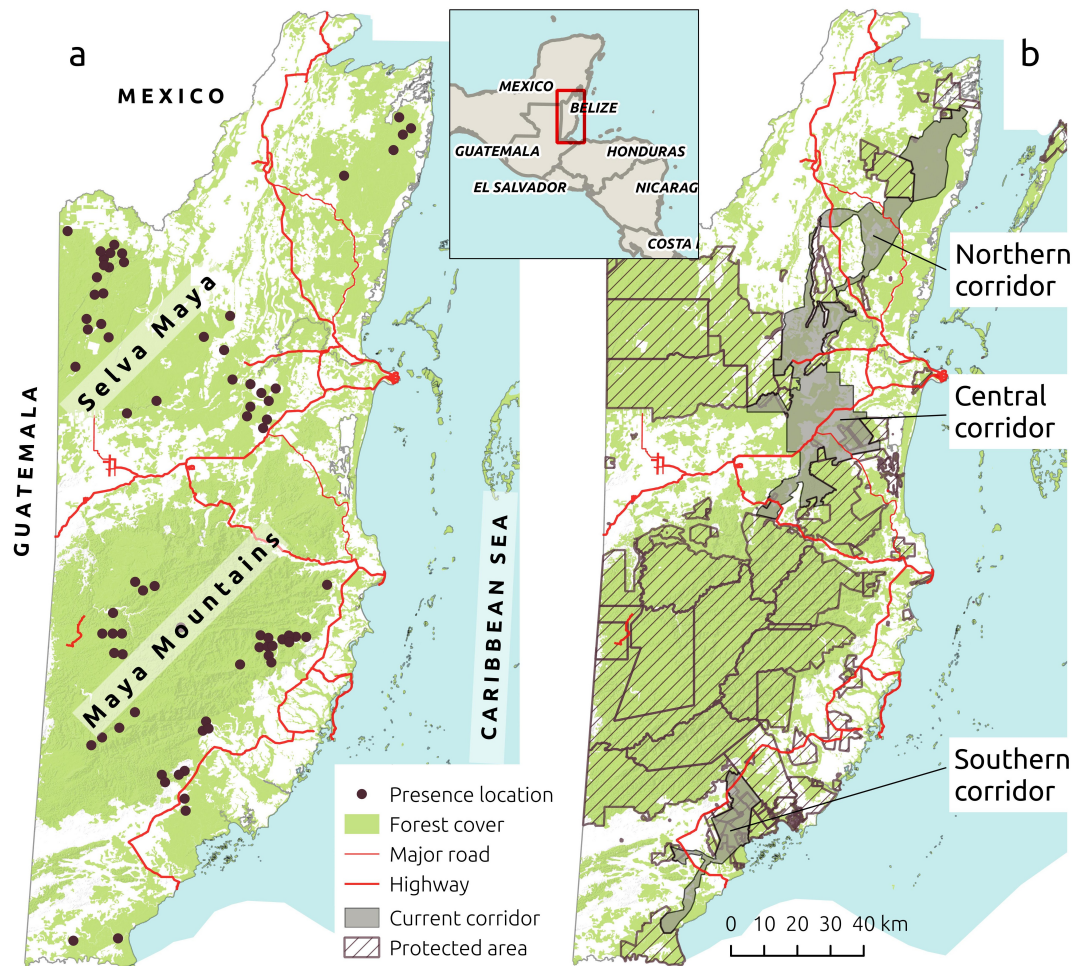
FIGURE 2.1: a) Location of Belize in Central America, showing the Maya Mountains and La Selva Maya, and the 75 presence-only points used for the habitat suitability analyses. b) All gazetted and candidate protected areas in Belize (*anno* 2010) and the currently suggested corridors between them.

2.2.2 Analytical framework

Our framework is based on the PCM framework by Rödder *et al.* (2016) and consists of four interrelated steps. First, we model species-specific habitat suitability using a range of environmental predictor variables and information on protected area effectiveness. Second, we objectively delineate nodes for the connectivity network and calculate a species-specific landscape resistance surface using the habitat suitability model constructed in step one. Third, we delineate corridors among the nodes based on the resistance surface. Finally, once the potential connectivity model is created (steps 1 to 3), we use graph-theory to quantify the relative importance of the network elements for overall landscape connectivity.

Step 1: Habitat suitability

We obtained 432 unique peccary observations, which we pruned to avoid issues with temporal and spatial autocorrelation (see Appendix A, section 2.1). We used the resulting 75 presence points (Figure 2.1a) as input for MaxEnt 3.3.3k (Phillips *et al.*, 2006), a widely used species distribution modelling software. We identified 23 environmental variables that potentially affect habitat suitability for peccaries (Table 2.1). To avoid multicollinearity, we excluded any predictor pairs with Spearman's Rho > 0.7 (Dormann *et al.*, 2013), and retained only the variable that we expected a priori to have the most direct relevance to the ecology of the species, based on our knowledge of the species' biology. To incorporate protected areas in the habitat suitability estimate, we constructed a 24th variable reflecting protected area effectiveness, based on the combination of (i) the IUCN Protected Area Categories (Dudley, 2008) updated for Belize according to Wildtracks (2013) and (ii) the management effectiveness according to a national study by (Walker & Walker, 2009, see Appendix A, Table 3). To illustrate the influence of including PA effectiveness (the PAEF model), we also constructed a CONTROL habitat suitability model that excluded PA effectiveness (Table 2.2).

Recent research suggests that species-specific tuning of MaxEnt models can improve their performance (Radosavljevic & Anderson, 2014). We used the package ENMeval (Muscarella *et al.*, 2014) in R 3.2 (R Development Core Team, 2015) to determine the optimal settings for the habitat suitability estimates (Warren & Seifert, 2011, see Appendix A, section 2.3), and ran 100 MaxEnt replicates using the package dismo (Hijmans *et al.*, 2015). The average predictions were used as the final habitat suitability models (CONTROL and PAEF). To test model accuracy, we compiled an additional set of 143 independently gathered presence locations for white-lipped peccaries in southern Belize, originating from satellite collar data and sightings of animals and tracks (Hofman *et al.*, 2016, B. Arevalo, *pers. comm.*). We randomly rotated and shifted (up to 3 km) these points 1000 times, and compared the average habitat suitability of the original points to the average habitat suitability of the permuted points, following Mueller & Fagan (2008).

Step 2: Node delineation and landscape resistance

To identify nodes based on the PAEF habitat suitability surface, we followed the approach used in Gnarly (Shirk & McRae, 2013), whereby we smoothed the surface by calculating the mean suitability across a moving window equal in size to the smallest reported annual white-lipped peccary home-range (21 km^2 — Fragoso, 1998, 2004) for each grid cell, and considered all grid cells with a smoothed suitability higher than 0.5 to be suitable. Cells

Metric type	Description	Metric
Environmental	Food tree occurrence (sum of food genera)	foodGenera
	Enhanced vegetation index	mEVI
	Mean annual rainfall	rain_wc
	Soil	soil
Land cover (class-level)	Distance to agriculture	distAgric
	Distance to broadleaf forest	distFor
	Distance to pine forest	distPif
	Distance to rivers	distRiv
	Distance to roads	distRoad
	Distance to savanna	distSav
	Distance to shrubland	distShrub
	Distance to urban area	distUrb
	Distance to waterbodies	distWat
Land cover (landscape-level)	Proportion of core forest	cfp
	Ratio of egde over core forest	ecp
	Frequency of fires	fire
	Landscape heterogeneity	lanhet
	Land cover type	weco
Political	Protected area effectiveness	paef2010
Topographic	Aspect	aspect
	Elevation	elev
	Slope	slope
	Topgraphic Position Index	tpi
	Terrain Ruggedness Index	tri

TABLE 2.1: Predictor variables used for the MaxEnt habitat suitability analyses. Variables in italics were excluded after correlation analysis.

	Current corridors*	CONTROL model	PAEF model
Habitat suitability model	Expert opinion	Environmental variables & Maximum Entropy modelling	Environmental variables + PA effectiveness & Maximum Entropy modelling
Nodes	Protected areas	Protected areas	High-suitability areas
Connectivity type	Structural/ Functional	Functional (Potential)	Functional (Potential)
Connectivity model	Expert opinion/ Least-cost	Least-cost	Least-cost + graph–theory

TABLE 2.2: Characteristics of the currently suggested biological corridors in Belize and the set of Potential Connectivity Models developed in this study. *based on (BERDS, 2005; J. Meerman, 2000; Petracca, 2010; Wildtracks, 2013)

with an original suitability value below 0.5 were removed, as were cells representing highways and major roads, since they constitute a division in any contiguous group of high-suitability grid cells. Of the resulting suitable areas, those smaller than 21 km^2 were removed. We added two nodes that were not identified by MaxEnt due to low habitat quality or small area, but represent areas where peccaries were recently observed and could potentially play a role in connectivity to neighbouring countries. These nodes were constructed by buffering one observation in each area with a circle of 21 km^2.

To obtain an approximation of landscape resistance to peccary movements, we followed Mateo-Sánchez *et al.* (2014) and converted the PAEF habitat suitability surface from Step 1 into a resistance surface using a negative exponential function (see Appendix A, section 3.3). In line with the PCM approach, we included movement barriers at this stage. Few absolute barriers exist for white-lipped peccaries within our study area (e.g. Fragoso, 2015), but we assumed a high resistance for highways and major roads (respectively 95% and 85% of the maximum value in the resistance surface).

Step 3: Corridor estimation using landscape resistance

We used a least-cost approach to identify the most suitable travelling routes between each pair of nodes (Adriaensen *et al.*, 2003), as provided by the Linkage Mapper toolbox version 1.0.9 (McRae & Kavanagh, 2011) in ArcGIS Desktop 10.3 (ESRI, 2015). This toolbox calculates the distance (in cost values) of the least-cost path between each pair of nodes and quantifies how much more costly the rest of the landscape is in proportion to the least-cost path. We delineated corridors by selecting all pixels having a cost-distance of maximum 25% higher than the cost-distance of the respective least-cost path between the two nodes. Note that, at this point, every pair of nodes was connected by a corridor because we did not limit the cumulative cost-distance to a relevant maximum for the species. This approach offers the possibility to locate suitable areas for corridor enhancement at a later stage in the process. For comparison, we also estimated corridors between nodes composed of blocks of PAs based on the CONTROL model (see Appendix A, section 4).We visually compared all three sets of corridors and quantitatively compared the distribution of suitability values inside them.

Step 4: Evaluating the network

To help evaluate the importance of predicted core areas and corridors, we identified potential stepping-stones in and around the corridors. Stepping-stones are habitat areas not sufficient in size and/or quality to maintain populations, but that can serve as stopovers when travelling through the unfavourable matrix between two nodes in the

network (Saura *et al.*, 2014). To identify stepping-stones, we selected areas that had a non-smoothed habitat suitability between 0.45 and 1. To exclude overlap between the stepping-stones and the nodes, we buffered the nodes with 3788 m (i.e. maximum daily movement distance recorded for T. pecari by Hofman *et al.*, 2016). We removed these buffered nodes from the potential stepping-stone areas, and excluded any stepping-stones that were smaller than half of the smallest reported annual white-lipped peccary home-range size.

We then used Conefor 2.6 (Bodin & Saura, 2010; Saura & Torné, 2009) to evaluate node, stepping-stone, and corridor importance. Conefor 2.6 can quantify overall landscape connectivity using a single graph-theoretic index (Probability of Connectivity), and estimates active links between patches. To determine the importance of nodes and stepping-stones in the network, each element of the corridor network is removed one at a time, and relative changes in three recently developed fractions of the Probability of Connectivity are recorded: dPC_{intra} represents the removed element's contribution in habitat area and quality, dPC_{flux} represents its contribution to the flux of dispersing organisms, and $dPC_{connector}$ the extent to which it acts as a connecting element (Bodin & Saura, 2010). We evaluated the importance of each node and stepping-stone by examining its $dPC_{connector}$ and dPC_{intra} values. The use of the Probability of Connectivity fractions in the optimisation of corridor networks has only recently become possible and, to our knowledge, has only been applied by Loro *et al.* (2015). The Conefor 2.6 links indicate which patches are currently connected (i.e. form a 'component' in the network), and thus provide an evaluation of which corridors are important for connectivity in the network. Corridors supported by active links suggest importance for maintaining current connectivity, while corridors with missing links suggest areas for improving connectivity. The links are drawn based on a user-defined, species-specific dispersal distance that is converted to a direct dispersal probability among patches based on an exponential dispersal kernel (Saura & Torné, 2009, 2012). We attributed a direct dispersal probability of 0.01 to a dispersal distance of 9495 m, which is the diameter of a circular average home-range for white-lipped peccaries (see A, section 5).

2.3 Results

The enhanced vegetation index and the protected area effectiveness variables contributed most to the PAEF habitat suitability model (28.6 and 21% respectively), while the proportion of core forest (15.8%) and the terrain ruggedness index (15.4%) contributed considerably as well. Land cover and the topographic position index each contributed less than 10% to the model (see A, Table 4). Only 50 out of 1000 permuted validation

sets had a higher average habitat suitability than the original validation set (P = 0.05). This is exemplified by the geographical fit of the validation points over the habitat suitability model (see A, Figure 5).In the CONTROL habitat suitability model, the overall ranking of the top contributing variables remained the same, but the relative importance of the enhanced vegetation index and the proportion of core forest increased by 10% and 15%, respectively (see A, Table 5).

Based on the PAEF habitat suitability surface, eleven nodes were identified (HS1–HS11), and each pair of nodes connected by least-cost corridor between them (PAEF corridors—Figure 2.2). The northern corridor between HS2 and HS4 showed an eastward shift from the existing corridor. The PAEF corridor between HS3 and HS6 overlapped to some extent with the current central Belize corridor, while two southwards corridors were suggested between HS3 and HS5. Node HS9 partially overlapped the southern corridor, and an alternative route was suggested between HS8 and HS11.

However, Conefor detected only 40 active links connecting 11 nodes and 31 stepping-stones, grouped in 12 separate components (Figure 2.2). Hence, many suggested PAEF corridors had missing Conefor links between their respective nodes. Ninety-five percent of the overall landscape connectivity was present within the nodes and stepping-stones (PC_{intra} = 95.18), and less than 5% through direct and indirect links. Nodes HS3, HS6, HS8 and HS9 contributed considerably to overall landscape connectivity due to their size and habitat quality (dPC_{intra} —Figure 2.2a). Stepping-stones and nodes of any size that were centrally located within their respective components played an important role as connecting patches ($dPC_{connector}$), whereby patches in the biggest components contributed most to overall landscape connectivity (Figure 2.2b).

2.4   Discussion

In this study, we applied a novel framework that combines habitat suitability models and least-cost corridor analysis, and adds graph-theory to robustly evaluate network connectivity. Our results extend current PCMs by accounting for PA effectiveness in the habitat suitability estimate and by estimating a corridor network between high-suitability areas rather than between PAs. Compared to existing, expert-derived corridors, our analysis suggests additional ecologically relevant locations for connectivity–enhancing measures and indicates potentially weak links in the network. Furthermore, our approach identifies areas that are particularly important for overall landscape connectivity. The model can easily be used to quantify the effect of different landscape planning options on overall connectivity (e.g. Mimet *et al.*, 2016), which is fundamental for prioritizing future conservation actions under logistical and financial constraints.
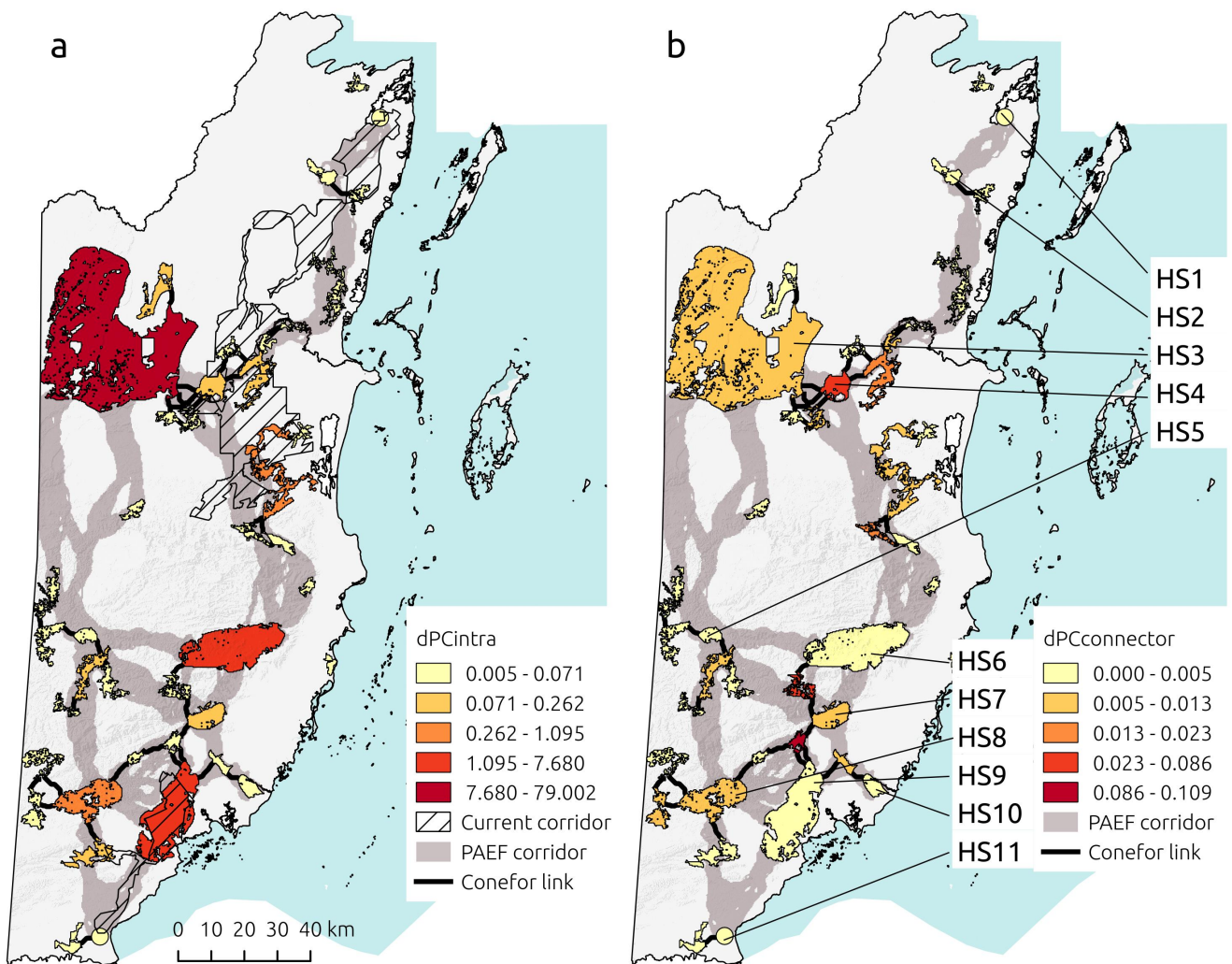
FIGURE 2.2: Hash-marked areas indicate the current corridors and grey shaded areas the PAEF corridors. Darker coloured nodes (denoted HS1–11) and stepping-stones (not denoted) indicate higher importance for connectivity, based on (a) their size and habitat suitability (dPC$_{intra}$), and (b) their role as a connecting patch (dPC$_{connector}$). Thick black lines indicate active Conefor links.

2.4.1 Habitat suitability and core areas

Our PAEF habitat suitability model accurately predicted actual occurrences of peccaries in Belize, and showed that PA effectiveness itself is an important predictor of habitat suitability for peccaries in Belize. This corroborates previous reports from Belize (Foster *et al.*, 2010) where white-lipped peccaries were predated by jaguars and pumas only inside PAs. Since 95% of the overall landscape connectivity was due to habitat area and quality inside the nodes and stepping stones, PCintra is by far the most important measure to evaluate their importance (2.2a). Overall, the model predicted that the largest and most centrally located patches in the Selva Maya and southeastern Maya

Mountains components are crucial for maintaining current landscape connectivity. The outline of identified nodes suggested that large PA blocks can contain substantial areas of highly suitable habitat or none at all, and anything in between (however, note that we have used a stringent threshold [see A, section 3.1], meaning that additional, slightly less suitable habitat outside the nodes might be available). Conversely, some unprotected areas were identified by the model as highly suitable and formed an important node in the network (e.g. HS9—2.2). Additionally, the absence of suitable habitat in some PAs (e.g. the northern node PA3—see A, section 4) caused alternative corridor routes to show up (e.g. for the northern corridor—2.2). These findings highlight the potential differences in corridor network design using core habitat areas instead of PAs as nodes.

2.4.2 Corridors

In some areas, the PAEF corridors suggested alternative routes for existing corridors, e.g. the more eastern alternative to the current northern corridor, while in other areas, the existing corridor outlines were supported (e.g. parts of the central and southern corridors). However, many corridor alternatives did not contain any Conefor links or stepping-stones, indicating that they are not currently of sufficient quality to potentially facilitate movement for white-lipped peccaries in Belize. For example, several links are predicted to be missing in all corridor alternatives between La Selva Maya from the Maya Mountains, suggesting these populations to be isolated from each other. Similarly, in the northern corridor between HS1, HS2 and HS4, several links are predicted to be missing to connect these nodes (2.2). In such cases, one of the main advantages of our framework is that the suggested PAEF corridor outlines can guide the search for the most suitable areas to implement conservation actions to improve connectivity.

2.4.3 Methodological considerations

The inclusion of protected area effectiveness in the PCM model reduces the variability of suitability values within our predicted corridors compared to the current and CONTROL corridors (see A, Figure 7). This suggests that corridor estimates are improved when basing node and corridor delineations on a habitat model that includes PA effectiveness, as compared to corridors estimated among PAs based on a habitat model excluding PA effectiveness. That said, we note that the corridor model (as opposed to the habitat suitability model) has not been validated in the field and may contain imprecisions. For example, contrary to the common assumption that connectivity within PAs is guaranteed, the component around node HS5 appeared to be separated from the component around nodes HS6 to HS10. This could be due to a ridge known as the Main Divide,

however accounts of anecdotal observations on the ridge may indicate that a lack of presence points in high terrain caused our model to underestimate suitability in such terrain. Moreover, we realise that the effect of PAs on habitat suitability is not just influenced by their effectiveness, but also by the time the area has been under protection. The longer it has been protected, the higher its naturalness (as in Beier *et al.*, 2011) is expected to be. However, due to insufficient data, we could not take this into account in our analysis. Indeed, information on PA effectiveness is probably the least available information in many conservation situations.

We compared our corridors with the current corridors within Belize rather than with corridors from a large-scale, functional connectivity assessment for jaguars (Rabinowitz & Zeller, 2010), because (i) the jaguar–specific corridors have largely confirmed the national level corridors between PAs, (ii) the limited spatial extent of our study area and (iii) the increased resolution of our analyses. Additionally, our modelling approach is based on data from a different umbrella species, the white-lipped peccary. Despite methodological and empirical uncertainties, umbrella species have been used in conservation studies for many years, and will likely continue to be so in the future for practical reasons (Caro & Girling, 2010). Krosby *et al.* (2015) questioned the use of umbrella species in studies at larger scales or in cases where exceptional dispersal distances and/or barrier sensitivity make them unsuitable for the purpose of studying connectivity. There is no data suggesting that either of these issues exist with peccaries in Belize. Instead of by individual or small-group, long-distance dispersers (which to our knowledge have never been reported for this species), dispersal and genetic exchange seem to occur primarily when home-ranges expand and overlap, and without bias towards either males or females (Altrichter *et al.*, 2002; Biondo *et al.*, 2011). Hence, observed movements of 5–10 km likely represent extended home-range movements and may also function as dispersal movements (de Almeida Jácomo *et al.*, 2013; Fragoso, 1998; Keuroghlian *et al.*, 2004). To evaluate the effect of our chosen dispersal distance on the identification of important nodes/stepping-stones in this study, we conducted a sensitivity analysis using a range of maximum dispersal distances (similar to Loro *et al.*, 2015) and found that the top 10 important nodes or stepping-stones remained remarkably stable (see A, Table 7). Consequently, we are convinced that the species is an ideal connectivity umbrella and that the scale of typical peccary movement matches that of our study area.

The applied framework relies on presence-only data for deriving habitat suitability, landscape resistance, and functional connectivity estimates. In general, presence-absence data and associated analysis methods (e.g. occupancy modelling) perform better in predicting habitat suitability, and prevent some methodological issues known to affect presence-only techniques such as those implemented in MaxEnt (Yackulic *et al.*, 2013). However, the available presence-absence data for our study area did not fully cover the

environmental conditions at known presence locations, preventing us from extrapolating to the full study area. Therefore we included them in the presence-only data for MaxEnt and used available techniques to account for MaxEnt's known methodological issues (see A, section 2). Nevertheless, the model may estimate habitat suitability conservatively. Furthermore, corridor delineation should ideally be based on actual data on movement or gene flow for the study species, i.e. representing 'actual' connectivity (Fagan & Calabrese, 2006; LaPoint *et al.*, 2013; Sawyer *et al.*, 2011). However, such data are not available for the while-lipped peccary and for many other species of conservation relevance. In such cases, the next best option is to consider 'potential' connectivity using indirect information on dispersal (e.g. occurrence data) to derive habitat suitability and landscape resistances (Fagan & Calabrese, 2006; Zeller *et al.*, 2012). Translating habitat suitability derived from presence-only data into resistances is not optimal for species that use different habitats for home-range movements versus dispersal movements, because the occurrence points may not adequately represent the way a species uses a landscape during actual dispersal (Abrahms *et al.*, 2016; Mateo-Sánchez *et al.*, 2015). However, this is unlikely an issue for our study, because peccaries move in sounders, and rather than showing distinct movement behaviours during foraging versus dispersal, dispersal likely occurs when home-ranges of different sounders overlap (see above). We used an exponential function to convert habitat suitability values into resistances, which greatly increases the usefulness of habitat models for connectivity estimations (Keeley *et al.*, 2016). Furthermore, basing resistance values on habitat suitability is a common starting point for connectivity analyses (Correa Ayram *et al.*, 2015) and increases repeatability as compared to expert opinion (Rayfield *et al.*, 2010; Rödder *et al.*, 2016).

A final methodological consideration is the fact that our PCM analyses were based on least-cost distances, which implicitly assume that the animal has complete knowledge of the study landscape and moves across it in an optimal way. We chose Linkage Mapper's least-cost approach because it has simple and intuitive algorithms that enable fast and widespread adoption of the framework by conservation practitioners. However, alternative movement models (e.g. including random walks) are available in user-friendly freeware (e.g. Circuitscape by McRae *et al.*, 2008). In sum, our results are robust to the methodological assumptions we made, and the framework can readily be adapted to other circumstances and settings.

2.5 Conclusions

Our study demonstrates the value of combining robust analytical approaches for designing and evaluating corridor networks. Using limited data, we derived a corridor network

for Belize that highlights alternative corridor routes, identifies potentially missing links and can be used to prioritize conservation actions in addition to reinforcing the value of existing corridor network elements.

We note that our corridor estimates only represent the ecologically most likely scenario for a single umbrella species. We recommend identifying a limited set of coarse habitat types based on species functional traits, and choose one or more suitable umbrella species for each habitat type (following Brodie *et al.*, 2014). Corridor areas can then be determined per umbrella species for the range of species that live in the same habitat types and have similar dispersal propensities. We encourage similar connectivity estimation efforts for other umbrella species representing different functional groups (e.g wetland species) using the landscape species concept (Sanderson *et al.*, 2002).

Since our corridor model has not been verified in the field yet, the next step in Belize could be to conduct a field validation of the suggested corridor alternatives, before integrating them with the current corridors. Moreover, reliable corridor prioritization is usually achieved by considering the future spread of development and its impact on the likelihood of completing planned habitat linkage projects (Spring *et al.*, 2010). Thus, evaluating the threats and opportunities of any planned developments in these corridor estimates is recommended to further inform prioritization of nodes, stepping-stones, and linkages.

While our results are specific to Belize, the methodological advances we present have merit for many other cases where optimal corridors are to be developed in a quantitative, objective manner. The toolbox for this extended PCM framework is becoming more accessible for conservation practitioners, and enables a shift from structural connectivity assessments between PAs towards potential functional connectivity assessments between high-suitability areas as a standard approach for informing landscape management. The framework illustrated here is based on rigorous modelling techniques and subsequent evaluation via graph-theoretic connectivity indices, and thus has the potential to lead to improved corridor networks that enhance conservation of threatened species.

2.6 Acknowledgements

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Chapter 3

Spatial ecology of a herd of white-lipped peccaries *Tayassu pecari* in Belize using GPS telemetry: challenges and preliminary results

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Abstract

Introduction. The Maya Mountains are a heavily forested mountain range in Belize and Guatemala supporting high levels of biodiversity. Due to environmental degradation around the range, it is in danger of becoming isolated from the largest contiguous forest in Central America. Forest connectivity in the area is vital for white-lipped peccaries. These social ungulates roam in herds of up to 300 individuals and need large forested areas to sustain populations. The species has not previously been studied in Belize and its distribution, population size, herd dynamics and movement patterns are unknown for the country. We aimed to estimate home-range size and investigate movement patterns of the species in southern Belize.

Methods. We present a preliminary 4-month data set from a herd of ca. 60 animals tracked by an individual fitted with a GPS satellite collar. We evaluated collar performance, habitat preference and movement characteristics, and estimated home-range size using a semi-variogram approach, suited for sparse and irregular data.

Results. Collar performance was poor, with 38% of the data not reaching the satellite, and a GPS fix success rate of 11.6% for the data that did reach the satellite. The semi-variogram home-range size was 55.2 km^2 . We observed a maximum daily movement distance of 3.8 km, and a preferential use of forest habitat over shrubland, savannah and cropland. We calculated a density of 1.09 ind/km^2 and make an informed guess of close to 100 herds in the broad-leaf forests of the Maya Mountains.

Discussion. Our study highlights some of the challenges faced when collaring white-lipped peccaries, as well as the performance of GPS-collars in tropical forests. It also provides a first glimpse of the home-range and movement behaviour of white-lipped peccaries in Belize.

3.1 Introduction

The Maya Mountains are a heavily forested mountain range in Belize and Guatemala, and form the southernmost part of La Selva Maya, the largest tropical forest block in the Americas after the Amazon (Briggs *et al.*, 2013; Radachowsky *et al.*, 2012). The diverse geology accounts for a range of different soil types and a dramatic topography, which result in a multitude of microhabitats. These characteristics, combined with tropical rainfall regimes, yield some of the highest levels of biodiversity in the region (Brewer & Webb, 2002; Dourson, 2012). The Maya Mountains are also part of the Mesoamerican Biological Corridor, a regional initiative to conserve connectivity among forests in

Central America (Herrera, 2003). On a national level, the Maya Mountains cover 22.2% of Belize's land mass, forming the largest contiguous forest in the country, and are regarded as a Key Biodiversity Area (Meerman, 2007). They are estimated to provide up to US\$1 billion worth of ecosystem services to the people of Belize (Hammond *et al.*, 2011), and constitute one of biggest resources in the country for local livelihoods, forestry and eco/agritourism (Briggs *et al.*, 2013). Despite the fact that most of the Belizean side of the mountain range consists of protected areas of various legal categories (Figure 3.1), increasing industrial and small scale clear-cutting have severed the connections between the Maya Mountains and the forests to the north in both Guatemala and Belize. Consequently, the Maya Mountains are becoming increasingly isolated (Briggs *et al.*, 2013).
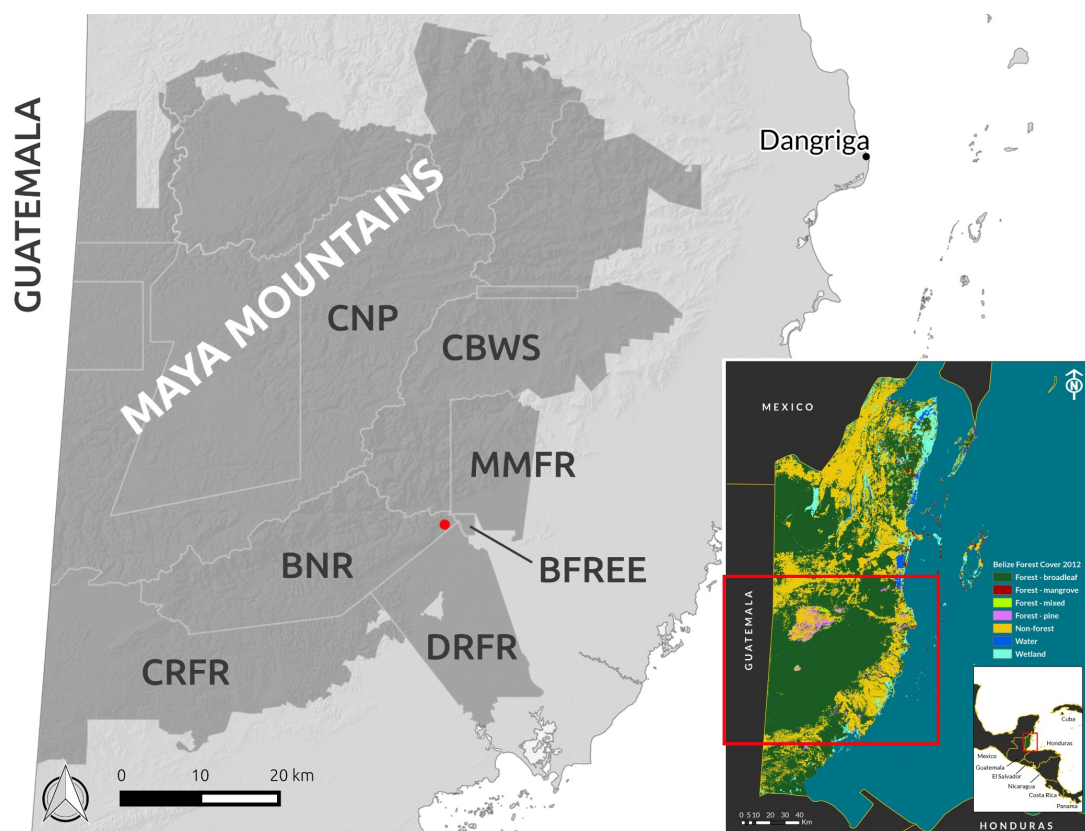
FIGURE 3.1: Location of Belize and the Maya Mountains. The protected areas of the Maya Mountains (as delineated by Briggs et al. 2013) are shaded grey and the trapping area is indicated by a red dot. Protected areas that are directly relevant to the study area are annotated. BFREE: Belize Foundation for Research and Environmental Education; BNR: Bladen Nature Reserve; CNP: Chiquibul National Park; CBWS: Cockscomb Basin Wildlife Sanctuary; CRFR: Columbia River Forest Reserve; DRFR: Deep River Forest Reserve;MMFR: Maya Mountain Forest Reserve.

The white-lipped peccary *Tayassu pecari* is often one of the first mammals to disappear with increasing forest fragmentation (Moreno & Meyer, 2014; Sowls, 1997). White-lipped peccaries are gregarious ungulates travelling in herds of 10 to 300 individuals (Altrichter *et al.*, 2012; Sowls, 1997), and although they are known to occur in mosaic

landscapes, they are regarded as typical forest dwellers (Desbiez *et al.*, 2009; Fragoso, 1999; Keuroghlian & Eaton, 2008b; Reyna-Hurtado *et al.*, 2009b; Reyna-Hurtado & Tanner, 2005; Tobler *et al.*, 2009). Due to the large herd size, they need to move frequently among different feeding spots, and in the process cover large distances through the forest. Home-range sizes throughout the species' range vary substantially, ranging from 20 to 200 km^2 (de Almeida Jácomo *et al.*, 2013; Fragoso, 2004; Keuroghlian *et al.*, 2004; Reyna-Hurtado *et al.*, 2009b). This variation reflects the environmental variability over the range of the species and illustrates its ability to cope with different conditions. Nevertheless, this flexibility seems to consist mainly of varying herd size (Fragoso, 2004) or splitting up in sub-herds (e.g. Keuroghlian *et al.*, 2004), rather than of changing habitat preferences. Thus, despite their ability to deal with different environmental conditions, white-lipped peccaries always depend on intact forest habitats of sufficient size and connectivity, rendering them highly susceptible to forest conversion and fragmentation. The Maya Mountains are assumed to offer continuous habitat and are expected to be home to several herds of white-lipped peccaries. However, no studies have been conducted on this species in Belize; their distribution, population size, herd dynamics and movement patterns are unknown for the country. The rugged topography of the Maya Mountains might render some parts of the forest unsuitable, and species-specific connectivity among suitable forest areas remains unstudied.

Here, we provide a preliminary report on data gathered from a herd of ca. 60 by tracking a single white-lipped peccary that was GPS-collared to investigate its home-range and movement patterns in the Bladen Nature Reserve, southern Belize. We assume that the location of the GPS-collared individual adequately represents the area used by its herd at the same point in time, because in many gregarious species the tendency of individuals to always move with the herd is very strong. In fact, this tendency has been used for management purposes in conservation. For example, Taylor & Katahira (1988) used the 'Judas goat'–approach to help eradicate feral goats *Capra hircus* on the Hawaiian Islands, and Campbell *et al.* (2004) and Cruz *et al.* (2009) used it for similar reasons on the Galpagos Islands. That is, goats fitted with a radio-collar (the Judas goats) were used to get information about the location of an entire herd of feral goats. All members of the discovered herds were killed, with the exception of the Judas goats, which would go on to find another herd, where the same scenario was repeated. A similarly strong herding tendency was described by Byers & Bekoff (1981) for collared peccaries *Pecari tajacu*, and we can confirm such cohesiveness for white-lipped peccaries too based on camera trap footage from within our study area (M. Hofman, *unpublished data*) and evidence from several earlier studies on the species elsewhere (Keuroghlian *et al.*, 2004; Reyna-Hurtado *et al.*, 2009b). For example, in neighbouring Calakmul, Mexico, collared animals were always seen with their respective herds for more than

700 observations (Reyna-Hurtado, *pers. comm.*). Hence, the collaring of additional individuals from the same herd would not necessarily yield additional information on home-range and movement patterns of that herd.

3.2 Methods

3.2.1 Study area

The Bladen Nature Reserve (BNR; 16.48, -88.88) is a strictly protected area (IUCN Cat. Ia) gazetted in 1990, covering about 40.5 km^2 of the southern Maya Mountains, and centred around the watershed of the Bladen branch of the Monkey River. Since 2008, the reserve has been managed by a local conservation NGO, the Ya'axché Conservation Trust, under mandate of the Belize Forest Department. Vegetation is almost exclusively lowland and submontane broad-leaf wet forest with relatively open understorey and a canopy height of 20–30 m (Iremonger *et al.*, 1995). Lowland areas are characterised by abundant *Astrocaryum mexicanum* and *Attalea cohune* palms, while tree diversity is dominated by the Fabaceae, Rubiaceae, Sapotaceae and Lauraceae families (Brewer & Webb, 2002; Iremonger *et al.*, 1995; Stott, 2014). The protected area also contains a sliver of seasonally inundated lowland savannah in its far eastern tip, and a pocket of pine forest. Due to its inaccessible terrain with steep slopes and extremely narrow valleys, the area holds some of the most undisturbed forests of Belize and is very high in biodiversity (Brewer & Webb, 2002; Briggs *et al.*, 2013; Dourson, 2012), with ongoing species discoveries (Polhemus & Carrie, 2013; Thompson & Dourson, 2013). Its elevation spans from 30 to 1050 m, some of the highest areas in Belize. It is one of the wettest areas in Belize receiving an average annual rainfall between 2,500 and > 3,000 mm, with 85% falling between mid-May and the end of November (Brewer & Webb, 2002), and an annual average temperature of around 26℃. The area has a distinct dry season from March to mid-May. It is bordered by six other protected areas with a lower protection status, which are equally likely to be used by white-lipped peccaries, given the contiguous habitat type and expected ranging behaviour of the species (Figures 3.1 and 3.3). The nearest human settlements are Medina Bank (∼300 inhabitants, mostly Q'eqch'i Maya) and Trio Village (∼3,000 inhabitants, mostly Q'eqch'i Maya and Mestizos from Guatemalan origin), and their agricultural areas border the Maya Mountain Forest Reserve and Belize Foundation for Research and Environmental Education. BNR is separated from a two-lane highway to the south-east by a five km wide stretch of savannah and lowland broadleaf forest, mostly within the Columbia and Deep River Forest Reserves.

White-lipped peccaries are occasionally spotted by Ya'axché field staff throughout the reserve, with estimated herd sizes between 60 and 100 individuals, but it has been unclear how many herds roam the area and whether or not they interact. Anecdotal reports from farmers and hunters suggest a declining population over the last 10 years in southern Belize. There are no reports about crop raiding by white-lipped peccaries in southern Belize and we assume that the animals in the research area have little or no contact with humans, with the exception of enforcement personnel and visiting researchers. Hunting pressure in eastern BNR is expected to be low due to long-term intensive enforcement activities in the area. In other parts of the reserve and in the surrounding areas, hunting pressure is expected to be higher (M. Hofman, *pers. obs.*).

3.2.2   Trapping

White-lipped peccaries have been trapped either by tracking or ambushing free-range animals (Fragoso, 1998; Fuller *et al.*, 2002; Reyna-Hurtado *et al.*, 2009b), or by using baited box and/or corral traps (Carrillo *et al.*, 2002; de Almeida Jácomo *et al.*, 2013; Keuroghlian *et al.*, 2004; Sowls, 1997, C. Richard-Hansen, *pers. comm.*). We used one box trap (1 x 1 x 2 m) and one corral trap ($\varnothing$ ca. 6 m, 1.5 m high, with handling compartment), spaced about 2.5 km apart, each in the proximity of a creek showing signs of peccary activity. The traps were deployed in July and August 2014, during the peak rainy season in southern Belize. Camera traps had indicated previous occasional presence at the corral trap site during two previous years. The traps were baited with various fruits; as well as cassava *Manihot esculenta* and cocoyam *Xanthosoma spp.* roots. Because only one collar was available, one adult female of appropriate size (estimated > 25 kg) was selected and isolated from the captured individuals, using recommended pig handling tools, including a confined restraining compartment, board and snare (Defra, 2003; Grandin, 2013). With the aim of minimizing the duration of the process, we did not use sedation. All animal trapping and handling followed the guidelines of the American Society of Mammalogists (Sikes & Gannon, 2011), and was permitted by the Belize Forest Department [Permit no. CD/60/3/14(37)]. The individual was fitted with a Telonics TGW-4570-3 GEN4 GPS/Iridium collar (Telonics, Mesa AZ, USA). The collar was programmed to start a fix attempt every three hours, theoretically yielding eight locations per day. If no GPS fix was obtained after 180 seconds, the fix attempt was aborted and classified as unsuccessful. Data were scheduled to transfer to the satellite every two days. Data remained on the sending list for 10 days, then would remain stored on-board but would not be sent.

3.2.3 Home-range size and movements

We used the semi-variance approach developed by Fleming *et al.* (2014) to detect whether the herd displayed home ranging behaviour, and to estimate the home-range size. The approach makes use of the auto-correlated nature of tracking data to investigate processes that occur over different time scales (e.g. foraging vs. migration or dispersal). The semi-variogram measures the distance between two relocations as a function of the time lag between them, and calculates the variability of distances among all relocation pairs with the same time lag. When an animal displays home ranging behaviour, increasing the time lag between relocations leads to an asymptote in distance covered, because animals would not usually travel further than their home-range diameter, even when given more time. Hence, the approach can be used both to detect home-range behaviour and to estimate home-range size. Since movement distances are averaged within time lags, the approach is robust in the face of irregular and sparse relocation data, i.e. varying fix intervals and long data gaps (Fleming *et al.*, 2014).

We used the `ctmm` package (Fleming *et al.*, 2015) for the R statistical environment (R Development Core Team, 2015) for all semi-variance calculations. Following Fleming *et al.* (2014), we calculated the empirical variogram, and selected the best fitting Semi-Variance Function (SVF) from a set comprised of i) a null-model (Brownian motion, i.e. random, undirected movement), ii) an Ornstein-Uhlenbeck motion model (OU—Brownian Motion within a home-range), and iii) an Ornstein-Uhlenbeck motion model with foraging included (OUF), i.e. assuming regular Brownian motion (while foraging) on a very short time scale, and Ornstein-Uhlenbeck motion on longer time scales. We used the Akaike Information Criterion corrected for small sample size (AICc) to select the best model.

Additionally, to allow comparisons with previous home-range estimates for the species, we used the `rhr` package (Signer & Balkenhol, 2015) in R to estimate 50, 95, 99 and 100% Minimum Convex Polygon (MCP) home-ranges, as well as 50, 95, 99 and 100% isopleths from a kernel density home-range estimate (KDE) with bandwidth set to the reference bandwidth. From the latter calculations, a core home-range area was estimated using the method of Seaman & Powell (1990) as provided in the `rhr` package (Appendix B). To investigate movement rates, we calculated step characteristics using the `rhr` package and summarized step lengths to indicate movement distances over three time spans: 6, 12, and 24 hours.

3.2.4 Habitat preference

To investigate habitat selection within home-ranges (i.e. third-order habitat selection; Johnson, 1980), we used the most recent land use/land cover map available in vector format based on 30m-resolution Landsat data, specifically for Belize from the Belize Environmental Resource Data System of Belize (BERDS, 2005), representing the 2011 situation with 18 land use/land cover classes. We considered the proportion of each land use/land cover class within the 100% MCP as available, and the proportion of relocations in each class as the proportion of habitat used. We tested for differences between available and used with a χ^2-test. Additionally, we calculated the Jacobs index (Jacobs, 1974) to detect which specific classes were used more often than expected from their availability in the landscape. The Jacobs index is a modified version of Ivlev's electivity index (Ivlev, 1961) that takes into account the relative abundance of a resource when identifying an organism's resource preferences (Jacobs, 1974). It is calculated as

$$D = (r - p)/(r + p - 2rp) \tag{3.1}$$

where r is the proportion of habitat used and p is the proportional habitat availability. D varies from -1 under strong avoidance to +1 under strong habitat preference. Values close to 0 indicate that the habitat is used in proportion to its availability.

3.3 Results

3.3.1 Trapping success

On April 22nd, 2015, we trapped 12 individuals from a herd of an estimated 60 in the corral trap. The individual selected for collar deployment was an adult female, estimated to weigh just over 25 kg. Fitting the collar took *ca.* five minutes, after which the animal was released from the handling compartment to join the others in the corral. Camera trap footage showed the collared female among the rest of the herd less than four hours after the trapping event, and with its young, both in good health, two weeks later.

GPS fix rate and data transfer. We report here on data collected between 22 April and 22 August 2015, i.e. 121 days of collar deployment. Data for *ca.* 47 days did not transfer to the satellite, meaning that 38.7% of the time we did not know whether a fix attempt had been successful, and where the animal was located. The average length of such data gaps was 6.7 ($\pm$ 3.0 SD) days, with a maximum of 12 days. From all the fix attempts that were transmitted to the satellite (n = 593), only 11.6% were successful, thus yielding a total of 69 GPS fixes over the study period.

3.3.2   Home-range

The empirical semi-variogram was best approximated by the semi-variance function representing Ornstein-Uhlenbeck motion including foraging (OUF; 2221.51 AICc), and thus showed evidence for home ranging behaviour over the four-month monitoring period (Figure 3.2). Only on very short time scales did the animal display random, undirected movement (2.53 hours, CI 0.92, 6.91) indicative of foraging. The OU and BM models followed with ΔAICc 8.11 and 1760.48 respectively. The estimated home-range size was 55.2 km^2 (CI 34.09, 81.32) which the animals could cover in 3.66 days (CI 1.70, 7.89; Figure 3.2). The 95% MCP home-range estimate was less than half that of the 95% KDE isopleth, while the core area estimate based on the KDE was closer to the 95% MCP (Table 3.1).
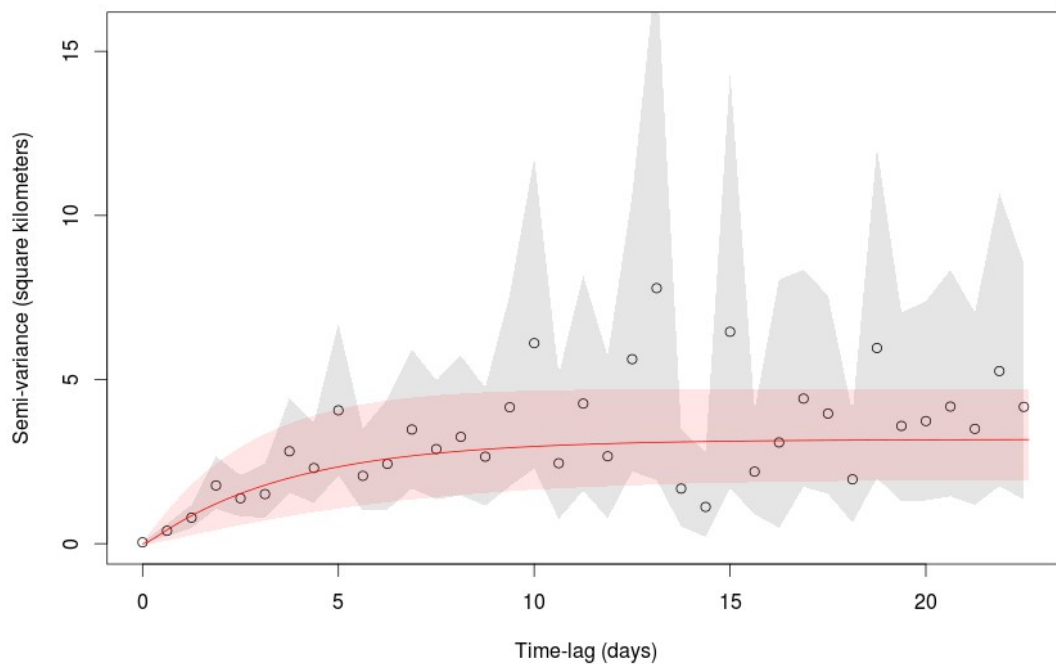
FIGURE 3.2: Semi-variogram of all GPS fixes of a single white-lipped peccary in southern Belize (n = 69). Circles represent the estimated semi-variance for each time-lag, with 95% confidence intervals estimated from the standard error of the mean semi-variance shaded light grey. The fitted OUF model (see text) is shown as a red solid line with its 95% confidence intervals estimated from the standard error of the best fit shaded light red.
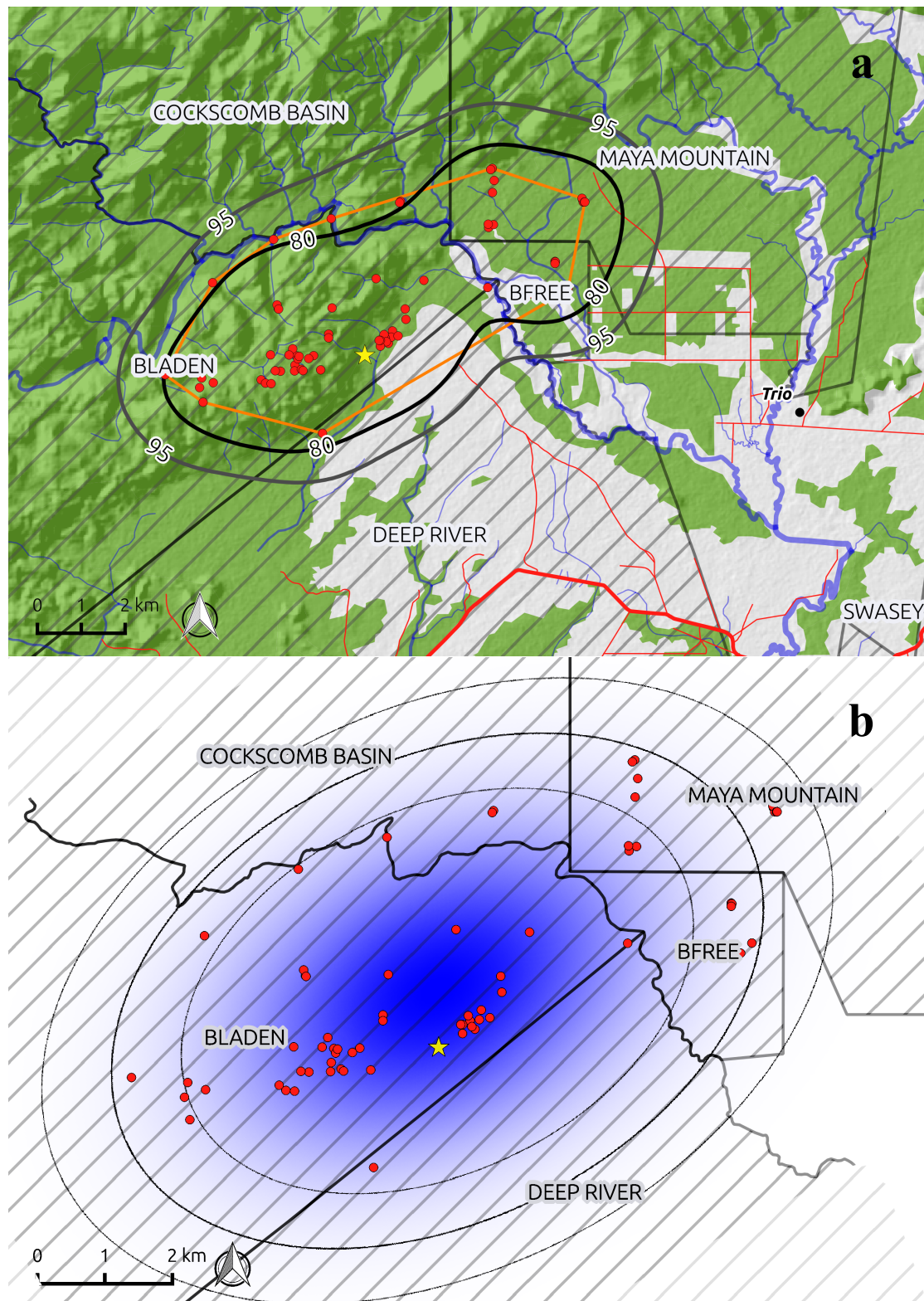
FIGURE 3.3: Spatial representation of the home-range estimates for a single white-lipped peccary herd in southern Belize. a) 95% Kernel Density Estimate home-range (dark grey line), Core area (80% KDE –black line) and 100% MCP home-range (orange line) over the relocations (red dots), rivers (blue) and roads (red lines). Black dots represent villages, the yellow star is the corral trap location. Forest cover is shaded green, grey shaded areas are non-forest (savannah, shrubs and agricultural lands), and grey diagonally line-filled areas with straight black boundaries are protected areas. b) Semi-variogram home-range estimate (black ellipse) with 95% confidence interval (grey ellipses) and utilisation density (blue shading).

	Level (%)	Area (km^2)
MCP	50	7.13
	95	33.48
	99	33.58
	100	33.59
KDE	50	17.67
	95	69.38
	99	96.71
Core area	79.8	41.01

TABLE 3.1: Minimum Convex Polygon (MPC) estimates, Kernel Density Estimates (KDE) and Core Area estimate of white-lipped peccary home-range size in southern Belize across different levels.

Step length (m)	n	Mean (SD)	Median	Maximum
$\Delta t <$ 6hrs	17	190 ($\pm$ 208)	119	802
6hrs $\geq \Delta t <$ 12hrs	11	910 ($\pm$ 814)	882	2380
12hrs $\geq \Delta t <$ 24hrs	13	1181 ($\pm$ 786)	1074	2260
$\Delta t \geq$ 24hrs	27	900 ($\pm$ 806)	792	3788

TABLE 3.2: White-lipped peccary step length statistics for different time intervals between GPS fixes.

3.3.3 Movement

Mean distances covered during fix intervals of six, 12 and 24 hours were 190, 910 and 1181 m respectively, while daily distances covered between subsequent fixes with multi-day fix intervals averaged around 900 m (Table 3.2). The maximum distance covered during fix intervals of up to one day was 2,380 m. For fix intervals longer than one day, the maximum observed speed was 3,788 m/day. Over all fix intervals, the maximum movement speed calculated was 270 m/h.

3.3.4 Habitat preference

Comparing the proportion of land use/land cover types for the relocations with the proportion of these classes in the 100% MCP area, a χ^2-test showed significant difference between use and availability ($\chi^2 = 15.133$ and P < 0.001 based on 2000 Monte Carlo replicates).

Jacobs D indicated a preference for broadleaf forest and a slight avoidance of shrubland (Table 3.3). Since no relocations were recorded in savannah and agricultural lands, the D index indicates total avoidance (-1.00). Note that we could not calculate significance levels for preferences of individual land cover classes, because our sample size of one does not allow us to calculate the relevant test statistics.

	Available	**Used**	***D***
Agriculture	0.69%	0.00%	-1
Broad-leaf forest	80.03%	95.65%	0.69
Savannah	12.54%	0.00%	-1
Shrubs	6.74%	4.35%	-0.23

TABLE 3.3: Proportion of land use/land cover classes available within the 100% MCP home-range (Available), the proportion of the relocations in each class (Used) and the corresponding Jacobs index (D).

3.4 Discussion

3.4.1 Home-range, density and population size

Even though white-lipped peccaries have been considered nomadic or migratory in early studies (Bodmer, 1990; Kiltie & Terborgh, 1983), the current consensus is that they use well-defined home-ranges that are large enough to encompass seasonal or multiannual movements (de Almeida Jácomo *et al.*, 2013; Fragoso, 2004; Keuroghlian *et al.*, 2004; Reyna-Hurtado *et al.*, 2009b).

All our home-range estimates fall within the range sizes reported for white-lipped peccaries from areas under various disturbance and rainfall regimes in Brazil, Costa Rica, and Mexico (Carrillo *et al.*, 2002; de Almeida Jácomo *et al.*, 2013; Fragoso, 1998, 2004; Keuroghlian *et al.*, 2004; Reyna-Hurtado *et al.*, 2009b). However, the time span covered by our estimates is four months for a single herd, whereas the other estimates cover multiple herds, each of which was tracked for a period of three months to more than one year. Despite the short time span, our data covers the end of the 2015 dry season and the beginning and peak of the wet season of the same year, and it remains to be seen whether our home-range estimates will shift or expand during the transition into the 2016 dry season, until the collar drops off in May 2016. However, although the semi-variogram indicated home ranging behaviour, it is impossible to say whether our location data adequately represent the entire home-range, given the numerous gaps in the data. For example, we suspect that the dense canopy in rugged terrain may more severely affect GPS fix success rate and satellite data transfer than relatively flat terrain, which would cause an underestimate of space-use in the more rugged areas.

Nonetheless, within the home-range estimated thus far, our habitat preference results agree with the preference for forested areas that is well-known for the species. Given the low availability of agricultural lands inside the MCP area and the limited number of relocations, the total avoidance of agricultural lands remains uncertain. With about 12.5% of the home-range covered by savannah, it is remarkable that no relocations were observed there, while almost 5% of the relocations were located in shrubland, which was

available at half the rate as savannah. This could be explained by i) shrubland providing better cover or food and ii) the patchy spatial configuration of shrubland throughout the forest making movement through these patches more likely than through the one continuous patch of savannah south of the forested areas. However, we emphasize that due to a sample size of one herd, significance testing of preference for specific habitats was not possible.

Due to its robustness with sparse data, we consider the semi-variogram estimate the most accurate for our data set. Using the home-range size estimate (and confidence intervals) of this approach and our estimated number of individuals in the herd (n = 60), we would obtain a density of 1.09 (CI 0.74, 1.76) ind/km^2 . If we (i) extrapolate these home-range and density estimates to other herds in the Maya Mountains (as delineated by Briggs *et al.*, 2013), and (ii) assume that all the broad-leaf forest habitats in the Maya Mountains are suitable for white-lipped peccaries, we estimate 99 (CI 67, 160) herds roaming the area, and a population size of 5,917 individuals (CI 4017, 9582). Clearly, the two assumptions for these estimates are untested and the estimates are therefore associated with very high uncertainty; we include them here in the discussion for indicative purposes only. Our density estimate of 1.09 ind/km^2 is in the lower half of the range of estimates from the Argentinian Gran Chaco (1.02 ind/km^2 , Altrichter, 2005), the Brazilian Cerrado (2.99 ind/km^2 , Desbiez *et al.*, 2010) and southern Brazil (4.5 ind/km^2 , Keuroghlian *et al.*, 2004), but still considerably higher than in the Calakmul Biosphere Reserve in Mexico (0.43 ind/km^2 , Reyna-hurtado, 2009) (0.43 ind/km^2 Reyna-Hurtado 2009), which is geographically closest to our study area. However, all of these areas are drier and/or less forested than our study area, which is expected to influence group size and density. For example, the high density in southern Brazil might be due to a crowding effect in the fragmented forests. We expect to have overestimated population size, because not all broad-leaf forests in the Maya Mountains are expected to be used by the species, and hunting pressure in the herd's home-range is expected to be lower than in most other parts of the area. Nevertheless, the estimates suggest that the Maya Mountains can potentially harbour a large number of while-lipped peccaries, warranting greater research emphasis and conservation incentives on the species in this region.

3.4.2   Collar performance

The numerous reports of successfully deployed GPS collars in different environmental settings convincingly illustrate the potential that this equipment holds for obtaining large quantities of high quality data in wildlife research (Edenius, 1996; Eriksen *et al.*, 2011; Harju *et al.*, 2013; Krofel *et al.*, 2013; Martins *et al.*, 2011). However, the use

of GPS collars often comes with unforeseen technical or data quality issues (Matthews *et al.*, 2013; Sager-Fradkin *et al.*, 2007). In particular, studies from tropical forests report imprecise locations or low GPS fix success rate (Barlow, 2009; Blake *et al.*, 2001; Coelho *et al.*, 2007; Hwang *et al.*, 2010; Lizcano & Cavelier, 2004; Phillips *et al.*, 1998). While we anticipated that the dense forest and steep terrain in our study area would pose a challenge for any telemetry-based research, we opted for GPS collars because (i) we wanted to obtain detailed information on movement patterns to parametrize a mathematical model for simulating potential movement paths of peccaries in Belize, and (ii) the cost of obtaining a limited number of GPS collars was estimated less than the personnel and equipment costs for running a large camera trap grid or transect network in the inaccessible area. Unfortunately, the fix success rate of 11.6% was much lower than expected from the literature, even for the given environmental conditions. However, collar malfunction cannot be excluded as a possible explanation. For logistical reasons, we could not perform collar tests in the field prior to deployment, but we stress that this should in fact be standard practice.The poor performance of one collar cannot be used to draw general conclusions about the viability of GPS collars in rugged tropical environments, but we suggest that a review on the usefulness of GPS collars specifically in such environments is needed to help researchers determine a priori the potential in their area. Nonetheless, we are confident that the data gathered during this study outperforms data collection using regular VHF collars in our area and for our highly mobile target species, both in terms of quantity and quality of locations obtained.

3.4.3 Movement

Movement data of high temporal resolution has been, and remains, difficult to obtain for white-lipped peccaries, and hence movement distances of white-lipped peccaries have mostly been described qualitatively in terms of home-range behaviour, migration and/or nomadism (Sowls, 1997). In this study, the herd of the tagged white-lipped peccary seemed to move about 1 km per day on average, but did at times travel at 270 m/h and covered up to 3,788 m per day, which enabled the herd to traverse its home-range in two to eight days. Due to our frequent sampling gaps however, our estimates likely underestimate the mobility of the species in our study area. For comparison, Fragoso (1998) reported distances from 1,200 to 2,600 m between VHF relocations of unknown time intervals, while Reyna-Hurtado *et al.* (2009b) mentioned a travel speed of up to 3,000 m/h, traversing seasonal home-ranges in one-day time intervals.

Based on observations elsewhere in Central and South America (Carrillo *et al.*, 2002; Moreira-Ramírez *et al.*, 2015; Tobler *et al.*, 2009), we expected white-lipped peccary activity to peak during mid-morning and mid-afternoon. However, from our movement

data (i.e. speed and distance measures), we were unable to detect any clear diurnal activity patterns (see Appendix B). We attribute this to the poor fix success rate of the collar. The fix success rate is lowest during the most active periods of the day (Figure 3.4), leading to a lack of information on movement distance and speed during these periods. This suggests that the behaviour of the animal is potentially an important factor influencing the success of our GPS collar, in line with previous findings (D'Eon & Delparte, 2005). The downward trend in fix success rate from the onset of the high activity period also suggests that time since the last successful fix is inversely correlated to the probability of obtaining a successful subsequent fix. The time lag between fix attempts has been found to negatively affect fix success rate in previous studies (Cain *et al.*, 2005; Moen *et al.*, 2001).
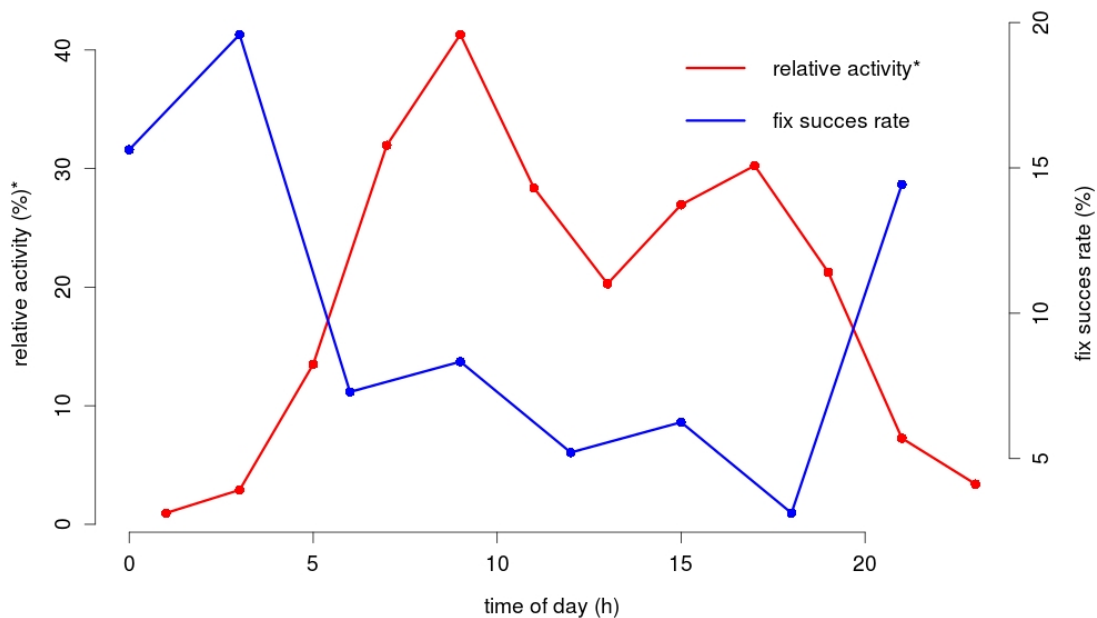
FIGURE 3.4: Fix success rate (%) was very low in general, but especially so during expected high activity peaks. [*Relative activity was calculated as the mean relative activity from the datasets presented in Carrillo *et al.* (2002), Tobler *et al.* (2009), and Moreira-Ramírez *et al.* (2015)]

3.4.4 Notes on behaviour

During the first six months, the animals visited the trap sites a total of five times with an average of 44.4 (± 51.9 SD) days in between. In the next two months, visit frequency increased, with an average of 11 (± 11.9 SD) days between subsequent visits. Note that the coefficient of variation in both cases is greater than one, indicating the unpredictability in time of the trap site visits. This visit frequency was generally lower

than in Manu National Park in the upper Amazon basin in Peru, where white-lipped peccaries passed by the same observation site every 4.25 days in the dry season, and every 14.5 days in the wet season (Kiltie & Terborgh, 1983). It is unclear whether this difference in visit frequency would be due to differences in food availability, wariness of human presence, or other factors. Other researchers have found similar time spans for the animals to increase trap visit frequency (three months to one year; C. Richard-Hansen, *pers. comm.*).

White-lipped peccaries have been reported in some cases to engage in aggressive behaviour towards a threat (Sowls, 1997), but we observed no direct attacks from the animals inside or outside the corral. Four of the trapped animals escaped upon our arrival as they managed to jump the fence using each other's backs as steps, while the remaining eight animals stood their ground and displayed a circular defence formation in the centre of the corral, in agreement with observations by Nietschmann (1972). Once the selected animal was isolated in the handling compartment out of view of the others, it was secured in place and let itself be handled without resistance.

3.5 Conclusions and recommendations

To our knowledge, white-lipped peccaries have so far been fitted with VHF-based radio-telemetry collars only, and no studies using GPS-collared white-lipped peccaries have been published. However such studies are being conducted in French Guyana, the Brazilian Pantanal and Mexico (C. Richard-Hansen, *pers. comm.*; A. Keuroghlian and R. Reyna-Hurtado, *pers. comm.*).

Our study illustrates some important challenges faced in trapping white-lipped peccaries and the use of GPS collars in dense tropical forests on rugged terrain. First, the time between the installation of the traps and the trapping success was considerably longer than anticipated. Second, collar performance was very poor in our area, presumably due to animal behaviour, canopy cover and terrain conditions. Recent implementations of the quick fix pseudo-ranging (QFP) system in terrestrial applications could improve the performance (Tomkiewicz *et al.*, 2010). Third, even though we found that collaring without sedation is possible, we have no information on the animal's stress levels while being handled other than the observation that the animal let itself be handled easily once isolated. Nogueira *et al.* (2015) simulated a hunting situation on captive white-lipped peccaries using a similar trapping set-up as was used in this study. They found that the psychological negative effect (i.e. increased wariness) of the trapping event lasted no longer than eight days. However, the approach also has the disadvantage of not allowing

for collecting body measurements or blood samples. For these reasons, we recommend using sedation when possible.

Despite the challenges, the preliminary results provide a much-needed glimpse of the spatial ecology of white-lipped peccaries in Belize. We present notes on behaviour, measurements of maximum and mean daily movement distances, habitat preference and home-range estimates. We cautiously provide density and population size estimates, but future studies should focus on estimating peccary densities directly (e.g. via camera-trapping or genetic mark-recapture), assess variability of herd size in Belize, and collar a greater number of individuals. We note that the relocations of our herd are spread over BNR and all five surrounding protected areas, highlighting the necessity to coordinate management of these areas so as to avoid spill-over effects of disturbances from one area to the other. Improving the management of, and knowledge about, the white-lipped peccary populations in the Maya Mountains is crucial for their survival in Belize as well as for monitoring and maintaining the connectivity of the area to neighbouring forests of La Selva Maya and the Calakmul area (Moreira-Ramírez *et al.*, 2015; Reyna-Hurtado *et al.*, 2009b).

3.6 Acknowledgements

Chapter 4

The performance of satellite telemetry units in terrestrial wildlife research: what does the evidence show?

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Abstract

Satellite telemetry is a promising technique for wildlife research. Large volumes of movement data at fine spatial and temporal resolution allow for a broad spectrum of ecological questions to be addressed. Its current widespread use reflects the technique's versatility. However, the performance of satellite telemetry units is influenced by many factors: the environmental and topographical conditions of the area in which they are deployed, the characteristics of the species carrying them, unit design and technical specifications, the constellation of satellites for geolocation, the methods and conditions for data transfer, and even the level of species knowledge and telemetry experience of the researchers deploying them. To avoid literature bias, we used questionnaires to collect data from over 3,000 units, deployed on 62 species in 142 study areas worldwide. We collated information from 167 projects worldwide, aiming to gain insight into the relative influence of all factors on different aspects of the performance of satellite telemetry units. We evaluated the success rate in obtaining fixes and transferring fixes to the user, and evaluated technical failure rates. We used boosted beta regression to model the units' performance as a function of a set of variables representing species and environment characteristics, deployment settings, and unit specifications. We found that average fix success and data transfer rates were high (85 and 94%, respectively), and were generally better predicted by species characteristics and unit specifications than measures of environmental characteristics. However, close to half of the unit deployments in an average project ended prematurely, and about 25% suffered a technical failure. Despite the challenges involved in satellite telemetry, the detail, amount, and quality of data often exceeds that of data gathered using traditional VHF telemetry or camera trap grids. Nevertheless, researchers should thoroughly consider the need for satellite telemetry to answer their specific research questions, given the sizeable investments involved for a scientifically sound and statistically robust result. We give a list of recommendations to consider before initiating a study involving satellite telemetry.

4.1 Introduction

Wildlife telemetry units (e.g. collars, harnesses) equipped with satellite functionality have opened up a very attractive set of options for remote observation across a large diversity of species. (Kays *et al.*, 2015). These telemetry devices allow for tracking movement on unprecedented temporal and spatial scales, yielding large amounts of detailed information. Since the early 1990s, GPS-based satellite tags have been used successfully in wildlife research (Thomas *et al.*, 2011; Tomkiewicz *et al.*, 2010), for example for studying predator-prey interactions (Eriksen *et al.*, 2011), activity patterns (Gottardi *et al.*,

2010), movement characteristics (Johnson *et al.*, 2002b; LaPoint *et al.*, 2013), habitat preferences (Chetkiewicz & Boyce, 2009), and behavioural modes (Forester *et al.*, 2007; Gurarie *et al.*, 2009). The scope of applications is still increasing due to improvements in technology and significant size reductions (Kays *et al.*, 2015). Due to the potential and wide range of uses of satellite telemetry, its use in research and conservation has increased considerably in the last decades, and an increasing number of scientific studies have been published using or evaluating the technique (see Figure 4.1 and Correa Ayram *et al.*, 2015).
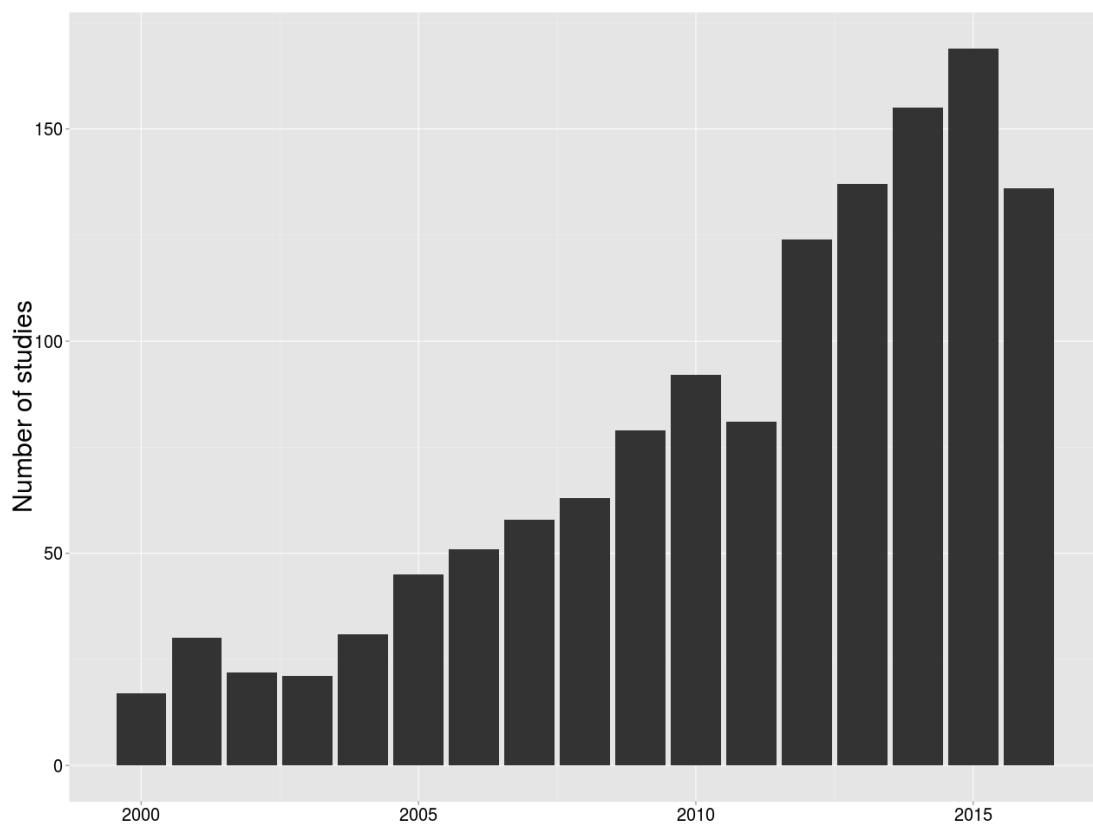
FIGURE 4.1: Number of publications over the last 16 years found on ISI Web of Knowledge using the search terms 'satellite wildlife telemetry', 'satellite wildlife tracking, 'GPS wildlife telemetry', 'GPS wildlife tracking', 'satellite animal telemetry', 'satellite animal tracking', 'GPS animal telemetry', and 'GPS animal tracking'.

Nonetheless, it is recognised that challenges related to the actual functioning of the units often result in lower data volume and quality than expected by the researcher (Johnson *et al.*, 2002a; Kaczensky *et al.*, 2010; Matthews *et al.*, 2013; Thomas *et al.*, 2011). The general operation of satellite telemetry units involves two steps (see Figure 4.2 on page 60). The first step is fix acquisition: whereby according to a pre-programmed, usually cyclic schedule, the satellite tag scans the sky for satellites and attempts to calculate the coordinates of its exact position on earth (a process often referred to astaking a fix'). The second step is data transfer: the stored results are transferred to the user either

via a physical connection to the unit or using one of the many options for remote data transfer (Thomas *et al.*, 2011; Tomkiewicz *et al.*, 2010). A number of factors affect the success of satellite telemetry units in both these steps.

First, fix acquisition is influenced to unknown extent by tag orientation (D'Eon & Delparte, 2005; Heard *et al.*, 2008), species behaviour (Bowman *et al.*, 2000; Mattisson *et al.*, 2010; Moen *et al.*, 2001; Sager, 2005), canopy cover/basal area of the habitat (Agouridis *et al.*, 2004; DeCesare *et al.*, 2005; Di Orio *et al.*, 2003; Hansen & Riggs, 2008), vegetation cover type (Phillips *et al.*, 1998), terrain ruggedness (Cain *et al.*, 2005; Lewis *et al.*, 2007) and the visibility to the sky to detect satellites (Cain *et al.*, 2005; Sager-Fradkin *et al.*, 2007). All of these can cause high variation in the volume and quality (i.e. geographic precision) of fixes stored on the unit.

Second, it is clear that the choice of data transfer method depends on the study species and environmental characteristics of the study area (Thomas *et al.*, 2011). However, to decide whether UHF, GSM or satellite based data transfer is more suited for a heavily forested and inaccessible area is not straightforward. Researchers need to judge whether the animals can be approached close enough for UHF data transfer and whether enough resources are available to visit the area frequently. Alternatively, they face difficult considerations about the effect of the density of the forest on the coverage of the GSM or satellite network. The chosen method of data transfer from the unit to the user can considerably impact the amount of data eventually available to the user, especially in cases where the chances of recovering the unit from the field are small (Gau *et al.*, 2004). Far fewer studies have addressed the success in transferring data from the unit to the user as compared to the fix acquisition rates.

Third, failures in the electronics and mechanics of satellite telemetry units are not uncommon. Failures due to production errors, battery malfunction, timed-release failure, the effects of harsh environments and species behaviour can all shorten a unit's operational life. The same is true for animal mortality due to natural causes, hunting, traffic or deployment-related issues (Gau *et al.*, 2004; Kaczensky *et al.*, 2010; Matthews *et al.*, 2013). Any premature end to the deployment of a telemetry unit undoubtedly causes further (potentially significant) losses in the expected data volume. Despite the availability of a number of data screening and processing techniques to deal with biased and/or missing positions (Frair *et al.*, 2010; Laver *et al.*, 2015; Nielson *et al.*, 2009), poor data quality and/or quantity can prevent units from providing sufficient data to answer specific research questions formulated based on the premise that larger amounts of high-quality data would be available. These limitations have led some authors to urge for caution when opting for satellite telemetry in wildlife research (Johnson *et al.*, 2002a).

One could expect that projects where the quantity and/or quality of information is insufficient to answer the main research question are unlikely to produce any peer-reviewed publications. Therefore, we expect the literature to be biased towards successful applications of satellite telemetry (Matthews *et al.*, 2013). For example, Campbell *et al.* (2015) report that approximately 50% of studies involving satellite transmitters in Australasia remained unpublished, either due to the time-lag between field work and publication, insufficient data quality or quantity, or a lack of time, funding, experience or motivation to publish in peer-reviewed journals. This means that evaluations of the performance of satellite telemetry in wildlife research based on literature review alone could lead to false conclusions. Because to our knowledge large-scale evaluations of fix success rates of satellite telemetry units relying on both published and unpublished data have not been conducted, the actual consistency of satellite telemetry units in providing the expected large amounts of high-quality data could be considered poorly known. Similarly, we do not know which factors determine the overall success of this promising research technique.

Here, we use a questionnaire approach to assess the performance of satellite telemetry units in terrestrial wildlife research across the globe, and evaluate the relative influence of environmental, technical and species-related characteristics. Our specific objectives were to investigate the average fix acquisition success, the average data transfer success, the overall success rate of units, the proportion of units malfunctioning due to technical or other failures, and how these rates are impacted by environment, species and unit characteristics.

4.2 Methods

4.2.1 Data collection

We used a standardised questionnaire format to collect information on satellite unit performance from past and ongoing wildlife research projects across the globe. We chose a questionnaire to obtain this information because we wanted to avoid a potential bias in published literature towards successful satellite telemetry studies.

To identify potential participants for the study—researchers who were willing to analyse and share information about the unit success rates for individual projects—we first used a short online form explaining the study, in which we invited researchers to submit their contact details if they were interested in participating. We shared the form on conservation and ecology related mailing lists, online wildlife and technology platforms, and social networks for scientists. We also mailed the invitation to contribute to personal

contacts, authors of satellite telemetry studies, and contributors to online animal movement databases. Second, data on satellite telemetry unit performance were collected from all interested participants in a standardised format using a questionnaire form (see Appendix C). The form consisted of 27 questions, grouped according to the topic they addressed: study area and animal characteristics, unit specifications, deployment details, unit costs, and researcher opinion on data quality and quantity and the usefulness for their career, for conservation, and for research.

The design of the questionnaire was guided by the general operation of satellite telemetry (see Section 4.1 and Figure 4.2). In the two-step process of data collection in satellite telemetry, the first step is fix acquisition. Nearly all recent, commercially available units for wildlife research use the Global Positioning System (GPS) satellite network for the purpose of obtaining fixes, although other methods exist (e.g. Argos with Doppler-effect, Global Navigation Satellite System or GLONASS for short, see Figure 4.2; Thomas *et al.*, 2011; Tomkiewicz *et al.*, 2010). Each programmed fix attempt by the unit either succeeds or fails in obtaining a fix, and this result is stored on an inbuilt memory device. The tag needs an unobstructed line-of-sight to at least four satellites to obtain a reliable 3D fix, with fewer satellites leading to lower spatial accuracy of the obtained coordinates (Al-Rabbany, 2002; Moriarty & Epps, 2015). Additionally, factors such as the spatial distribution of satellites in the sky and the distortion of the satellites' radio signals due to atmospheric effects can introduce imprecision in the obtained positions (Al-Rabbany, 2002). This imprecision is measured as the geometric dilution of precision (DOP). The number of available satellites and the DOP for each fix attempt are usually—but not always—included in the fix result information provided to the user by the unit or the manufacturer. Furthermore, the programmed fix attempt frequency itself can influence the success of the fix attempts. If the time lag between fix attempts is short, the unit can reuse the satellites' ephemeris data, reducing the time and battery power needed to determine the next location (Cain *et al.*, 2005; McGregor *et al.*, 2016; Moriarty & Epps, 2015). The second step in data collection is the transfer of the obtained locations from the unit to the user. Several options for transferring data are available (Thomas *et al.*, 2011; Tomkiewicz *et al.*, 2010), including:

(1) The store-on-board unit is retrieved from the field, and the user extracts the data using a physical connection between the unit and a computer.

(2) An Ultra High Frequency (UHF) tag on the unit enables the user to download the data, typically using a UHF receiver from a relatively short distance.

(3) The unit is equipped with a GSM sim card and messages containing the fix results are sent directly to the user's phone.

(4) An additional satellite tag on the unit transmits the fix results to a commercial communication satellite network (e.g. Argos, GlobalStar, Iridium or Inmarsat), usually providing global or near-global coverage.

Where the additional weight is not of concern, satellite telemetry units can be equipped with an automated timed-release mechanism to avoid having to recapture the animal to retrieve the collar. Additionally, the units usually come with traditional Very High Frequency (VHF) tags for on-the-ground triangulation or homing-in, as well as activity and environmental sensors that provide supplementary information (Kays *et al.*, 2015). This supplementary information is not usually included in remote data transfer to reduce the size of the individual data packages to be transferred.

4.2.2 Standardised questionnaire

In the questionnaire, we used the following general principles and terminology. In line with Figure 4.2, we considered the number of *expected* fixes to be the number of scheduled fix attempts that were initiated by the unit between the day of deployment and the moment the unit failed, the animal deceased or until the last data download. A fix was considered *successful* when a scheduled fix attempt succeeded in obtaining the unit's location and the user subsequently managed to retrieve the time and coordinate information for this fix from the unit. We considered a fix to be *unsuccessful* when a scheduled fix attempt failed in obtaining the unit's location, but the user still managed to subsequently retrieve the available info for this attempt from the unit. Note that the available information for unsuccessful fixes will include variables such as date, time and number of visible satellites, but will lack coordinates. Fixes with obviously improbable coordinates were also counted as unsuccessful. Any scheduled fix attempt for which no information was transferred to the user—hence it is unknown whether the unit succeeded or failed to obtain its location—was considered a *not-retrieved* fix. We neglected the quality of individual fixes (DOP, 2D/3D) for the purposes of this study, because the diversity of ways to measure the quality would have increased the complexity of our questionnaire disproportionately. Moreover, the quality of fixes is governed by more detailed processes than the actual fix success rate (e.g. the position of satellites relative to one another), and and it has been studied on smaller scales on several occasions (Cain *et al.*, 2005; D'Eon *et al.*, 2002; Frair *et al.*, 2010; Ganskopp & Johnson, 2007; Gau *et al.*, 2004; Hansen & Riggs, 2008; Jung & Kuba, 2015; Lewis *et al.*, 2007; Matthews *et al.*, 2013; Sager-Fradkin *et al.*, 2007). Hence, only the quantity of fixes was considered for the evaluation of the unit success. Some projects involved flexible fix acquisition schedules whereby fix frequencies varied depending on the activity level of the animal or the

crossing of a 'virtual fence' in the landscape. We included only those projects where the number of expected fixes could be accurately calculated or estimated.
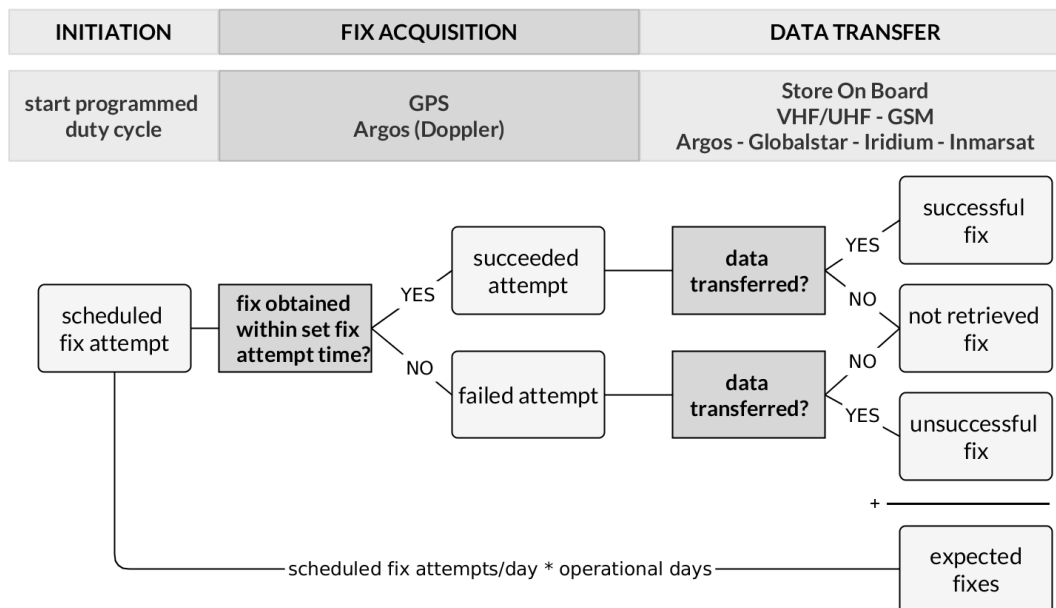

FIGURE 4.2: The general two-step operation of terrestrial satellite telemetry units, and the possible fix outcomes of the process. The number of expected fixes equals the sum of successful, unsuccessful and not-retrieved fixes.

4.2.3 Unit performance and its co-variates

We compiled a set of co-variates that potentially influence the different measures of unit success. Several of these co-variates were derived directly from the questionnaire information, while area-based co-variates were calculated from study area coordinates (see Table 4.1). We used five measures to evaluate unit success. Three of these covered different parts of the actual satellite telemetry data gathering process, while the other two measured the rate of failures in the units.

(1) **fix success rate** – To evaluate the fix acquisition, we calculated the fix success rate as *successful / (successful + unsuccessful)* fixes.

(2) **data transfer rate** – To evaluate the data transfer success, we calculated the data transfer rate as *(successful + unsuccessful fixes) / expected* fixes. We excluded projects where not-retrieved fixes were downloaded from units with remote data transfer (GSM, UHF, satellite) after recovering them from the field.

(3) **overall success rate** – To evaluate how many fixes were eventually available to the user we calculated an overall success rate as *successful / expected* fixes. In

previous research, the overall success rate is often referred to as the fix success rate (Adams *et al.*, 2013; Gau *et al.*, 2004; Sager-Fradkin *et al.*, 2007), whereby authors have either assured or assumed complete data transfer.

(4) **unit failure rate** – The proportion of units that failed for any given reason (animal-related, technical or unknown) to evaluate the overall unit failure rate and

(5) **technical failure rate** – The proportion of units that failed exclusively due to known technical issues (including failure of timed-release mechanism) to evaluate the technical failure rate.

4.2.4   Statistical analysis

To evaluate the relative importance of covariates for the fix success and overall success rates, we used boosted beta regression models (Schmid *et al.*, 2013). The boosted beta regression approach combines the beta regression framework, as a special case of the Generalised Additive Models for Location, Scale and Shape (GAMLSS) class of regression models (Mayr *et al.*, 2012; Rigby *et al.*, 2005), with the gradient boosting framework. Beta regression is a commonly used technique in natural sciences to model a continuous response bounded between 0 and 1, with essentially the same interpretation as logistic regression (Cribari-Neto & Zeileis, 2010; Schmid *et al.*, 2013). The flexibility of the beta distribution allows for complex responses to be modelled, while the GAMLSS class allows precise model specification as it enables the fitting of not only the conditional mean, but also other parameters of the distribution of the response variable (location, scale, and shape) as a function of explanatory variables and/or random effects (Rigby *et al.*, 2005). Additionally, where classical beta regression usually uses maximum likelihood to optimise regression coefficients and requires the user to select variables based on model-selection criteria (e.g. AIC), the boosted beta regression approach uses an algorithm called gamboostLSS (Mayr *et al.*, 2012). The algorithm uses the gradient boosting framework to optimise the models for all distribution parameters (see Hofner *et al.*, 2014; Mayr *et al.*, 2014). The family of beta distributions, as implemented in the R package `gamboostLSS` (Hofner *et al.*, 2016a,b), has two parameters: *mu* is the conditional mean, while *phi* is the precision or overdispersion parameter. The conditional variance of the outcome is then given as *mu (1 − mu) / (1 + phi)*. Essentially, boosted beta regression assesses the relative importance of covariates simultaneously on the mean (*mu*) and on the variability (in terms of overdispersion *phi*) by iteratively fitting simple regression functions of the effects of each covariate to the negative gradient for *mu* and *phi*. Relative variable importance for the models of both parameters is given as the

Name	Description	Type	Level
Purchase date	Weighted mean of the year of purchase of all units in the project	Quantitative	Unit
Time-to-fix	Weighted mean of the time-to-fix of all units in the project	Quantitative	Unit
Burowing/ Hibernating	Boolean indication of burrowing and/or hibernating individuals in the project	Qualitative	Species
Height	Weighted mean of the species shoulder height across all individuals in the project	Quantitative	Species
Forest type	Type of forest in the study area as indicated in the questionnaire. Levels: No forest cover; Temperate evergreen; Temperate deciduous; Temperate mixed; (Sub)Tropical evergreen; (Sub)Tropical deciduous; (Sub)Tropical mixed.	Qualitative	Environment
Forest cover (qualitative)	Percentage of forest cover as indicated in the questionnaire. Levels: 0-25%; 26-50%; 51-75%; 76-100%	Qualitative	Environment
Forest density	"Density of forest in the study area as indicated in the questionnaire. Levels: Dense understory & closed canopy; Open understory & closed canopy; Dense understory & intermediate canopy cover, Open understory & intermediate canopy cover; Dense understory & sparse canopy cover; Open understory & sparse canopy cover; No forest cover.	Qualitative	Environment
Terrain ruggedness	Terrain ruggedness as indicated in the questionnaire. Levels: Steep slopes and narrow valleys, flat areas and gentle slopes are rare ($< 20\%$); Steep slopes, interspersed with flat areas and/or gentle slopes; Mostly flat area and/or gentle slopes, with occasional steep slopes ($< 20\%$); Mostly flat area or gentle slopes ($< 5\%$ steep slopes).	Qualitative	Topography
Transfer method	The main data transfer method used in the project. Levels: GSM; Satellite; Store-on-board; VHF/UHF.	Quantitative	Environment
Forest cover (quantitative)	Mean forest cover in the study area as derived from the GlobCover dataset using the coordinates provided in the questionnaire.	Quantitative	Environment
Terrain Ruggedness Index	Mean Terrain Ruggedness Index across the study area, as derived from the best available Digital Elevation Model for the study area. This variable was used as a proxy for available view to the sky.	Quantitative	Topography
Number of units	The number of units deployed in the project	Quantitative	Unit

TABLE 4.1: Co-variates for the boosted beta regression on the fix success rate and overall success rate of satellite telemetry units.

percentage of boosting iterations in which a covariate was selected as the best fit to the respective parameter of the outcome. When the algorithm is appropriately tuned, e.g. via cross validation, it has the major added advantage of having an in-built mechanism for variable selection (Hofner *et al.*, 2016b; Schmid *et al.*, 2013). All covariates described above were entered in the overall success model, while the main data transfer method variable was excluded for the fix success rate model. We included the main unit brand used in each project as a random variable, and weighted each project by the number of telemetry units deployed.

4.3   Results

We collated information from 167 projects in 142 study areas across 42 countries and 6 continents (see Figure 4.3). The geographic distribution was uneven, with just over half of all study areas located in Europe, 20% in Africa and less than 10% in each of the other continents. Projects lasted on average 3.5 years, and ranged anywhere between 60 days and 14.3 years. Across all projects, a total of 3,695 individuals of 62 species were equipped with 3,130 telemetry units of 16 different brands. Most units were purchased between 2006 and 2015. Reptiles and (ground-dwelling) birds were tagged in four and two study areas respectively, whereas medium to large mammals were the study object in all other areas. Moose *Alces alces* comprised 15.6% of all reported individuals, 10.7% were reindeer *Rangifer tarandus tarandus* and 8.2% mouflon sheep *Ovis gmelini musimon x Ovis sp.*. Cheetah *Acinonyx jubatus* and roe deer *Capreolus capreolus* each represented 5.8% of all reported individuals, and chamois *Rupicapra rupicapra* 5.0%. All other species each represented less than 5.0%.

4.3.1   Overall unit performance

In the average project, units performed well in terms of both fix acquisition and transfer. On average 85.2% (7.5–100%) of transferred fix attempts succeeded, and 93.6% (23.4–100%) of fix information was transferred successfully from the units to the user. Note that the data transfer rate not only includes data that was transferred remotely but also data that was downloaded from retrieved units. In 64 out of 125 projects in which data was transferred remotely, retrieved units provided additional fixes to the remotely transferred fixes. Eventually, users obtained on average 77.5% (6.7–100%) of the fixes that they could have expected to obtain during the total time that units were deployed and functioning properly in the project. However, 25% (0–100%) of all unit deployments in an average project ended prematurely due to technical failure, irrespective of the unit's price or purchase date. Additionally, about as many deployments
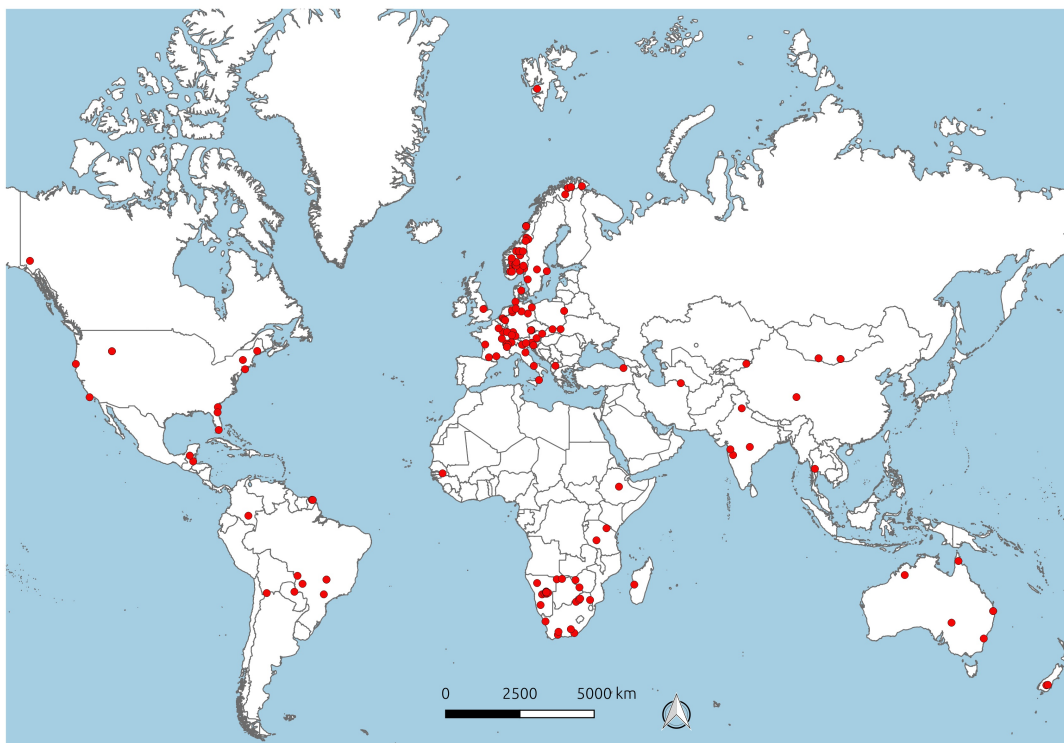
FIGURE 4.3: The geographic distribution of all projects that provided information the performance of satellite telemetry units.

ended prematurely due to animal related issues or for unknown reasons, such that 48% (0–100%) of all unit deployments in an average project ended earlier than was planned.

4.3.2 Exploratory trend analysis

We observed a number of weak trends in the data. Both qualitative forest cover and density tended to negatively influence overall success rate, with effects visible mostly in the decline in fix success rate and to a lesser extent data transfer rate. The quantitative forest cover derived from GlobCover showed similar trends. We noted a slight tendency of the evergreen forests (both [sub]tropical and temperate) to result in lower fix success rates than their deciduous or mixed variants, which was again most notable in the fix success rate rather than in the data transfer rate. The qualitative measure of terrain ruggedness of the study area did not show a consistent trend in either direction, but an increasing trend in overall success rate was observed with decreasing quantitative terrain ruggedness. The overall success rate showed an upward trend with increasing mean year of purchase of the units (weighted by the number of collars), again mostly affecting the fix success rate, and a similar trend was observed with increasing mean shoulder height (weighted by the number of individuals). The overall success rate of units with GSM or UHF based data transfer tended to be higher than store-on-board units or units

Variable	Selection frequency	
	mu	*phi*
Height	18.60%	
Time-to-fix	13.95%	20.00%
Purchase date	11.63%	10.00%
Forest Density	11.63%	30.00%
Burrowing/Hibernating	9.30%	
Forest type	9.30%	
Terrain ruggedness (qualitative)	6.98%	
Forest cover (qualitative)	2.33%	
Terrain Ruggedness Index	2.33%	10.00%

TABLE 4.2: Selection frequencies of co-variates in the boosted beta regression model for the fix success rate

with satellite-based data transfer. The price range of the telemetry units did not tend to influence their success rates. Hence, most trends were more pronounced in the fix success and overall success rates than in the data transfer rate. However, trends for all co-variates were weak and showed high variability, calling for a more in-depth analysis using boosted beta regression.

4.3.3 Fix success rate

The boosted beta regression model for the fix success rate selected the shoulder height of the study species as the most important variable, followed by the maximum time to fix, the purchase date of the units and forest density (Table 4.2). The model predicted fix success rate to increase nearly linear with species shoulder height up until 1 meter, and then flatten off for taller standing species (Figure 4.4). Generally, allowing a longer time for the unit to obtain a fix improved fix success rate, and fix success rate was higher for more recently purchased units (Figure 4.4). Where we observed a reduced fix success rate with increasing forest density in our data exploration, this was not predicted in the fix success rate model. Burrowing and/or hibernating behaviour reduced the fix success rate, and was selected in less than 10% of the boosting iterations, as were the qualitative environmental variables (forest type, forest cover and terrain ruggedness) and the mean Terrain Ruggedness Index. The modelled responses for forest type and qualitative forest cover were roughly in line with the observed data trends, and the response for qualitative and quantitative terrain ruggedness lacked any consistent trend, as was the case in the observed trends. Forest density, especially closed canopy, was an important factor increasing the variability in fix success rate, while an increased time to fix and more recent purchase date of units decreased its variability. Intermediate and high values of mean Terrain Ruggedness Index impacted the variability of the fix success rate slightly.
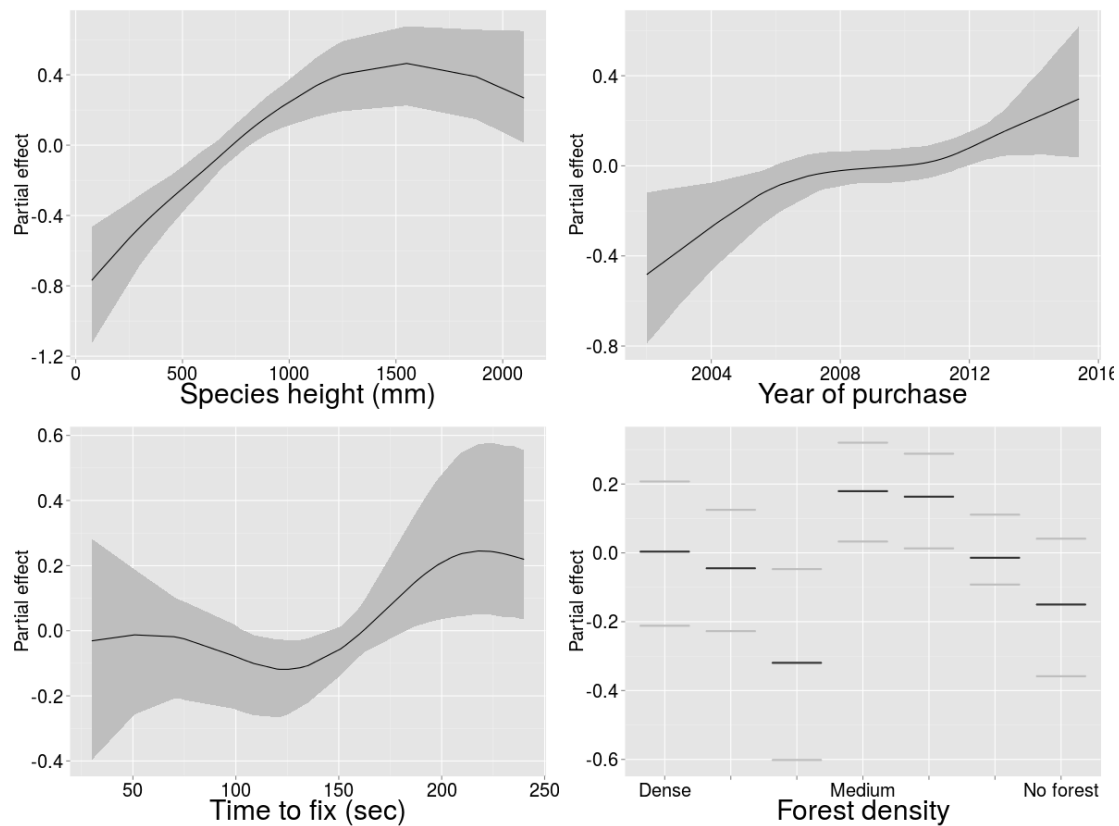
FIGURE 4.4: Mean-centred partial effects of the most important variables predicting the mean fix success rate of satellite telemetry units (empirical confidence intervals in grey). Partial effects display the effect of the variable while accounting for all other variables in the model.

4.3.4 Data transfer rate

In 15% of all projects, the majority of units were store-on-board units, where the data transfer was entirely dependent on the successful retrieval of the units from the field. All remaining projects used remote data download methods to transfer the information from the units to the user. GSM was the main data transfer method in 40.1% of all projects, while 23.1% mainly used satellite communication and 21.8% mainly VHF/UHF. Of all the units with satellite data transfer, 86.3% attempted sending data at least once per day, 11.3% at least once every three days, and the remaining at least once per month.

To isolate the effects of the data retrieval method on the overall success rate, we needed to exclude those projects where retrieved units provided fixes in addition to those down-loaded remotely. That is, we selected only projects where either all fixes were transferred via a physical connection (store-on-board units), or all fixes were obtained through re-mote data download (remote transfer units). The observed trend in the data indicated that data transfer success using communication satellite systems was lowest and most variable, while VHF/UHF was most effective in data transfer (see Figure 4.5). However,

due to the reduced number of projects, some factor levels had insufficient sample sizes for a boosted beta regression approach to produce usable results (B. Hofner, *pers. comm.*). Hence, we could not determine the relative importance of different factors affecting the transfer rate for each transfer method.
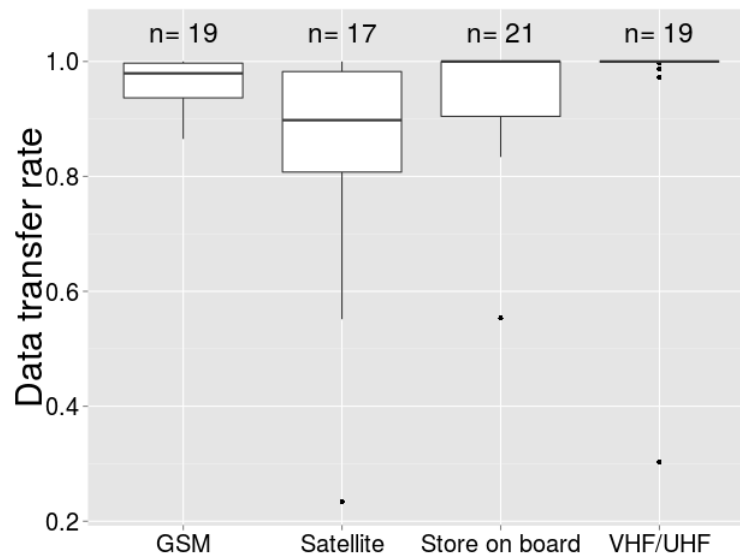

FIGURE 4.5: Data transfer rate per primary transfer method used in the projects. (Projects with remote transfer units where retrieved units yielded additional fixes were removed from the analysis.)

4.3.5 Overall success rate

The overall success rate model was the same as the fix success rate model, but with the main data transfer method added as a variable. Here, the maximum time to fix was most influential, while species shoulder height, transfer method, burrowing or hibernating behaviour, and forest density were somewhat less important. Forest type and qualitative forest cover were selected only infrequently (Table 4.3). The maximum time to fix showed a strong effect on overall success rate, while the effect of species shoulder height was reduced compared to its effect on fix success rate alone (Figure 4.6). Overall success rate was higher for GSM and VHF/UHF-based data transfer units, as compared to satellite and store-on-board units (Figure 4.6). The variability of the overall success rate was mostly determined by quantitative forest cover. Areas with intermediate levels of forest cover increased the variability of the overall success rate estimates. To a lesser extent, a higher mean Terrain Ruggedness Index increased variability, whereas a longer time to fix decreased it. Variability in overall success rate was also decreased in more recent units. Forest type and density did not show consistent effects.

Variable	Selection frequency	
	mu	*phi*
Time-to-fix	15.79%	10.00%
Height	10.53%	
Transfer method	10.53%	
Burrowing/Hibernating	10.53%	
Forest Density	10.53%	10.00%
Forest type	5.26%	10.00%
Forest cover (qualitative)	5.26%	
Forest cover (GlobCov)		20.00%
Purchase date		10.00%
Terrain Ruggedness Index		10.00%

TABLE 4.3: Selection frequencies of co-variates in the boosted beta regression model for the overall success rate
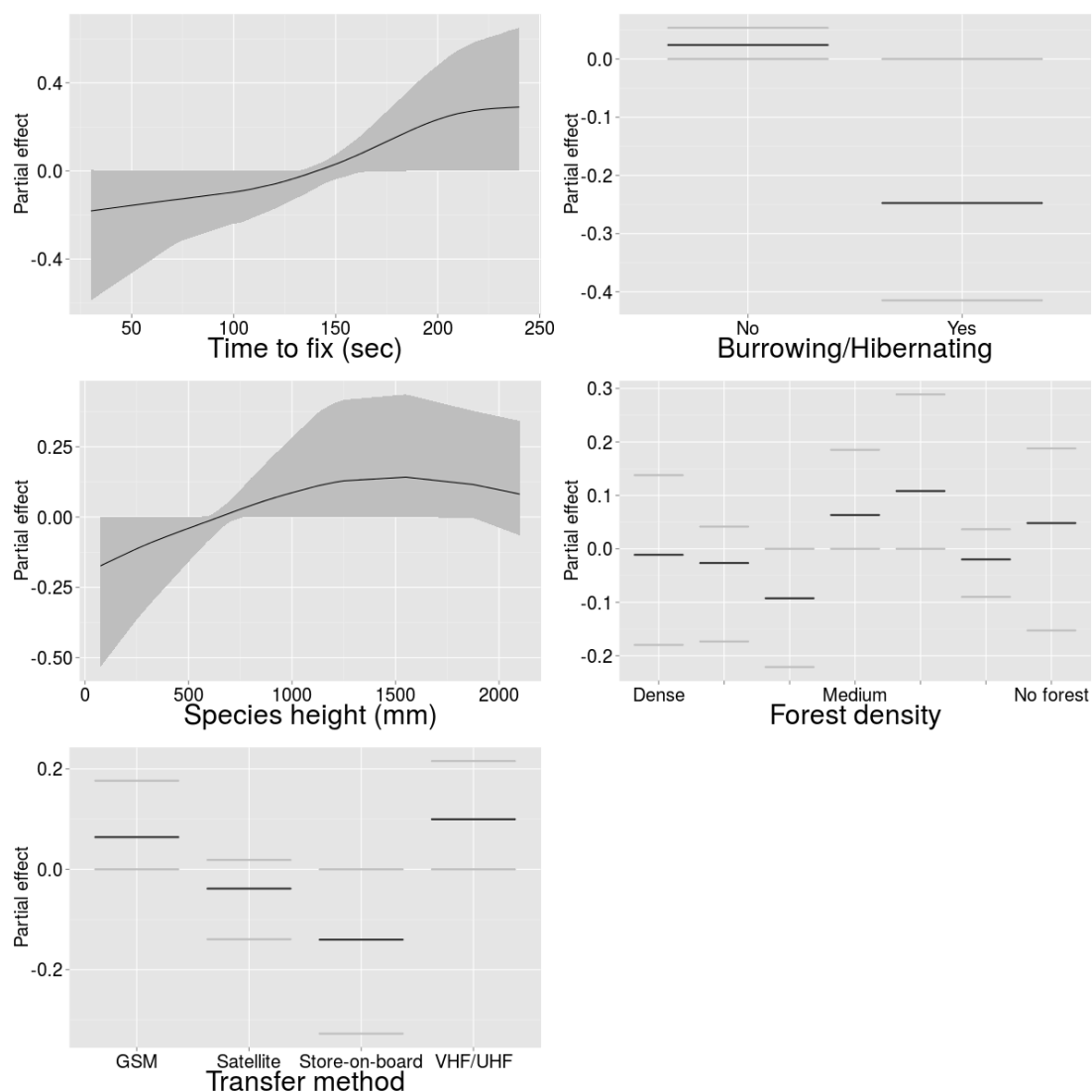

FIGURE 4.6: Mean-centred partial effects of the most important variables predicting the mean overall success rate of satellite telemetry units (empirical confidence intervals in grey). Partial effects display the effect of the variable while accounting for all other variables in the model.

4.3.6 Failure rates

Of all reported unit deployments (n = 2124), 61.2% were either successfully ongoing or ended as planned, while 18.9% ended due to technical malfunctioning. Technical malfunctions were due to battery failures (51.4%), electronic (36.2%) or mechanical problems (12.5%). Approximately 1 out of 10 unit deployments ended for unknown or non-specified reasons, and a similar amount ended due to either animal mortality (8.6.%) or unit removal by the animal (0.9%). The price range of the telemetry units did not tend to influence their technical failure rate.

4.3.7 Scientific output and subjective evaluation by researchers

The scientific output was relatively low. Of all the projects that reported on scientific output, 63.8% declared that no peer-reviewed papers had been published from the obtained data, while 17.2% published just one paper. However, 79.7% of the studies reported that they were gathering additional data or waiting for external factors to allow for publication. Almost half of all projects produced at least one publication that was not peer-reviewed (47.8%). Although 32.1% of the projects did not report whether the data was uploaded to Movebank, 79.8% of the reporting studies did not upload their data, and the most important reasons for this were that researchers did not know of this online data system (35.9%) or were not familiar with its uses (23.08%).

Most researchers considered a fix success rate of around 90% or more to be good, while anything lower than 80% was regarded poor. However, an overall success rate of more than 75% was considered good. Whereas researchers' opinions of their projects' contribution towards the field of applied conservation, ecological and conservation biology research or their career development tended to remain stable or even increase with lower fix success rates, opinions appeared to be negatively affected by higher unit failure rates. We also found that the data loss resulting from low success rates and high unit failure rates sometimes led to reduced scientific output of the project: 11.6% of the researchers indicated the lack of sufficient data quantity/quality as the reason for the low number of publications arising from the study.

4.3.8 Costs

The purchase costs of units was between US$2,001-2,500 in 39.7% of the projects, US$2,000 or cheaper in 32.9%, and more expensive than US$2,500 in 27.4%. In over half of the projects (52.3%), the additional costs for software licences and/or hardware extensions were US$50 or less, however in 19.6% of the projects these costs exceeded

US$500. Units with GSM or satellite data transfer tended to be more expensive to purchase and have higher recurring costs. Monthly costs for GSM contracts or satellite services can accumulate fast. In 57.2% of all projects, these monthly costs remained below US$10, while in 14.5% these costs were more than US$50.

4.4   Discussion

Our analyses revealed that performance of satellite telemetry in terrestrial wildlife research is more strongly influenced by unit and species characteristics, rather than environmental conditions in a study area. Furthermore, imperfect overall success rates were mostly due to issues with fix acquisition and unit failure, rather than problems with data transfer. Below, we discuss these findings in detail before deriving recommendations for the use and future development of satellite telemetry devices in wildlife research.

4.4.1   Fix success rate

The average fix success rate was about 85%, which is on the high end of published fix success rates. For example, Johnson *et al.* (2002a) recorded an average fix success rate of 59% for 26 collars deployed on woodland caribou *Rangiferus tarandus caribou*, while fix success rates were 81.4 and 85.6% for 15 collars on wolves *Canis lupus* and 26 on deer *Cervus elaphus*, respectively (Hebblewhite *et al.*, 2007). Both of these studies were conducted in the Canadian Rocky Mountains.

Our boosted beta regression analysis suggested that fix success rate is best predicted by the species shoulder height, the allowed time to fix and the year of unit purchase. Specifically, taller species, longer time to fix and more recently purchased units increase the fix success rate. An increased fix success rate for taller standing species intuitively makes sense because the units' satellite view is generally less obstructed by understory. Smaller animals are also more likely to seek cover during resting periods. Fix success rate was higher in more recent telemetry units, probably due to the improved sensor technology and GPS satellite constellation. For example, in 2011 the GPS network was expanded from a 24 to a 27-slot constellation, which improved coverage in most parts of the world (NCO, 2016). Unsurprisingly, burrowing or hibernation decrease fix success rate. Generally, forest type, density, cover and terrain ruggedness were less important predictors of fix and overall success, but contributed stronger to the variability of the success rates. Higher forest density and terrain ruggedness were predicted to increase the variability of the fix success rate in an area.

4.4.2 Data transfer rate

The fact that the average overall success rate was lower than the fix success rate implied that the data transfer process itself involved loss of data. That is, some fix attempt information that was successfully stored on the unit, did not get transferred to the user. We could not directly compare data transfer rates between transfer methods, but the observed trend was that data transfer was most effective in VHF/UHF units. Store-on-board units and GSM units also performed well, whereas data transfer over communication satellite systems was lowest and most variable. For the purposes of this study, we have assumed that the data transfer process did not discriminate between transferring succeeded or failed fix attempts, i.e. both are equally likely to be transferred. However, in cases were remote data transfer is accomplished using satellite services, we would expect that when conditions are good enough for data transfer, the fix success will have been high just before the data transfer, whereas in periods of failing data transfer, we expect the fix success rate to be lower. This would imply that, for projects using units with satellite data transfer (and without additional downloads after unit retrieval), succeeded fix attempts would have a higher chance of transmission than failed fix attempts, leading to an inflated fix success rate. Argos[1], Iridium[2], GlobalStar[3] and Inmarsat[4] all claim global or near global coverage (Inmarsat and GlobalStar do not cover polar regions, and GlobalStar's coverage in sub-Saharan Africa only began in 2015). Data transfer via satellite faces similar challenges to the fix acquisition step, and data loss during transfer can be expected.

4.4.3 Overall success rate

Overall success rate was 78% across projects, meaning that studies should account for receiving at least 22% less fixes than expected under a given fix acquisition frequency. This excludes data loss due to lost or failing units. Previous studies reporting overall success rates include Matthews *et al.* (2013), who compiled data from 280 deployments in 24 studies across Australia and found an average overall success rate of 66%. Gau *et al.* (2004) noted overall success rates of between 61 and 87% on average for 71 deployments on bears *Ursus arctos* in western Canada.

The time to fix was the most important predictor of overall success rate, reaching about the same selection frequency than in the fix success rate model. The effect size of species shoulder height was reduced, but was still equally important as burrowing or hibernating

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[1]http://www.argos-system.org
[2]http://www.iridium.com
[3]http://www.globalstar.com
[4]http://www.inmarsat.com

behaviour and forest density, both of which kept their level of importance as compared to the fix success rate model. All variables showed similar effects on the overall success rate than on the fix success rate. The data transfer method came in at the same level of importance as species height, and confirmed the trend observed in the data exploration: VHF/UHF and GSM units have higher overall success rates than satellite and store-on-board units. The lower overall success rate in satellite transfer units was due to both lower fix success rate and lower data transfer rate, whereas it was primarily due to lower fix success rate for store-on-board units. The lower fix success rate in store-on-board units could be because they were usually older than the satellite transfer units. Similar to the results of the fix success rate model, an earlier unit purchase date and a higher mean Terrain Ruggedness Index increased the variability in the overall success rate. Intermediate levels of mean forest cover and mixed forests also increase its variability.

4.4.4 Failure rates

Importantly, in the average project, close to half of all units stopped working properly sooner than expected, and about 25% suffered a technical failure. Johnson *et al.* (2002a) reported a failure rate of 69.2%, of which all were suspected to be due to technical issues, while Gau *et al.* (2004), Hebblewhite *et al.* (2007), andMatthews *et al.* (2013) experienced an overall unit failure rate of 53.3%, 47.0%, and 47.6% respectively, comparable to the average in this study. Matthews *et al.* (2013) also found that in 24% of all collars with timed-release mechanism, the mechanism failed to release the unit on the scheduled time, or at all. In our study, 10.5% of all unit deployments ended for unknown reasons. Most of the units with an unknown cause of malfunction were due to the fact that the unit could not be retrieved from the field, i.e. the 'lost' units. This is comparable to the average of 10% of collars reported as lost by Matthews *et al.* (2013), and slightly lower than the 18.3% reported by Gau *et al.* (2004). Any number of failing or lost units can result in considerable loss of data and investment (Gau *et al.*, 2004; Kaczensky *et al.*, 2010; Matthews *et al.*, 2013). Our questionnaire asked for the number and reason of prematurely terminated deployments, but the loss in expected data volume was not quantified in this study because not all unit manufacturers provide predictions on the number of fixes each unit should yield. We did find that, more so than low fix or overall success rates, the unit failure rate was perceived to reduce the contribution of a project towards the field of applied conservation, ecological and conservation biology research or the researcher's career development, suggesting that researcher reliance upon this technology has career-long ramifications.

Some studies reported instances where telemetry units performed fix attempts much more frequently than programmed in the schedule, resulting in a much higher number

of fixes than expected, and a much shorter battery lifespan. Matthews *et al.* (2013) also report this, as well as units failing to log fix results during (part of) the deployment period, resulting in considerable data loss. It is unclear though whether the reported underperformance was due to data storage or data transfer issues. In this study, where fix rates were investigated on a project level, we were not able to quantify the number of units affected by such unintended shifts in duty cycle.

4.4.5 Study limitations

Our approach of using a questionnaire to obtain information on the performance of satellite telemetry devices had the clear advantage of avoiding a potential publication bias towards successful studies. However, there are also some caveats to the approach.

First, geographic distribution of projects in our data set was biased towards European studies. We attribute this distribution to the willingness to participate, the density of studies conducted, and communication reach of the study's primary authors (e.g. limited information from Asia and Latin-America due to language barriers). We recognise that the relatively low number of studies reported from North America in this paper is not an accurate representation of the work that has been conducted in the region, and we are aware of several papers being published using satellite telemetry for wildlife research by universities and government bodies in North America (Chetkiewicz & Boyce, 2009; Cushman & Lewis, 2010; Hansen & Riggs, 2008; Heard *et al.*, 2008; Hebblewhite *et al.*, 2007; Joly *et al.*, 2015; Jung & Kuba, 2015; Sawyer *et al.*, 2009)). This geographically uneven distribution of studies might have influenced the representation of different brands and our findings on the relatively low publication output of wildlife satellite telemetry studies.

Second, we acknowledge that the role of the quantitative measures of forest cover and terrain ruggedness could be imprecise because they represent mean values across study areas, which could mask more localised effects due to variation across the study area or habitat preferences of the study species. Thus, even though the qualitative forest cover and terrain ruggedness measures are inherently subjective, we assume they are more representative because they were assigned based on the landscape and species knowledge of the researchers.

Third, the data used for the overall success rate model included all projects, including those where data was both transferred remotely and downloaded from retrieved units. The additional fixes downloaded after retrieval can significantly add to the overall success rate of the project. This means that the overall success rate was determined not just by the combined effect of the fix success rate and the data transfer success, but also by

the number of retrieved units. However, separating the fixes transferred remotely from those downloaded after retrieval was not possible because most researchers were not able to distinguish between these fixes in their final datasets.

Fourth, we were not able to estimate the cost efficiency of satellite telemetry devices. Purchase and running costs for units with satellite and GSM data transfer are usually higher than for VHF/UHF or store on board units. However, the overall running costs for VHF/UHF transfer and store-on-board systems are difficult to calculate due to the increased field effort required to retrieve the data and/or units (Thomas *et al.*, 2011). A better alternative for estimating cost efficiency of wildlife satellite telemetry is to calculate the cost per fix (Matthews *et al.*, 2013; Thomas *et al.*, 2011). However, because our data collection and analysis was on the project level, we could not calculate a cost per fix for the average collar.

Fifth, trapping of wild animals and deploying telemetry devices is a highly invasive procedure, often plagued by unforeseen circumstances, and carrying risk of injury or fatality of the animal (Kaczensky *et al.*, 2010; Matthews *et al.*, 2013). We did not take into account the trapping and collaring experience of the researcher for each project, but are aware that this can influence the rate of failure due to animal issues (death, collar removal), and the choice of optimal fix schedule. Although the ethical considerations of trapping and tagging are important for the welfare of the studied animals, our questionnaire did not contain questions to specifically quantify the number of injuries or animal mortalities due the impact of the tagging procedure. Animal welfare was not within the intended scope of our study and we felt that asking these sensitive questions would have greatly reduced the number of participating scientists.

Finally, even though many researchers would probably appreciate advice on which company to buy from for a specific study, our study was not designed to evaluate the relative performance of different brands of satellite devices. For a number of reasons, we cannot draw reliable conclusions about the performance of individual brands. For example, we determined the main brand of a project on the basis of simple majority, meaning that the use of multiple brands in one project (which was the case in 12% of all projects) could confound the brand-specific effect. Also, the sample size (i.e. number of projects) for many brands was too low for any statistically valid comparisons. This is especially important because different brands were also used with varying frequency across years, and we found a substantial improvement of success rates with increasing year of purchase. Thus, instead of incorrectly treating main brand as an actual co-variate, we chose to include it as a random variable in our boosted regression model. This was necessary, because our main goal was not to do a brand comparison, but to identify environmental, species and technical variables that determine the units' success rates. As a random

factor, the main brand had a strong influence on the average fix and overall success rates (selection frequency of 13.95 and 31.58%, respectively), but also had the strongest impact on the variability in success rates (30% selection frequency for both fix and overall success rates). In other words, predictions of mean success rates for each brand were associated with high uncertainties. This unpredictability could come, for example, from the rate of uptake of new technological advances throughout the years by different brands, or the deployment of the same brand on species of different sizes across years. Overall, we cannot give meaningful recommendations for choosing specific brands. Nevertheless, we can derive several important recommendations from our results, both for researchers wishing to deploy satellite telemetry devices, and for manufacturers of such devices.

4.5 Recommendations

The scope of possibilities and the detail of obtained information in satellite telemetry are major advantages of the technique for answering a range of ecological and conservation questions. However, given the considerable investment and the variability of the effects that many aspects of study design have on the success rate, we recommend to carefully consider project objectives, study design and budget constraints before investing in satellite telemetry units (Johnson *et al.*, 2002a; Thomas *et al.*, 2011). Below, we list a number of recommendations that arose from our study. For potential users, we present important considerations for deciding if and which satellite telemetry units are useful to deploy in future studies. For manufacturers, we recommend ways to actively contribute to the improvement of satellite telemetry application in wildlife research.

4.5.1 User recommendations

Evaluate the need for satellite technology – The acquisition of satellite telemetry units generally involves a considerable financial investment. The relative scarcity of funds for applied conservation and conservation research may inhibit the investment needed for a statistically valid study design. Researchers run the risk of resorting to accept low sample sizes, limiting the potential relevance of their inferences, conclusions, and indeed their investment (Hebblewhite & Haydon, 2010). Hence, we recommend to carefully consider whether the research questions really require satellite telemetry to obtain the necessary data. For studies where infrequent data points over a limited area suffice to answer the research questions, money might be better spent on VHF telemetry or non-invasive surveys (e.g. camera trapping, genetic analysis) instead of satellite telemetry (Thomas *et al.*, 2011). Similarly, where the behaviour of animals is of interest, these

methods might be optimal as the researcher needs to go to the effort of observing the animals anyway (i.e. GPS telemetry only provides spatio-temporal information). If satellite telemetry is the preferred option, ensure sufficient funds are available for the acquisition of the necessary units to produce statistically robust results (see below). If available funding is inadequate, consider postponing project implementation until additional funds are secured, or changing research questions, in order to avoid the risk of misguided conclusions or loss of investment.

Use more units than necessary – We found that 10% of all units were lost, while close to 20% suffered technical failures. When planning a project, we suggest to budget for 10–20% more units than strictly necessary for the study, in accordance with previous suggestions (Matthews *et al.*, 2013). If the acquisition of extra units is financially not possible, consider budgeting extra costs for retrieving units and sending them back for repair. If the acquisition is possible, be aware of the additional logistical challenges that the deployment of the extra units can involve.

Get recently developed units – The technologies underlying satellite telemetry continue to improve. Our results showed that the more recently produced units generally have higher and more consistent fix success rates, suggesting that manufacturers are making use of the latest technology developments to improve their products. Consequently, especially in challenging conditions, choosing the more recently produced units is a sensible choice.

Test different brands – Given the high variability in brand performance in our study, we recommend testing different brands for their suitability in a particular study before ordering the full amount of units needed. Brands provide different unit designs that might be affected to various extent by e.g. forest cover and species height or behaviour.

Use a higher-than-necessary fix rate – The average fix success rate was 85%, while the overall success rate was only 78%. Whenever possible (i.e. when not restricted by study species size and thus battery size), we recommend to set the fix frequency 15-25% higher than strictly necessary for the study design. This will not compensate for data loss due to animal mortality or unit failures, but can counteract data loss that originates from species behaviour, unit orientation or environmental factors temporarily obstructing satellite view.

Choose a longer time to fix – If the trade-off between battery life and fix frequency allows for it, consider choosing a longer rather than a shorter maximum allowed time to fix. In favourable conditions, the time to get a fix will be short and battery usage low anyway, while in challenging conditions, any extra seconds search time might make the difference in obtaining a fix.

Data transfer method – In cases where remote data transfer is necessary, our study results suggest that researchers should favour GSM or VHF/UHF data transfer, if study design and practical circumstances (species, terrain, etc.) allow for it. Especially in studies with challenging conditions (e.g. closed canopy, rough terrain), it might be worth investigating the GSM coverage in detail before deciding to choose satellite data transfer. An added advantage of GSM or VHF/UHF data transfer is that units tend to weigh less and are cheaper in purchase costs.

Test the units – Besides the common-sense pre-deployment test to verify proper functioning of the device, we believe it should be a prerequisite in all telemetry studies to specifically test units at known reference sites that are representative for the study area to get an idea of location error and fix success rate (Gitzen *et al.*, 2013; Hansen & Riggs, 2008). When interpreting the results of these tests, researchers should take into account that performance of units deployed on animals is reduced by up to 25% as compared to stationary tests (Blackie, 2010; Cain *et al.*, 2005; Hebblewhite *et al.*, 2007). The test results can be used later to screen and filter incoming data (Laver *et al.*, 2015).

Report specifications and settings in publications – Satellite telemetry users should report unit specifications and settings in scientific publications (or their supplementary materials) to facilitate comparison between species, environments and settings for different research questions (e.g. home-range, dispersal, connectivity, etc.). Important information includes the brand, type and purchase date of the unit, the fix frequency, the maximum allowed time to fix, and the data transfer method. Also the weight of the unit and the attachment technique (e.g. collar, harness, glued-on tag, etc.) are useful information. Ideally, the period of deployment and information on the number of expected, successful, unsuccessful and not-retrieved fixes should be included, as well as the datum and coordinate system of the fixes' coordinates. Furthermore, to interpret the fix success rates, it is useful to know the number of units that was recovered from the field and whether or not the recovered units yielded additional fixes to those downloaded remotely. Also, indicating price ranges for purchase and running costs can be useful information for other researchers considering the use of the technique.

Upload data and meta-data – Additionally, researchers could use existing collaborative e-infrastructures to store and manage their data (e.g. Movebank, Eurodeer, and others—see Campbell *et al.*, 2015; Kays *et al.*, 2015). Importantly, meta-data on unit specifications and settings as described above should be included in the upload, in as far as the database design allows for it. Online animal movement databases usually have options to let you decide if, when and how contributed data can be accessed by third parties.

Report success rates, technical issues, etc. – We also encourage researchers to report issues and successes encountered in the field to the manufacturers and bring up species-specific behaviour that may require custom unit design. Work with manufacturers to improve the technique under a variety of circumstances and for different species (Matthews *et al.*, 2013).

4.5.2 Manufacturer recommendations

Standardise data transferred to user – We encourage manufacturing companies to collaborate with scientists and practitioners to develop minimum standards for the data type and format that is stored on the units and/or transferred to users. For example, some brands only provide a record of successful fixes to the user, and do not inform the user about the fate of the remaining fix attempts. However, it is useful for the user to know whether the remaining fix attempts went wrong during fix acquisition or data transfer in order to evaluate the suitability of either the collar specifications or the data transfer method in a given study area (Matthews *et al.*, 2013). Another example is the variety of ways that the precision of fixes is measured. Many manufacturers provide data on the number of satellites used for the fix, or the fix dimension (2D/3D). Some provide data on Positional Dilution of Precision (PDOP), while others only report on the horizontal component of PDOP (HDOP). Sometimes only horizontal error estimates are reported based on undisclosed proprietary algorithms. Producing a standard reporting format for data originating from animal-borne devices would be beneficial for the management and analysis of such data in collaborative e-infrastructures (e.g. Movebank, Eurodeer), and would increase the efficacy of satellite telemetry for large-scale studies (Campbell *et al.*, 2015). Additionally, it would increase the feasibility of reviews such as this one. This standard reporting should streamline the data types and units, and variable names and definitions.

Customise devices – Given the importance of species characteristics for fix success rates in our study, companies should offer ways to customise devices for particular species (e.g. collar shape, antenna placement).

Reduce technical failure rates – All deployments that last shorter than expected result in a reduction in envisioned data volume, jeopardising the usefulness of the technique for wildlife research. We found that 25% of the units in an average project suffered a technical failure, and about as many failed due to animal-related issues. While animal mortality or tag removal are hard to eliminate as a cause for premature deployment end, reducing unit or data loss by avoiding technical failures would potentially present a considerable increase in the final data volume obtained.

Unit failure feedback – Both users and manufacturers would benefit from an easy and standardised feedback mechanism where users can provide details on unit successes and failures. In cases where the units cannot be sent back for diagnostics, knowing the circumstances of the failures could help recognising the underlying cause. Manufacturers should actively work with researchers on a standardized way for reporting success and failure rates.

Improve fix success rate – While data transfer is less of an issue, the average fix success rate of 85% in our study leaves scope for improvement. In the last decade, commercial satellite applications (e.g. hand-held GPS devices and smartphones) have started to make use of both the GPS and GLONASS satellite networks. The addition of the GLONASS network nearly doubles the amount of satellites used for geolocation, which results in faster acquisition of more precise locations (Cai & Gao, 2007). Using chipsets that provide access to both systems could increase fix success rates in challenging settings. Another opportunity is the recent development of minute gyroscopes, accelerometers and digital compasses, which allows for determining the location of a unit using Inertial Navigation System technology. An Inertial Navigation System determines the location of an object relative to an initial location without an external reference frame by using the velocity (measured by the accelerometer) and attitude (measured by the gyroscope and compass) of the object (Grewal *et al.*, 2007). The combination with GPS-based locations has opened up the possibility to determine the location of a unit in between fixes, and periodically update the accumulated location Inert Navigation System error using the coordinates of successful GPS fixes (Hubel *et al.*, 2016; Tomkiewicz *et al.*, 2010; Wilson *et al.*, 2013). Additionally, it allows for detailed behavioural data to be gathered. The technique has a lot of potential for further development.

In conclusion, the results of our study are very promising. Technological advances and product improvements seem to have increased success rates over the years, and reduced the influence of canopy and terrain characteristics on these success rates. We are starting to take advantage of the knowledge generated through field experiences and are gaining insights in how to further improve the technique. With this study, and in all our recommendations, we want to highlight the exciting opportunity for closer collaboration between manufacturers and scientists to find creative ways to solve any current and future problems encountered. Eventually, improved design and performance of satellite telemetry units will allow researchers to do better science, and will increase the use of the technique across the broad spectrum of biological questions that can be answered by it.

4.6   Acknowledgements

Chapter 5

Conclusions

As natural habitat is incessantly being converted for anthropogenic uses, maintaining connectivity between the remaining natural areas has become of vital importance. In fragmented landscapes, only adequate amounts of functional connectivity can prevent the loss of biodiversity and the inherently linked loss in ecological and evolutionary resilience of ecosystems worldwide. Conservation networks have been established across the globe and landscape ecologists have spent much effort developing models to understand and measure landscape connectivity, making use of the technological advances being made in wildlife telemetry and remote sensing areas. Land managers and conservationists generally make good use of the existing structures on the ground (such as protected areas) to design conservation networks based on expert-informed decisions about optimal linkages. This approach compiles valuable information for kick-starting action to safeguard connectivity, but includes few of the landscape ecological developments that aim to optimise the ecological realism of connectivity estimates for conservation network design. That is, it can lead to misguided management actions because it runs the risk of not well representing the ecological requirements of certain species that are meant to use the outlined corridors. Incorporating more biological information is thus desirable.

5.1 An overview

In this dissertation, we have seen that the incorporation of ecological detail on movement of species is possible, but the data availability, resolution and quality determines how much detail can be included. This dessertation has highlighted some of the opportunities and challenges in increasing the use of functional connectivity estimates in connectivity conservation.

Chapter 2 has shown that including more landscape and species details in connectivity models can provide potential connectivity estimates that augment the available information for effective conservation network design. Specifically, the use of occurrence data for white-lipped peccaries and a range of remotely-sensed environmental variables enabled the calculation of a habitat suitability surface, while the inclusion of protected area effectiveness in this calculation influenced the precision of the least-cost corridor estimates based on it. In addition, estimating corridors between highly suitable areas instead of between protected areas resulted in the identification of alternative corridors and brought to light highly suitable core areas that currently lack official protection. Furthermore, the use of graph-theoretic connectivity indices helped to evaluate least-cost corridors and identify priority areas for connectivity conservation. Potential connectivity for white-lipped peccaries in Belize was modelled to be mostly provided within, rather than among, core habitat patches. This yielded insight in the importance of maintaining protection of certain areas, and in the value of working on improved corridor functionality in other areas.

Chapter 3 compiled useful insights into the movement ecology of white-lipped peccaries for their conservation in Belize. A recently developed method was used for home range estimates from sparse movement data, and found the home range size of white-lipped peccaries in Belize to align with average home range sizes across its range. A relatively low maximum daily movement distance of 3,788 m was recorded, and the species' preference for forest ecosystems confirmed. The chapter also highlighted potential challenges of using satellite telemetry for obtaining high resolution movement data in Belize. Trapping success was influenced by animal behaviour and unforeseen logistical problems, which prevented the trapping schedule to be conducted as planned. Furthermore, fix acquisition success and data transfer rates were very low in the study area, leading to movement data that was too sparse to be used for the parametrisation of a resistance surface for actual connectivity purposes. Nonetheless, the gathered information provided evidence that the species behaviour was a factor influencing the success rate of fix acquisition attempts.

Chapter 4 provided a more general and large-scale assessment of the functionality of satellite telemetry in providing the quality and quantity fine-scale movement information it has become expected to provide. While the fix success rate of satellite telemetry units was generally high, the eventual amount of obtained data barely satisfied most researchers. The success rates were mostly influenced by species characteristics (such as shoulder height and burrowing behaviour) and unit specifications (such as the brand, the purchase date and the maximum allowed time to fix), while environmental and topographical factors contributed stronger to the variation in the success rates. Data transfer

over communication satellites generally performed worse than GSM or VHF/UHF systems, which confirms the observed fate of the collar used in Chapter 3. When retrieved from the field, this unit provided about three times the number of fixes than what was transferred over satellite connection alone. After application of the Quick-Fix-Pseudoranging method (a post-hoc data enhancement— Tomkiewicz *et al.*, 2010), the number of successful fixes increased to an order of magnitude larger than the remotely-downloaded fixes. Importantly, average failure rates due to both technical malfunctions and animal-related issues were high, impacting the perceived contribution of projects to conservation and research due to potentially significant loss of data and investment.

Throughout this dissertation, the issue of data availability and quality has been of importance. Low data availability is a day-to-day reality in applied conservation, limiting the extent to which management decisions can be based on robust science. Shortage of data to parametrise or validate models can provide incomplete or inaccurate information and hence limit the scientific validity of the conclusions drawn. In each chapter, I have acknowledged the shortage of available data where appropriate and point towards the possible shortfalls this may have caused in the obtained results and their interpretation.

5.2 Functional connectivity approaches in connectivity conservation

Even though data on landscape characteristics and animal movement is available in increasing detail, and landscape ecology is providing tools and metrics, the integration of increased biological detail in the multidisciplinary approaches used in landscape management and applied conservation has generally been considered troublesome (Bennett *et al.*, 2006; Opdam *et al.*, 2002; Resasco *et al.*, 2016). The application of functional connectivity models in conservation settings depends many on factors. For example, the availability of concise, intuitive, and broadly applicable connectivity metrics determine the uptake of the developed methods in applied conservation network design (Bennett *et al.*, 2006). As outlined in the introduction, a number of metrics and tools have been developed to make functional connectivity models accessible for applied connectivity conservation. Functional connectivity models and some of the developed tools have already been used in applied situations in certain areas of the world. For example, McHugh & Thompson (2011) used a set of umbrella species tied to priority habitats and a set of decision rules to delineate habitat extensions and improve ecological networks in the UK, while Pouwels *et al.* (2002a,b) used similar approaches in the Netherlands. Hofman *et al.* (2010) used expert-informed resistance surfaces for a set of target species to calculate least-cost corridors in a port area in Belgium. Mateo-Sánchez *et al.* (2014)

used available software for estimating a habitat suitability model, least-cost path density maps and graph-theoretic metrics to delineate corridors for brown bears *Ursus arctos* in Spain. Roever *et al.* (2013) used telemetry-based movement data and circuit theory to evaluate corridors for elephants *Loxodonta africana* across southern Africa. LaPoint *et al.* (2013) mapped and evaluated corridors for fisher *Martes pennanti* using tracking data, resource selection functions and least-cost approaches in New York, USA, while Zeller *et al.* (2016) used step selection function and circuit theory to predict corridors for pumas *Puma concolor* in California, USA.

Notably, most of these examples of applications of functional connectivity in conservation so far are limited to industrialised nations. In many other areas in the world, especially developing nations, conservationists still use much cruder information and modelling techniques for the delineation of conservation networks. Possible reasons are that many industrialised nations have a relatively long history of landscape planning and ecological data collection, and more or less adequate funds for compiling the necessary information and available capacity to produce functional connectivity estimates necessary to design conservation networks (Bennett, 2004). Even though Belize is listed as a Small Island Developing State (SIDS) by UN (UNCTAD, 2017), it is unusual in that it has an active and organised conservation community. The community is supported by local and international NGOs and academic institutions, which enables the compilation of environmental and biological data from many sources, some providing data dating back at least 25 years (BERDS, 2005). This is what enabled the potential connectivity estimates presented in Chapter 2.

This leads us to a second factor determining the likelihood of functional connectivity models used in conservation network design: data availability and quality. Chapter 2 and the previous paragraph show that data for the use of functional connectivity models in applied connectivity conservation is available in certain cases, but the data availability for using actual connectivity models faces more challenges. The advent of satellite telemetry has enabled large amounts of data to be gathered, but detailed data on ecosystem processes underlying connectivity studies (e.g. dispersal) remain hard to obtain. Furthermore, satellite telemetry performance is highly variable across a range of factors, and methods for handling and analysing telemetry data for the use in connectivity estimates are still under development. Additionally, the reality of available remotely-sensed data dictates that a certain discrepancy between fine-scale movement information and coarser-scale landscape data will be unavoidable in functional connectivity studies. This makes current applications of actual connectivity models in conservation network design difficult.

Moreover, even when tools and data are available, practicalities that are outside the realm of landscape ecology constrain the implementation of conservation networks based on functional connectivity models. For example, because functional connectivity implies a species-specific approach, its implementation in conservation network design requires the selection of one or more target species. Potential functional connectivity requires a minimal set of target species' occurrence records, while actual functional connectivity often involves recording movement tracks of the species, usually using telemetry. The challenge of collecting such species-specific movement data for even a single species has put off conservationists from using more ecologically realistic models to inform network design (e.g. Crouzeilles *et al.*, 2011). In addition, depending on the degree of overlap between estimated corridors for the different target species, one or more sets of corridors might have to be included in the conservation network. This can result in a significant increase in implementation costs and practical obstacles such as land ownership. Further practical limitations include e.g. land managers frequently having to work with degraded or absent linkages between the remnants of natural habitat that remain after development (Pulsford *et al.*, 2015). And lastly, socio-political issues, such as land tenure, support from local communities, management capacity and integration within other sectors of society can influence the feasibility of ecologically optimised conservation networks (Bennett, 2004).

In conclusion, understanding and modelling functional connectivity with increasing ecological realism is a prerequisite for effective conservion network design and thus ultimately for conserving biodiversity in fragmented landscapes. However, it is also challenged by technological shortcomings, by limited availability of adequate movement data, and by potential mismatches of environmental data and relevant ecological processes. These challenges jeopardize the ecological realism in current connectivity network design, especially in developing countries where some species of conservation concern are highly understudied and logistic and financial constraints often lead to limited data availability. Here, expert-informed approaches and cruder models will be necessary until sufficient data can be collected. In other parts of the world, using potential connectivity modelling seems an achievable objective for current applied connectivity conservation initiatives to increase ecological realism. Actual connectivity modelling techniques are developing fast but currently mostly remain testing ground for landscape ecological research. Nevertheless, several authors prove to that efforts are being made to achieve a tight integration between the theoretical domain and the empirical and applied domains of connectivity conservation (Aben *et al.*, 2014; Benz *et al.*, 2016; Correa Ayram *et al.*, 2015; Lechner *et al.*, 2015; Loro *et al.*, 2015; Mateo-Sánchez *et al.*, 2014; Roever *et al.*, 2013; Thurfjell *et al.*, 2014; Zeller *et al.*, 2016; Zetterberg *et al.*, 2010). It is at the cross-road of these domains that true connectivity conservation happens (Bennett *et al.*, 2006).

Appendix A

Supplementary material to Chapter 2

Supplementary material

to the article

"Enhancing conservation network design with graph-theory and a measure of protected area effectiveness: refining wildlife corridors in Belize, Central America"

by

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Introduction

This document provides more details about the methods, results and conclusions outlined in the article and presents additional analysis that were too lengthy to be included. Throughout the document, we follow the steps of the analysis framework presented in the article, which are included here for ease of reference (see below). Information referred to in the article will be presented in the analogous step in this document. R code for all of the analysis steps described in the paper and this document can be requested by contacting the corresponding author via maarten.hofman@forst.uni-goettingen.de.

1   Analysis framework

The framework presented in the paper is based on the Potential Connectivity Model framework from Rödder et al. (2016), which involves a two step process. First, a species distribution model is produced, which is then used as the basis for a resistance surface in a connectivity analysis, taking into account barrier effects. Our framework splits up the workflow into four interrelated steps, to extend and modify the PCM framework in several ways (Figure 1). First, we model species-specific habitat suitability using a range of environmental predictor variables as well as information on protected area effectiveness. Second, we objectively delineate nodes for the connectivity network and calculate a species-specific landscape resistance

surface using the habitat suitability model constructed in step one. Third, we delineate least-cost corridors among the nodes based on the resistance surface. Finally, once the potential connectivity model has been created through steps 1 to 3, we identify additional stepping-stones and use graph-theory to quantify the relative importance of identified nodes, stepping-stones and corridors for overall landscape connectivity. We illustrate the framework using data from the white-lipped peccary *Tayassu pecari* as an umbrella species within Belize, where a currently existing corridor network has previously been suggested based on expert opinion (Meerman 2000; Petracca 2010; Wildtracks 2013).
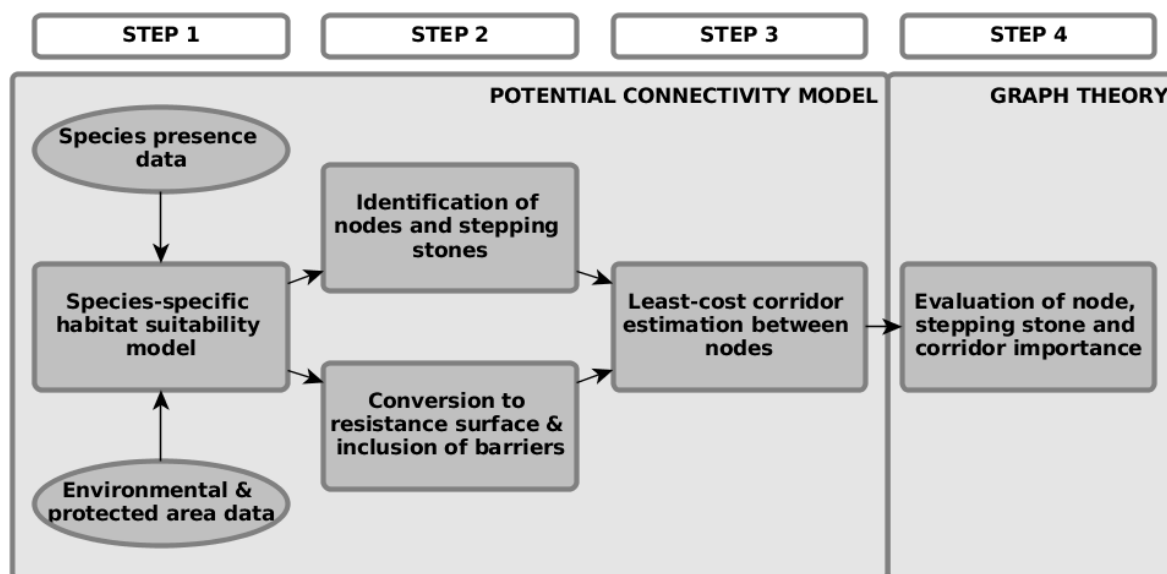

Figure 1: Illustration of analysis framework: the combination of a Potential Connectivity Model, evaluated using a graph-theoretic approach.

2 Step 1: Habitat suitability

We used MaxEnt 3.3.3k (Phillips et al. 2006) for estimating habitat suitability, MaxEnt is open-source and freely available, and is a commonly used and well-tested species distribution modelling tool (Franklin, 2010). It needs presence-only points and environmental variables as inputs, and compares the environmental situation at presence locations to that at a large number of background locations. MaxEnt allows for customised number and location of background points.

2.1 Presence and background points selection

We obtained 432 peccary observations from camera trap surveys, targeted monitoring and opportunistic sightings, partially originating from a national database (BERDS 2005), partially from camera trapping grids by R. Foster and B. Harmsen (Panthera Belize) and by M. Kelly (Virginia Tech), and partially from transect monitoring and camera trapping grids by Ya'axché Conservation Trust. Only points with a location error of 1000 m or less were retained for further analysis. The data contained spatial and temporal clusters that arose from survey or monitoring grids. To avoid issues with temporal autocorrelation, we removed observations recorded at different times at the exact same location (most of these locations concerned consecutive records from camera trap surveys). Since this approach essentially results in snapshots of presence in different time periods, we reviewed the land use change at the presence localities to check for changes that would render older observations invalid at this point in time. Based on our own additional field observations and on Cherrington et al. (2010), we concluded that the landscape at the occurrence points experienced little change over the time span on either side of the time stamp of the landscape data (i.e. 2011). After removing temporal autocorrelation, 149 presence points remained. To remove spatial autocorrelation (clustered observations within monitoring or camera trap grids), we used

Ward's cluster analysis method (implemented as `ward.D2` in the standard `stats::hclust` function – R Development Core Team 2015) to identify spatial clusters. We set k=75 clusters, which we considered the fairest trade-off between a) the best representation of the range of environmental conditions in all known presence locations and b) the lowest level of spatial clustering. From each cluster we retained only one observation that was chosen at random, and used these as input for MaxEnt.

We also expected a strong bias in sampling effort (e.g. more areas are sampled closer to roads or populated areas). To factor out this bias, we calculated a kernel density estimate of sampling effort across the country and rescaled this estimate to values between 0 and 1 by dividing each grid cell by the sum of all cells. The result was used as a probability surface to select 10,000 background points as input for MaxEnt. This approach has been suggested by Fourcade et al. (2014). For the presence data originating from BERDS, the sampling effort was determined by all "Target Group" observations in the database (Phillips & Dudík 2008). Target group observations are presence records of species that are detected using similar methods and frequency over the same time period as the focal species data was collected. We used observations from Baird's tapir *Tapirus bairdii*, jaguar *Panthera onca*, jaguarundi *Puma jagouaroundi*, margay *Leopardus wiedii*, ocelot *Leopardus pardalis*, puma *Puma concolor*, red brocket deer *Mazama americana*, tayra *Eira barbara*, and white-tailed deer *Odocoileus virginianus*. For presence data originating from separate camera trap grids, we determined sampling effort as all camera trap locations from the grid. We used the kernel density estimate instead of the traditional target group approach, because the combined number of target group records and camera trap locations would result in a less than optimal number of background points as suggested by Phillips and Dudík (2008).

2.2 Predictor variable preparation

Twenty-three (23) environmental variables were obtained from different source data sets (Table 1 and 2) and resampled to the same 250m resolution base grid. We added a 24th variable reflecting protected area effectiveness in the PAEF model to incorporate protected areas in the habitat suitability estimate. This variable was based on the combination of (i) the IUCN Protected Area Categories (Dudley 2008) updated for Belize according to Wildtracks (2013) and (ii) the management effectiveness according to a national study by Walker & Walker (2009). The two factors were classified in four categories, and their categories were summed to obtain values from 2 to 8. If a protected area was lacking a rating for one or both of these variables, it received the value 1, and unprotected land received the value 0. Table 3 summarises the construction of the protected area effectiveness variable. After the correlation analysis, our final set of 24 predictors for our habitat suitability modelling was reduced to 20 variables in the PAEF model, and 19 in the CONTROL model (Table 2).

Table 1. Data sources used to produce the predictor variables for the habitat suitability analyses

Data set	Type	Source	Based on	Original resolution
DEM	Raster	Emil Cherrington/CATHALAC	SRTM, ASTER	1 arcsecond (30m)
Ecosystems	Vector	Biodiversity & Environmental Resource Data System of Belize (BERDS)	Meerman & Sabido 2001 + updates	222m
Rivers	Vector	BERDS	Unknown	NA
Roads	Vector	BERDS	Unknown	NA
Fire occurrence	Vector	Fire Information for Resource Management System (FIRMS) by EOSDIS	MODIS	NA
Rainfall	Raster	WorldClim climate data	WorldClim	0.0083333 dec degrees (1000m)
Rainfall	Vector	National Meteorological Service of Belize (Hydromet)	field data	NA

Data set	Type	Source	Based on	Original resolution
Enhanced Vegetation Index	Raster	Institute of Surveying, Remote Sensing and Land Information (IVFL) of the University of Natural Resources and Applied Life Sciences (BOKU), Vienna	MODIS	250m
Protected areas 2014	Vector	Land Information Center (LIC) of the Government of Belize	field data	NA
Soils	Vector	BERDS	Wright 1959	NA
Food plant occurrence	Vector	Global Biodiversity Information Facility	Compiled datasets	NA

Table 2. Predictor variables used for the MaxEnt habitat suitability analyses. Variables in italics were excluded after correlation analysis. (R code for the construction of these variables on request).

Metric type	Description	Metric
Environmental	Food tree occurrence (sum of food plant genera potentially occurring in the grid cell)	foodGenera
	Enhanced vegetation index	mEVI
	Mean annual rainfall	rain_wc
	Soil	soil
Land cover (class-level)	Distance to agriculture	distAgric
	Distance to broadleaf forest	distFor
	Distance to pine forest	*distPif*
	Distance to rivers	distRiv
	Distance to roads	distRoad
	Distance to savanna	distSav
	Distance to shrubland	distShrub
	Distance to urban area	*distUrb*
	Distance to waterbodies	distWat
Land cover (landscape-level)	Proportion of core forest within moving window of 71km^2 (average home range)	cfp
	Ratio of egde over core forest within moving window of 71km^2 (average home range)	ecp
	Frequency of fires	fire
	Landscape heterogeneity within moving window of 71km^2 (average home range)	lanhet
	Land cover type	weco
Political	Protected area efficiency	paef2010
Topographic	Aspect	aspect
	Elevation	*elev*
	Slope	*slope*
	Topgraphic Position Index	tpi
	Terrain Ruggedness Index	tri

Table 3: Conversion table for construction of the protected area effectiveness predictor variable (paef2010) in the PAEF habitat suitability analysis.

IUCN PA Cat.[1]	Mgmt. Effectiveness[2]	Category value	Final protected area effectiveness value
Ia, Ib	Very good	4	
II	Moderate	3	Between 2 and 8 (sum of category values from [1] and [2])
III, IV	Fair	2	
V, VI	Poor	1	
	Either variable unknown		1
	Non-protected area		0

[1] (Wildtracks 2013); [2] (Walker & Walker 2009)

2.3 Model complexity

Recent research has suggested that species-specific tuning of MaxEnt models can improve the models' performance (Radosavljevic and Anderson, 2014). We used the package ENMeval (Muscarella et al. 2014) in R (R Development Core Team 2015) to determine the optimal MaxEnt settings for our PAEF and CONTROL models. ENMeval evaluates the performance of a set of models with different feature classes and regularisation multipliers by calculating AUC and modified AICc values among other evaluators of model fit and accuracy (Warren and Seifert, 2011; Muscarella et al., 2014). Feature classes represent transformations of the predictor variables (linear, quadratic, hinge, product and threshold) that allow for more complex fits to the observed data, while the regularisation multiplier determines the penalty of including predictors that provide little 'gain' to the model, thereby reducing chances of overfitting of the model.

We tested the full range of feature classes and varied the regularisation multiplier between 1 and 50, with increments of 0.5. The PAEF model with the lowest AICc used linear and quadratic features and a regularisation multiplier of 6.5. The best CONTROL model used only linear features and a regularisation multiplier of 8. We then ran 100 MaxEnt replicates with the identified settings from within R using the package dismo (Hijmans et al. 2015), and used the average predictions as the final habitat suitability models (CONTROL and PAEF).

2.4 Results

PAEF – The protected area effectiveness variable ranked second in contribution to the PAEF model with 21% (after the Enhanced Vegetation Index – Table 4). A slightly broader range of variables contributed more evenly to the model than in the CONTROL model (see Table 5). The habitat suitability was influenced by the presence of protected areas: unprotected areas became less suitable under the PAEF model as compared to the CONTROL, while any level of protection effectiveness generally increased the habitat suitability, but only the highest level of effectiveness did so considerably (Figure 2 &3).

CONTROL - A set of three variables were the main contributors to this model: Enhanced Vegetation Index, the proportion of core forest within an average sized home range and the terrain ruggedness (Table 5). Land use/land cover class also contributes, but much less.
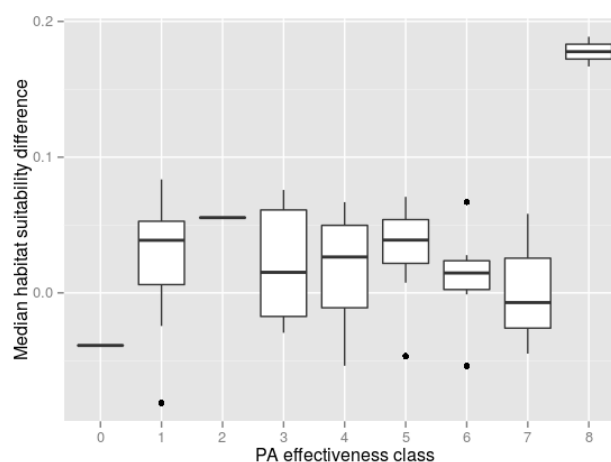

Figure 2: The median difference in habitat suitability among all pixels within each protected area.

The change in the top variable contributions between the CONTROL and PAEF habitat suitability models indicated that PAs mainly contribute undisturbed, high-productive core forests. Nevertheless, our results clearly showed that PA effectiveness itself is an important predictor of habitat suitability for peccaries.

Table 4. Variable contribution to the PAEF model

PAEF	
Variable	**Percent contribution**
mEVI250	28.6
paef2010250	21.0
cfp250	15.8
tri250	15.4
weco250	7.3
tpi250	4.9
lanhet250	2.3
distWat250	2.1
distAgric250	0.6
distFor250	0.5
foodGenera250	0.4
distSav250	0.3
distShrub250	0.3
distRiv250	0.2
distRoad250	0.1
fire250	0.1
aspect250	0
rain_wc250	0
soils250	0

Table 5. Variable contribution to the CONTROL model

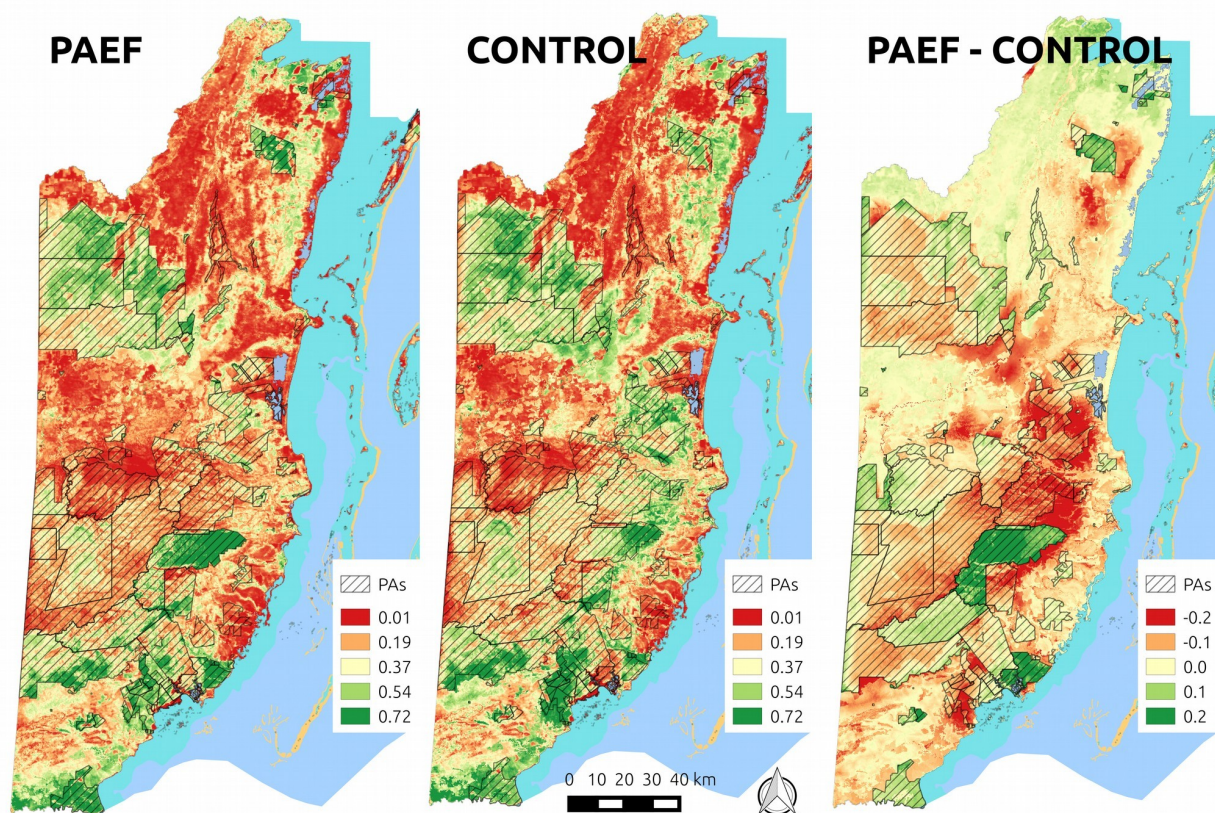| CONTROL	
Variable	**Percent contribution**
mEVI250	38.1
paef2010250	---
cfp250	31.5
tri250	20.4
weco250	4.9
distWat250	1.5
lanhet250	0.9
distShrub250	0.8
distSav250	0.5
distRiv250	0.5
distFor250	0.4
distAgric250	0.2
foodGenera250	0.1
distRoad250	0.1
tpi250	0.1
rain_wc250	0
soils250	0
aspect250	0
fire250	0

Figure 3. Logistic habitat suitability for (a) the PAEF and (b) the CONTROL model. Higher values indicate higher suitability. Panel c shows the subtraction of the CONTROL from the PAEF model, with positive values indicating higher suitability in the PAEF model and negative values indicating higher suitability in the CONTROL model. (PAs = protected areas)

To test model accuracy, we compiled a set of 143 independently gathered presence locations for white-lipped peccaries in southern Belize, originating from satellite collar data and sightings of animals and tracks (Hofman et al., 2016; B. Arevalo, pers. comm.). We visually investigated the fit of the validation points over the habitat suitability prediction (Figure 4). To evaluate the fit quantitatively, we rotated and shifted (up to 3 km) the validation points 1000 times in random directions, and compared the average habitat suitability of the original points to the average habitat suitability of the permuted points, similar to Mueller et al. (2008). Only 50 out of 1000 permuted validation sets had a higher average habitat suitability than the original validation set (p = 0.05).
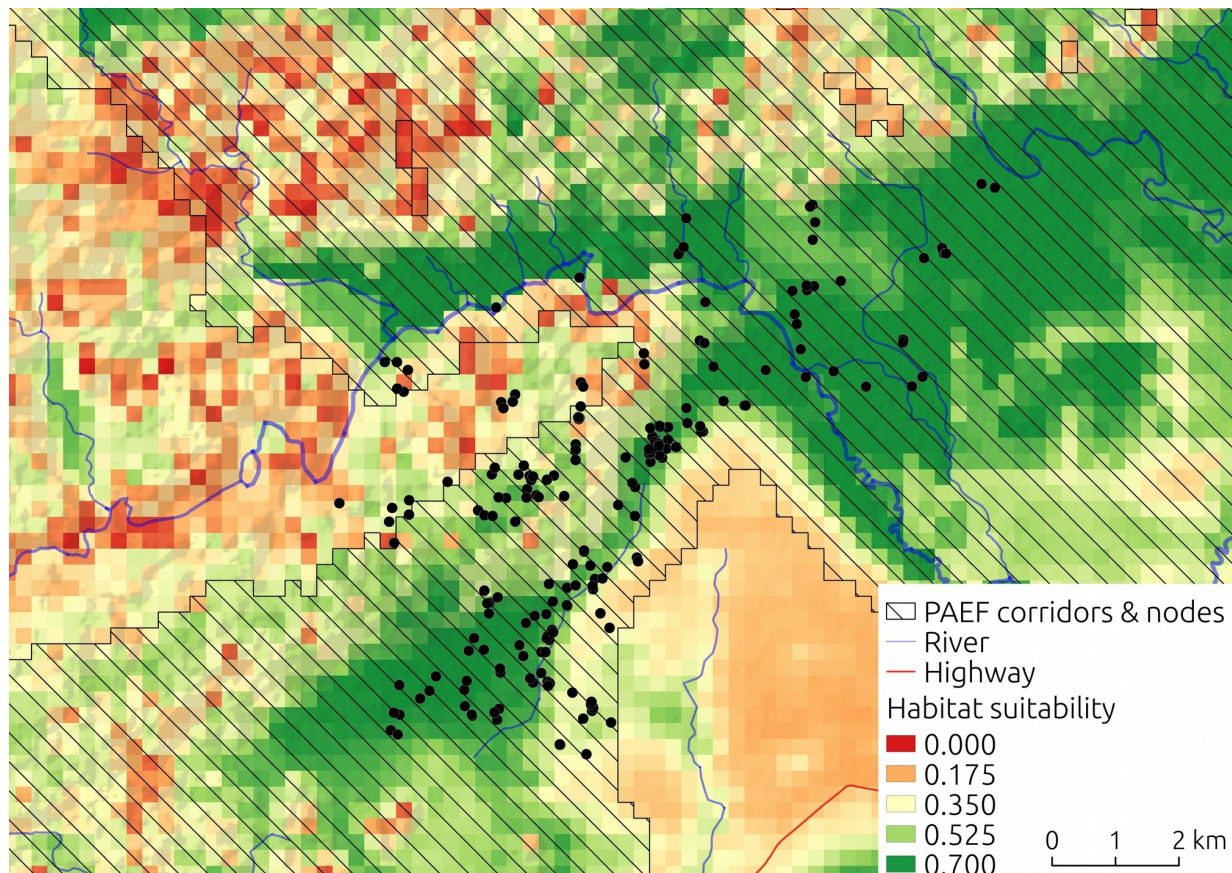
Figure 4. PAEF habitat suitability model fit with independent relocation data and corridor outlines.

3   Step 2: Node delineation and landscape resistance

3.1   High suitability node delineation

To identify nodes based on the PAEF habitat suitability surface, we followed the approach used in Gnarly (Shirk & McRae 2013), whereby we smoothed the surface by calculating the mean suitability across a moving window equal in size to the smallest reported annual white-lipped peccary home range (21 km^2 – Fragoso 1998, 2004) for each grid cell, and considered all grid cells with a smoothed suitability higher than 0.5 to be suitable. Note that this threshold is much more stringent than the commonly recommended threshold for MaxEnt (the maximized sum of specificity and sensitivity – 0.3 in this case) in order to select only the highest-quality habitat. Cells with an original suitability value below 0.5 were removed, as were cells representing highways and major roads, since they constitute a division in any contiguous group of high-suitability grid cells. Of the resulting suitable areas, those smaller than 21 km^2 were removed and the remaining areas were considered suitable nodes.

3.2   Protected area node delineation

In addition to the nodes for the PAEF model, we compiled a set of nodes for the CONTROL model. Since our aim was to account for protection status but the protected area effectiveness was not taken into account in the CONTROL habitat suitability model, these nodes needed to be based on the actual protected areas in the study region. The set of PA nodes was formed by the outlines of all terrestrial protected areas, excluding non-gazetted and most private reserves, to resemble the set of features used for the delineation of the current set of corridors used in the country. Adjacent areas were grouped into a single node, and nodes smaller than the average known home range size (i.e. 71 km^2, see Fragoso 1998, 2004; Carrillo et al. 2002; Keuroghlian et al. 2004, 2014; Reyna-Hurtado et al. 2009; de Almeida Jácomo et al. 2013) were removed, yielding 8 PA nodes (PA1 – PA8; see Figure 5).

3.3 Resistance surface and movement barriers

We calculated the resistance surface by converting the habitat suitability estimates using the negative exponential equation outlined in Mateo-Sánchez et al. (2014):

$$\left(\frac{R'}{R'min}\right)^2$$

where R' is (1 – *habitat suitability*) in a given pixel and $R'min$ is the minimum value of (1 – *habitat suitability*) across all pixels in the study area.

Few absolute barriers exist for white-lipped peccaries within our study area. The species is known to swim across 2 km wide rivers (Fragoso 2015), and according to local residents, herds can occasionally be seen crossing roads. Nonetheless, we assumed a reasonably high resistance for highways and major roads throughout study area, and set their respective resistance values to 95% and 85% of the maximum value in the resistance surface.

4 Step 3: Corridor estimation using landscape resistance

The resistance surface resulting from the PAEF habitat suitability was used to calculate the corridors between high-suitability nodes, while the resistance surface resulting from the CONTROL habitat suitability was used to calculate the corridors between the PA nodes. Corridors were estimated with Linkage Mapper toolbox version 1.0.9 (McRae & Kavanagh 2011) in ArcGIS Desktop 10.3 (ESRI 2015), and their delineation was determined by including all pixels that had a cost-distance value that was maximum 25% higher than the cost-distance value of the respective least-cost path between the nodes.

The currently proposed corridors were largely contained within the CONTROL corridors between PA nodes, which were generally broader and followed similar trajectories (Figure 5a & b). Additional corridor routes between PA5 and PA6, PA6 and PA7, and PA6 and PA8 appeared in the CONTROL model. The corridor configuration in the PAEF model changed as compared to the current and CONTROL scenarios (Figure 5c). The northern corridor route between HS2 and HS4 was displaced eastwards. Nodes PA3 and PA7 did not show up among the habitat suitability-based nodes, and thus the corridors connecting these were not present in the PAEF model. Conversely, the western corridors connecting nodes HS3 and HS5 only appeared in the PAEF scenario.
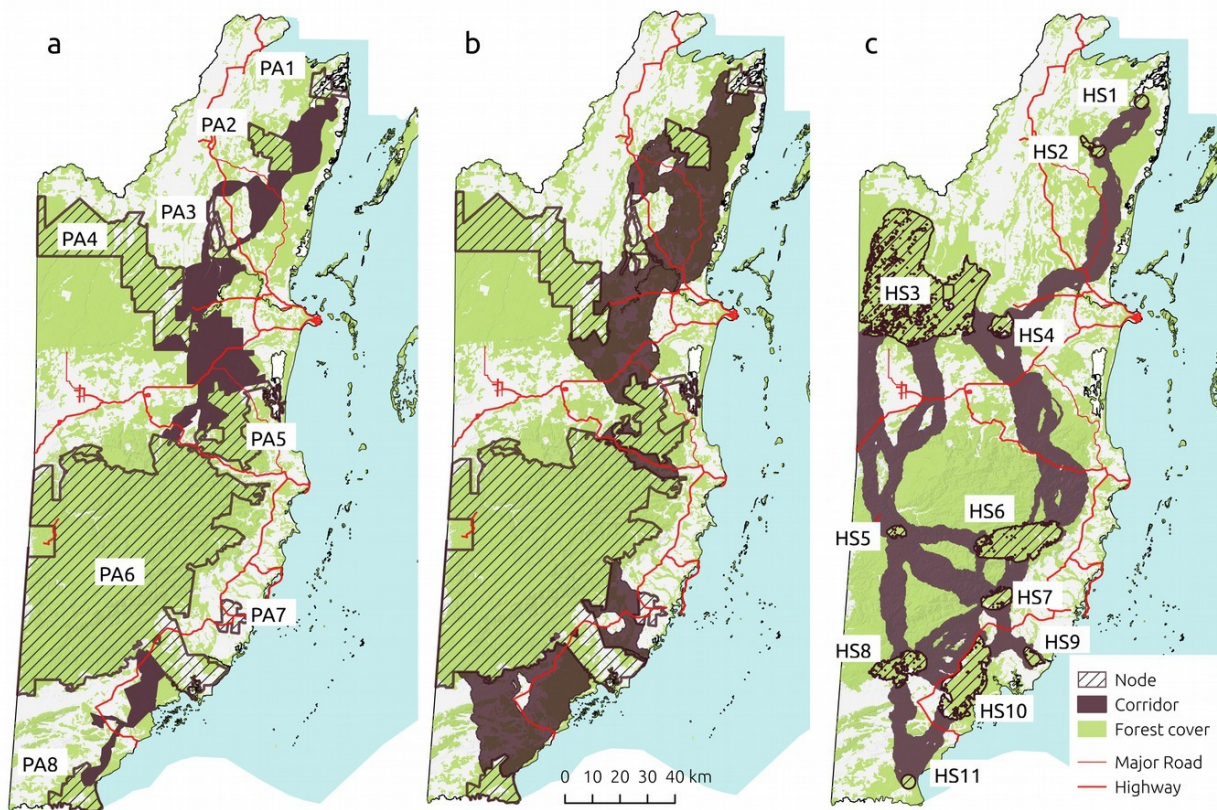
Figure 5. Comparison of (a) the currently proposed corridors between protected areas (PA1-PA8), (b) the corridors estimated between protected areas using a resistance surface based on the CONTROL habitat suitability model and (c) the corridors estimated between high-suitability nodes (HS1-HS11) using a resistance surface based on the PAEF habitat suitability model.

The frequency distribution of suitability values in the PAEF corridors was more centred around mid to high suitability than in the current corridors, and as compared to the suitability across the entire study area (Figure 6). The portion of the PAEF corridors that falls within the protected area nodes used for the current corridors was excluded for the calculation of Figure 6c.
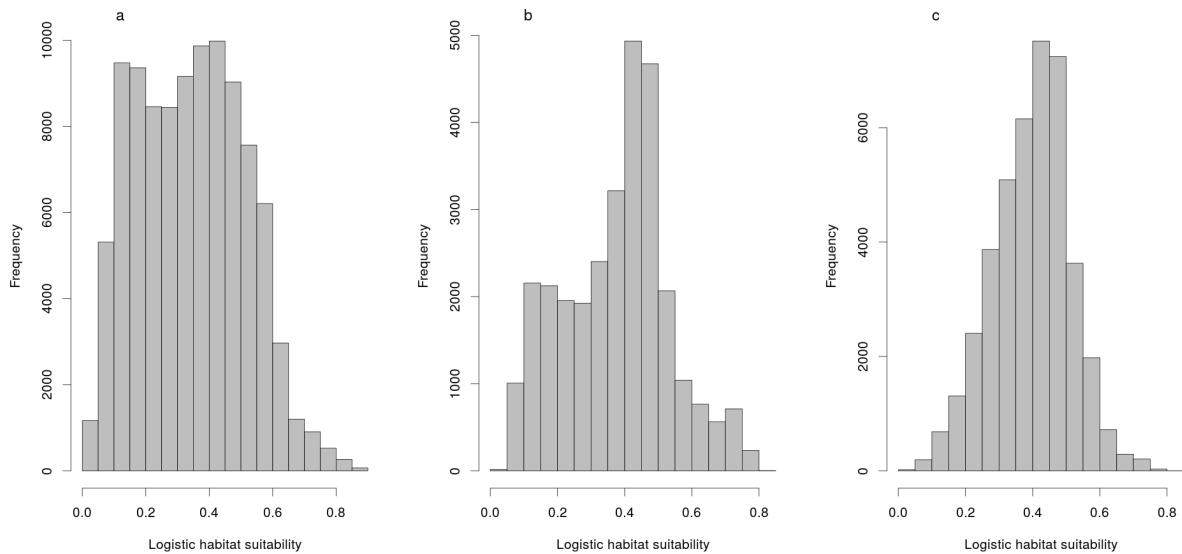
Figure 6: Distribution of habitat suitability values in (a) the whole study area, (b) the current corridors and (c) the corridors resulting from the PAEF model. All distributions differ significantly from each other (Kolmogorov-Smirnov; p < 0.001).

5 Step 4: Evaluating the network

To evaluate the importance of predicted core areas and corridors, we additionally identified potential stepping-stones in and around the corridors. We then used Conefor 2.6 (Saura & Torné 2009; Bodin & Saura 2010) to evaluate importance of all nodes, stepping-stones, and corridors. Conefor 2.6 can quantify overall landscape connectivity using a single graph-theoretic index (Probability of Connectivity). To determine the importance of nodes and stepping-stones in the network, each of them is removed one at a time, and the relative changes in three fractions of the Probability of Connectivity are recorded: dPC_{intra} represents the removed element's contribution in habitat area and quality, dPC_{flux} represents its contribution in the flux of dispersing organisms, and $dPC_{connector}$ the extent to which it acts as a connecting element (see Bodin and Saura, 2010). We evaluated the importance of each node and stepping-stone for overall network connectivity by examining at its $dPC_{connector}$ and dPC_{intra} values.

To evaluate the importance of each corridor in the network, we examined the Conefor 2.6 links between patches. These links indicate which patches are actually connected (i.e. form a 'component' in the network) based on a species-specific dispersal distance, set by the user. This distance is converted to a direct dispersal probability among patches based on an exponential dispersal kernel (Saura & Torné 2009, 2012). The dispersal kernel is a decreasing negative exponential function of distance (e.g. Bunn et al., 2000; Urban and Keitt, 2001; Saura and Pascual-Hortal, 2007) that matches with the probability-distance values specified by the user, as follows:

$$p_{ij} = e^{-k \cdot d_{ij}}$$

where d_{ij} is the distance between nodes i and j, p_{ij} is the probability of direct dispersal between nodes i and j (i.e. the probability that an organism is able to disperse a distance equal to or larger than the distance between those nodes), and k is a constant set to make the function match to the probability-distance values specified by the user. We attributed a direct dispersal probability of 0.01 to a dispersal distance of 9495 m, which is the diameter of a circular average home range for white-lipped peccaries (based on 71 km^2, see Fragoso 1998, 2004; Carrillo et al. 2002; Keuroghlian et al. 2004, 2014; Reyna-Hurtado et al. 2009; de Almeida Jácomo et al. 2013), resulting the dispersal kernel in Figure 7. For use within the Conefor 2.6 software, we converted the Maximum dispersal distance from Euclidean distance to cost-distance by calculating the average ratio of cost-based over Euclidean distance for all least-cost paths between each pair of nodes and/or stepping-stones.
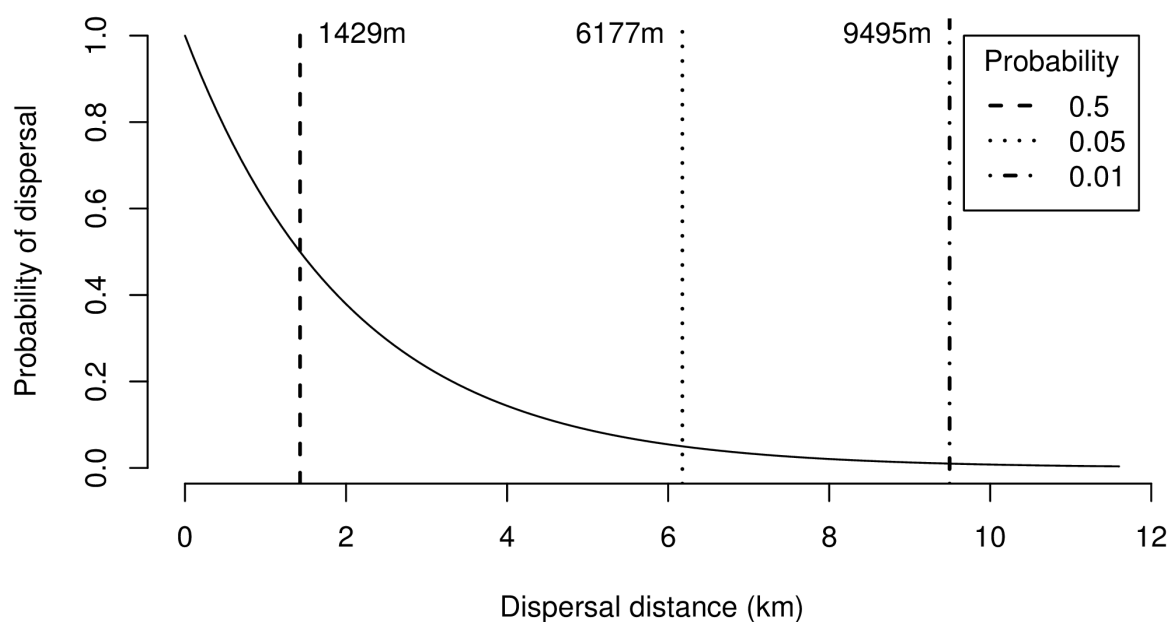
Figure 7. Dispersal kernel used in the PAEF model

To evaluate the effect of this chosen dispersal distance on the identification of important nodes/stepping-stones in this study, we did a sensitivity analysis by varying the maximum dispersal distance and evaluating the effect on $dPC_{connector}$. To generate a broad range of distance values, we used each of the distance values in Table 6 as a median (p = 0.05) and maximum dispersal distance (at p = 0.05 and p = 0.01) in subsequent Conefor runs (each using the corresponding dispersal kernel). Hence we ended up with a total of 21 dispersal kernels (three for each distance value). However, because the first two distance values were too small to be considered a maximum dispersal distance for our species, we only used them as a median (p = 0.5), reducing the number of kernels to 17.

Table 6. The set of distance values used for the sensitivity analysis of the maximum dispersal distance. With the exception of the first two values, each value was used to calculate 3 dispersal kernels. First the value was used as the median (p = 0.5) dispersal distance, then as maximum dispersal distance at p = 0.05, and lastly as the maximum dispersal distance at p = 0.01.

Distance (m)	Used as median	Used as maximum	Source
589	Yes	No	Median dispersal distance following Bowman et al. (2012)
1000	Yes	No	Low guesstimate
3366	Yes	Yes	Maximum dispersal distance following Bowman et al. (2012)
3788	Yes	Yes	Maximum daily movement distance in southern Belize (Hofman et al. 2016)
4748	Yes	Yes	Radius of average annual home range in the literature (see text)
9495	Yes	Yes	Diameter of average annual home range in the literature (see text)
10000	Yes	Yes	High guesstimate

We estimated the maximum dispersal distance for white-lipped peccaries following Bowman et al. (2012) to be 3,366 m, which was lower than the maximum daily movement distance observed in southern Belize (Hofman et al. 2016) and has been reported as a distance covered in one hour in Mexico (Reyna-Hurtado et al. 2009). Hence, we used this estimate as our lowest maximum dispersal distance (see Figure 8). To obtain our highest maximum dispersal distance, we calculated the dispersal kernel with 10,000 m as the median dispersal distance (which sets the maximum dispersal distance at p = 0.01 to 66,439 m – see Figure 9).
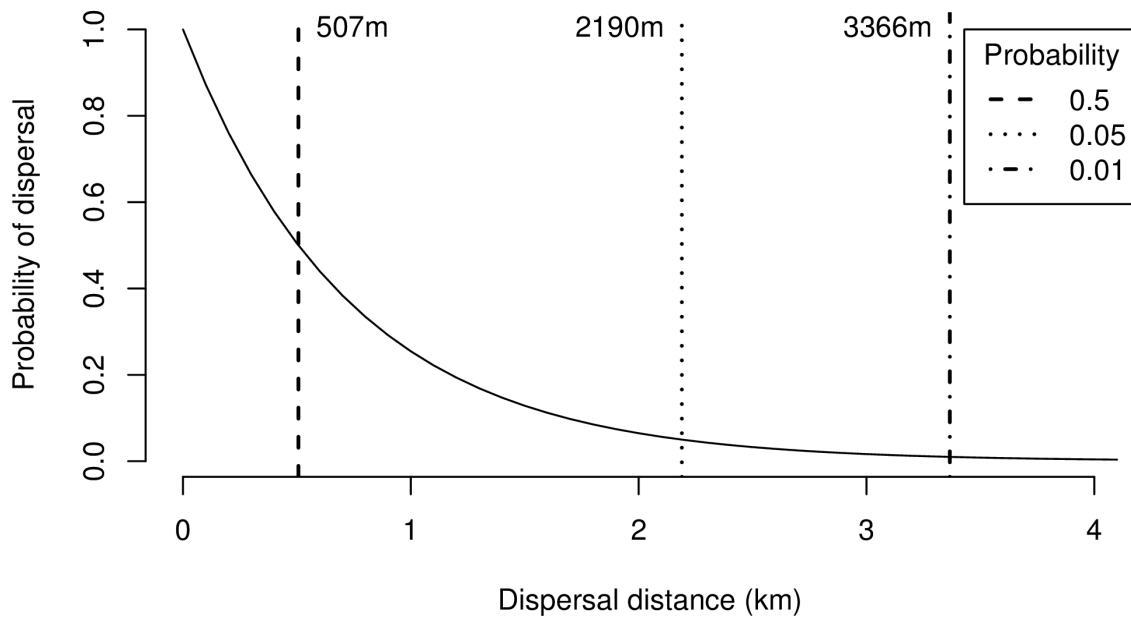
Figure 8. The dispersal kernel corresponding to the lowest maximum dispersal distance used in the sensitivity analysis.
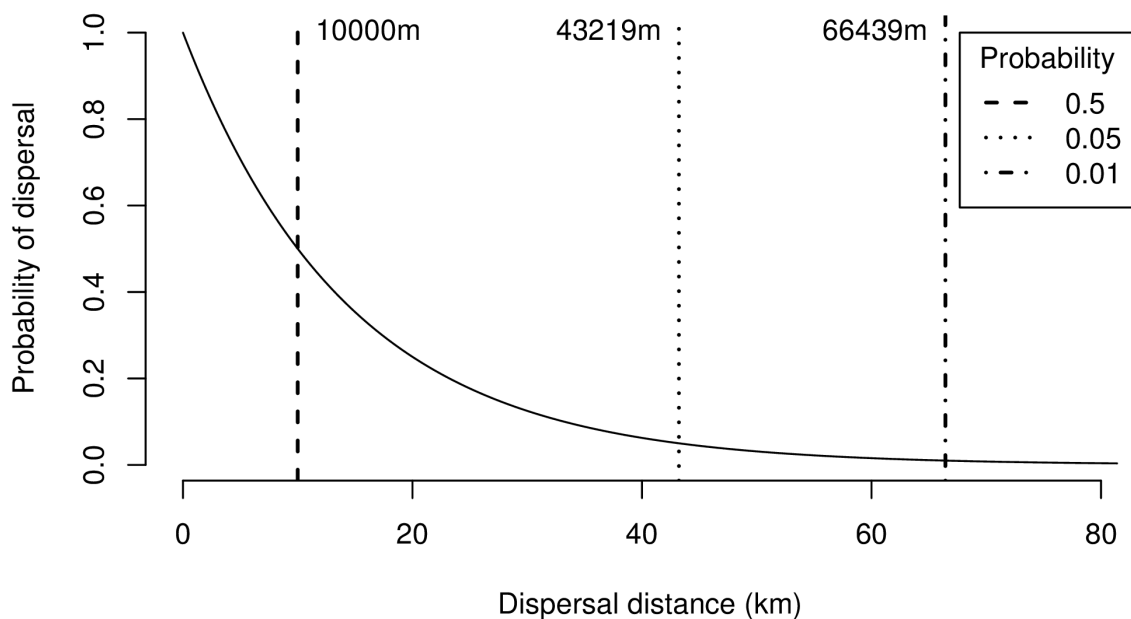

Figure 9. The dispersal kernel corresponding to the highest maximum dispersal distance used in the sensitivity analysis.

We then examined the effect on the $dPC_{connector}$ of all nodes and stepping-stones (similar to Loro et al. 2015). We found that the top 10 important nodes or stepping-stones remained remarkably stable across distances. The top 4 important source patches in our model, also occurred in the top ten of all other dispersal distances (Table 7).

Table 7. Node and stepping-stone IDs ranked according to decreasing dPCconnector values across the full range of maximum dispersal distances evaluated.

Distance value*	589	589	1000	1000	3366	3788	589	4748	3366	3788	1000	4748	**9495**	10000	9495	10000	3366	3788	4748	9495	10000
at p =	0.01	0.05	0.01	0.05	0.01	0.01	0.5	0.01	0.05	0.05	0.01	0.05	**0.01**	0.01	0.05	0.05	0.5	0.5	0.5	0.5	0.5
Maximum dispersal distance (at p = 0.01)	589	905	1000	1537	3366	3788	3913	4748	5174	5823	6644	7299	**9495**	10000	14596	15372	22363	25167	31545	63083	66439
Rank 1	NA	NA	NA	NA	25	35	35	35	35	35	35	35	**35**	35	4	4	4	4	33	33	33
Rank 2	NA	NA	NA	NA	35	25	25	25	25	33	33	33	**4**	4	33	33	33	33	4	4	22
Rank 3	NA	NA	NA	NA	17	17	17	33	33	25	4	4	**33**	33	35	35	35	35	35	22	4
Rank 4	NA	NA	NA	NA	30	30	30	17	4	4	25	25	**19**	19	19	19	19	19	19	35	35
Rank 5	NA	NA	NA	NA	20	20	20	30	30	30	19	19	**25**	25	7	7	7	7	32	19	19
Rank 6	NA	NA	NA	NA	19	33	33	20	17	19	30	30	**3**	3	3	3	8	8	9	32	32
Rank 7	NA	NA	NA	NA	33	19	19	19	20	17	17	17	**37**	37	37	37	32	32	8	9	9
Rank 8	NA	NA	NA	NA	22	22	22	4	19	20	20	20	**7**	7	8	8	9	9	7	8	26
Rank 9	NA	NA	NA	NA	3	4	4	22	3	3	3	3	**30**	30	25	17	3	3	17	26	8
Rank 10	NA	NA	NA	NA	4	3	3	3	22	22	39	37	**17**	17	17	25	37	17	3	16	16

* From Table 6

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Appendix B

Supplementary material to Chapter 3

Hourly variation in movement distance of white-lipped peccaries

Methods. From studies in Costa Rica, Peru and Guatemala, white-lipped peccaries known to be diurnal animals with peak activity during mid-morning and mid-afternoon (Carrillo et al. 2002; Tobler et al. 2009; Moreira-Ramrez et al. 2015). We expected that white-lipped peccary activity patterns in Belize are similar to those observed elsewhere. We calculated step characteristics using the rhr package and compared movement rates (speed and distance) for different time periods during the day, using only time lags shorter than six hours.

Results. Speed and distance during different time periods during the day did not show the expected pattern of increased mobility during mid-morning and mid-afternoon activity peaks. However, no steps shorter than 6 hrs were available for points with fix time of 9 am or 15 pm, while between two and seven were available for low-activity periods (Table B.1). This suggests that during the most active periods no successful fixes were obtained, and thus no information on speed or distance is available for these critical times of the day. Therefore, we could not detect any significant signs of increased mobility during the expected activity peaks.

Time of day (h)	n	Max. speed (km/h)	Mean speed (km/h)	SD speed (km/h)	Median speed (km/h)	Max. distance (m)	Mean distance (m)	SD distance (m)	Median distance (m)
00:00:00	2	0.08	0.06	0.03	0.06	224.97	172.19	74.64	172.19
03:00:00	7	0.27	0.06	0.09	0.03	802.11	209.43	279.31	101.76
06:00:00	3	0.09	0.05	0.04	0.03	277.85	138	123.03	89.72
09:00:00	0	-	-	-	-	-	-	-	-
12:00:00	1	0.07	0.07	NA	0.07	224.23	224.23	NA	224.23
15:00:00	0	-	-	-	-	-	-	-	-
18:00:00	1	0.04	0.04	NA	0.04	119.49	119.49	NA	119.49
21:00:00	3	0.09	0.04	0.05	0.03	552.09	218.36	291.55	89.76

TABLE B.1: Diurnal variation in step length and speed. Time of day reflects the fix schedule programmed in the GPS-collar. Only steps with Δt < 6 hours were included.

Home range analysis with rhr

This is an automatically generated report summarizing from a range analysis with rhr started: [2015-09-28 11:50:40]

Site Fidelity

Method was not requested

Time to Statistical Independence

Method was not requested

Minimum Convex Polygon

Parameter values used

Parameter	Value
levels	50, 95, 99, 100

Results for Animal1
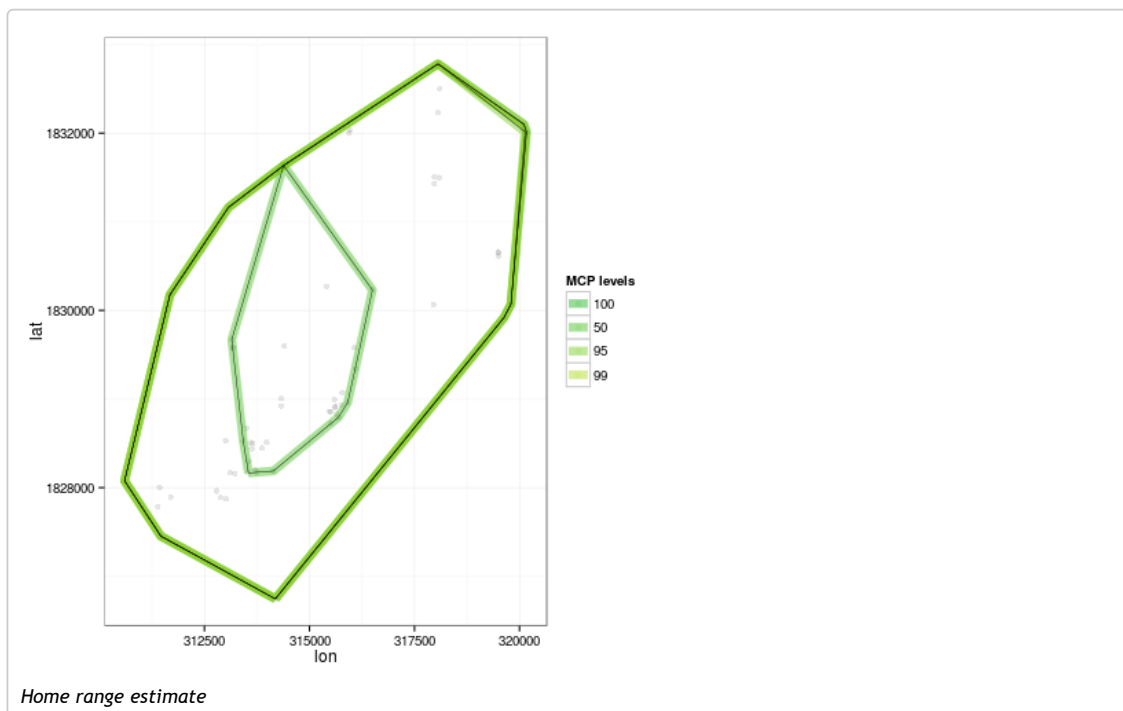
Home range estimate

Home Range Area

Level	Area
50	7.134122
95	33.476011
99	33.582523
100	33.591851

Home range areas

Kernel Density Estimation

Parameter values used

Parameter	Value
levels	50, 95, 99, 100
trast	RasterLayer (nrow:100; ncol:157; res:146.363,146.363)
h	href
userh	

Results for Animal1
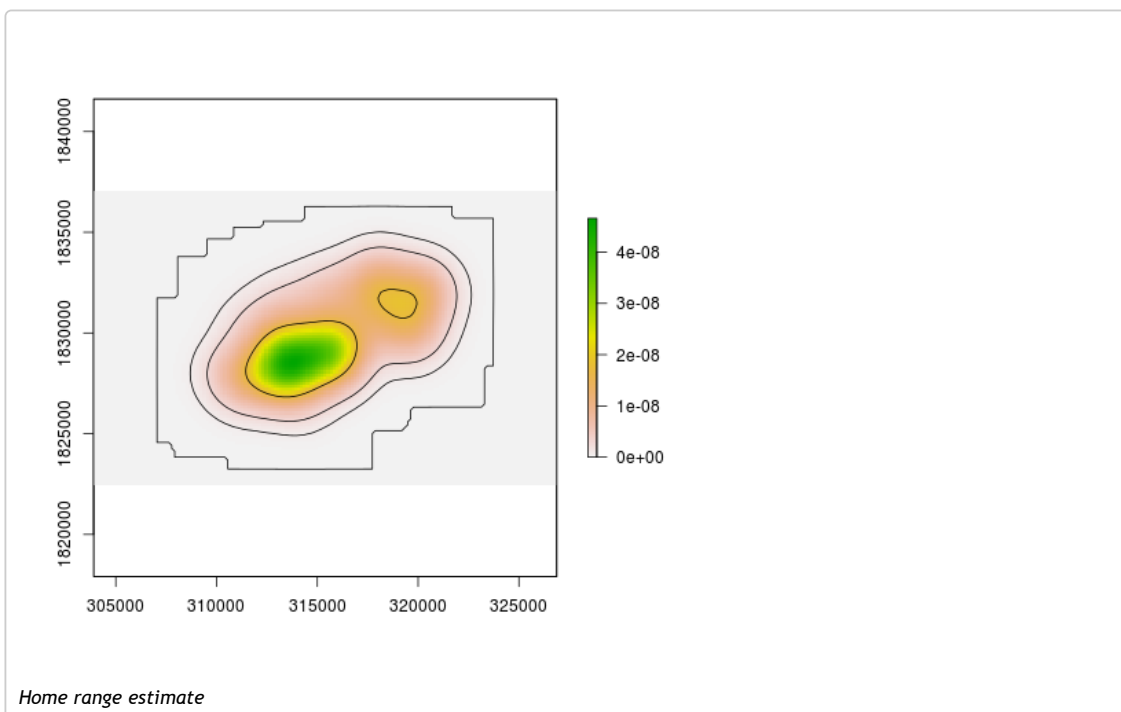
Home range estimate

Tuning parameter (bandwidth)

The used value for bandwidth (h) is: 1059.24, 1059.24

Home Range Area

Level	Area
50	17.67451
95	69.38215
99	96.70847
100	183.06389

Home range areas

Home Range Core Area
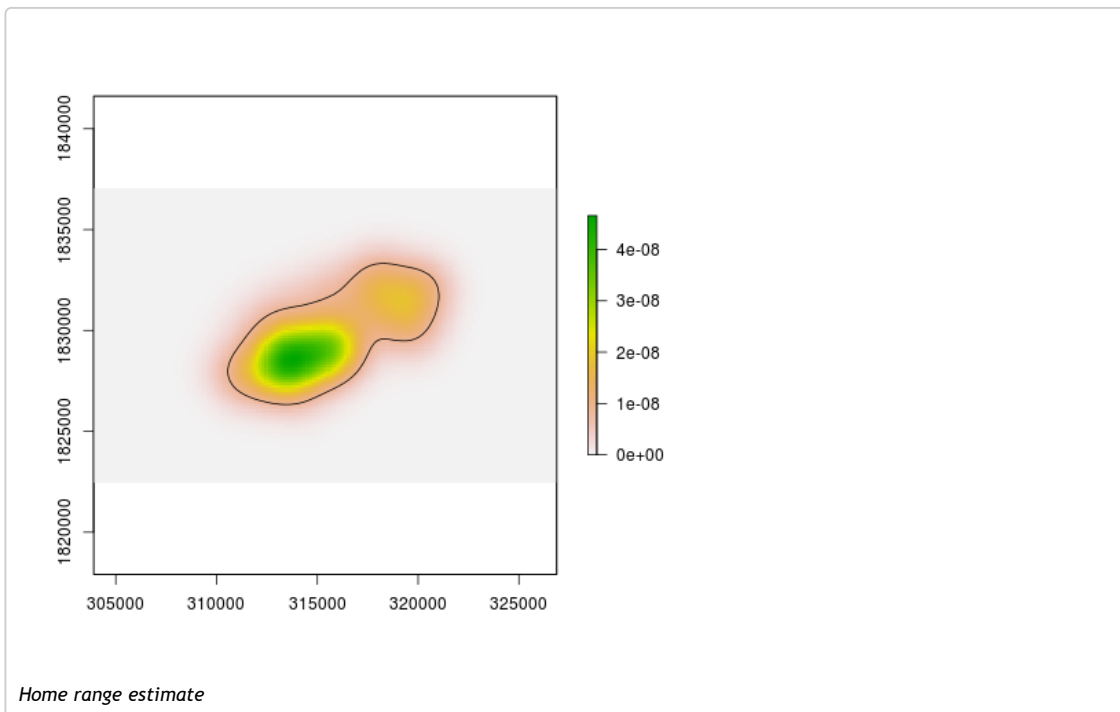
Home range estimate

Level	Area
79.79618	41.00779

Area of home range core area

Local Convex Hull

Method was not requested

Brownian Bridges

Method was not requested

Unimodal bivariate Normal

Method was not requested

Bimodal bivariate Normal

Method was not requested

Session info

For the sake of reproducibility, you should always include your session info. This shows which version of R and different packages you were using.

```
## R version 3.2.2 (2015-08-14)
## Platform: x86_64-pc-linux-gnu (64-bit)
## Running under: Ubuntu 14.04.3 LTS
##
## locale:
##  [1] LC_CTYPE=en_GB.UTF-8       LC_NUMERIC=C
##  [3] LC_TIME=en_US.UTF-8        LC_COLLATE=en_GB.UTF-8
##  [5] LC_MONETARY=en_US.UTF-8    LC_MESSAGES=en_GB.UTF-8
##  [7] LC_PAPER=en_US.UTF-8       LC_NAME=C
##  [9] LC_ADDRESS=C               LC_TELEPHONE=C
## [11] LC_MEASUREMENT=en_US.UTF-8 LC_IDENTIFICATION=C
##
## attached base packages:
## [1] grid      stats     graphics  grDevices utils     datasets  methods
## [8] base
##
## other attached packages:
##  [1] xtable_1.7-4        markdown_0.7.7      knitr_1.10.5
##  [4] lubridate_1.3.3     brew_1.0-6          shinyBS_0.61
##  [7] shiny_0.12.1        rhr_1.2.002         Rcpp_0.12.0
## [10] dplyr_0.4.2         adehabitatHR_0.4.14 adehabitatLT_0.3.20
## [13] CircStats_0.2-4     boot_1.3-17         MASS_7.3-44
## [16] adehabitatMA_0.3.10 ade4_1.7-2          deldir_0.1-9
## [19] rJava_0.9-6         pvclust_1.3-2       SDMTools_1.1-221
## [22] sparr_0.3-6         spatstat_1.41-1     usdm_1.1-12
## [25] Hmisc_3.15-0        ggplot2_1.0.1       Formula_1.2-1
## [28] survival_2.38-3     lattice_0.20-33     maptools_0.8-36
## [31] rgdal_1.0-4         dismo_1.0-12        trajectories_0.1-3
## [34] raster_2.4-15       sp_1.1-1            ctmm_0.2.8
##
## loaded via a namespace (and not attached):
##  [1] jsonlite_0.9.16    splines_3.2.2      R.utils_2.0.2
##  [4] assertthat_0.1     highr_0.5          latticeExtra_0.6-26
##  [7] digest_0.6.8       RColorBrewer_1.1-2 polyclip_1.3-0
## [10] colorspace_1.2-6   htmltools_0.2.6    httpuv_1.3.2
## [13] Matrix_1.2-2       R.oo_1.19.0        plyr_1.8.3
## [16] scales_0.2.5       intervals_0.15.0   tensor_1.5
## [19] mgcv_1.8-7         rstudio_0.98.1087  nnet_7.3-11
## [22] proto_0.3-10       magrittr_1.5       mime_0.3
## [25] evaluate_0.7       memoise_0.2.1      R.methodsS3_1.7.0
## [28] nlme_3.1-120       xts_0.9-7          foreign_0.8-66
## [31] tools_3.2.2        formatR_1.2        stringr_1.0.0
## [34] munsell_0.4.2      cluster_2.0.3      spacetime_1.1-4
## [37] rstudioapi_0.3.1   goftest_1.0-2      labeling_0.3
## [40] gtable_0.1.2       abind_1.4-3        DBI_0.3.1
## [43] reshape2_1.4.1     R6_2.0.1           zoo_1.7-12
```

```
## [46] rgeos_0.3-11        KernSmooth_2.23-15  stringi_0.5-5
## [49] parallel_3.2.2      rpart_4.1-10        acepack_1.3-3.3
## [52] rgl_0.95.1201
```

Appendix C

Supplementary material to Chapter 4

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PERFORMANCE OF SATELLITE COLLARS IN WILDLIFE RESEARCH: WHAT DOES THE EVIDENCE SHOW?

A survey by Maarten P.G. Hofman[1,2], Matthew W. Hayward[2], Julia P.G. Jones[2] and Niko Balkenhol[1]
[1] Dept. of Wildlife Sciences, University of Göttingen, Germany
[2] School of Environment, Natural Resources and Geography, Bangor University, Wales, UK

Dear colleague,

Telemetry collars equipped with GPS functionality are a very attractive option in wildlife research, because they allow for tracking of movement and activity on a very fine temporal and spatial scale. However, one limitation of this technology is that GPS fix success rates and positional errors are highly variable, and are affected to unknown extent by collar orientation, canopy cover, terrain ruggedness, etc. These confounding factors often cause bias in the locations obtained, and in some cases might prevent the device from obtaining sufficient data to answer research questions, forcing to change or abandon project objectives. This has led some authors to urge for caution when opting for satellite collars. Unfortunately, most unsuccessful studies do not get published, their analysis not completed and/or their results discarded. The literature therefore is biased towards successful applications of satellite collars, giving the general impression that the technique is useful under most circumstances. With this survey, we want to give the chance to such unsuccessful studies to still contribute to the field of wildlife research. We want to tap into both unsuccessful and successful research projects using satellite collars to see if we can find out whether there is an identifiable set of circumstances under which the technique should be a safe bet to yield useful data and/or under which circumstances it might be advisable to look for alternative methods to answer the questions at hand.

The survey will likely require you to dig up data and/or publications and perform some calculations, but we hope that this will not discourage you from contributing to the assessment of satellite collars as a wildlife research technique. Filling out the survey will take anywhere between 20 minutes and half a day, depending on the size of your dataset and how close you have your data at hand.

The survey will be closed by May 31th, 2016.

If you wish so, you will receive a summary of the results when the study is finished. In this case, please indicate so in the form on the next page.

We thank you for taking this survey, and hope you will bear with us as we guide you through the questions. Throughout the form, questions marked with an asterix (*) need to be filled out in order for your project to be used in the analyses.

Let's start!

First, we would like to get a minimal amount of background data on our respondents. Remember that we will take into account the preference you have indicated in our online form regarding your personal details to be permanently removed at least 5 months after the end of the study.

Please provide your personal information.
(All personal details will be treated strictly confidential and will only be used for this survey. Note that you can choose not to fill out your personal details, in which case all your deployment data will be treated as strictly anonymous throughout the study.)

Last name		**First name**	

Affiliation

	Yes	No
Would you like to be informed about the results when the study is finished? (If yes, please provide contact details below)	○	○
Can we contact you for further information, if necessary? (If yes, please provide contact details below)	○	○
Would you like to remain anonymous in any acknowledgements for this study?	○	○

Contact details
(Note that you can choose to leave the fields blank. In this case, you will not be informed about the results or contacted for further information about the data you provide.)

Email		**Phone**	

Thank you! This got us started.
Please save this document for later submission. We will now go on to input the deployment data.

We have assumed most studies will have the requested data stored on a project basis. Hence, we have chosen the project as the level of data entry. By clicking the "Add project data" button below, you will be prompted to download a PDF form from the server at the University of Göttingen. Bear in mind that most browsers will not allow you to fill out the form inside the browser. You will need to save it to your local computer and open it with the latest version of your PDF viewer. Our Linux server is clean, safe and well-maintained; you can trust the file for download. The form will allow you to enter all collar deployment information pertaining to one project. If you have conducted more than one project, you will have the opportunity to start adding the data for any additional project(s) at the end of the downloaded form.

Please save this form and press the "Add project data" button to start entering your deployment data.

> Add project data

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PERFORMANCE OF SATELLITE COLLARS IN WILDLIFE RESEARCH: WHAT DOES THE EVIDENCE SHOW?

A survey by Maarten P.G. Hofman[1,2], Matthew W. Hayward[2], Julia P.G. Jones[2] and Niko Balkenhol[1]
[1] Dept. of Wildlife Sciences, University of Göttingen, Germany
[2] School of Environment, Natural Resources and Geography, Bangor University, Wales, UK

PROJECT INFORMATION FORM

Throughout the form, questions marked with an asterix (*) need to be filled out in order for your project to be used in the analyses.

I.   PROJECT AREA

To start off, we would like the location and extent of the project area to be filled out in the table below. Please, bear in mind the following:

›   If your project involves collars deployed in disjunct areas and/or under clearly distinct environmental circumstances, please consider filling out separate forms for each of these areas.
›   If your project area(s) cross(es) an international border, you can list all countries involved.
›   The extent is indicated by the geographic (non-projected) coordinates of the lower left and upper right corner of the rectangle that best describes your project area. Coordinates need to be in the WGS84 coordinate system and in decimal degrees format (see Figure 1 and the first row of the Project area table).
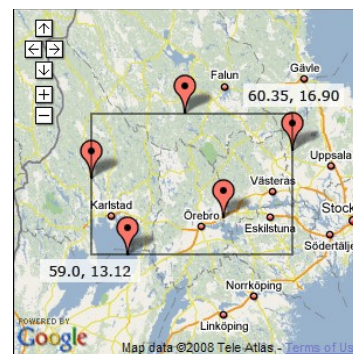
Figure 1: Example map illustrating the measurement of the project area extent

> Assistance
> To convert your project area extent from your local coordinate system to WGS84 (GPS), you can use this online tool.
> To find out the coordinates of a point in Google Maps, right click the point and choose "What's here?" from the pop-up context menu.

1. Area name*	Country*	Latitude 1*	Longitude 1*	Latitude 2*	Longitude 2*
Example area Örebro**	Sweden	59.0000	13.1200	60.3500	16.9000

** see Figure 1

Now we would like to get a general impression of the environmental situation in your project area.

2. Forest cover in the landscape*	
3. Dominant forest type*	
4. Typical forest density in the area*	
5. Terrain ruggedness*	

Importantly, we also need to know the time span over which the project was conducted.

6. Project period from* [   ] **until*** [   ]

II. SPECIES

Please enter the number of individuals of all species for which deployment data is provided. If possible, group the counts per sex and age combination. Please contact us if more species have been collared than fit in the provided fields.

7. Colloquial name	Scientific name*	Sex	Age	Number*
TOTAL				

III. COLLARS

We are now getting closer to the core information needed, and dive a little deeper into the characteristics of the collars. In the table below, please provide the number of collars deployed per brand (and type, if possible) and year of purchase. Again, please contact us if more collars have been deployed than fit in the provided fields.

8. Brand*	Type	Year of purchase*	Number*
TOTAL			

Before we go on with some further information on the collars, please have a look at the following diagram to clarify the terminology used. What is the fix attempt time and when is a fix successful?
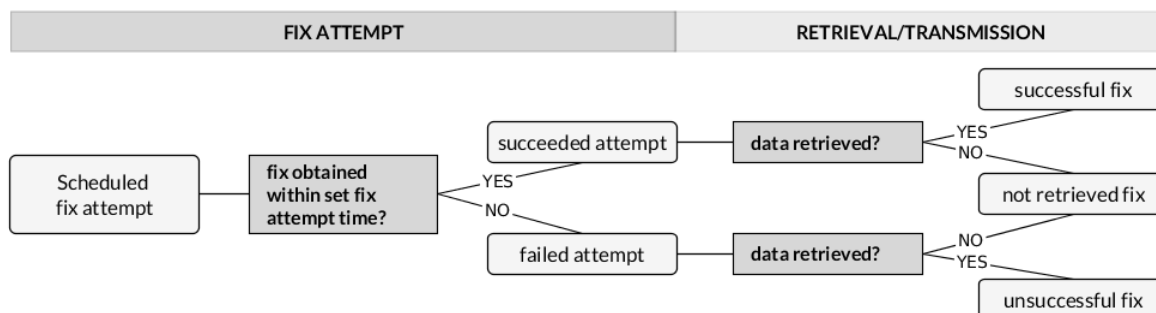
Figure 2: From fix attempt to usable geographic information. When is a fix successful?

The **fix attempt time** (the first step in Figure 2) is defined as the time span over which a collar is allowed to search for sufficient satellites to obtain a fix before the attempt is classified as failed. A fix attempt is considered **successful** if it (i) succeeded in obtaining the collar's geographical position within the set fix attempt time and (ii) was successfully transmitted/retrieved from the collar. A fix attempt is labelled **unsuccessful** if it failed to obtain a position, and it is labelled '**not retrieved**' when information on its status (succeeded/failed) could not be obtained from the collar (Figure 2). There are three general ways of **obtaining data** from a collar (the second step in Figure 2 - retrieval/transmission). First, data can be obtained directly from the collar upon its recovery from the field. Second, data can be retrieved remotely using regular VHF/UHF or GSM systems. And third, data is transmitted through satellite-based systems, e.g. Argos, Globalstar or Iridium, and then forwarded to the end user, usually via email.

9. For how many collars was the programmed maximum fix attempt time of the following length?

Fix attempt time	Number
≤ 60sec	
61-90sec	
91-180sec	
> 180sec	
Unknown	

10. How many collars** used the following methods to retrieve the GPS fixes (see text above)?

Data retrieval method	Number
Upon collar retrieval	
VHF/UHF	
GSM	
Argos	
Globalstar	
Iridium	
Unknown	
Other	

**Please include all deployed collars, regardless of whether they actually yielded fixes or not.

IV. DEPLOYMENT

Good. So far we are aware of the number and type of collars that were deployed at the project site for any duration within the project period. Now, we need to know some more deployment details. How often was data transmitted? How many fix attempts were obtained? How did the deployment end? Etc.

11. For all collars using satellite data transmission, how many sent the obtained positions to the satellite at the following frequencies?

no collars with satellite data transmission were used ☐

more than 1 transmission attempt per day	
1 transmission attempt every 2-3 days	
1 transmission attempt every 4-7 days	
1 transmission attempt every 2-4 weeks	
less than 1 transmission attempt per month	
Unknown	
Other	

12. For how many collars did the deployment period end as follows? (Please include all deployed collars)

It hasn't ended yet	
As planned (drop-off, battery dead, collar retrieved, project end)	
Unexpected battery failure	
Electronic failure (software/sensor/electronics)	
Mechanical failure (e.g. collar damaged)	
Unknown (e.g. collar lost)	
Other	

13. From all collars with remote data retrieval (VHF/UHF, GSM or satellite), how many yielded additional successful fixes after they were retrieved from the field?

We have now arrived to the key number of the questionnaire: the **fix success rate**. We calculate the fix success rate as the proportion of all scheduled fix attempts that was successful, as defined in Figure 2. Therefore, we need the number of expected (scheduled) fixes, the number of fixes that could not be retrieved, and the number of successful fixes.

14. Over all deployed collars, what was the total number of *expected fixes* over the project period? That is, when all scheduled fix attempts over the project period would have been successful, how many fixes would there have been?*

15. Over all deployed collars, how many scheduled fix attempts were *not retrieved* (e.g . because of poor satellite connection, failing GSM network, failing VHF or just data loss)? That is, the status (failed/succeeded) of these fixes is unknown.*

16. Over all deployed collars, how many *successful fixes* were eventually obtained over the project period, regardless of positional error (e.g. DOP) or number of satellites involved?*

V.   PROJECT OPERATION AND EVALUATION

We are now nearing the end of the questionnaire, and would like to know some more details about the operation and evaluation of the project. For example, what are the average costs involved in projects using satellite collar techniques. We are only interested in broad cost classes to investigate the profitability of the approach under different environmental circumstances and varying fix success rates.

17. What was the average purchase price range per collar?
(including drop-off mechanism, shipping and/or import costs, excluding accessories and software)

18. What were the average additional _non-recurring_ costs per collar?
(e.g. additional hardware, software, etc.)

19. What were the average _recurring_ running costs _per collar per month_?
(e.g. satellite service, GSM network, battery replacement)

Knowing you have invested these resources into your project hoping for helpful and insightful results, we want to gauge to what extent you were satisfied with the amount and quality of the data you obtained using the satellite collar technique.

20. How well do the following two statements reflect your impressions about the collars in your project?

	Very poor	Poor	Neutral	Good	Very good	I don't know
The amount of data obtained (i.e. fix success rate and transmission success) met my expectation.	○	○	○	○	○	○
The data quality (position error) met my expectation.	○	○	○	○	○	○

And finally, we are interested whether the results of this project were useful for ecological or conservation research? Was the data useful for furthering your career? Was it used in publications?

21. How well do the following statements reflect your impressions on the usefulness of the project results?

	Very poor	Poor	Neutral	Good	Very good	I don't know
The project results were useful for applied conservation.	○	○	○	○	○	○
The project results were useful for the field of ecological or conservation research I am active in.	○	○	○	○	○	○
The project results were useful for furthering my career.	○	○	○	○	○	○

22. How many publication(s) report on the data from these collars?

Peer-reviewed journal publications

Other publications

23. Please provide citations for any peer-reviewed journal publications mentioned in Question 22.

24. If none, why did the project not result in any publications?

25. Have you uploaded any of your data to Movebank?   ○ **Yes**   ○ **No**

Movebank is a free, online database of animal tracking data hosted by the Max Planck Institute for Ornithology, helping researchers to manage, share, protect, analyse, and archive their data, including unpublished datasets.

26. If you have not done so, what was the most important reason?

VI. REMARKS AND FURTHER INFORMATION

27. If you have any further remarks about the project details, specific collar details, etc. please provide them here.

Please verify that you have answered all 27 questions, or at least those marked with an asterix (*).
If so, you have provided all necessary deployment data for your study to be included in our analysis, and you will find out how you can submit this form on the next page.

THANK YOU!

If you have conducted any additional projects and you would like to add their deployment data as well, you can use the "Add another project" button below to start entering the data for these project(s) using a new form.

If you have no further projects to add, send us the filled out form(s) following these instructions:
  – save this project information form under a unique name (e.g. the name of the project area),
  – combine this project information form (and those for any additional projects) with your previously filled out personal information form in a compressed folder (e.g. .zip), and
  – send the compressed folder to maarten.hofman@forst.uni-goettingen.de with in the subject line: "Satellite collars in wildlife research"

To add another project, please save this form as mentioned above and press the "Add another project" button to start entering the deployment data of your next project.

Add another project

For more information about this survey:
Maarten Hofman,
Department of Wildlife Sciences,
University of Göttingen
Büsgenweg 3, 37077 Göttingen,
Germany
+49 (0)551 39 33583
maarten.hofman@forst.uni-goettingen.de

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PERFORMANCE OF SATELLITE COLLARS IN WILDLIFE RESEARCH: WHAT DOES THE EVIDENCE SHOW?

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ADDITIONAL GUIDELINES FOR THE PROJECT INFORMATION FORM

Q1: Ideally, the coordinates should be the bounding box of the observed locations of all collared animals in the project, or the bounding box of their compiled home ranges.

Q2-5: Think about the general area within the bounding box that was actually used by the individuals.

Q6: If some of the collars are still deployed and providing data, the end date of the project should be set to the date up until which you have calculated the expected fixes (see Q14).

Q7: Include all animals that were collared at least once during the project.

Q8: Include all collars that were deployed at least once during the project, regardless of whether they were refurbished. Include the year of original purchase.

Q9: We are interested in the maximum time that the collar was programmed to look for a GPS fix during a fix attempt. Please include all deployments (collar-animal combinations) that occurred during the project. That is, the sum of all numbers in this question should equal the number of deployments during the project.

Q10: We are interested in the mode of data transfer that was originally intended to be used. If the collar is equipped to transfer data using the GSM network, this would be the intended method of data transfer, even if you downloaded most fixes directly from the collar after retrieving it from the field. (All collars from which you downloaded additional fixes after retrieval should be listed in Q13). Please include all deployments (collar-animal combinations) that occurred during the project.

Q11: Please include all deployments (collar-animal combinations) that occurred during the project.

Q12: Please include all deployments (collar-animal combinations) that occurred during the project. Animal mortalities can be included in the "Other" section, but indicate the number of mortalities in the specification.

Q13: What we are after here, is the number of retrieved collars from which you downloaded fixes (e.g. using cable connection to a laptop) that you weren't able to download remotely using VHF/UHF, GSM or a satellite network (Argos, Globalstar, Iridium, …) while the collar was deployed.

Q14: In general, 'Expected' in our questionnaire means: how many fixes could all the collars deployed during the project period have made during the time they were active and functioning according to schedule? That is, every fix attempt scheduled on the collars from the start of deployment till the end of deployment or until failure detection is expected to yield a successful fix. As soon as the collars malfunctioned, we are not expecting to get any fixes from them any more.
For any collars that are still deployed, you can choose a date in the recent past up until which you will calculate the expected fixes for all collars. This will also be the project end date (Q6) for the purposes of our study.

<u>Q15-16:</u>
There are in fact three possible outcomes of a fix attempt (defined in Fig. 2 in the questionnaire):
- **Successful** = GPS position obtained during fix attempt by the collar, and this information was retrieved from the collar (Q16)
- **Unsuccessful** = GPS position NOT obtained during fix attempt by the collar, and this information was retrieved from the collar (calculated from Q14 to Q16)
- **Not retrieved** = Information on the scheduled fix attempt could not be retrieved from the collar. It is unknown whether the collar managed to obtain a GPS position. (Q15)

such that:
Expected fixes (Q14) = Successful fixes (Q16) + Unsuccessful fixes + Not retrieved fixes (Q15)
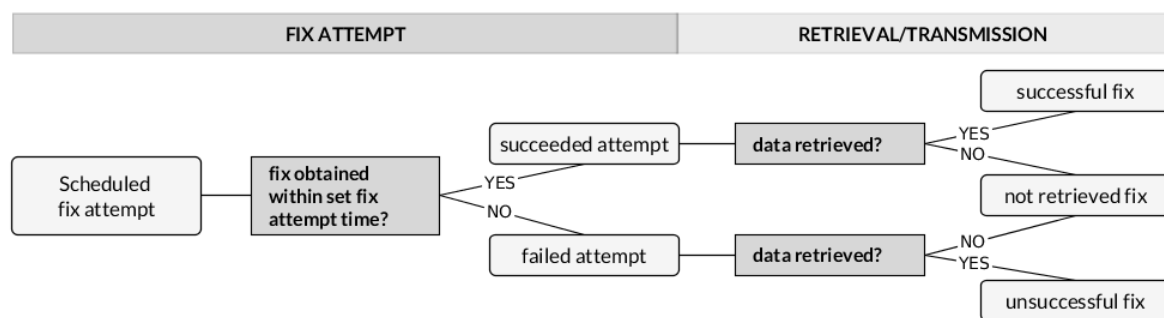
Figure 1: From fix attempt to usable geographic information. When is a fix successful?

> **An example:**
>
> When I get data from my Iridium collars, the files include information on every scheduled fix attempt that the Iridium network managed to download from the collars, regardless of whether it succeeded or not.
>
> That is, the file includes information such as:
> - start time of fix attempt
> - end time of fix attempt (time to fix) - this will say '>180sec' if the fix attempt failed
> - coordinates - these will be blank for a failed fix attempt
> - DOP/coordinate precision - again blank for failed attempts
> - No. of satellites
> - etc.
>
> The fix attempts with coordinates are the **successful** fixes.
> From the fix attempts with blank coordinates, I can tell that a fix was **unsuccessful**.
> The fix attempts that were scheduled, but are missing from the Iridium files, could not be downloaded from the collar by the Iridium network, and are therefore considered **not retrieved**.

Some collar manufacturers only provide the user with the fix attempts that were successful, while not specifying the fate of the other scheduled fix attempts. In that case you would not be able to distinguish between unsuccessful and not retrieved fixes, and you can leave Q15 blank. <u>Please make note of this in the remarks section (Q27).</u>

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