

The Ecology and Conservation of Animal Movement in Changing Land- and Seascapes

By

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Abstract

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Anthropogenic habitat fragmentation is a primary driver of species endangerment across the globe and has compounding effects on species diversity and ecosystem function. While efforts to enhance habitat connectivity are therefore essential to protecting biodiversity, a fundamental behavioral and ecological understanding of animal movement is first needed to successfully protect species movements. Understanding the role of behavior in determining animal movement patterns is essential to conservation planning, yet the extent to which an animal's behavioral state (e.g. foraging, dispersing) influences its movements and resource selection has largely been ignored as part of conservation planning efforts. Further, because empirical studies of animal movement are most-often site- and species-specific, the processes underlying observed movement patterns are not well understood across taxa. This dissertation seeks to elucidate the processes that shape animal movements to advance the biological grounding of connectivity science and inform conservation efforts.

A systematic review of connectivity studies employing resource selection analysis examined how researchers have incorporated animal behavior into connectivity planning, and highlighted promising approaches for identifying wildlife corridors. The review revealed that most of the research done to date has superficially considered all animal location data as representative of resource selection patterns, despite recognition that an animal's behavioral state can be an important component of space use. Those studies in the review that validated connectivity predictions with independent movement data indicate that general patterns of resource selection are not always a suitable proxy for movement preference during dispersal, and failure to recognize this distinction may have important consequences for species-specific efforts to preserve habitat connectivity.

Using high-resolution GPS and activity data from African wild dogs (*Lycaon pictus*), an Endangered species highly sensitive to habitat fragmentation, resource selection and responses to roads were measured across three behavioral states identified from activity data (hunting, resting, and traveling). The response of wild dogs to roads varied markedly with both the behavioral and landscape contexts in which roads were encountered, ranging between strong selection for and avoidance of roads depending on behavioral state. A comparison of these outputs to a full model that did not parse for behavior revealed that these patterns were not evident when all movement

data were considered together in the full model. This study indicates that including behavioral information in resource selection models is critical to understanding wildlife responses to landscape features and suggests that successful application of resource selection analyses to conservation planning requires explicit examination of the behavioral contexts in which movement occurs.

The effects of behaviorally-mediated patterns of resource selection were then applied in a habitat connectivity modeling context. To illustrate the importance of behavioral information in connectivity assessments, behavior-specific predictions of connectivity were tested against long-distance dispersal movements of African wild dogs. Findings demonstrated that including only directed-movement behavior when measuring resource selection reveals far more accurate patterns of habitat connectivity than a model measuring resource selection independent of behavioral state. Results of this work suggest that connectivity studies that rely on resource selection analysis alone may be insufficient to target movement pathways and corridors for protection. This research highlights the value of incorporating animal behavior into connectivity planning.

To examine how basic movement processes scale up to produce emergent patterns for multiple species, movement data from over a dozen marine and terrestrial vertebrate species spanning three taxonomic classes, continents and orders of magnitude in body size were compared with computer-simulated idealized movement paths. This comparative approach revealed that similar movement patterns and properties recur in highly dissimilar ecological systems, and showed that a simple set of metrics can reliably classify broad-scale movement patterns such as migration, nomadism, and territoriality in disparate taxa. This classification system can be applied to inform predictions in multiple areas of ecological research, such as how an individual or species' movement classification influences its response to climate change or its invasion potential in an exotic environment. In addition, this work provides researchers with a standardized set of movement metrics for expediently analyzing animal trajectories over time to detect any changes in movement pattern that may be indicative of environmental change.

Taken together, the body of work presented in this dissertation provides new approaches for researchers and practitioners to understand the ecology and conservation of animal movement, and in particular for measuring wildlife responses to widespread habitat alteration. Given limited conservation resources and rapidly changing environments, these contributions mark a key step in developing effective strategies to preserve critical wildlife movement processes.

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Table of Contents

ACKNOWLEDGEMENTS	iii
CHAPTER 1	
INTRODUCTION	1
CHAPTER 2	
LESSONS FROM INTEGRATING BEHAVIOUR AND RESOURCE SELECTION: ACTIVITY-SPECIFIC RESPONSES OF AFRICAN WILD DOGS TO ROADS	6
CHAPTER 3	
DOES WILDLIFE RESOURCE SELECTION ACCURATELY INFORM CORRIDOR CONSERVATION?	23
CHAPTER 4	
CLASSIFICATION OF MOVEMENT SYNDROMES ACROSS INDIVIDUALS AND SPECIES	49
CHAPTER 5	
CONCLUSIONS	72
REFERENCES	75

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1. Introduction

Anthropogenic habitat fragmentation, the process of breaking apart and reducing intact habitat through human land conversion (Fahrig 2003), is a primary driver of species endangerment across the globe (Czech & Krausman 1997; Pimm & Raven 2000; Sala *et al.* 2000). Beyond the effects of habitat loss itself, fragmentation has been shown to increase genetic isolation of populations, interrupt dispersal routes leading to higher mortality rates, increase edge effects, and disrupt species' abilities to shift ranges in response to long-term environmental change (Fahrig 2003).

Today, nearly one fifth of all vertebrate species are classified as Threatened (Vulnerable, Endangered or Critically Endangered) on the International Union for Conservation of Nature (IUCN) Red List (Hoffmann *et al.* 2010). For wide-ranging species with large area requirements like large carnivores, the rate is significantly greater. Sixty one percent of extant large carnivore species are Threatened, and 77% of these species are experiencing ongoing population declines (Ripple *et al.* 2014). Habitat fragmentation, compounded with the loss of the important regulatory role of large carnivores in ecosystems (Terborgh *et al.* 2001; Estes *et al.* 2011), have cascading effects on species diversity and ecosystem function (Fahrig 2003; Prugh *et al.* 2008; Forister *et al.* 2010).

Yet, evidence that conservation actions have prevented some 18% of bird and mammal species on the IUCN Red List from further declining in status offers reason for optimism (Hoffmann *et al.* 2010). Effective efforts to mitigate habitat fragmentation are essential to protecting biodiversity, and scientific methods to enhance landscape connectivity, the degree to which a landscape facilitates or impedes movement among habitats (Taylor *et al.* 1993), are consequently burgeoning (Beier, Majka & Spencer 2008; Gilbert-Norton *et al.* 2010; Rudnick *et al.* 2012). To successfully target these efforts for the protection of critical movement processes, a fundamental behavioral and ecological understanding of animal movement is first needed (Sawyer, Epps & Brashares 2011). This dissertation seeks to elucidate the internal and external processes that shape animal movements to advance the biological grounding of connectivity science and inform conservation efforts.

Corridor ecology: theory, approaches and limitations

The ability of animals to move through their landscapes has profound effects on their survival and population dynamics. Landscape connectivity influences demography (Clobert *et al.* 2001), promotes dispersal and colonization (Hanski 1998), maintains genetic diversity through gene flow (Hendrick 2005), increases a species' ability to respond to environmental change (Heller & Zavaleta 2009), and supports long term persistence of populations (Swingland & Greenwood 1983). Thus, a great deal of attention within the ecological and conservation literature is increasingly given to understanding and predicting animal movement processes and patterns (Nathan *et al.* 2008).

Wildlife corridors are an important conservation tool for protecting animal movement and promoting landscape connectivity (Gilbert-Norton *et al.* 2010). Corridors, defined as a linear habitat connecting two or more larger habitat patches within a non-habitat matrix (Beier and Noss 1998), have been shown to facilitate movement between habitat patches (Haddad *et al.*

2003; Gilbert-Norton et al. 2010) and reduce individual mortality during dispersal (Kenneth Dodd, Barichivich & Smith 2004; Glista, DeVault & DeWoody 2009). At a population and meta-population scale, corridors can theoretically reduce genetic isolation and local extinction and allow immigration to new habitat patches if currently occupied habitat becomes unsuitable (Caro, Jones, and Davenport 2009).

A requisite first step in protecting corridors for movement is the identification of areas on the landscape where movement between habitat areas is most likely to occur. Resistance surface modeling is the leading analytical technique for predicting animal movements across broad spatial scales to inform corridor planning (Sawyer, Epps & Brashares 2011; Zeller, McGarigal & Whiteley 2012). Resistance surface models assign a value in a landscape grid cell to each environmental variable of interest (e.g. elevation, land cover) that represents the energetic or survival cost to the study species of moving through that spatial position (Adriaensen *et al.* 2003), or the willingness of the individual to cross the cell (Zeller, McGarigal & Whiteley 2012). Low cost (or resistance) values indicate a suitable habitat type while high values indicate less suitable habitat or habitat which impedes movement, for example rivers, roads, or urban areas. Corridors intended for protecting dispersal movements among habitat areas, for instance, may then be identified by evaluating paths of least resistance over the cost surface (Adriaensen *et al.* 2003; McRae *et al.* 2008).

While resistance surface modeling provides a strong analytical framework for evaluating landscape connectivity and predicting movement pathways, it has a number of limitations that necessitate further research to improve its efficacy. First, because resistance surface modeling typically uses the inverse of habitat suitability as a proxy for cost, it runs the risk of misappropriating movement preferences by treating all behaviors as equal (Zeller et al. 2012). Just as humans don't drive over houses nor sleep on highways, animals may not select the same habitat they would for dispersal as they would for denning or any other behavior. In fact, there is increasing recognition that an animal's behavioral state (e.g. resource use vs. dispersing) can strongly mediate its patterns of resource selection (Wilson, Gilbert-Norton & Gese 2012; Roever *et al.* 2013; Abrahms *et al.* 2016). Thus, the degree to which connectivity predictions are sensitive to behavior-specific estimates of resource selection must be better understood.

Second, little direct evaluation exists of how well resistance surface models predict actual animal movement paths (Driezen et al. 2007). Empirical evidence is lacking on how assigned resistance values correlate with on-the-ground species' movements (Beier and Noss 1998; Sawyer, Epps, and Brashares 2011). Not only is there no consensus as to which analytical approaches yield the most accurate resistance values, but there is little exploration of the sensitivity of model output to the chosen methodology (Zeller et al. 2012). These limitations are highly problematic, as managers may base land use and acquisition decisions on inaccurate and/or unevaluated models (Simberloff et al. 1992).

With the advancement of GPS collar technology that includes kinematics data and allows for the collection of movement data at unprecedented scales, there is great opportunity for better understanding the role of behavior in shaping animal movements, determining the efficacy of connectivity models, and evaluating movement as an indicator of environmental change.

Study system

African wild dogs (*Lycaon pictus*) serve as the focal species for the greater part of my dissertation uses. African wild dog GPS movement data was collected in the Okavango Delta region of northern Botswana.

Okavango Delta, Botswana

The Okavango Delta in north-western Botswana is a World Heritage Site and boasts one of most diverse assemblages of large carnivores in the world (Ripple *et al.* 2014). It supports populations of cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), brown hyenas (*Hyaena brunnea*), leopards (*Panthera pardus*), lions (*Panthera leo*), and one of the world's largest African wild dog populations (c. 500 individuals) (Woodroffe, McNutt & Mills 2004). The Delta's highly productive environment also supports some of the highest herbivore densities seen across Africa, including African buffalo (*Syncerus caffer*), African elephants (*Loxodonta africana*), impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchelli*) (Ramberg *et al.* 2006).

My study site was located just east of the Delta's main floodwaters (c. 2600 km²; 19°31'S, 23°37'E; elevation: c. 950 m) and was bordered to the west and northwest by the Delta's permanent swamp, including a portion of the Moremi Game Reserve. This area is part of the greater Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), which was recently instituted to re-establish ecological connectivity in southern Africa. The KAZA-TFCA encompasses a network of reserves and corridors across Botswana, Zimbabwe, Namibia, Zambia, and Angola, including Moremi Game Reserve. Adjacent to Moremi Game Reserve are designated Wildlife Management Areas in which photographic and trophy hunting tourism are the only human activities permitted. The Okavango Delta's rich wildlife communities attract over two million tourists annually, and, between 1995 and 2005, tourism in Botswana grew nearly 15%, leading to the threat of rapid development for tourism infrastructure (Harrison & Maharaj 2013; *Tourism Statistics Annual Report* 2015).

African wild dogs: natural history and population trends

The African wild dog, otherwise known as the African hunting dog or African painted dog, is among the most iconic species of sub-Saharan Africa. African wild dogs are known for their unique social hierarchy and cooperative behavior, which are rare among mammals, living and breeding in hierarchical social groups called packs (Creel & Creel 2002). Packs range in size from 2-27 individuals and increasing pack size has been shown to contribute to additive hunting and reproductive success (Creel & Creel 2015; Hubel *et al.* 2016). Their main prey species vary by region and include impala, kudu (*Tragelaphus strepsiceros*), Thomson's gazelle (*Eudorcas thomsonii*), wildebeest, and steenbok (*Raphicerus campestris*) (Creel & Creel 2002). Breeding among African wild dogs is typically restricted to the dominant male and female of the pack and occurs once annually. Because they are obligate cooperative breeders, African wild dogs are vulnerable to inverse density dependence at low densities (i.e. the 'Allee effect'), whereby the probability of pack survival dramatically decreases below a pack size threshold (Courchamp, Clutton-Brock & Grenfell 1999; 2000). Dispersal occurs when individuals of either sex reach maturity typically between the ages of two and three years, and functionally serves to avoid inbreeding by emigrating to a new breeding range (McNutt 1996).

Along with the Ethiopian wolf (*Canis simensis*), the African wild dog is considered one of the top two most endangered carnivore species of Africa, and is listed as Endangered on the IUCN Red List (Woodroffe & Sillero-Zubiri 2013). The species currently occupies 12% of its historical range, with fewer than 1,500 mature adults estimated remaining in the population (Woodroffe & Sillero-Zubiri 2013). Anthropogenic habitat fragmentation is consistently identified as its principal threat (Creel & Creel 1998; Woodroffe & Sillero-Zubiri 2013; van der Meer *et al.* 2013). African wild dogs have among the largest space requirements of large carnivores, which is attributed to avoidance of competitively dominant sympatric predators (lions and hyenas) (Creel & Creel 1996). In northern Botswana, African wild dog home range sizes are estimated at a mean of 739 km² and have been observed to be as large as 1,608 km², making them highly vulnerable to reduction and fragmentation of suitable habitat (Pomilia, McNutt & Jordan 2015). Habitat fragmentation increases direct mortality of African wild dogs from human-wildlife conflict and disease transmission from domestic animals, and increases barriers to movement for long-distance disperses, thereby increasing the genetic isolation of wild dog populations and risk of inbreeding depression (Woodroffe 2011). Indeed, strong genetic structuring recently shown among nine wild dog subpopulations, indicating the loss of gene flow, reveals the genetic signature of extensive habitat fragmentation across sub-Saharan Africa (Marsden *et al.* 2012). Consequently, the IUCN has identified “determining the landscape features which facilitate (or prevent), wild dog movement over long distances and hence promote (or block) landscape connectivity” among its top five scientific needs (Woodroffe & Sillero-Zubiri 2013).

Because African wild dogs are highly wide-ranging, sensitive to habitat fragmentation, and are of immediate conservation concern, they provide an ideal focal species for examining the behavioral and environmental influences on movement and dispersal and identifying methods to protect these processes.

Overview of Dissertation

In the second chapter, I investigate the role of behavior in determining responses of African wild dogs to one of the most widespread forms of landscape alteration globally: road systems. Understanding how anthropogenic features affect species’ abilities to move within landscapes is essential to conservation planning and requires accurate assessment of resource selection for movement by focal species. Yet, the extent to which an individual’s behavioral state influences resource selection has largely been ignored. I collected high resolution GPS and activity data from 13 wild dogs over a two-year period. I employed a step selection framework to measure resource selection across three behavioral states identified from activity data (high-speed running, resting, and traveling) and across a gradient of habitats and seasons, and compared these outputs to a full model that did not parse for behavior. The response of wild dogs to roads varied markedly with both the behavioral and landscape contexts in which roads were encountered. Specifically, wild dogs selected roads when traveling, ignored roads when high-speed running, and avoided roads when resting. This distinction was not evident when all movement data were considered together in the full model. When traveling, selection of roads increased in denser vegetative environments, suggesting that roads may enhance movement for this species. These findings indicate that including behavioral information in resource selection models is critical to understanding wildlife responses to landscape features and suggest that successful application of

resource selection analyses to conservation planning requires explicit examination of the behavioral contexts in which movement occurs. Thus, behavior-specific step selection functions offer a powerful tool for identifying resource selection patterns for animal behaviors of conservation significance.

In the third chapter, I review current connectivity literature and use an empirical case study on African wild dogs to demonstrate that including only directed-movement behavior when measuring resource selection reveals markedly different, and more accurate, patterns of landscape connectivity than a model measuring resource selection independent of behavioral state. I reviewed sixteen years of connectivity studies employing resource selection analysis to evaluate how researchers have incorporated animal behavior into corridor planning, and highlight promising new approaches for identifying wildlife corridors. This review indicated that most connectivity studies conflate resource selection with connectivity requirements, which may result in misleading estimates of landscape resistance, and lack validation of proposed connectivity models with movement data. To illustrate the importance of behavioral information in such analyses, I presented an empirical case study to test behavior-specific predictions of connectivity with long-distance dispersal movements of African wild dogs. Results of this work suggest that resource selection analyses that fail to consider an animal's behavioral state may be insufficient in targeting movement pathways and corridors for protection. This study highlights the crucial importance of incorporating behavioral information into connectivity planning.

In the fourth chapter, I move beyond a single species analysis to investigate whether broad-scale movement patterns can be characterized across diverse taxa and environments, and develop a system of measures for how the study of movement can be used as an indicator of environmental change. Because empirical studies of animal movement are most-often site- and species-specific, ecologists lack a generalized understanding of the mechanisms underlying broad movement patterns. By combining movement data from 13 marine and terrestrial species spanning three taxonomic classes, continents and orders of magnitude in body size with computer-simulated idealized movement paths, I examine how fundamental movement metrics scale up to predict emergent movement patterns across multiple taxa. I introduce a classification scheme for movement syndromes, which are suites of correlated movement traits seen across taxa (e.g. migration, nomadism), and show that a simple set of metrics can reliably classify movement syndromes across highly disparate vertebrate taxa. This movement syndrome classification scheme provides a general framework for linking movement patterns to movement process, and facilitates new understanding of relationships between movement and environmental factors such as landscape configuration and climate. In the final chapter, I discuss key conclusions from this body of work and provide recommendations for future areas of research.

2. Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads

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Abstract

Understanding how anthropogenic features affect species' abilities to move within landscapes is essential to conservation planning and requires accurate assessment of resource selection for movement by focal species. Yet, the extent to which an individual's behavioural state (e.g. foraging, resting, commuting) influences resource selection has largely been ignored. Recent advances in GPS tracking technology can fill this gap by associating distinct behavioural states with location data. We investigated the role of behaviour in determining responses of an endangered species of carnivore, the African wild dog (*Lycaon pictus*), to one of the most widespread forms of landscape alteration globally: road systems. We collected high resolution GPS and activity data from 13 wild dogs in northern Botswana over a two-year period. We employed a step selection framework to measure resource selection across three behavioural states identified from activity data (high-speed running, resting, and traveling) and across a gradient of habitats and seasons, and compared these outputs to a full model that did not parse for behaviour. The response of wild dogs to roads varied markedly with both the behavioural and landscape contexts in which roads were encountered. Specifically, wild dogs selected roads when traveling, ignored roads when high-speed running, and avoided roads when resting. This distinction was not evident when all movement data were considered together in the full model. When traveling, selection of roads increased in denser vegetative environments, suggesting that roads may enhance movement for this species. Our findings indicate that including behavioural information in resource selection models is critical to understanding wildlife responses to landscape features and suggest that successful application of resource selection analyses to conservation planning requires explicit examination of the behavioural contexts in which movement occurs. Thus, behaviour-specific step selection functions offer a powerful tool for identifying resource selection patterns for animal behaviours of conservation significance.

Keywords

resource selection, animal behaviour, linear features, movement ecology, step selection functions, conservation planning, landscape permeability, *Lycaon pictus*

Introduction

Understanding animal movement is essential to effective in-situ conservation planning. An animal's ability to move through its landscape has fundamental consequences for both individual fitness (e.g. resource acquisition, survival) and long-term population persistence (e.g. dispersal, gene flow; Swingland & Greenwood 1983; Dingle 1996; Hanski 1999; Clobert *et al.* 2001). Management efforts aimed at preserving landscape connectivity have thus skyrocketed, and the effect of natural and human-built landscape features on animal movement and resource selection has become a central issue in ecology and conservation (Turner 1989; Nathan *et al.* 2008). In particular, conservation planners use estimates of resource selection to identify important habitat for wildlife populations, assess how wildlife responds to specific landscape features, and delineate wildlife corridors where animal movement is predicted to occur (Manly *et al.* 2002; Chetkiewicz & Boyce 2009).

The extent to which an animal's behavioural state (e.g. foraging, resting, commuting) influences resource selection has largely been ignored as part of these conservation planning efforts (Wilson, Gilbert-Norton & Gese 2012). Behavioural state has been shown to be an important component of habitat selection and space use in multiple taxa including elk (*Cervus elaphus*) (Fryxell *et al.* 2008), killer whales (*Orcinus orca*) (Ashe, Noren & Williams 2010), Bluefin tuna (*Thunnus maccoyii*) (Pedersen *et al.* 2011), lions (*Panthera leo*) (Elliot *et al.* 2014) and elephants (*Loxodonta africana*) (Roever *et al.* 2013). While both behavioural patterns and habitat use vary substantially among these species, these studies are similar in demonstrating that behaviour is an important determinant of how animals use their landscape. Thus, appropriate land management decisions rely on correctly identifying patterns of resource selection for the specific behaviours that are of conservation interest.

Recent advances in GPS tracking and mapping technology promise to improve efforts to link behavioural traits and patterns of habitat use, thereby providing conservation practitioners with a greater understanding of animal space use (Nams 2014). Animal-attached accelerometers in particular are being increasingly used to collect high-resolution activity data that can be paired with GPS locations (Brown *et al.* 2013). This collar technology allows not only precise quantification of resource selection, but also assessment of the behavioural contexts in which landscape features are selected for or avoided. Here, we demonstrate the importance of combining location and activity data to determine the role of behavioural state in resource selection and response to human habitat modification. Specifically, we investigate how behavioural state affects responses of African wild dogs (*Lycaon pictus*; Fig. 1) to one of the most widespread forms of landscape alteration globally: road systems (Bennett 1991; Trombulak & Frissell 2013). Roads have been shown to impede movement and dispersal by small-bodied species, particularly in areas with high human traffic (e.g., Fahrig *et al.* 1995; Shepard *et al.* 2008; Benítez-López, Alkemade & Verweij 2010). In contrast, a growing body of literature suggests that larger and more vagile species such as carnivores may use low traffic volume roads as movement corridors; roads may therefore increase the permeability of the encompassing landscape for these species (Latham *et al.* 2011; Whittington *et al.* 2011). Because of their vagility and sensitivity to human disturbance (Creel & Creel 1998), African wild dogs offer a particularly appropriate system for exploring behavioural variation in responses to road

networks. Given that road construction is accelerating throughout Africa, including in areas critical to the remaining African wild dog populations, detailed understanding of interactions between road networks and African wild dog behaviour is necessary for effective management of this endangered species.

To determine if resource selection patterns by African wild dogs vary with behavioural state, we evaluated fine-scale individual responses to roads using step selection functions. This approach is ideal for estimating resource selection for continuous movement data as it accounts for changes in resource availability as the animal moves through its environment (Fortin *et al.* 2005; Thurfjell, Ciuti & Boyce 2014). We modeled resource selection across three behavioural states (high-speed running, resting, and traveling) measured across multiple habitats and seasons to test the hypothesis that roads increase landscape permeability for African wild dogs. In addition to providing the first behaviourally explicit analysis of movements by African wild dogs, our analyses demonstrate the importance of including behavioural information in conservation-planning efforts.

Materials and Methods

Study Area

Our study area (Fig. 1) was located in northern Botswana's Okavango Delta (*c.* 2700 km²; centered at 19°31'S, 23°37'E; elevation *c.* 950 m) and included the southeastern portion of Moremi Game Reserve and surrounding Wildlife Management Areas. The region is characterized by highly seasonal fluctuations in precipitation, which correlate with vegetative growth. The dry season extends from April to October, peaking September-November (hereafter, peak dry season). The wet season extends from November to March with annual rainfall of 300-600 mm (McNutt 1996), peaking January-March (peak wet season). At our study site, the peak of the Delta's annual flood pulse typically occurs between August and September, which coincides with the wild dog denning season June-August (flood/denning season). Five major habitat types can be distinguished based on vegetation composition and structure: swamp (open structure), grassland (open structure), mixed woodland (medium structure), mopane (medium-dense structure), and riparian (dense structure). Broekhuis *et al.* (2013) provide detailed descriptions of these habitats and the methods used to distinguish them. An extensive and growing network of unpaved (sand) roads in this area (Fig. 2) is used primarily to support ecotourism.

Data Collection

Between November 2011 and 2013, we fitted thirteen adults from six wild dog packs with custom-designed GPS radiocollars (mean fixes per collar = 22350 ± 18676; Table S1). Each collar included a GPS unit and an Inertial Measurement Unit (IMU) consisting of a three-axis accelerometer and gyroscope to record position, velocity, and acceleration data. The GPS units within the collars were programmed to move between different operating states depending on the measured activity status of the animal. For all collars, the default state ('resting') took hourly fixes when the animal was stationary but transitioned into a 'traveling' state with five-minute fixes when activity data indicated that the animal was moving consistently. In addition, 10 collars included a 'running' state of five fixes per second, or 5-Hz intervals, triggered by

acceleration equivalent to galloping (38.2 m/s²). Field validation has shown that the number of runs recorded by the collars agree with reported data on average chases of prey per individual per day (Wilson *et al.* 2013). Wilson *et al.* (2013) provide additional information regarding the specifications of the collar design.

Movement Analyses

We chose roads as our focal landscape feature for evaluating patterns of resource selection since roads are a ubiquitous form of human landscape alteration and have been shown to influence animal movement patterns (e.g., Whittington, St. Clair & Mercer 2005; Shepard *et al.* 2008). To determine if responses to roads by African wild dogs vary with behavioural state, we employed a case-control design using step selection functions (SSFs; Fortin *et al.* 2005). SSFs use conditional logistic regression to estimate the relative probability of selecting a step by comparing the attributes of observed steps with those in a set of random control steps. When analyzing GPS-derived data, a step is typically measured as the straight line segment between two consecutive fix locations, and is described by its step length and turn angle (Turchin 1998). Following Forester *et al.* (2009), we generated five control steps for each observed step by sampling random step lengths from an exponential distribution and random turn angles from a uniform distribution from 0 to 2π . We chose to create only five control steps per observed step since a low number of control steps has been shown to have no effect on coefficient estimation for large datasets (Thurfjell *et al.* 2014). The binary response variable of our step selection model was used (1) and control (0) locations, with predictor variables being step length, turn angle, and distance to nearest road, measured continuously. We checked these predictor variables for collinearity using pairwise Pearson correlation coefficients with a correlation threshold of $|r| > 0.6$ (Latham *et al.* 2011); based on this threshold, no variables were discarded.

We estimated a SSF for all movement data without parsing by behaviour ('combined model'), and then estimated separate SSFs for each of the three behavioural states. Since SSFs rely on constant telemetry fix rates, for the combined model we matched the 5-minute fix intervals for traveling by interpolating the hourly resting data, during which the animal was stationary, and subsampling the 5 Hz running data. We conducted a sensitivity analysis to ensure post-hoc modification of fix rates did not affect parameter estimation; we found no significant difference between estimates for the resting and running data at the modified fix rates. For models partitioned by behaviour, we subsampled the running data to 1 Hz and did not alter the fix rates of the resting or traveling data. To consider the potential role of lack of independence between individuals occurring within the same pack, we repeated this and the following analyses with only one individual from each pack. The results of this more conservative approach were consistent with those presented in this paper (Table S2, Fig. S1 and S2).

To explore effects of roads on landscape permeability when traveling, we included a distance-to-road by habitat type interaction term in the traveling model; data on habitat type were derived from a GIS layer of the five habitat classes (Broekhuis *et al.* 2013). We performed a Fourier Transform for the traveling data and included an interaction between distance to road and the sine- and cosine-transformations of day of year to examine changes in selection over season (Priestley 1981). Finally, we calculated movement speed as displacement divided by time and turn angle as the change in direction of heading for each step in the traveling dataset. We used a linear model to test for relationships between average speed or turn angle as response variables

and a binary on-road/off-road predictor variable. To look at variation in these relationships over season, we created separate models with data from the peak wet, flood/denning, and peak dry seasons. All statistical analyses were performed using R 3.1.0 (R Core Team 2014). Conditional logistic regression was performed with R package *survival* and p-values for coefficient estimates were calculated with Wald tests (Therneau 2014).

Results

Behaviourally-mediated variation in responses to roads

There were no effects of roads on step selection in a full model (“combined”) that included the entire GPS dataset and all behavioural categories ($p = 0.54$; Table 1). However, when locations were partitioned by behavioural state and run in separate models, we found that patterns of road use varied markedly among the focal behaviours. African wild dogs selected for roads when traveling ($p < 0.01$) but selected locations far from roads when resting ($p = 0.015$). No effect of roads was evident for high-speed running ($p = 0.55$). The positive and negative effects of roads on step selection for these behavioural categories explain the absence of a road effect in the combined model.

Movement responses to roads across space and time

When an interaction term between distance-to-road and habitat type was included in the model for traveling, we found significant road selection across all habitat types ($p < 0.01$; Fig. 3). However, the magnitude of the selection coefficient, corresponding to the degree to which roads were selected for, varied greatly among habitats. Road selection was lowest in open habitat types (swamp, $|\beta| = 1.05e-04$; grassland, $|\beta| = 1.4e-04$), and increased with increasing habitat density (woodland, $|\beta| = 1.95e-04$; mopane, $|\beta| = 2.56e-04$), although road selection was only moderate in the densest habitat category, riparian ($|\beta| = 1.65e-04$). Results from the Fourier Transform showed similar significant variation in road selection over time (Fig. 4). Road selection was strongest during the peak wet season, January-March (min $\beta = -2.6 e-04$), and weakest during the peak dry season, September-November (max $\beta = 2.18e-05$). A second peak in road selection occurred in June-August (min $\beta = -1.04e-04$), which corresponds with the flood/denning season.

Movement statistics of road travel

In our traveling data set, comparisons of the distribution of turn angles for observed steps on roads versus observed steps off roads revealed that movement steps on roads had a greater proportion of small or zero magnitude turn angles (Fig. 5). Our linear model showed that turn angles were 25% smaller on roads (intercept = 1.00, slope = -0.25, $p < 0.01$). Average speeds calculated from the traveling dataset were higher on roads than off-road across all seasons (Fig. 4). Average off-road travel speeds were 27% less than on-road speeds in the peak wet season (0.81 vs. 1.03 m/s, SE=0.01, $p < 0.01$), 50% less in the flood season (1.02 vs. 1.53 m/s, SE=0.006, $p < 0.01$), and 23% less in the peak dry season (0.72 vs. 0.17 m/s, SE = 0.006, $p = 0.04$).

Discussion

Behaviour-specific patterns of resource selection

Conservation and development planning require a comprehensive understanding of how anthropogenic landscape features affect resource selection and landscape connectivity. Our results emphasize the importance of explicitly considering the behavioural, landscape, and climatic contexts in which the landscape features under study are encountered by the study species. Importantly, we show that failure to consider these factors yields notably different and potentially misleading outcomes compared to models that incorporate behaviour. Specifically, while African wild dogs selected for roads when traveling, they avoided roads when resting. This distinction was not evident when all movement data were considered together, thus illustrating the need to consider the specific behavioural context in which movement is measured in order to understand fully how anthropogenic features affect wildlife. In our case, separating patterns of resource selection by behavioural state was required to determine roads effects on landscape permeability for African wild dogs.

Road effects on landscape permeability

Understanding the effects of landscape features such as roads on the energetic or survival cost of animal movement is critical for accurately assessing connectivity and for protecting linkages for wildlife movement (Rudnick *et al.* 2012; Cozzi *et al.* 2013). Yet, despite the global ubiquity of roads, little research has described their impacts on fine-scale behavioural responses of wide-ranging species. While roads increase landscape resistance for many species, our findings indicate that unpaved roads can significantly enhance landscape permeability for a large carnivore of conservation concern. Our finding that African wild dogs selected for movement on roads when traveling is consistent with previous studies on large carnivore use of anthropogenic linear features (Dickson, Jenness & Beier 2005; Whittington *et al.* 2005); our use of high resolution spatial data partitioned by behavioural state provided a novel opportunity to link road use to enhancement of landscape permeability.

Results of two analyses supported our hypothesis that roads increase landscape permeability for African wild dogs when traveling. First, African wild dogs selected roads more strongly in habitat types with high vegetation density, suggesting that roads are more preferred for movement as the vegetation surrounding them becomes less permeable (Fig. 3). One exception to this trend occurred in riparian habitat, where road selection was lower than in either mixed woodland or mopane forest habitats. While riparian habitat was the most densely vegetated, the riverbanks and ground cover immediately abutting riparian areas was more open and may have served as movement corridors, a pattern that has been demonstrated for other large carnivore species (Hilty & Merenlender 2004; Dickson *et al.* 2005). Second, road selection tracked seasonal changes in vegetation, peaking during the peak wet season when vegetative growth is highest, and dropping during the peak dry season when ground cover is relatively sparse (Fig. 4). A second peak in road selection occurred during the Delta flood pulse, which coincides with the denning season for African wild dogs. This peak in road selection may reflect the benefits of efficient travel to and from den sites. Topographically, the study area is extremely flat, with no correlation between road locations and elevation; as a result, we found no evidence that road selection during the wet or flooding seasons is an artifact of animals simply selecting higher ground to avoid flooded areas. A potential alternative hypothesis for road use is that prey species

of African wild dogs use roads for travel or foraging and the dogs simply followed their prey. However, our results do not support this explanation as road selection was greatest in mopane habitat, which is the habitat type most strongly avoided by their primary prey species, impala (*Aepyceros melampus*; Bonyongo 2005), and this hypothesis does not explain the seasonal variation in road use exhibited by African wild dogs.

Roads also significantly influenced the turn angle and speed parameters of African wild dog movement, which may result in energetic benefits. Smaller turn angles (Fig. 5) and greater travel speeds may reflect reduced energetic costs of traveling on this type of open surface. These tendencies were most pronounced during the denning season, a finding that is consistent with work by Zimmermann *et al.* (2014), who reported that breeding wolves traveled faster than non-breeding wolves, especially on roads. Increased travel speeds during the denning season might be explained by two contributing factors: den site habitat characteristics and the nature of central place foraging. Wild dogs frequently choose den sites in relatively prey-poor habitat which has been attributed to comparatively low predator densities (Meer *et al.* 2013). Commuting relatively long distances through less prey-productive habitats could contribute to direct steady, and therefore faster, travel until reaching comparatively high prey density hunting areas. Secondly, the return trip to provision pups during the denning season represents a direct and purpose-driven commute from wherever they are to a known destination (i.e., central place). Elimination of the need to maintain cohesion as a social group while traveling (because the common destination is predetermined), as well as the relatively direct return trip commute, would contribute to increased average travel speeds during this period.

In addition to increasing landscape permeability, road use may have other behavioural advantages. One potential advantage of road use is demarcation of pack territories, as has been proposed for wolves (Zimmermann *et al.* 2014). African wild dogs regularly use roads as scent-marking sites since roads may act as transmission corridors for olfactory information (Parker 2010). Roads may also confer benefits for hunting behaviour. For example, roads may increase the line-of-sight to prey for African wild dogs (Latham *et al.* 2011). Indeed, Whittington and colleagues (2011) showed that encounter rates between wolves and caribou increased near linear features such as roads. Finally, while roads may increase the probability of encounters with other carnivore species (e.g., lions), road use may reduce the risk of potentially detrimental outcomes due to increased visibility along roads; this potential consequence of road use by traveling African wild dogs will be investigated as part of future studies of the movement patterns of this species.

These results suggest that unpaved roads do not reduce, and may in fact enhance, landscape permeability for African wild dogs in wildlife areas of northern Botswana. This can and should be incorporated into landscape-level connectivity assessments for this species, though managers must be careful to align conservation action with the specific behaviour of conservation concern. For example, our results indicate that preservation of suitable habitat for African wild dog rest sites would be markedly different to that for movement pathways. Future research should explore the potential negative impacts of roads on other behaviours such as denning (Meer *et al.* 2013), and the direct impact of vehicle strikes or other effects of human presence in human-dominated areas (Woodroffe *et al.* 2007).

Conclusions

Our findings emphasize the importance of considering the behavioural contexts in which animal movements occur when attempting to assess habitat preferences and responses to landscape features (Beyer *et al.* 2010; Wilson *et al.* 2012). Resource selection analyses are commonly used to inform landscape resistance surfaces in order to identify wildlife corridors (Chetkiewicz & Boyce 2009; Zeller, McGarigal & Whiteley 2012). We assert that conservation biologists should limit application of these data to localities identified when members of the target species are in an appropriate behavioural state; failure to do so risks misidentification of movement corridors (Elliot *et al.* 2014). While behaviour has been used to inform recommendations for conservation planning in marine systems (Ashe *et al.* 2010), it has yet to be similarly incorporated into land management for terrestrial species, particularly for the preservation of functional landscape connectivity. The use of behaviour-specific step selection functions as implemented here provides a powerful tool for analyzing fine-scale resource selection as part of efforts to conserve habitats critical to endangered wildlife.

Acknowledgements

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Table 1. Summary of step selection coefficients for “distance to road” by collar-derived behaviour categories (n = 13 individuals). Negative beta values indicate increasing “distance to road” has a negative effect on step selection, therefore negative values correspond to selection for locations nearer roads (road selection); positive values indicate selection for locations farther from roads (road avoidance). All beta and standard error values are multiplied by 10^{-4} . P-values were calculated from Wald tests.

Behaviour	# observed steps	β	SE	<i>p</i>
Combined	82840	-0.16	0.26	0.54
Traveling	70550	-1.47	0.20	<0.01*
Running	5934	-1.63	2.70	0.55
Resting	6356	3.23	0.13	0.015*

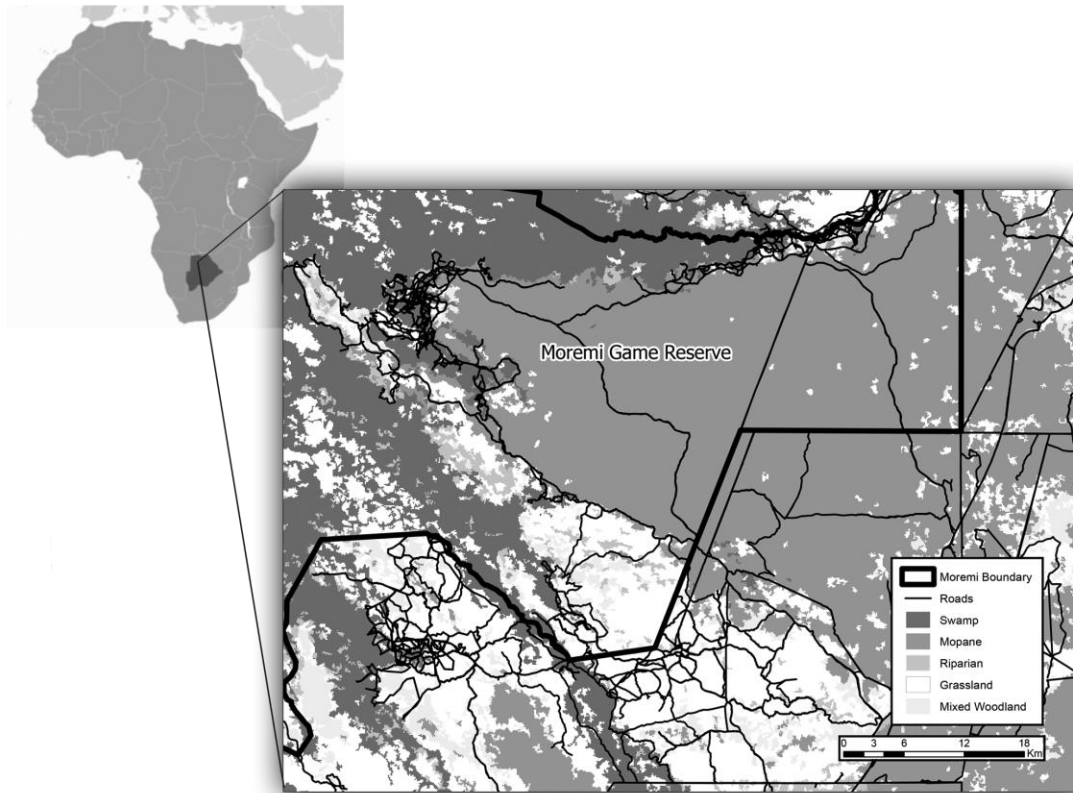


Figure 1. Map of study area (c. 2700 km²; centered at 19°31'S, 23°37'E) and major vegetation types.



Figure 2. A pack of African wild dogs (*Lycaon pictus*) on a typical sand road in the study area located in northern Botswana's Okavango Delta region.

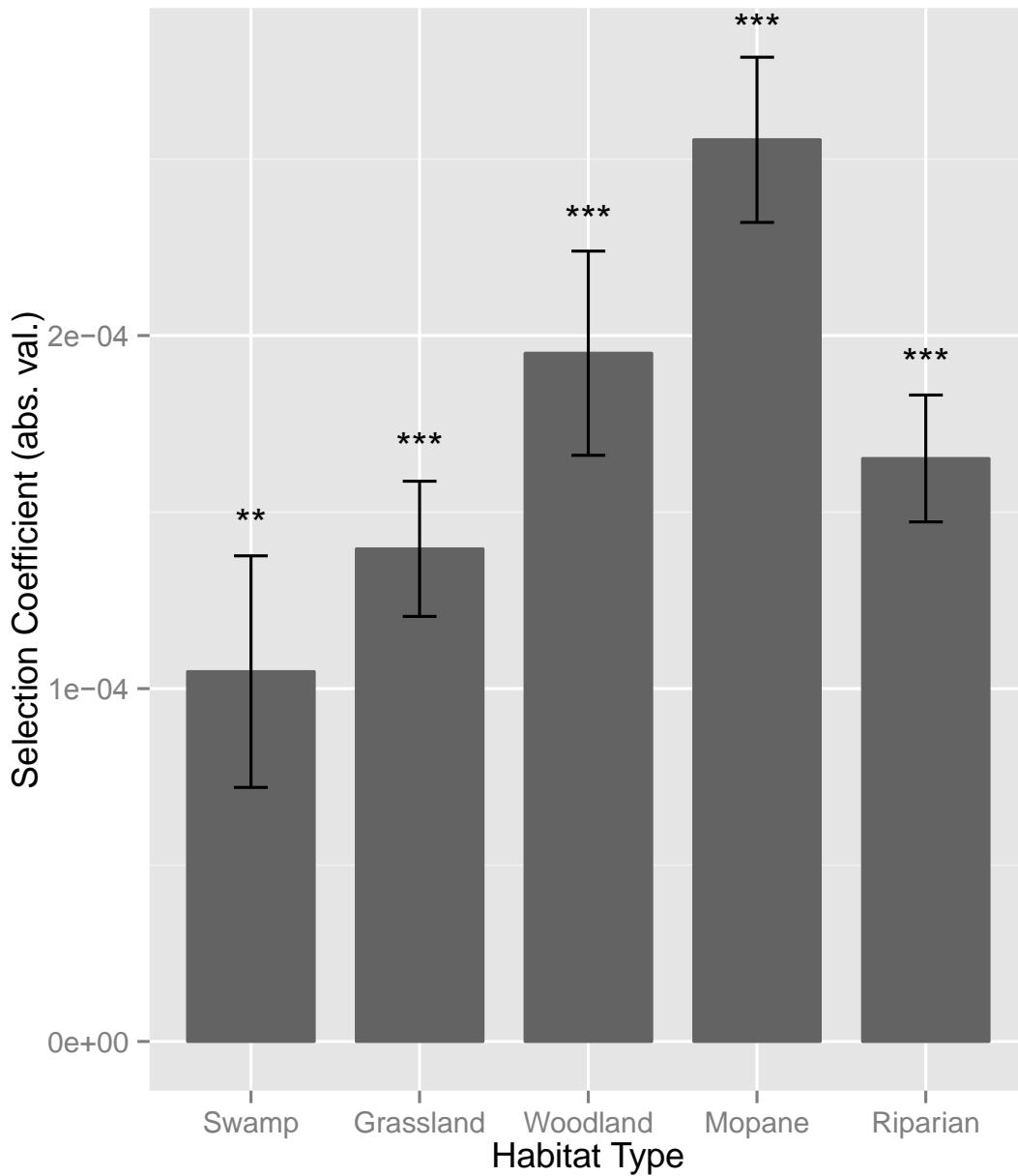


Figure 3. The strength of road selection as a function of habitat type for African wild dogs moving consistently (“traveling”, $n = 70550$ steps). Selection coefficients were calculated with step selection functions; larger values indicate stronger road selection. Habitats are listed in increasing order of vegetation density from left: swamp (open structure), grassland (open structure), mixed woodland (medium structure), mopane forest (medium-dense structure), and riparian (dense structure). With the exception of riparian habitat (see Discussion), the strength of road selection increases in denser habitat types.

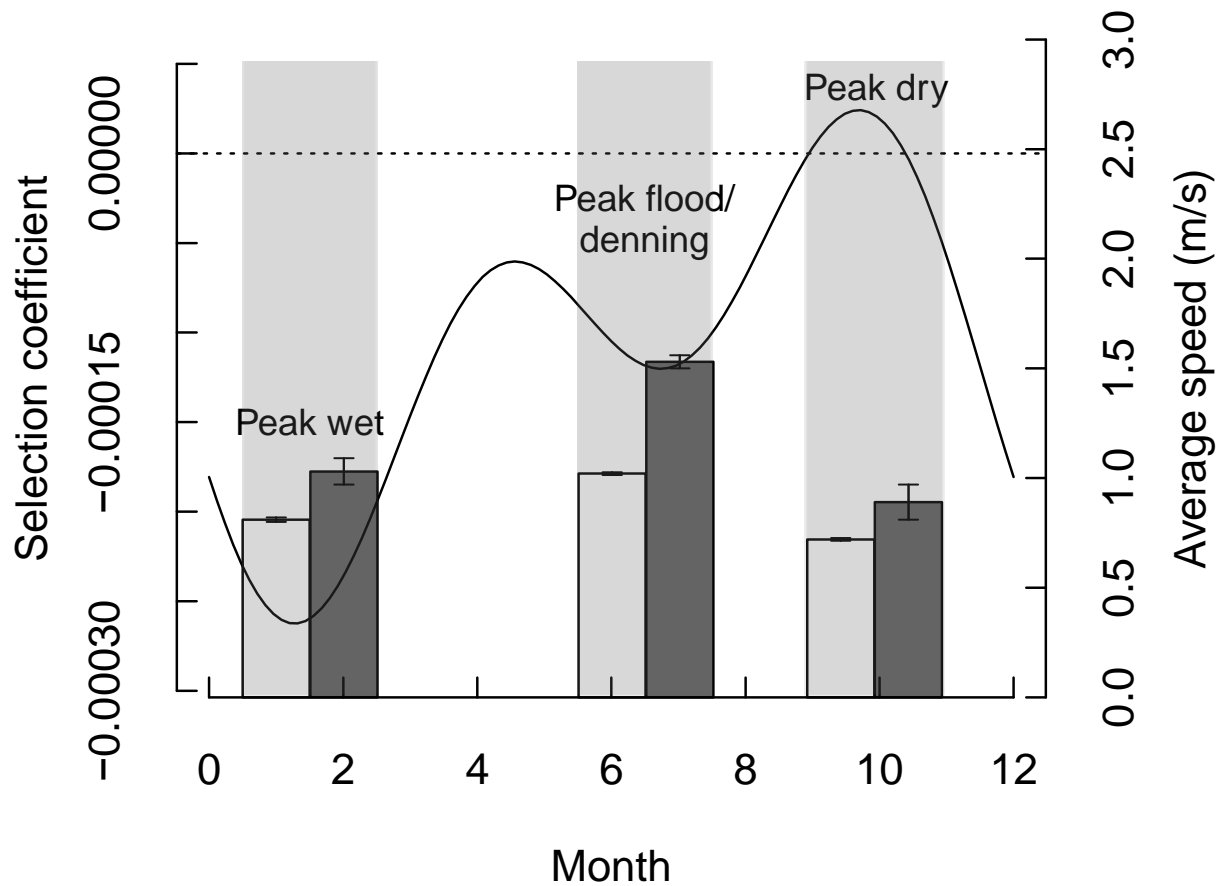


Figure 4. Variation in road selection over time of year (black line) when African wild dogs were moving consistently (“traveling”, $n = 70550$ steps) and corresponding travel speeds averaged within each season (light grey bars = average off-road travel speed; dark grey bars = average on-road travel speed). Negative step selection coefficients correspond to selection for locations nearer roads (road selection); positive values indicate selection for locations farther from roads (road avoidance). Three distinct climatic seasons are highlighted: peak wet, peak flood, and peak dry seasons.

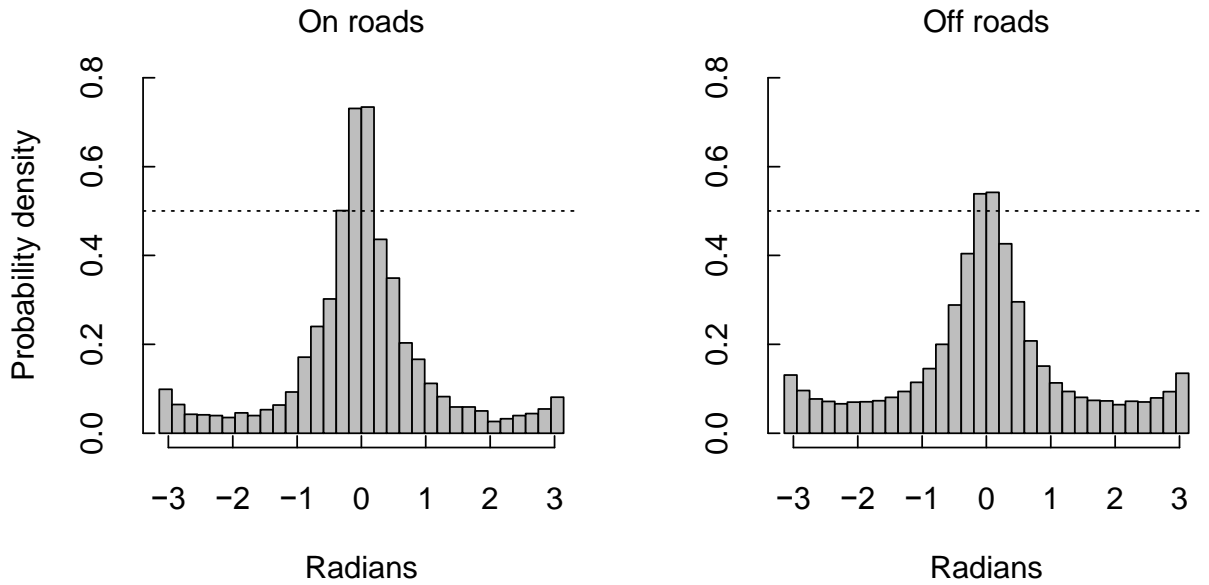


Figure 5. Probability density of turn angles for steps on roads and off roads when African wild dogs were moving consistently (“traveling”, $n = 70550$ steps). The dotted line highlights the 50% probability density for comparison between plots. Turn angles were measured as the change in bearing from the previous step.

Supplementary Material

Table S1. Pack identities and data collected per collared individual.

Individual	Gender	Pack ID	Study Period	# GPS locations
Accra*	F	KB	Apr.-Sep. 2012	64,192
Timbuktu	F	KB	Apr.-Sep. 2012	38,366
Scorpion	M	KB	Apr. 2012-Oct. 2013	50,411
Kobe	M	KB	Apr.-July 2012	24,852
Gomer*	M	HW	Nov. 2011-Nov. 2012	23,023
Bongwe	M	HW	Apr.-Dec. 2012	17,378
Bobedi	F	HW	Nov. 2011-July 2012	20,676
Yolo*	M	MT	Nov. 2011-2012	21,131
Stetson	M	MT	Nov. 2011-Apr. 2012	8,906
Brian	M	MT	Apr.-July 2012	5,604
Dar*	F	CT	Apr.-Aug. 2012	1,447
Kubu*	F	MK	Apr.-Oct. 2012	8,587
Jesus*	M	SA	Mar.-July 2012	5,983

* Individuals included in the more conservative analyses excluding multiple individuals from the same pack.

Table S2. Summary of step selection coefficients for distance to road by collar-derived behaviour categories excluding multiple individuals from the same pack ($n = 6$ individuals). Negative beta values correspond to selection for locations nearer roads (road selection); positive values indicate selection for locations farther from roads (road avoidance). All beta and standard error values are multiplied by 10^{-4} . P-values were calculated from Wald tests.

Behaviour	# observed steps	β	SE	p
Combined	29326	-0.47	0.55	0.461
Traveling	25601	-2.18	0.27	<0.01*
Running	1794	-11.7	8.1	0.151
Resting	3168	2.96	1.64	0.07

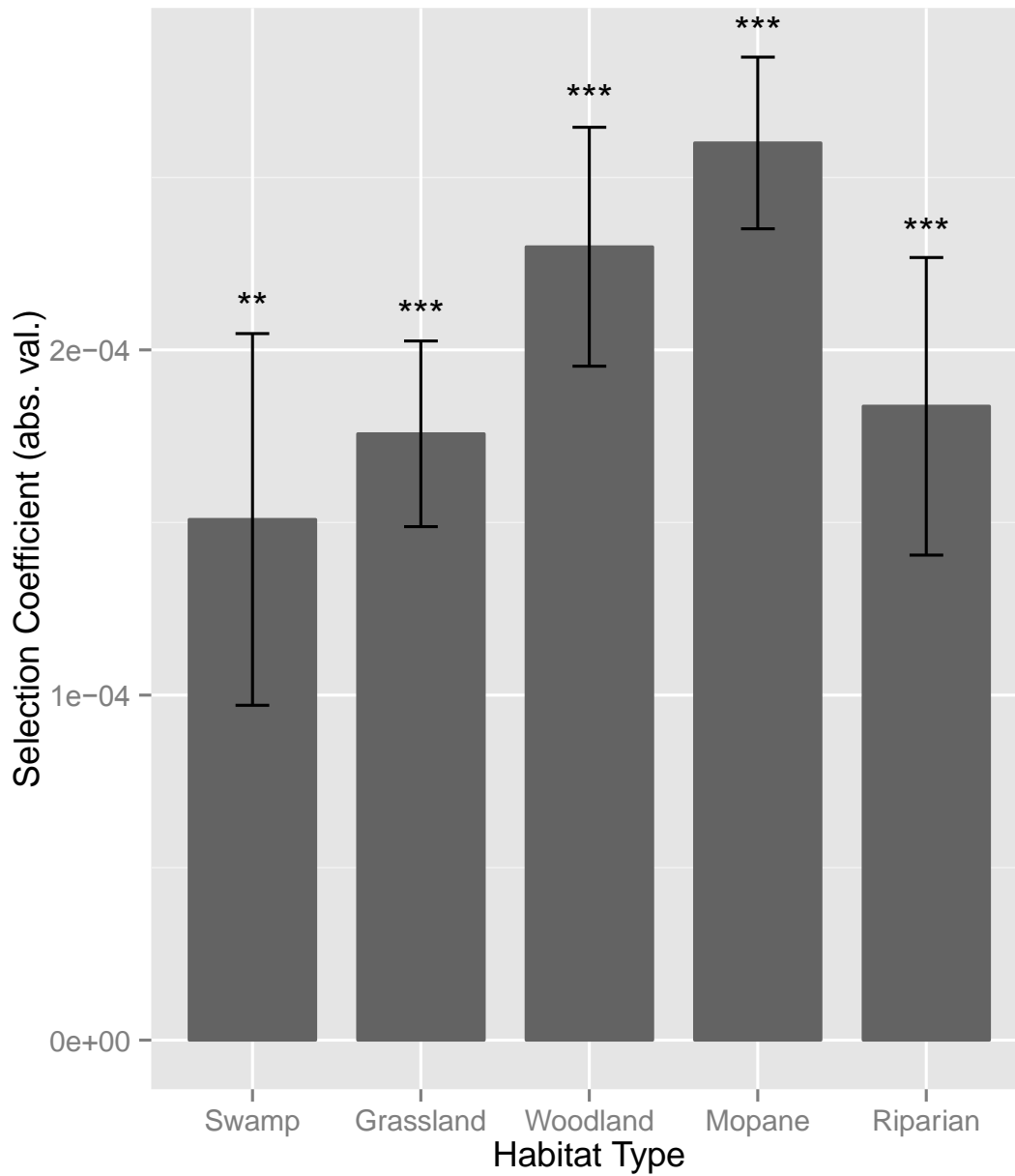


Figure S1. The strength of road selection as a function of habitat type for African wild dogs moving consistently, excluding multiple individuals from the same pack (“traveling”; $n = 6$ individuals, 25601 steps). Selection coefficients were calculated with step selection functions; larger values indicate stronger road selection. Habitats are listed in increasing order of vegetation density from left: swamp (open structure), grassland (open structure), mixed woodland (medium structure), mopane forest (medium-dense structure), and riparian (dense structure). With the exception of riparian habitat (see Discussion), the strength of road selection increases in denser habitat types.

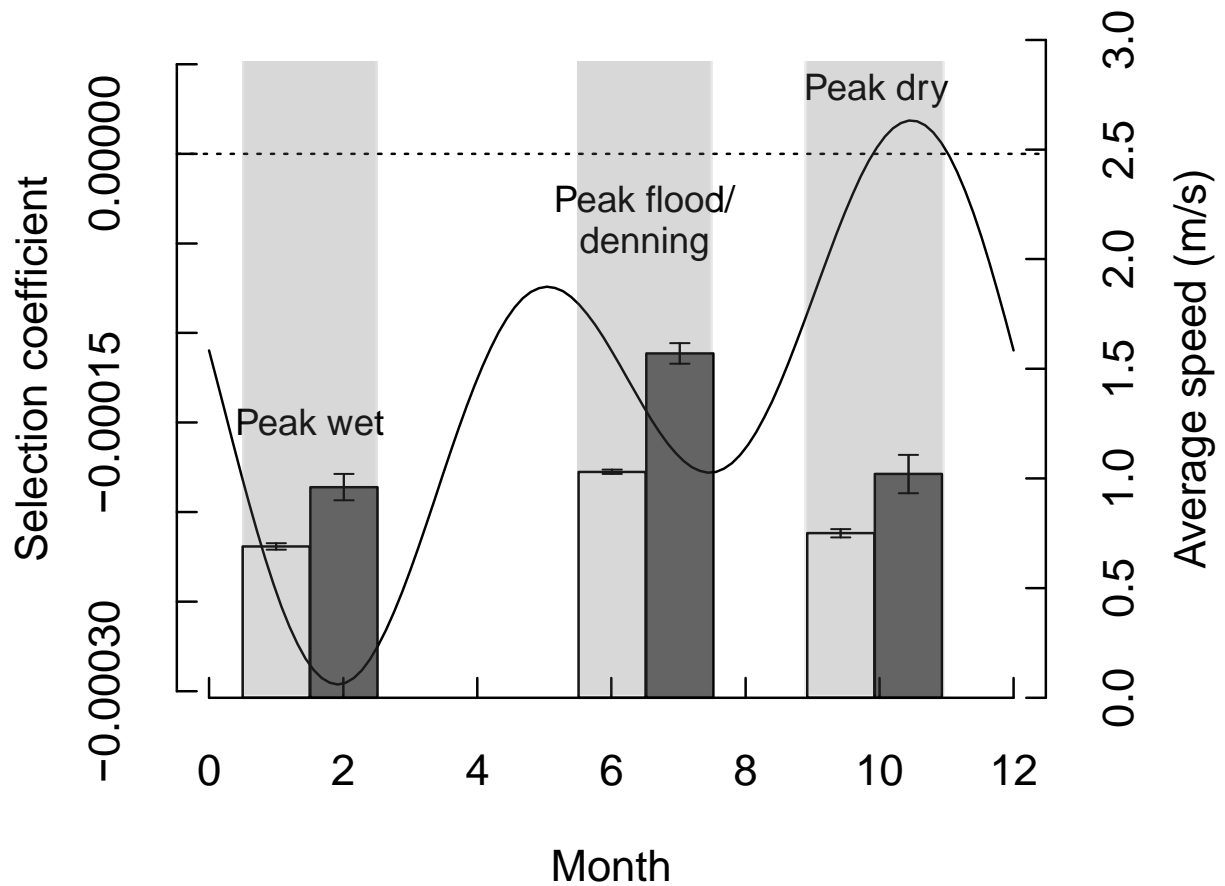


Figure S2. Variation in road selection over time of year (black line) when African wild dogs were moving consistently, excluding multiple individuals from the same pack (“traveling”; $n = 6$ individuals, 25601 steps), and corresponding travel speeds averaged within each season (light grey bars = average off-road travel speed; dark grey bars = average on-road travel speed). Negative step selection coefficients correspond to selection for locations nearer roads (road selection); positive values indicate selection for locations farther from roads (road avoidance). Three distinct climatic seasons are highlighted: peak wet, peak flood, and peak dry seasons.

3. Does wildlife resource selection accurately inform corridor conservation?

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Abstract

1. Evaluating landscape connectivity and identifying and protecting corridors for animal movement have become central challenges in applied ecology and conservation. Currently, resource selection analyses are widely used to focus corridor planning where animal movement is predicted to occur. An animal's behavioural state (e.g. foraging, dispersing) is a significant determinant of resource selection patterns, yet has largely been ignored in connectivity assessments.
2. We review sixteen years of connectivity studies employing resource selection analysis to evaluate how researchers have incorporated animal behaviour into corridor planning, and highlight promising new approaches for identifying wildlife corridors. To illustrate the importance of behavioural information in such analyses, we present an empirical case study to test behaviour-specific predictions of connectivity with long-distance dispersal movements of African wild dogs *Lycaon pictus*. We conclude by recommending strategies for developing more realistic connectivity models for future conservation efforts.
3. Our review indicates that most connectivity studies conflate resource selection with connectivity requirements, which may result in misleading estimates of landscape resistance, and lack validation of proposed connectivity models with movement data.
4. Our case study shows that including only directed-movement behaviour when measuring resource selection reveals markedly different, and more accurate, connectivity estimates than a model measuring resource selection independent of behavioural state.
5. *Synthesis and applications.* Our results, using African wild dogs as a case study, suggest that resource selection analyses that fail to consider an animal's behavioural state may be insufficient in targeting movement pathways and corridors for protection. This failure may result in misidentification of wildlife corridors and misallocation of limited conservation resources. Our findings underscore the need for considering patterns of animal movement in appropriate behavioural contexts to ensure the effective application of resource selection analyses for corridor planning.

Keywords

behavioural state, conservation planning, corridor ecology, dispersal, landscape connectivity, landscape resistance, movement ecology, resource selection, step selection

Introduction

Connectivity, i.e., the degree to which a landscape facilitates or impedes movement between resources or habitats (Taylor *et al.* 1993), is a key aspect of land management for the conservation of species and communities. Connectivity influences demography (Clobert *et al.* 2001), promotes dispersal and colonization (Hanski 1998), maintains genetic diversity (Hendrick 2005), increases a species' ability to respond to perturbations and changing climates (Heller & Zavaleta 2009), and supports long term persistence in heterogeneous landscapes (Vasudev *et al.* 2015). Consequently, increasing landscape connectivity has been identified as a fundamental strategy for mitigating impacts of climate change on biodiversity (Heller & Zavaleta 2009).

The identification and protection of wildlife corridors, i.e., land allowing movement of focal species between two or more habitat areas (Beier *et al.* 2008), has become a critical tool for the maintenance of landscape connectivity (Gilbert-Norton *et al.* 2010). As a response to global concerns about habitat fragmentation, climate change, and loss of landscape connectivity, establishment of wildlife corridors has accelerated in the last decade and half. Today, studies aimed at evaluating connectivity and determining where to establish corridors have become central to conservation science and practice (Beier, Majka & Spencer 2008; Beier *et al.* 2011; Rudnick *et al.* 2012).

Here, we systematically review sixteen years of studies using wildlife resource selection to estimate landscape connectivity and highlight promising new approaches for identifying wildlife corridors. We argue that failure to assess resource selection in appropriate behavioural contexts may lead to misidentification of wildlife corridors and misallocation of limited conservation resources.

Methods for identifying wildlife corridors

Accurate identification of functional corridors depends on knowledge of a species' dispersal requirements (Vasudev *et al.* 2015). Currently, estimating landscape resistance to movement is the most widely used technique to focus corridor planning on areas where dispersal is considered most likely to occur (Sawyer, Epps & Brashares 2011). Landscape resistance models – or 'resistance surfaces' – assign a value in a landscape grid cell to each environmental variable of interest (e.g. elevation, land cover) that represents the energetic or survival cost to the study species of moving through that spatial position (Adriaensen *et al.* 2003), or the willingness of the individual to cross the cell (Zeller, McGarigal & Whiteley 2012). Earlier efforts to estimate landscape resistance based on expert opinion (e.g., LaRue & Nielsen 2008; Shen *et al.* 2008) have been greatly advanced by technological and analytical tools that now allow researchers to evaluate resistance directly from empirical data (Zeller, McGarigal & Whiteley 2012). Methods for estimating resistance based on empirical data fall into the following two main approaches, landscape genetics and resource selection functions.

Landscape genetics approaches measure the correlation of observed genetic distance between individuals or subpopulations separated by hypothesized values of landscape resistance (Cushman *et al.* 2006; Epps *et al.* 2007). Thus, landscape genetics infers the influence of landscape variables on gene flow. These methods are a gold standard in connectivity modelling

when the process of interest is genetic connectivity. However, the few studies that have attempted to validate genetic results with movement data indicate that while resistance models derived from landscape genetics are useful in understanding large-scale effects on the process of gene flow, they may not be as useful for predicting pathways of wildlife movement at finer, management-relevant scales (Reding *et al.* 2013; Graves, Beier & Royle 2013). Additionally, genetically-derived connectivity estimates can reflect past landscape permeability, due to the time-lag to detect barriers (15-100 generations depending on methods and species traits; Langduth *et al.* 2010), and thus may not capture current movement in rapidly evolving landscapes, changing climates or for species dispersing short distances.

Given the uncertainties associated with applying landscape genetics to landscape planning at finer spatial and temporal scales, we focused our review on the use of resource selection functions (RSFs). In contrast to landscape genetic analyses, estimates of landscape resistance derived from RSFs are thought to be effective at predicting areas for wildlife movement at more immediate and fine scales; as a consequence, this approach is highly applicable to management decisions (Chetkiewicz & Boyce 2009). Resource selection functions calculate the probability of use of a given landscape variable (e.g., habitat type, elevation, slope) by statistically comparing the characteristics of locations used by the study species with those in a control set of random locations deemed available to, but presumably unused by, that species (Manly *et al.* 2002). These analyses have recently been improved by the introduction of step selection (Fortin *et al.* 2005; Thurfjell, Ciuti & Boyce 2014) and path selection (Cushman & Lewis 2010) functions, which characterize movement as a series of linked steps or paths rather than a distribution of independent points. Thus, while traditional RSFs, also known as point selection functions, are well-suited for detection data, step and path selection analyses tend to be more useful for relocation data because they account for changes in resource availability as an animal moves through its landscape (Zeller, McGarigal & Whiteley 2012).

The role of behaviour

Use of RSFs in connectivity planning is largely based on the assumption that a habitat occupied/selected by a species is predictive of the landscape conditions or features necessary for successful dispersal (Vasudev *et al.* 2015). This critical assumption has been the subject of debate, specifically regarding the degree to which resource selection models provide an accurate proxy for movement preference as an animal navigates through a landscape (Beier, Majka & Spencer 2008; Zeller, McGarigal & Whiteley 2012; Fattebert *et al.* 2015). Resource selection during dispersal may differ significantly from selection exhibited during daily residential activities (Elliot *et al.* 2014; Vasudev *et al.* 2015; Gastón & Cabrera 2016). In particular, there is increasing recognition that an animal's behavioural state (e.g. resource use vs. searching, territory maintenance vs. dispersing) can strongly mediate patterns of resource selection (Wilson, Gilbert-Norton & Gese 2012; Roever *et al.* 2013; Abrahms *et al.* 2016).

Behaviourally-mediated differences in resource selection can have important effects on estimates of landscape resistance and resulting conservation actions. For example, a recent study by Zeller and colleagues (2014) found opposite patterns of resistance to some landscape variables for pumas *Puma concolor* in a 'resource use' behavioural state versus a directed 'movement' state. Similarly, Elliot and colleagues (2014) found that landscape resistance differed between

dispersing and resident male lions *Panthera leo*. Thus, failure to assess resource selection in appropriate behavioural contexts may lead to misidentification of corridors for animal movement and ineffective use of limited conservation funding (LaPoint *et al.* 2013; Elliot *et al.* 2014). Because dispersal events are often difficult to detect in the field, resource selection measured during directed movement states may provide an important proxy that can be used to infer functional connectivity in addition to or in lieu of direct dispersal data. Yet, little work has validated RSF-derived predictions of landscape connectivity with long-distance movement data to assess this possibility.

We surveyed recent RSF-derived connectivity studies to 1) evaluate the extent to which these efforts have incorporated movement behaviour and 2) identify best practices for considering movement behaviour for future connectivity studies. While the range of definitions for animal movement is vast (Nathan *et al.* 2008), we define ‘movement behaviour’ in the context of connectivity science as directed movement toward a new location (i.e., taxis), typical of movement between rest sites or resource patches (Schick *et al.* 2008). Using this definition, we evaluated published studies with regard to how movement behaviour was considered in estimating landscape resistance and predicting connectivity. Using data drawn from our studies of African wild dogs, we demonstrate the sensitivity of corridor models to behavioural state and test the validity of model predictions against empirical movement data. Specifically, we use high-resolution GPS data from African wild dogs in northern Botswana to create least-cost path predictions from two RSF-derived resistance models, one that ignores behavioural state and one that isolates movement behaviour. We then test these predictions against observed long-distance dispersal paths. We conclude by providing a framework and recommending strategies for researchers and managers to develop more realistic connectivity models for future corridor planning efforts.

Materials and Methods

Literature review

To capture current trends in the literature, we searched ISI Web of Science for papers published between January 2000 and February 2016 that contained the following key words: Topic = (landscape resistance OR cost-distance OR effective distance) AND (corridor OR connectivity OR linkage). We filtered the resulting 157 papers by restricting our search to the subject areas Ecology, Environmental Sciences, Environmental Studies, Zoology, Biology, Biodiversity Conservation, or Remote Sensing; this resulted in a subset of 137 papers. We further restricted our review by excluding studies that did not use resource selection to estimate landscape resistance and/or did not explicitly aim to model connectivity for the purpose of predicting wildlife movement, resulting in a final set of 28 papers (Table 1). For each of the selected papers, we evaluated: (1) the source of biological data (study species and data collection method), (2) type of RSF employed (e.g., point selection, step selection), (3) whether movement behaviour was explicitly considered in developing connectivity models, and (4) whether modelled corridors were validated with independent movement data.

African wild dog case study

To determine whether isolation of directed movement behaviour improves predictions regarding long-distance movement paths, we collected high-resolution GPS data from 15 free-ranging African wild dogs in northern Botswana (Abrahms *et al.* 2016). African wild dogs are both the widest ranging and most endangered of Africa's large carnivores; the International Union for Conservation of Nature (IUCN) has linked the decline of wild dog populations to the species' high sensitivity to habitat fragmentation (Woodroffe & Sillero-Zubiri 2013). Consequently, these animals are a highly relevant focal species for assessing functional landscape connectivity.

Using collar-mounted accelerometers, we classified GPS locations into three discrete behavioural states: traveling, chasing, and resting (Hubel *et al.* 2016). We used step selection functions to quantify resource selection for a 'combined model' that included all available data, ignoring behavioural state, and for a 'movement model' that included only the traveling dataset (Thurfjell, Ciuti & Boyce 2014). Three of the 15 collared wild dogs exhibited long-distance dispersal movements during the study period; these animals were excluded from the step selection analysis to serve as test data against corridor model outputs. The data from the remaining 12 individuals used to parameterize our models were collected from 12 different packs to minimize risk of pseudoreplication. Habitat cover, land use type, proximity to road, and proximity to human settlements were included as initial covariates after testing for collinearity based on known influences on African wild dog space use (Woodroffe 2010; Whittington-Jones *et al.* 2014; Abrahms *et al.* 2016; Table 2). We used AIC forward model selection to determine which to retain in our final models (Burnham & Anderson 2002). We used significant selection coefficients from each model to create two corresponding resistance surfaces (Squires *et al.* 2013). For each resistance surface we used least-cost path (LCP) analysis to predict the dispersal paths of the three dispersers, as this represents the most commonly used method for designing wildlife corridors (Sawyer, Epps & Brashares 2011). Finally, to address the uncertainty inherent in least-cost modelling we estimated least-cost corridors that overcome the single-pixel width limitation of LCPs (Beier, Majka & Newell 2009). Following published recommendations (Harrison 1992; Beier, Majka & Spencer 2008), we buffered our LCPs by a conservative estimate of half the average home range width for African wild dogs (8km; Woodroffe 2010) to determine biologically-informed corridor widths of 16 km.

To evaluate our models, we used two metrics as suggested by a recent study comparing the utility of connectivity modelling validation methods (McClure, Hansen & Inman 2016). Firstly, we calculated the percentage of observed dispersal relocations overlapping with predicted least-cost corridors, a metric relevant to conservation practitioners in assessing the proportion of movement that would be protected by a potential corridor (Poor *et al.* 2012; McClure, Hansen & Inman 2016). Secondly, we measured the path deviation of each model's LCP from the observed dispersal paths, a straightforward statistic of how well the model agrees with the data (Pullinger & Johnson 2010). All statistical analyses were performed using R 3.1.0 (R Core Team 2014). We used ESRI ArcMap 10.2 to create resistance surfaces and Linkage Mapper software (McRae & Kavanagh 2011) to generate least-cost paths. See Appendix S1 for full methods details.

Results

Literature review

The majority of studies (82%) used animal relocation data from either GPS or VHF collars to assess resource selection, while five (18%) relied on measures of indirect detection such as animal sign or camera trap data. None of the detection-based studies made efforts to focus on movement-related habitat use. In total, 11 of the 28 studies evaluated included efforts to explicitly incorporate movement behaviour into their connectivity analyses. The remaining studies assumed that resource selection indicated connectivity requirements.

Only five studies (18%) validated connectivity predictions with movement data. LaPoint *et al.* (2013) found poor agreement between corridor predictions for fishers *Martes pennanti* based on GPS locations versus ‘animal-defined’ corridors delineated by quick, repeated, and linear fisher movements. Deployment of camera traps demonstrated greater use by fishers of animal-defined corridors than cost-based corridors. In contrast, Harju and colleagues (2013) found that connectivity estimates based on resource selection during traveling and relocating movement states for sage-grouse *Centrocercus urophasianus* were strong predictors of an independent test set of locations for these movement states. Finally, Trainor *et al.* (2013) found a strong correlation between connectivity predictions for red-cockaded woodpeckers *Leuconotopicus borealis* based on resource selection during exploratory forays and an independent dataset of short-distance dispersals.

African wild dog case study

The highest ranked movement model based on AIC model selection retained habitat cover, land use type, and distance to roads as predictor variables; the highest ranked combined model retained habitat cover and land use type (Table S2). Step selection results showed different, and in some cases opposing, responses to landscape variables between the movement model and the combined model (Fig.1, Table S3); these differences were reflected in the divergent patterns of landscape resistance between the two models and resulting LCPs (Fig. 2). Least-cost corridors from the movement model overlapped with the large majority of GPS locations from the three dispersal paths (range 62 -100%, mean 87%; Table 3) while those from the combined model included a lower percentage of GPS locations (range 0-100%, mean 33%). Path deviations between the movement model LCPs and observed paths were significantly lower than those between the combined model LCPs and observed paths.

Discussion

Literature review: inclusion of movement behaviour in corridor planning

Collectively, the studies in our review that validated connectivity predictions with independent movement data point to the importance of incorporating behavioural data in connectivity models as a key step toward generating management strategies. As showcased by several such studies, multiple data collection, technological and analytical approaches exist to aid conservation scientists and practitioners in including movement behaviour in corridor planning. The eleven studies that considered animal movement behaviour in their connectivity predictions provide

informative examples for working with relocation data (Table 4). From these studies, we identified two principal scales at which movement behaviour has been addressed: a behavioural level and a demographic level. At the behavioural level, several studies identified the subset of locations at which animals displayed behavioural states categorized broadly as movement behaviour. These categorizations included a) ‘traveling’, ‘relocating’, or ‘moving’ based on step-length distributions (Harju *et al.* 2013; Zeller *et al.* 2014); b) ‘large-scale movements’ delimited by a threshold for movement rate (Pullinger & Johnson 2010); and c) ‘active’ versus ‘resting’ behaviour based on both step-length and turn angle distributions (Squires *et al.* 2013). At the demographic level, three studies employed a demographic approach by collaring and collecting relocation data from juvenile dispersers (Richard & Armstrong 2010; Trainor *et al.* 2013; Elliot *et al.* 2014). While behavioural and demographic approaches may be used in concert, we distinguish a demographic approach from a behavioural one in that it may include all behavioural states of a disperser. This approach may be ideal for determining how dispersers navigate their landscape, but it is logistically challenging because it requires predicting which individuals in the population will disperse. Perhaps not coincidentally, two of these three studies focused on birds, where identification and tagging of juvenile dispersers is easier than it is for many other vertebrates (Zeller, McGarigal & Whiteley 2012). To focus on dispersal movements, three other studies collected location data during known dispersal seasons for their study species (Cushman & Lewis 2010; Walpole *et al.* 2012; Roever, van Aarde & Leggett 2013).

Advances in GPS collar technology over the last decade can contribute to connectivity science by coupling discrete behavioural states with patterns of space use and movement preference. In particular, activity sensors such as collar-mounted accelerometers, magnetometers, and physiological loggers are becoming increasingly popular for classifying behavioural states remotely (Brown, Kays & Wikelski 2013; Wilson *et al.* 2013; Nams 2014). However, the literature also provides many methods for inferring behavioural state without the expense of activity sensors, even for collars that operate at coarse spatiotemporal scales. For instance, Pullinger & Johnson (2010) classified two behavioural states of resource use versus long-distance movement for caribou *Rangifer tarandus* by examining movement rate between 3-hour GPS fix intervals. Similarly, pairing movement rate with turn angle distributions revealed a clear distinction between sedentary and exploratory behavioural states in elephants (Roever *et al.* 2013). Patterns of GPS clustering have been used to further partition relocation data, including identifying kill sites, dens, and scent marking areas for pumas (Wilmers *et al.* 2013) and feeding and bedding behaviours in grizzly bears (Cristescu, Stenhouse & Boyce 2015). The wide variety of existing methods for inferring behavioural states necessitate the development of best practices for their application and interpretation in the context of connectivity modelling.

As mentioned previously, advances have also been made in the analytical procedures associated with resource selection analyses, such as the addition of step selection (Fortin *et al.* 2005; Thurfjell, Ciuti & Boyce 2014) and path selection functions (Cushman & Lewis 2010). Both of these analytical approaches can help to quantify selection specifically for movement paths, though for the purposes of connectivity modelling care must still be taken to ensure resource selection is measured for the appropriate behavioural state(s). In addition, the rapidly growing field of movement ecology (Schick *et al.* 2008; Nathan *et al.* 2008) offers many analytical approaches for remote identification of behavioural states such as hidden Markov (Patterson *et*

al. 2009) and state-space models (Jonsen, Flemming & Myers 2005; Patterson *et al.* 2008) that have been developed for effectively analysing noisy or imperfect animal movement data.

Our result that none of the detection-based studies focused on movement-related habitat use highlights a ripe opportunity for advancement. Indirect detection methods are often less costly than obtaining direct relocation data and are sometimes the only feasible option for rare or elusive species. For those using indirect detection based on sign to identify movement corridors (e.g., Walpole *et al.* 2012; Mateo-Sánchez, Cushman & Saura 2014), locations with sign of resource-use behaviour (e.g. gorilla nesting/feeding sign, McNeilage *et al.* 2006; grizzly bear bedding sites, Munro *et al.* 2006) can be excluded from resource selection analyses in favour of travel-related sign (e.g., gorilla trampled vegetation, dung, footprints; Sawyer & Brashares 2013) to limit inferences to more movement-focused habitat use. For studies relying on camera trap data to identify corridors (e.g., Brodie *et al.* 2014; Wang *et al.* 2014), there are several improvements that can be made beyond using standard abundance estimates to infer areas with high connectivity. If individual identification from photos is possible, spatially-explicit movement rates can be measured and related to landscape variables through spatial capture-recapture methods (Royle *et al.* 2013a; b). If individual identification is not possible, camera trap data can be used to associate habitat use with activity patterns of the study species (Rowcliffe *et al.* 2014). Given that nearly 20% of the connectivity studies we evaluated relied on indirect detection for their resource selection analyses, development and application of methods to better assess movement behaviour in these data sets is greatly needed.

We propose a series of steps that can be taken through the data collection and analysis stages of resource selection estimation to better emphasize movement behaviour in connectivity modelling (Fig. 3). As is the case with all ecological fieldwork, the processes we suggest depend first on what data can be feasibly collected for the target species. However, since location data are often used for a variety of purposes and thus may not have been collected specifically for connectivity analyses, we suggest that researchers working with such data sets apply the analytical approaches outlined above to focus inferences on movement behaviour regardless of the methods employed during the data collection stage.

African wild dog case study

Results from our African wild dog case study mirror a small set of recent publications (e.g., Harju *et al.* 2013; Trainor *et al.* 2013) indicating that including only movement behaviour in resistance surfaces analyses reveals markedly different patterns of connectivity than models measuring resource selection without consideration of behavioural state. For the goal of predicting and protecting dispersal, the movement model (i.e., only GPS positions when the dogs were in a ‘traveling’ behavioural state) outperformed the combined model (i.e., all available GPS positions independent of behavioural state) according to both validation metrics used in our analysis (Table 3). The movement model least-cost corridor (LCC) fully incorporated two of the three observed dispersal paths, overlapping with a total of 87% of movement locations compared with only 33% for the combined model LCC. In addition, the path deviation statistic indicated greater agreement between the least-cost paths derived from the movement model and the observed wild dog dispersal paths than those from the combined model. These results suggest

that a general resource selection analysis may be insufficient in predicting and protecting movement pathways for African wild dogs.

The divergent patterns of resource selection by African wild dogs revealed by our models have significance for the conservation and management of this species. African wild dogs displayed large differences in habitat preference when traveling compared to when behavioural state was not considered. Our behaviourally informed model also revealed that African wild dogs showed a higher tolerance for human-modified landscapes and features (pastoral areas, roads) when dispersing, an outcome that has been reported for other dispersing carnivores including lions (Elliot *et al.* 2014) and Iberian lynx *Lynx pardinus* (Gastón & Cabrera 2016). While the ability of dispersing carnivores to navigate potentially hostile landscapes may allow populations to maintain greater levels of connectivity than previously thought (Mateo-Sánchez *et al.* 2015), this also places them at higher risk of human-wildlife conflict. Because of increased tolerance for human disturbance and proclivity to range beyond protected areas, African wild dogs in a dispersing or exploratory state are more prone to human-caused mortality (Woodroffe *et al.* 2007; Davies-Mostert *et al.* 2012) and thus it is essential that creation of corridors for large carnivore movement be paired with efforts to mitigate human-carnivore conflict (Elliot *et al.* 2014).

Caveats

A number of caveats and assumptions to this work are important to note. First, this work is focused on corridor design for terrestrial vertebrates, and not for entire community assemblages. The latter would rely less upon single-species dispersal requirements than broader estimates of structural connectivity, such as landscape ‘naturalness’ (Theobald *et al.* 2012). We also focus on connectivity as viewed through movement corridors, rather than the more spatially-expansive lens of habitat contiguity. The first emphasizes the maintenance of pathways for effective dispersal between populations while the second seeks to preserve viable habitat to ensure occupancy of a focal species across fragmented landscapes. This distinction is important in the context of our review because resource selection functions or other general assessments of habitat use may be effective on their own where the conservation goal is simply to preserve a connected system of occupied habitats.

We chose to employ least-cost path (LCP) analysis for our case study because it is the most popular method for managers to delineate corridors (Sawyer, Epps & Brashares 2011), however it requires a number of assumptions that may not be upheld in all cases. First, it assumes a defined start and end point, which is appropriate when determining a connection between two protected areas, or in our case a natal and dispersal range, but this assumption is often violated when clear habitat patches cannot be demarcated. Similarly, LCP analysis cannot evaluate multiple potential pathways between more than two patches. In addition, by weighting the cumulative cost of a pathway by its total Euclidean distance, LCP analysis implicitly assumes that animals have total knowledge of their landscape, which is especially likely to be violated when animals are dispersing into new territory. Ultimately, when evaluating whether to use a least-cost or alternative approach such as circuit-theory modelling, the movement ecology of the focal species and the landscape context are key determinants that should be considered (McClure, Hansen & Inman 2016).

A final and important limitation to our case study is the small number of known dispersal paths for our study animals, despite data collection over a four-year period, highlighting the challenge of collecting long-distance movement data for evaluating functional landscape connectivity. Efforts such as ours to directly compare behaviour-informed predictions of connectivity with known long-distance dispersal movements are accordingly rare. Nevertheless, the strong effect sizes of our model validation metrics lend confidence to our inference that consideration of behavioural state is critical, and that by focusing connectivity analyses on movement behaviour, researchers can eliminate much of the noise that comes from analysing all data points.

Conclusions and future directions

While the protection of corridors for animal movement involves sociopolitical, economic and other considerations that were not addressed in this assessment, our review and case study suggest that the success of corridor efforts also relies on an accurate understanding of how animals move through their environment. Resource selection within an animal's home range may be a suitable proxy for movement preference during dispersal for some species (Fattebert *et al.* 2015), though researchers and conservation practitioners should be aware this is not always the case and failure to recognize this distinction may have important consequences for preserving landscape connectivity. Our findings underscore the need for examining animal movement in appropriate behavioural contexts to ensure effective application of resource selection analyses for corridor planning. Advances in monitoring technology are fostering new opportunities to study wildlife movements that promise to enhance corridor conservation. At the same time, current analytical tools that rely on indirect location data can be improved to more accurately inform connectivity models. Given limited conservation resources and rapidly changing environments, efficient and accurate corridor identification, establishment and management is a critical need in conservation planning. Unifying the fields of movement ecology and connectivity science promises to advance our knowledge of – and thus our ability to preserve – the fundamental process of wildlife movement.

Acknowledgements

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Data Accessibility

African wild dog dispersal path data are available from the Dryad Digital Repository:
<http://dx.doi.org/10.5061/dryad.66kc7>.

Table 1. Summary of studies evaluated that used resource selection analyses to model connectivity for wildlife movement.

<i>Study</i>	<i>Species</i>	<i>Data Collected</i>	<i>RSF Type^d</i>	<i>Consideration of Movement Behavior</i>	<i>Validation of Connectivity Predictions with Independent Movement Data</i>
Braaker et al. 2014	<i>E. europaeus</i>	Relocation – GPS	PSF	None	None
Brodie et al. 2014	<i>H. derbyanus</i> ; <i>H. malayanus</i> ; <i>N. diardi</i> ; <i>R. unicolor</i> ; <i>M. nemestrina</i>	Detection – Camera trap	PSF	None	None
Carvalho et al. 2015	<i>G. genetta</i>	Relocation – VHF	PathSF	None	None
Chetkiewicz & Boyce 2009	<i>U. arctos</i> ; <i>P. concolor</i>	Relocation – GPS	PSF	None	None
Clark et al. 2015	<i>U. americanus luteolus</i>	Relocation – GPS	SSF	Removed relocations <100 meters apart	None
Cushman & Lewis 2010	<i>U. americanus</i>	Relocation – GPS	PathSF	None	None
Elliot et al. 2014	<i>P. leo</i>	Relocation – GPS	PathSF	Resource selection of dispersing individuals	None
Harju et al. 2013	<i>C. urophasianus</i>	Relocation – GPS	SSF	Resource selection during traveling and relocating states	Validated with independent GPS data in traveling and relocating states
Kautz et al. 2006	<i>P. concolor coryi</i>	Relocation – VHF	PSF	None	None
Kindall & Manen 2007	<i>U. americanus</i>	Relocation – VHF	PSF	None	None
LaPoint et al. 2013	<i>M. pennanti</i>	Relocation – GPS	PSF	None	Validated with ‘animal-defined’ corridors based on rate of fast, linear movement
Mateo-Sánchez, Cushman & Saura 2014	<i>U. arctos</i>	Detection – Sign	PSF	None	None

McClure, Hansen & Inman 2016	<i>C. elephas; G. gulo</i>	Relocation – GPS, VHF	PSF	Resource selection for migratory or dispersal-related movements	Validated with independent GPS data for long-distance movements
O'Brien et al. 2006	<i>R. tarandus caribou</i>	Relocation – GPS	PSF	None	None
Proctor et al. 2015	<i>U. arctos</i>	Relocation – GPS	PSF	None	None
Pullinger & Johnson 2010	<i>R. tarandus caribou</i>	Relocation – GPS	SSF	Resource selection during large-scale movements	Validated with independent GPS data identified as long-distance movement
Reding et al. 2013	<i>L. rufus</i>	Relocation – VHF	PathSF	None	None
Richard & Armstrong 2010	<i>P. longipes</i>	Relocation – VHF	SSF	Resource selection of dispersing individuals	None
Roever, van Aarde & Leggett 2013	<i>L. africana</i>	Relocation – GPS	PSF	None	None
Squires et al. 2013	<i>L. canadensis</i>	Relocation – GPS	SSF	Resource selection during movement state	None
Sutcliffe et al. 2003	<i>A. hyperantus; H. virgaureae</i>	Relocation – Mark-recapture	MSF	Resource selection for matrix with highest passage rates	None
Thatcher, van Manen & Clark 2009	<i>P. concolor coryi</i>	Relocation – VHF	HSF	None	None
Trainor et al. 2013	<i>P. borealis</i>	Relocation – VHF	PSF	Resource selection of dispersing individuals	Validated with frequency of dispersal events within predicted corridors
Verbeylen et al. 2003	<i>S. vulgaris</i>	Detection - Sign	MSF	None	None

Walpole <i>et al.</i> 2012	<i>L. canadensis</i>	Detection – Sign	PSF	None	None
Wang <i>et al.</i> 2014	<i>A. melanoleuca</i>	Detection – Camera Trap	PSF	None	None
Zeller <i>et al.</i> 2014	<i>P. concolor</i>	Relocation – GPS	PSF	Resource selection during movement state	None
Zeller <i>et al.</i> 2015	<i>P. concolor</i>	Relocation – GPS	SSF, PathSF	Removed relocations <200 meters apart	None

¹PSF = point selection function, SSF = step selection function, PathSF = path selection function, MSF = matrix selection function, HSF = home range selection function (categories as defined by Zeller *et al.* 2012).

Table 2. Landscape variables used to quantify resource selection of African wild dogs.

<i>Category</i>	<i>Variable Name</i>	<i>Description</i>	<i>Source</i>
Habitat Cover	Swamp	Moist and seasonally flooded floodplains	Broekhuis <i>et al.</i> 2013
	Grassland	Former floodplains characterized by shrubbed grassland	
	Woodland	Mixed woodland dominated by <i>Acacia</i> spp.	
	Mopane	Woodland composed primarily of <i>Colophosphermum mopane</i> shrubs and trees	
Land Use Type	Game Reserve	IUCN Category IV Protected Area	Botswana Department of Lands
	National Park	IUCN Category II Protected Area	
	Wildlife Mgmt Area (WMA)	Community-managed land gazetted for photographic and hunting tourism	
	Pastoral	Non-wildlife area dominated by pastoralism	
Anthropogenic Features	Road	Distance to nearest road	Okavango Delta Information System
	Settlement	Distance to nearest human settlement	

Table 3. Percentage overlap between least-cost corridors (LCC) and GPS points along observed dispersal paths, and path deviation between modelled and observed paths with p-values indicating significant differences between model performance.

<i>Model</i>	LCC Overlap	Path Deviation		
	%	<i>Mean (km)</i>	<i>SD</i>	<i>p</i>
Path 1- Movement	62	7.16	2.28	<0.001
Path 1- Combined	0	25.5	3.18	
Path 2- Movement	100	2.65	1.92	<0.001
Path 2- Combined	0	29.8	6.08	
Path 3- Movement	100	.34	.75	0.07
Path 3- Combined	100	1.93	1.55	

Table 4. Approaches for using movement behaviour to inform connectivity conservation.

<i>Approach</i>	<i>Description</i>	<i># Studies</i>	<i>Example studies</i>
Behavioral	Use localities when the individual is in a traveling/exploratory state versus a resource use state	7	Pullinger & Johnson 2010; Squires et al. 2013; Zeller et al. 2014
Demographic	Use localities from dispersing vs. resident individuals in the population	3	Elliot et al. 2014; Richard & Armstrong 2010; Trainor et al. 2013
Seasonal	Collect location data during the known dispersal season	3	Cushman and Lewis 2010; Roever et al. 2013; Walpole et al. 2012

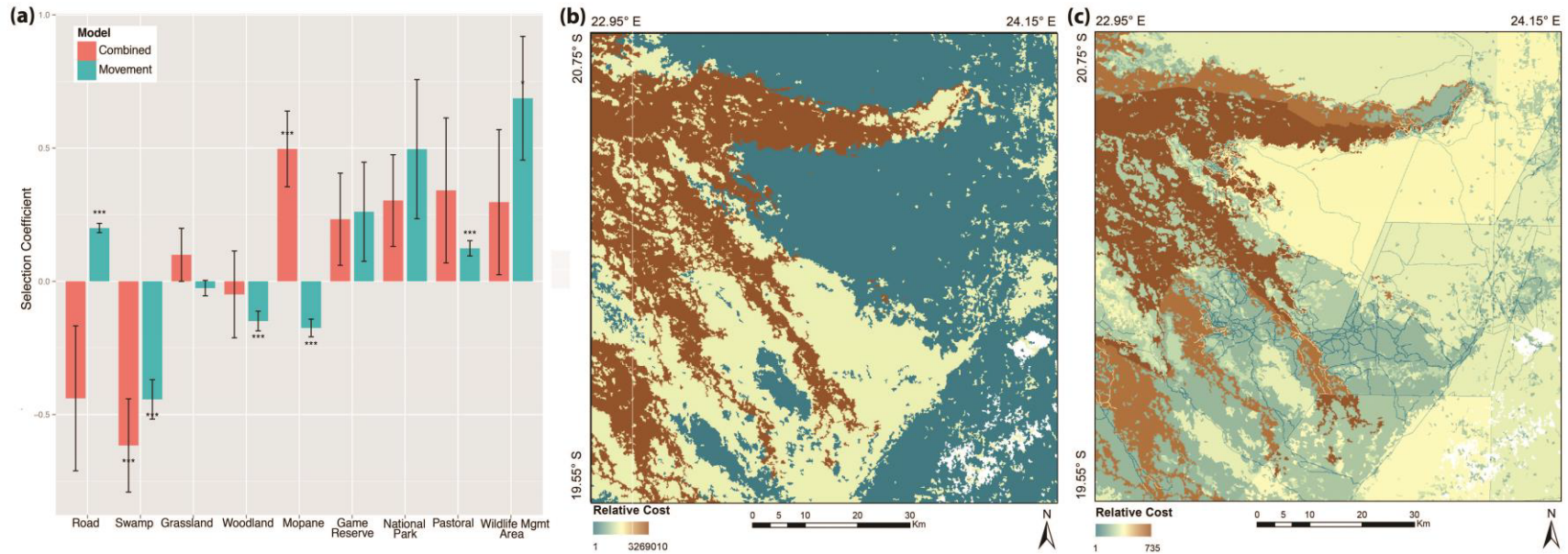
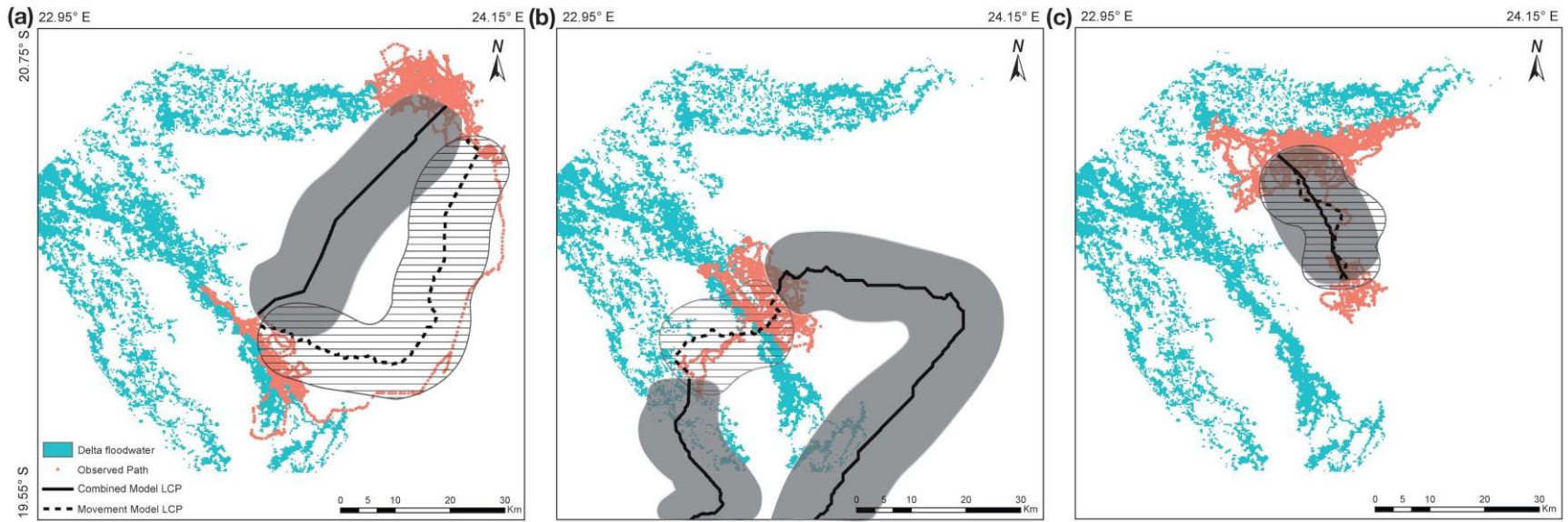


Figure 1. (a) Comparison of step selection parameter estimates and standard errors for the combined model, measuring resource selection for all location data independent of behavioural state, and the movement model, measuring resource selection only when wild dogs were in a ‘traveling’ behavioural state (see Table S3 for listed values). Negative selection coefficients indicate avoidance of corresponding landscape variables; positive values indicate selection for corresponding variables. P-values were calculated from Wald tests. (b) Resistance surface derived from significant selection coefficients ($p < 0.05$) in the combined model. Resistance values were calculated as the inverse of scaled ‘probability of use’ values $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots)$ where β_i is the selection coefficient for landscape variable x_i . Blue cells and orange cells indicate low and high resistance to movement, respectively. (c) Resistance surface derived from significant selection coefficients in the movement model.



41

Figure 2. Comparison between least-cost corridors derived from combined model (solid black lines), movement model (dashed black lines), and GPS-captured paths (orange dots) from three distinct dispersal events in (a) October 2014, (b) August 2013 and (c) January 2012 (Table S1). Okavango Delta floodwaters (light blue) are included for spatial reference.

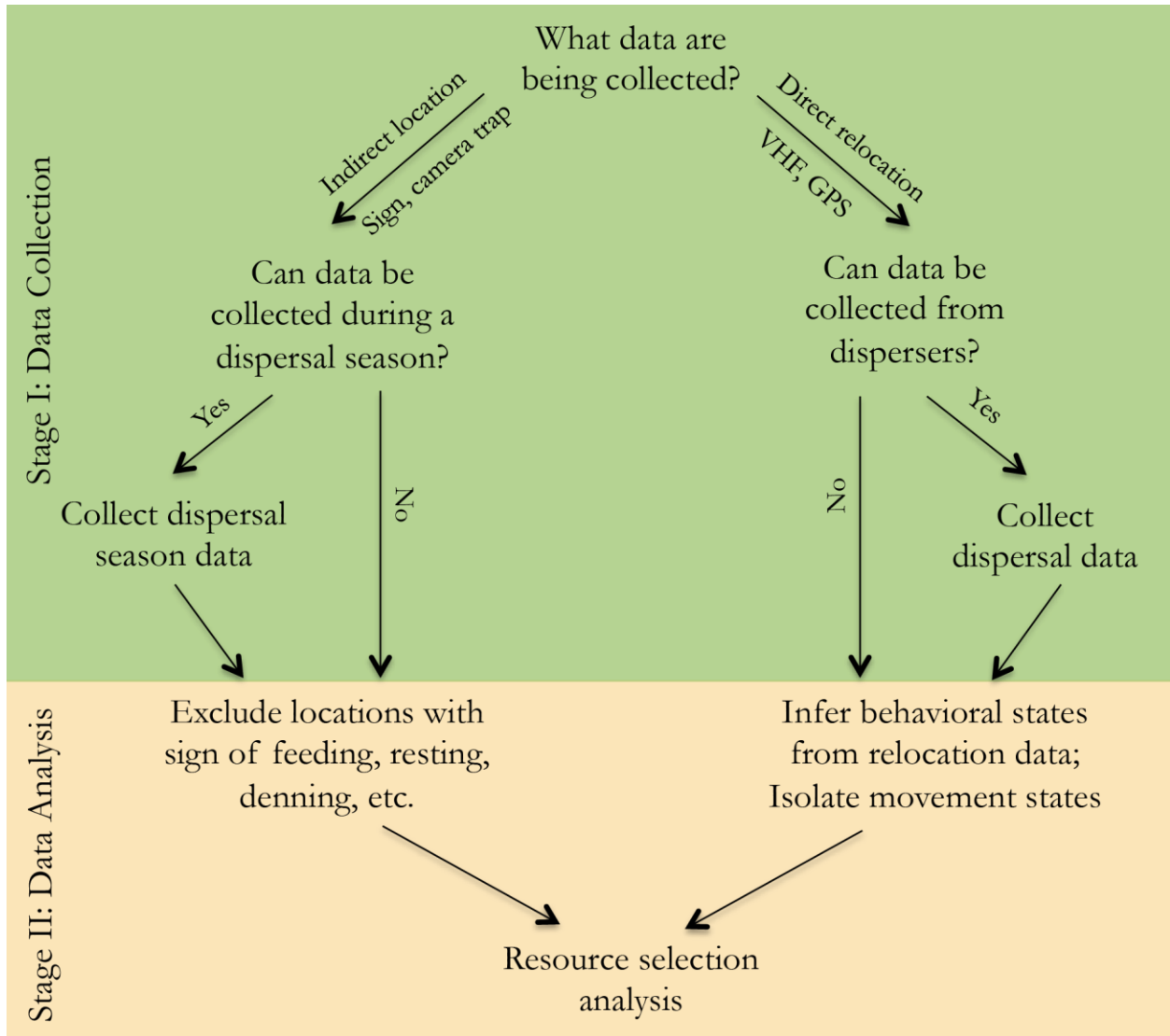


Figure 3. A decision tree for focusing resource selection analyses on animal movement for connectivity planning. At the data collection stage, decisions are made as to the type of data that can be collected and whether collection can be targeted toward dispersal seasonally or demographically. At the data analysis stage, the collected data can be analysed and cleaned to isolate locations for movement before inputting the dataset into a resource selection analysis.

Supplementary Material

Appendix 1. Detailed methods for African wild dog case study.

To collect movement data from African wild dogs, between November 2011 and March 2015 we fitted 15 adults from 13 packs in northern Botswana's Okavango Delta region with custom-built GPS-accelerometer collars (Abrahms *et al.* 2016). Capturing and collaring of all animals was performed under approval from the Government of Botswana (permit #EWT 8/36/4 XXIV) and the University of London Royal Veterinary College Ethics & Welfare Committee and conformed to the guidelines of the American Society of Mammalogists for the use of wild mammals in research. The GPS units in the collars moved between different operating states depending on the measured activity status of the animal derived from the accelerometers (Hubel *et al.* 2016). The default state took hourly fixes when the animal was stationary but transitioned into a 'traveling' state with five-minute fixes when activity data indicated that the animal was moving consistently between consecutive locations; acceleration equivalent to galloping (38.2 m/s^2) triggered the collars into a third 'running' state of five fixes per second. See Hubel *et al.* (2016) for further specifications on collar design.

We created two separate step selection models to quantify resource selection (Fortin *et al.* 2005; Thurfjell, Ciuti & Boyce 2014). We used conditional logistic regression to compare the landscape attributes of each observed step with those of five matched control steps (see Abrahms *et al.* 2016 for details on step selection methods). For the combined model, we included all available GPS data, resampled to a consistent fix rate of five-minute intervals. For the movement model, we used only GPS data when the animals were in the 'traveling' state. To determine the sensitivity of model output to GPS fix interval, we repeated these analyses using an hourly fix rate; this conservative approach did not significantly alter our coefficient estimates (see Table S4).

Three of the fifteen collared wild dogs exhibited long-distance dispersal movements (movement from a natal or breeding range to a new potential breeding range; Clobert *et al.* 2001) during the study period; these animals were excluded from the step selection analyses to serve as test data against corridor model outputs. The data from the remaining 12 individuals used to parameterize our models were collected from 12 different packs to minimize risk of pseudoreplication. Because African wild dogs travel in packs and retain a high degree of spatial proximity to one another (Hubel *et al.* 2016), we assumed that the movement pattern of a given pack member is representative of other members of the pack, with the exception of denning females which were not included in this study. The following landscape variables were included in the models based on known influences on African wild dog space use (Woodroffe 2010; Whittington-Jones *et al.* 2014; Abrahms *et al.* 2016): habitat cover, land use type, proximity to road, and proximity to human settlements (Table 1). Topography was not included as there was little to no topographic variation in the study area. All GIS layers were resampled to 100 m resolution to maintain consistent grain size. We tested for independence between all landscape variables using Pearson pairwise correlations and used the standard threshold for non-independence of $|r| > 0.6$. No variables were characterized by correlations greater than $|r| = 0.38$ and thus no landscape variables were discarded. We used AIC forward model selection to determine which variables to include in our final models (Burnham & Anderson 2002).

We used significant selection coefficients ($p < 0.05$) from the combined model and movement model to create two corresponding resistance surfaces. First, we calculated the probability of use of each grid cell using the equation $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots)$ where β_i is the selection coefficient for landscape variable x_i (Thurfjell, Ciuti & Boyce 2014). Following (Squires *et al.* 2013), we scaled the probability of use values to between 0 and 1 by dividing each grid cell value by the maximum probability value; we then inverted these values to create each resistance surface such that $\text{resistance} = 1/\text{scaled}(w(x))$. We used least-cost path analysis to predict the movement paths of the three dispersing individuals, as this represents the most commonly used method for designing wildlife corridors (Sawyer, Epps & Brashares 2011). This approach finds the least costly path between two user-defined points on a resistance surface by minimizing the Euclidian distance weighted by the cumulative resistance values of all cells traversed (Adriaensen *et al.* 2003; Sawyer, Epps & Brashares 2011). For our analyses, we used the center of each natal and dispersal home range centroid as our start and end points. Finally, to address the uncertainty inherent in least-cost modeling we estimated least-cost corridors that overcome the single-pixel width limitation of LCPs (Beier, Majka & Newell 2009). Following published recommendations (Harrison 1992; Beier, Majka & Spencer 2008), we buffered our LCPs by a conservative estimate of half the average home range width for African wild dogs (8km; Woodroffe 2010) to determine biologically-informed corridor widths of 16 km.

Table S1. Pack identities and data collected per collared individual.

Individual	Gender	Pack ID	Study Period	# GPS locations
<i>Residents</i>				
Accra	F	KB	Apr.-Sep. 2012	64,192
Gomer	M	HW	Nov. 2011-Nov. 2012	23,023
Yolo	M	MT	Nov. 2011-2012	21,131
Dar	F	CT	Apr.-Aug. 2012	1,447
Kubu	F	MK	Apr.-Oct. 2012	8,587
Jesus	M	SA	Mar.-July 2012	5,983
Augustus	M	BW	June-Sept. 2013	4,841
Xerxes	M	AP	June 2014-Mar. 2015	26,345
Pula	M	FV	July-Nov. 2014	11,295
Bali	F	HT	Dec. 2013-Nov. 2014	22,556
Aztec	M	ZU	Feb.-Oct. 2014	19,488
Adiga	M	MB	Aug. 2013-Mar. 2015	37,648
<i>Dispersers</i>				
Scorpion	M	KB	Apr. 2012-Nov. 2013	156,099
Stetson	M	MT	Nov. 2011-Apr. 2012	8,906
Lupe	M	KM	July 2014-Jan. 2015	14,494

Table S2. AIC model selection for Combined and Movement step selection models; L = Step length; A = Absolute relative turn angle; S = Distance to nearest human settlement; R = Distance to nearest road; H = Habitat type; M = Land use type.

<i>I</i>	<i>Model</i>	Combined SSF				Movement SSF			
		<i>AIC</i>	ΔAIC	<i>w</i>	<i>LogLi</i>	<i>AIC</i>	ΔAIC	<i>w</i>	<i>LogLik.</i>
0	L + A	21231	151.	0	-	198269.2	3207.1	0	-
1	L + A + S	21233	153.	0	-	198269.8	3207.6	0	-
2	L + A + R	21233	153.	0	-	198126.3	3064.1	0	-
3	L + A + H	21093	14.1	0	-	195366.0	303.85	0	-
4	L + A + M	21211	131.	0	-	198074.5	3012.4	0	-
5	L + A + H + M	21079	0	0.4	-	195196.1	134.01	0	-
6	L + A + H + R	21095	15.9	0	-	195220.8	158.61	0	-
7	L + A + H + S	21095	16.1	0	-	195368.0	305.81	0	-
8	L + A + H + M + R	21080	1.1	0.2	-	195062.1	0	0.53	-
9	L + A + H + M + S	21081	1.9	0.1	-	195194.8	132.61	0	-
1	L + A + H + M +	21082	3.0	0.1	-	195062.3	0.20	0.47	-

Because there was support for inclusion of distance to roads in the combined model ($\Delta AIC=1.1$), we included this variable in our initial step selection analysis for comparison with the movement model, though its selection coefficient proved non-significant and was not given weight in the corresponding resistance surface ($p=0.35$). There also was modest AIC support in each model type for including distance to settlement as a predictor variable, but selection coefficients for this variable were not significant ($p>0.5$) in either step selection model and we did not include this parameter in our final models.

Table S3. Step selection parameter estimates (β) and standard errors for the combined model, measuring resource selection for all location data independent of behavioural state, and the movement model, measuring resource selection only when wild dogs were in a ‘traveling’ behavioural state. Negative selection coefficients indicate avoidance of corresponding landscape variables; positive values indicate selection for corresponding variables. P-values were calculated from Wald tests.

Variable	Movement Model			Combined Model		
	β	<i>SE</i>	<i>p-value</i>	β	<i>SE</i>	<i>p-value</i>
Road	0.200	0.017	<0.001	-0.439	0.472	0.35
Grassland	-0.025	0.029	0.38	0.099	0.131	0.45
Mopane	-0.175	0.033	<0.001	0.497	0.142	<0.001
Woodland	-0.149	0.037	<0.001	-0.049	0.163	0.76
Swamp	-0.443	0.074	<0.001	-0.616	0.175	<0.001
Game Reserve	0.261	0.286	0.36	0.233	0.473	0.62
National Park	0.496	0.301	0.10	0.303	0.206	0.52
Pastoral	0.124	0.029	<0.001	0.341	0.472	0.47
WMA	0.687	0.282	0.01	0.297	0.472	0.53

Table S4. Results of sensitivity analysis for 1-hour fix intervals. Step selection parameter estimates (β) and standard errors for the combined model, measuring resource selection for all location data independent of behavioural state, and the movement model, measuring resource selection only when wild dogs were in a ‘traveling’ behavioural state. Negative selection coefficients indicate avoidance of corresponding landscape variables; positive values indicate selection for corresponding variables. P-values were calculated from Wald tests.

Variable	Movement Model			Combined Model		
	β	<i>SE</i>	<i>p-value</i>	β	<i>SE</i>	<i>p-value</i>
Road	0.180	0.016	<0.001	-0.489	0.425	0.25
Grassland	-0.028	0.031	0.36	0.082	0.232	0.72
Mopane	-0.169	0.034	<0.001	0.478	0.137	<0.001
Woodland	-0.150	0.039	<0.001	-0.051	0.171	0.76
Swamp	-0.419	0.067	<0.001	-0.602	0.183	<0.001
Game Reserve	0.268	0.282	0.34	0.187	0.510	0.71
National Park	0.515	0.320	0.11	0.332	0.251	0.19
Pastoral	0.102	0.031	<0.001	0.362	0.494	0.46
WMA	0.574	0.292	0.05	0.282	0.486	0.56

4. Classification of movement syndromes across individuals and species

This chapter has been prepared for publication and is reproduced here with kind permission of the contributing authors: Dana P. Seidel, Eric Dougherty, Elliot L. Hazen, Steven J. Bograd, Alan M. Wilson, John W. McNutt, Daniel P. Costa, Stephen Blake, Justin S. Brashares and Wayne M. Getz.

Abstract

Patterns of animal movement have critical implications for multiple aspects of biology, including the ecology, evolutionary biology, and long-term persistence of wildlife populations. Because empirical studies of animal movement are most-often site- and species-specific, it is difficult to gain a generalized understanding of the mechanisms underlying broad movement patterns. By combining movement data from 13 marine and terrestrial species spanning three taxonomic classes, continents and orders of magnitude in body size with computer-simulated idealized movement paths, we provide the first empirical examination of how fundamental movement metrics scale up to predict emergent movement patterns across multiple taxa. We introduce a classification scheme for movement syndromes, which are suites of correlated movement traits seen across taxa (e.g. migration, nomadism), and show that a simple set of metrics can reliably classify movement syndromes across highly disparate vertebrate taxa. Our movement syndrome classification scheme thus provides a general framework for linking movement patterns to movement process, and facilitates new understanding of relationships between movement syndromes and physiological, behavioral and life-history traits.

Introduction

Ecology links community, population, and ecosystem patterns with individual and interactive level processes at multiple scales of inquiry (Levin 1992). Animal movement is one such process that is also an essential component of individual fitness (e.g. resource acquisition, survival), with critical implications for population persistence (e.g. dispersal, gene flow), species distributions, and ecosystem function (e.g. ecosystem engineering, propagule dispersal) (Swingland & Greenwood 1983; Lawton & Jones 1995; Hanski 1998; Clobert *et al.* 2001). Further, in the so-called Anthropocene, movement will play a critical role in species and community responses to environmental change (Tingley *et al.* 2009; Hazen *et al.* 2012; Bost *et al.* 2015). Because of the profound importance of movement in driving the spatial dynamics of multiple levels of ecological organization, the identification of common mechanistic underpinnings for complex movements has recently been identified as a research priority in ecology and conservation biology (Hays *et al.* 2016). A stronger conception of how movement processes lead to higher-level patterns will facilitate the integration of movement into other areas of ecology to inform predictions, such as the invasive potential of exotic species (Peterson 2003), how diseases will spread through contact-networks (Peterson 2008), or how species will respond to climate change (Schloss *et al.* 2012).

In behavioral ecology, the concept of *behavioral syndromes*, i.e. suites of correlated behaviors, has aided quantification of behavioral types and their ecological and evolutionary implications (Sih *et al.* 2004). Analogously, current efforts to characterize *movement syndromes*, i.e. suites of correlated movement traits seen across taxa such as migration or nomadism (Sih *et al.* 2004; Dingle 2006), have generated a number of promising methods and metrics (Schick *et al.* 2008). Several important theoretical contributions have linked basic movement metrics (i.e., mechanism/process) with broad-scale movement syndromes (i.e., pattern) (Börger *et al.* 2008; Mueller & Fagan 2008; Nathan *et al.* 2008), but few empirical studies have confirmed these links (Mueller *et al.* 2011). Moreover, it is unclear which metrics have the greatest utility for identifying movement syndromes, information that is critical both to developing appropriate data collection procedures and to conducting efficient analyses of movement. Given that the majority of empirical movement studies have focused on single species, our ability to generalize findings is limited (Holyoak *et al.* 2008). Different taxa not only have different modes of movement (e.g., swimming versus terrestrial locomotion), but also move across spatial and temporal scales that differ by orders of magnitude. Thus, a more unified understanding of the processes underlying emergent movement syndromes requires an examination across a broad array of taxa, movement modes, and body sizes.

Here, we provide the first empirical examination of the extent to which simple measures of animal movement can be used to identify movement syndromes across widely disparate taxa, in effect linking movement process with pattern. Three movement syndromes appear repeatedly in the literature from which we draw upon: range residency, nomadism, and migration (Mueller & Fagan 2008; Bunnefeld *et al.* 2010; Mueller *et al.* 2011; Bastille-Rousseau *et al.* 2016). Range residency can be further expanded upon to include central place foraging and territoriality, yielding four movement syndromes classically defined as: 1) central-placed foraging, in which individuals return to fixed locations between foraging trips (Orians & Pearson 1979); 2) territoriality, in which individuals actively demarcate the boundaries of fixed areas against conspecifics (Howard 1920); 3) nomadism, in which individuals move unpredictably with little to no site fidelity (Weins 1976); 4) migration, in which individuals move with persistence from one habitat area to another, bi-directionally and with temporal predictability (Williams 1957). These movement syndromes may be lifetime descriptors correlated with life history types, or life history stage descriptors of significant movement phases associated with particular events (e.g. breeding, resource pulses, etc.). While these four syndromes differ conceptually and qualitatively, we develop a novel methodology for their quantitative distinction.

We expected similar forms and characteristics of movement to underlie the same syndrome across species and spatial scales. To evaluate this prediction and test whether simple metrics reliably identify movement syndromes, we assessed five key movement metrics for GPS trajectories of individuals from 13 species spanning three taxonomic classes, continents, movement modes, and orders of magnitude in body size. Using these metrics, we performed a cluster analysis to determine if our study organisms fell into statistically distinct groupings. We compared these groupings with simulations of four idealized syndromes – central place foraging, territoriality, nomadism, and migration – which revealed that observed groupings were explained by common movement syndrome. This approach provides a framework for a rigorous large-scale movement classification scheme that may facilitate the integration of animal movement into

other areas of ecology by pairing an animal's movement syndrome with other ecological data to develop and test predictions.

Methods

Empirical Data

We gathered GPS-derived movement data for the following species: African buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*), African wild dog (*Lycaon pictus*), black-backed jackal (*Canis mesomelas*), California sea lion (*Zalophus californianus*), cheetah (*Acinonyx jubatus*), Galapagos albatross (*Phoebastria irrorata*), Galapagos tortoise (*Geochelone nigra*), African lion (*Panthera leo*), northern elephant seal (*Mirounga angustirostris*), plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), and white-backed vulture (*Gyps africanus*). Species were chosen to represent an array of taxa, environments, and body sizes, but were restricted by the availability of datasets with sufficient quality in terms of resolution and duration. All data were collected with fix intervals of 1-hour or less and subsampled to 1-hour resolutions to achieve consistent fix rates for comparison, with the exception of Galapagos albatross data which were collected at 90-min intervals and interpolated to a 1-hour resolution. See Table S1 in supporting information for a detailed summary of GPS data.

Movement Metrics

We employed five metrics widely applied in current movement studies and grounded in ecological theories of animal movement in heterogeneous landscapes. Turn angle correlation and net-squared displacement are two central parameters in random-walk (RW) models, which are extensively used to evaluate animal search strategies and foraging efficiency (Viswanathan *et al.* 1999; Bartumeus *et al.* 2005; Codling, Plank & Benhamou 2008; Reynolds & Rhodes 2009). Variations of random walk models have been shown to approximate nomadic movement via uncorrelated RWs (Bunnefeld *et al.* 2010), central-place foraging via biased RWs (Börger, Dalziel & Fryxell 2008), and territorial behavior via correlated RWs (Moorcroft, Lewis & Crabtree 2006). When spatially-explicit information about the landscape is known, ecologists have employed a variety of time-use metrics to quantify how animals exploit resources. In heterogeneous landscapes, for example, animals are predicted to adjust their residence times and/or return times to a given area in response to variation in resource quality (Turchin 1991; Barraquand & Benhamou 2008; van Moorter *et al.* 2015); these two properties have been linked to emerging patterns of home range residency (van Moorter *et al.* 2015). Over longer timescales, measures of home range stability, such as the amount of overlap between seasonal home ranges, can inform theory on how animals respond to temporal predictability of resources (Alcock 2009) and have been used to identify migration patterns (Cagnacci *et al.* 2015). Because movement processes are often scale-dependent and those of a given syndrome may be observable at one or more spatiotemporal scales (Benhamou 2013), we also considered that our metrics were relevant over a range of timescales — in our case, hour, day, month, and lifetime of trajectory. Thus, for each individual in our dataset, we calculated five movement metrics suitable for analysis over these timescales as follows:

1. *Mean turn angle correlation* (TAC). Following Dray et al. (2010), we calculated angular autocorrelation S_A as the sum of squares of chord distances between N successive turn angles ρ :

$$S_A = \frac{1}{N} \sum_{n=1}^{N-1} [(\cos \rho_{n+1} - \cos \rho_n)^2 + (\sin \rho_{n+1} - \sin \rho_n)^2]$$

Thus, small chord distances resulting in low S_A values correspond to high turn angle correlation (Dray, Royer-Carenzi & Calenge 2010).

2. *Mean residence time* (RT). Residence time was measured as the number of hours the animal spends inside a circle of a given radius centered on each location without leaving the radius for more than a specified cut-off time (van Moorter *et al.* 2015). We tested the sensitivity of a subset of our dataset to radii of mean step length (SL), 2 x mean SL, 4 x mean SL, and 8 x mean SL, where SL was calculated as the mean Euclidean distance between successive relocations, and cut-off times of 12 and 24 hours. Consistent time-use patterns were observed across these thresholds, so following van Moorter et al. (2015), we used a radius of mean SL and a 12-hour cut-off time.

3. *Mean time-to-return* (T2R). Time-to-return was measured as the number of hours the animal spends beyond a specified cut-off time before its return to a circle of a given radius centered on each location (van Moorter *et al.* 2015). We conducted the same sensitivity analysis for this metric as above, and finding consistent patterns across thresholds, we again used a radius of mean SL and a 12-hour cut-off time.

4. *Mean volume of intersection* (VI). Volume of intersection was measured by the between monthly 95% kernel density home ranges (Millspaugh *et al.* 2004; Fieberg & Kochanny 2005). Volume of intersection varies between 0 and 1, with increasing values corresponding to increasing overlap between monthly home ranges, and is thus VI is a measure of home range stability.

5. *Maximum net squared displacement* (MNSD). Maximum net squared displacement was calculated as the maximum squared Euclidean displacement from the first relocation of the trajectory over the full course of the trajectory (Kareiva & Shigesada 1983). To make comparisons among individuals across species that have orders of magnitude different motion capacities, we scaled this parameter for each individual by dividing by the smallest MNSD observed for its species.

All movement metrics were calculated using the *adehabitatLT* package (Calenge 2015) in R 3.2.3.

Cluster Analysis

To elucidate any underlying structure in our dataset, we performed a principal components analysis (PCA) on the five movement metrics calculated from our empirical datasets. PCA is a widely used technique for summarizing a multivariate dataset into a reduced number of

uncorrelated dimensions, or *principal components*, while minimizing the loss of information in the original dataset (King & Jackson 1999). We used the Broken-stick criterion to retain important composite (PC) axes, whereby only the eigenvalues that are greater than those expected from a random model are considered significant. Comparative analyses of component retention methods have shown the Broken-stick model to be among the most reliable techniques (King & Jackson 1999; Peres-Neto, Jackson & Somers 2003). To normalize the dataset for this analysis we first log-transformed the data, followed by centering around the mean and dividing by the variance (Jolliffe 2014).

Finally, we applied Ward's agglomerative hierarchical clustering algorithm to the resulting PCA values (Ward 1963). This approach clusters the most similar pair of points based on their squared Euclidean distance at each stage of the algorithm, and is an efficient method to identify clusters based on minimum within-cluster variance without making an *a priori* determination of the number of clusters to generate (Gordon 1987). These clusters can be viewed as functional movement groups, analogous to functional types first theorized for plant communities, which provide a non-phylogenetic classification based on shared responses to environmental conditions (Gitay & Noble 1997). To determine the significance of the resulting cluster arrangement, we calculated *p*-values for each cluster via multi-scale bootstrap resampling with 1000 bootstrap replications (Shimodaira 2004). By simulating the following idealized movers and determining their cluster assignments, we were able to identify these clusters by movement syndrome.

Simulated Data

As a baseline for comparison, we developed spatially-explicit models simulating four movement syndromes: central place foraging, territorial, nomadic, and migratory (Fig. 1). Central place foragers and territorial individuals were assumed to have stable home ranges, whereas nomadic and migratory individuals moved without boundary constraints. For each syndrome, we simulated six individuals, using rules described below. In all cases, we drew step length and turning angle randomly from probability distributions, enabling variation in the movement paths of individuals within the same syndrome. We simulated data for each individual for 3600 time steps at hourly intervals, with the exception of migratory individuals, which we simulated for 7200 time steps to incorporate a return migration.

Central Place Foragers (CPF). For CPF, we assumed that resources are optimal at the center of the home range (the 'central place'; (Ford 1983). We drew steps within the core of the home range from a uniform distribution and weighted them by the distance to the edge of the home range to simulate greater space use within the core. Upon reaching the home range boundary, we drew turning angles from a normal distribution with a mean 180° from the direction the simulated individual was traveling rather than a uniform distribution, leading to its return to the home range center.

Territorialists. The territorial individual functioned in an opposite fashion from CPFs in terms of its selective use of the outer edges of its home range – in effect demarcating or defending the territory (Giuggioli, Potts & Harris 2011). Thus, steps were weighted by the distance to the home range center. However, turning angles were adjusted as for CPFs to maintain home range stability.

Nomads. We assigned these individuals randomly to one of two states: foraging or dispersing (Morales *et al.* 2004). The probability of switching from one state to the other in nomads was 0.05 based on empirical estimates ranging from 0.018-0.09 (Fryxell, Wilmshurst & Sinclair 2004; Haydon *et al.* 2008). The foraging state was meant to simulate movement patterns in the vicinity of high quality resources, so we applied lower weights to step sizes for the foraging state than for the dispersing state. We drew turning angles from a uniform distribution for the foraging state and a normal distribution for the dispersal state with a mean of the initial direction after switching from the foraging state.

Migrants. We assigned these individuals to one of two states: sedentary or migratory (Morales *et al.* 2004). In the sedentary state, we defined movement by uniform step size and turning angle distributions. We defined the migratory state by highly directional movement, with long step sizes and highly correlated turning angles (Dingle & Drake 2007). After an approximately four-month period of residence, the individuals migrated for about two months before entering a sedentary state for another four months at their new location, then returned to their origin location over the course of a two month return migration.

Results

The first two principal components (PC) of the PCA explained 70% of the variance among the five movement metrics and thus PC1 and PC2 were retained for the cluster analysis using the Broken-stick criterion (Table 1). Plotting our data along the minor PC axes (PCs 3, 4, and 5) did not provide informative clusters, suggesting that the first two PCs are sufficient for classifying individuals by syndrome (Fig. S3). Because of evidence of collinearity between metrics (Fig. 2B), we also ran the PCA using different combinations of a reduced set of three variables (Fig. S4). Despite potential collinearity, we found that including only three variables performed less well than including all five, presumably because some variables play a larger role in classifying particular syndromes than others (Fig. 3).

Using acronyms VI (Volume of Intersection), RT (Residence Time), T2R (Time-to-Return), TAC (Turn Angle Correlation) and MNSD (Maximum Net Squared Displacement), the first PC represented a contrast primarily between VI+RT and TAC+MNSD, with a somewhat smaller contribution of T2R, to the latter. From left to right along PC1 were clustered CPFs/territorial individuals, nomads, and migrants (Fig. 2B), suggesting this axis indicates a spectrum of random walk movement from diffusive (low directional persistence) to advective (high directional persistence) movement (Codling, Plank & Benhamou 2008).

The second PC represented a contrast primarily between T2T and TAC+MNSD. Along PC2 territorial individuals had low values and CPFs had high values, suggesting this axis indicates a continuum of low to high repeated use of resources, as territorial animals may limit returns to previously visited sites in exchange for patrolling a greater proportion of their territory (Giuggioli, Potts & Harris 2011), while CPFs by definition have high site fidelity and return rates to their ‘central place’ (Ford 1983). There is also a clear trend along this axis differentiating terrestrial species and marine species. Marine species — here, migratory Northern elephant seals and central placing foraging Galapagos albatrosses and California sea lions — had lower mean

T2R and higher MNSD and TAC than their terrestrial counterparts. These differences are likely due to the high motion capacity of marine organisms (Nathan *et al.* 2008), facilitation of movement in air and water with few static barriers requiring circumnavigation (Shillinger *et al.* 2012), and greater dispersion of resources in pelagic environments (Sorte 2012).

The cluster analysis identified four statistically significant groupings (Fig. 2A). All individuals of the four simulated movement syndromes fell into separate groups (see Fig. S1 for a full dendrogram displaying individual leaves within clusters), suggesting each grouping represents a different movement syndrome. The heights of the associated dendrogram branches correspond to the squared Euclidean distances between clusters in PCA-defined movement ecology space (Fig. 2B). Thus, clusters that diverge at lower heights (have shorter branches) have greater similarity. Multiple species were represented in more than one cluster, showing that more than one movement syndrome may occur within a monospecific population (Table 2; Fig. S1).

Analysis of the movement metrics for each cluster revealed distinct differences between putative syndromes (Fig. 3). Specifically, individuals in the migrant cluster had the highest average turn angle correlation, times to return, and maximum net squared displacement, and the lowest average residence times and volume of intersection. In contrast, individuals in the central place cluster had the highest average RT and VI and lowest T2R. Individuals in the territorial cluster had next-to-highest T2R and VI, and lowest MNSD. Finally, individuals in the nomadic cluster had intermediate values for all metrics.

Discussion

A generalized understanding of the basic mechanisms underlying broad movement patterns across taxa is limited by the species-specific nature of movement studies, often due to constraints in funding or feasibility (Holyoak *et al.* 2008). By combining movement data from 13 taxonomically diverse species with simulated movement trajectories constructed for the four syndromes, we show that a simple set of metrics provides a framework that we can use to reliably classify the trajectories of organisms over large time scales into movement syndromes. Our analysis found that movement syndromes transcend species membership and revealed that similar movement patterns and properties recur in highly disparate ecological systems. The movement syndromes were conserved across ecotype, even though marine systems change more rapidly than terrestrial habitats (Scales *et al.* 2016). Ultimately, classifying individuals by movement syndromes provides a window to predicting spatial and broader life history patterns.

Importantly, our movement syndrome classifications did not simply divide by species membership, but instead indicated movement strategies common across individuals within their syndrome cluster. For some species, such as the black-backed jackal, all individuals were assigned to the same syndrome (Table 2). For other species, assignments were made to more than one syndrome. For instance, half of the Galapagos tortoises in our dataset exhibited seasonal altitudinal migrations (Blake *et al.* 2012) and were appropriately classified as migrants while the remaining resident tortoises were classified as CPFs (see Fig. S5 for movement paths). This highlights the value of examining intraspecific variability in movement behavior when assessing population-level movement patterns. It also emphasizes the need to consider the degree to which

populations of a species contain multiple movement syndromes, particularly when developing conservation and management plans.

No single metric could be used to distinguish the four movement syndromes, suggesting that these metrics must be assessed in concert. While significant headway has been made applying a single statistic such as Net Squared Displacement to differentiate between sedentary home range behavior, migration and nomadism in a single taxon (Bastille-Rousseau *et al.* 2016), distinguishing between more complex forms of sedentary behavior such as territoriality versus central place foraging, and among disparate taxa, is a greater challenge. Thus, we recommend evaluating movement with multiple metrics in order to capture metric- or scale-dependent patterns. Our choices of metrics reflect those prevalent in current studies of movement ecology and were selected to represent multiple time scales of analysis relevant to resource use on land- and seascapes. Our results indicate that the metrics used here can serve as informative synoptic measures to classify a broad array of organisms into movement syndromes. However, future research should test the utility of other movement metrics in classifying organisms into additional meaningful classes in ecology.

For any given individual movement trajectory, our approach provides a method for quantifying the degree of intermediacy among syndromes, akin to fractional trophic levels in community ecology (Pauly *et al.* 1998). This quantification is achieved by comparing the relative distance measured in terms of node heights within the dendrogram where the trajectory diverges from two different syndrome clusters. The “degree of intermediacy” can be defined in terms of ratios of the distances among neighboring clusters (measured by going ‘down’ or ‘up and then down’ the relevant node heights, as illustrated in Fig. S7). For purposes of discussion, we define the lowest node that includes all the simulated cases from one syndrome as the “strict cluster node.” If a particular trajectory is contained within this “strict syndrome cluster” then, following phylogenetic practices, we classify it as being that syndrome *sensu stricto*. On the other hand, if a particular trajectory falls outside the strict syndrome cluster but within the greater syndrome cluster (cf. Fig. S7), then we classify this trajectory as being the syndrome *sensu lato*. In this case, we can take the further step of calculating the relative distance of that trajectory’s node to its defining *sensu stricto* cluster node compared with its distance to another *sensu stricto* cluster nodes. To illustrate using our dendrogram in Fig. S1, the trajectory of Elephant Seal #13 (ES13) is migrant (MG) *sensu stricto*. In contrast, African Wild Dog #5 (WD05) is CPF *sensu lato*, but because its distance to the CP node is roughly 4 and to the strict territorial (TE), nomad (NM), and migrant (MG) nodes are roughly 9, 9 and 17 respectively, we can make statements such as, this individual’s trajectory is $9/4=2.25$ times more CPF-like than TE- or MN-like, and $17/4=4.25$ times more CPF- than MG-like.

While we cannot validate the classification of each study animal in our dataset, their assignments are consistent with how we understand their movement processes, such as the tortoise assignments described above (Blake *et al.* 2012). *A priori* predictions for individual African wild dogs, lions and cheetahs based on behavioral observations made during movement data collection also match their classifications (Botswana Predator Conservation Trust, *personal communication*). Because the classification scheme is determined by our syndrome simulations, assignments may exist that are contrary to expectations and these may prompt deeper investigation into the ecology of the study system. For example, all of the California sea lions in

our dataset were breeding females restricted to central place foraging and were correctly assigned as CPFs except one: this individual exhibited foraging trips an order of magnitude greater in distance than its conspecifics, and as a result was classified as a migrant (Table 2; see Fig. S6 for movement paths). This result could subsequently direct researchers to more closely examine the behavior and ecology driving this intraspecific variation in foraging pattern.

It is important to note that individuals may transition between syndromes seasonally or during different life stages. One such example (not analyzed here) is the Pacific salmon (*Oncorhynchus* spp.), which undertakes a one-time migration as juveniles (Quinn 2005). Individuals can also experience seasonal transitions, such as male springbok that enter a highly territorial phase (Lyons, Turner & Getz 2013) or pelagic seabirds that become CPFs (Shaffer *et al.* 2006; Kappes *et al.* 2015) during their breeding season. These transitions can explain why some individuals within a species that have the same life history pattern may be categorized differently, or appear at the interface between two syndromes. For example, among African wild dogs, which have annual denning periods during which they are restricted to central place foraging (Mbizah *et al.* 2014), most were classified as CPFs while some were classified as territorial and one was nomadic (Table 2). These differences can reasonably be explained by the life history stage of an individual during data collection. Developing methods for dividing an individual's movement path into constituent movement syndromes is an arena ripe for future research.

Our findings reveal that a relatively simple set of metrics can reliably predict movement syndromes across taxa, environments, and spatial scales. By linking movement with higher-level patterns of organization, we open the way to further studies relating movement syndromes to life history traits, such as examining the extent to which traits can be inferred from belonging to different movement syndromes. This has important implications for current attempts to incorporate species traits into climate change predictions (Angert *et al.* 2011). For example, the inclusion of coarse classifications of species' movement capacities (permanent resident, short-distance migrant, and long-distance migrant) into species distribution models has been shown to improve predictions of the probability of range shifts in response to climate change (Tingley *et al.* 2012). The movement syndrome concept can also inform predictions in a number of other areas of ecological research. For example, movement syndromes can be applied to macroecology to test whether species-area relationships vary between syndromes, in parallel to how they are expected to vary among taxa or geographic regions (Rosenzweig 1995). Classifying organisms by movement syndrome can also inform predictions regarding the spatial dynamics of invasive species and disease ecology (Peterson 2003; 2008) as well as the spatial distribution of resources in the organism's environment (Turner 1989). Moreover, movement syndrome types could be informative for conservation biology, for example in assessing landscape connectivity solutions for each generalized syndrome when assessments for thousands of individual species are not feasible. To our knowledge, this is the first attempt to summarize measures of animal movement into broad movement syndromes evident across diverse systems — a framework that forges new links between movement pattern and process and that enables the generation of new insights into multiple aspects of ecology and conservation biology.

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Table 1. Contributions of variables to and cumulative percentage of variance explained by principal components. Significant components based on the Broken-stick criterion and retained for the cluster analysis are shaded.

	PC1	PC2	PC3	PC4	PC5
Turn Angle Correlation	0.47	0.47	-0.12	-0.55	-0.50
Residence Time	-0.46	0.17	0.72	0.04	-0.50
Time-to-Return	0.35	-0.68	0.46	-0.45	0.08
Volume of Intersection	-0.50	0.23	-0.00	-0.67	0.49
Maximum Net Squared Displacement	0.44	0.48	0.51	0.21	0.51
Cumulative Percentage of Variance Explained	51.5%	70.1%	84.4%	94.8%	100%

Table 2. Summary of 130 individuals within 13 species analyzed into cluster classifications.

<i>Species</i>	<i>N individuals</i>	Migratory	Central place	Nomadic	Territorial
African buffalo	5	-	-	2	3
African elephant	8	-	1	4	3
African wild dog	13	-	9	1	3
Black-backed jackal	15	-	15	-	-
California sea lion	15	1	14	-	-
Cheetah	5	-	-	-	5
Galapagos albatross	8	-	8	-	-
Galapagos tortoise	8	4	4	-	-
Lion	9	-	1	1	7
N. elephant seal	15	15	-	-	-
Plains zebra	9	-	-	6	3
Springbok	10	2	4	4	-
White-backed vulture	10	-	2	3	5

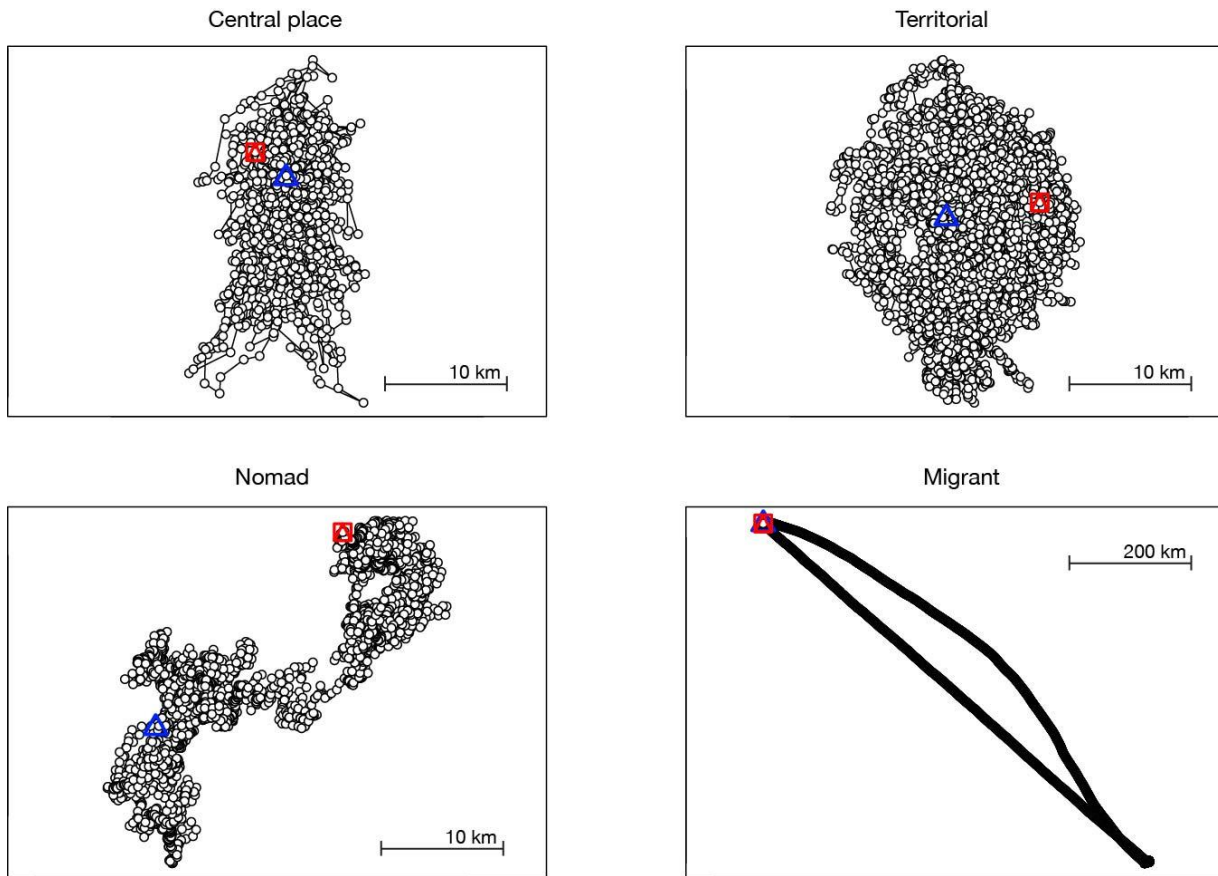


Figure 1. Sample path simulations for four idealized movement syndromes. Movement paths begin at the blue triangle and end at the red square.

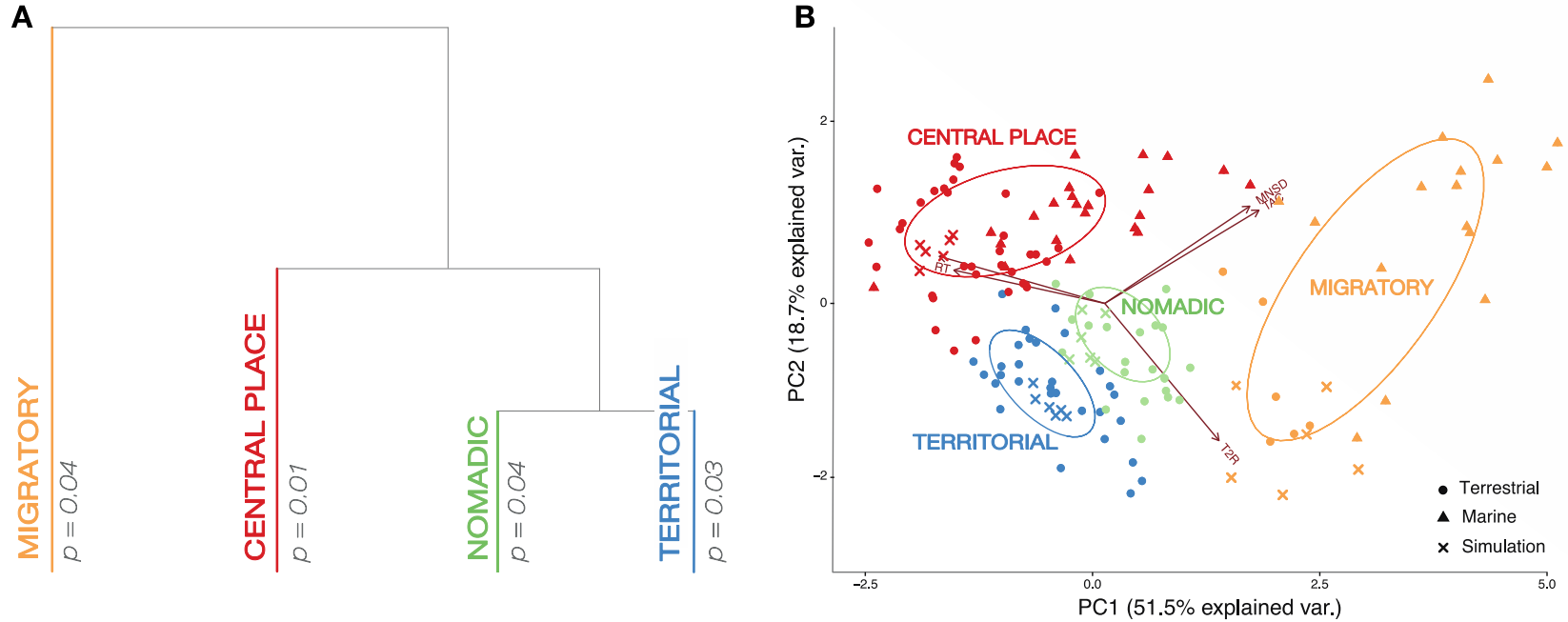


Figure 2. A) Dendrogram tree displaying results of Ward hierarchical cluster analysis of all individuals based on PC1 and PC2 values, and bootstrapped p -values for each cluster. See Fig. S1 for full display of individual leaves within each major cluster. B) Scatterplot of classified individuals based on PCA-defined axes. See Fig. S2 for scatterplot with species identities. Ellipses represent the 50% probability contour for cluster classifications. Simulated individuals are plotted for reference, although not included in the PCA.

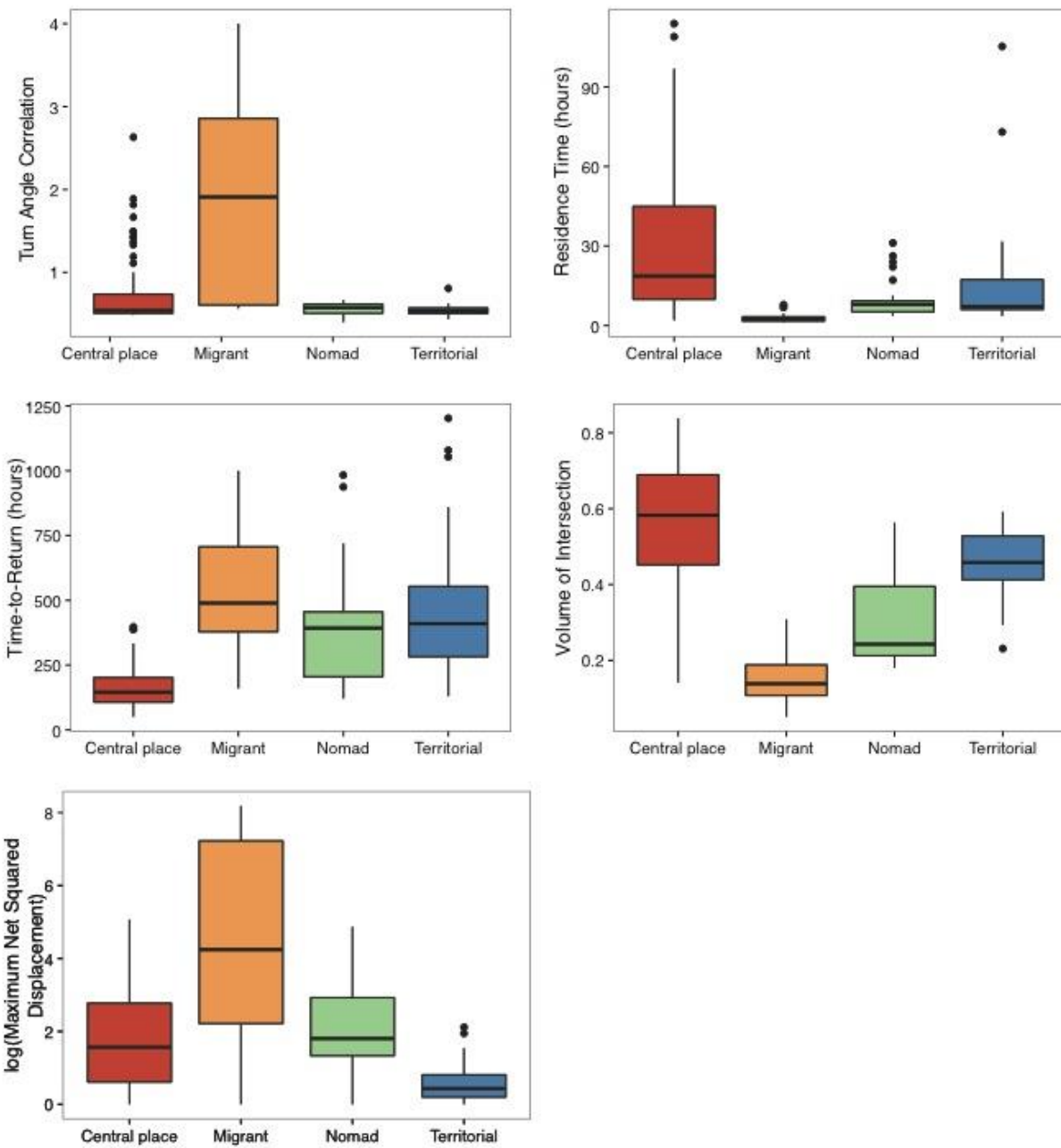


Figure 3. Boxplots of movement metrics for syndrome classifications, excluding simulated individuals.

Supplementary Material

Table S1. Summary and sources of GPS data used in analyses.

Species	N individuals	Total fixes	Duration (mo.)	Source
African buffalo	5	14449	5 ± 2.2	Bar-David et al. 2009
African elephant	8	93590	17.5 ± 5.2	Unpublished ⁴
African wild dog	13 (1 per pack)	55675	7 ± 2.3	Abrahms et al. 2016
Black-backed jackal	15	98691	9.4 ± 4.7	Bellan et al. 2012
California sea lion	15	34088	2.4 ± 0.3	Unpublished ¹
Cheetah	5	25421	7 ± 3.6	Wilson et al. 2014
Galapagos albatross	8	17123	3 ± 0.9	Dodge et al. 2013
Galapagos tortoise	8	103663	18 ± 2.7	Blake et al. 2013
Lion	9	41278	7 ± 3.3	Unpublished ²
N. elephant seal	15	120353	7.5 ± 0.5	Robinson et al. 2012
Springbok	10	59608	8.7 ± 2.3	Lyons et al. 2013
White-backed vulture	10	30454	8.5 ± 4.9	Spiegel et al. 2013
Zebra	9	67835	11.8 ± 3.1	Unpublished ³

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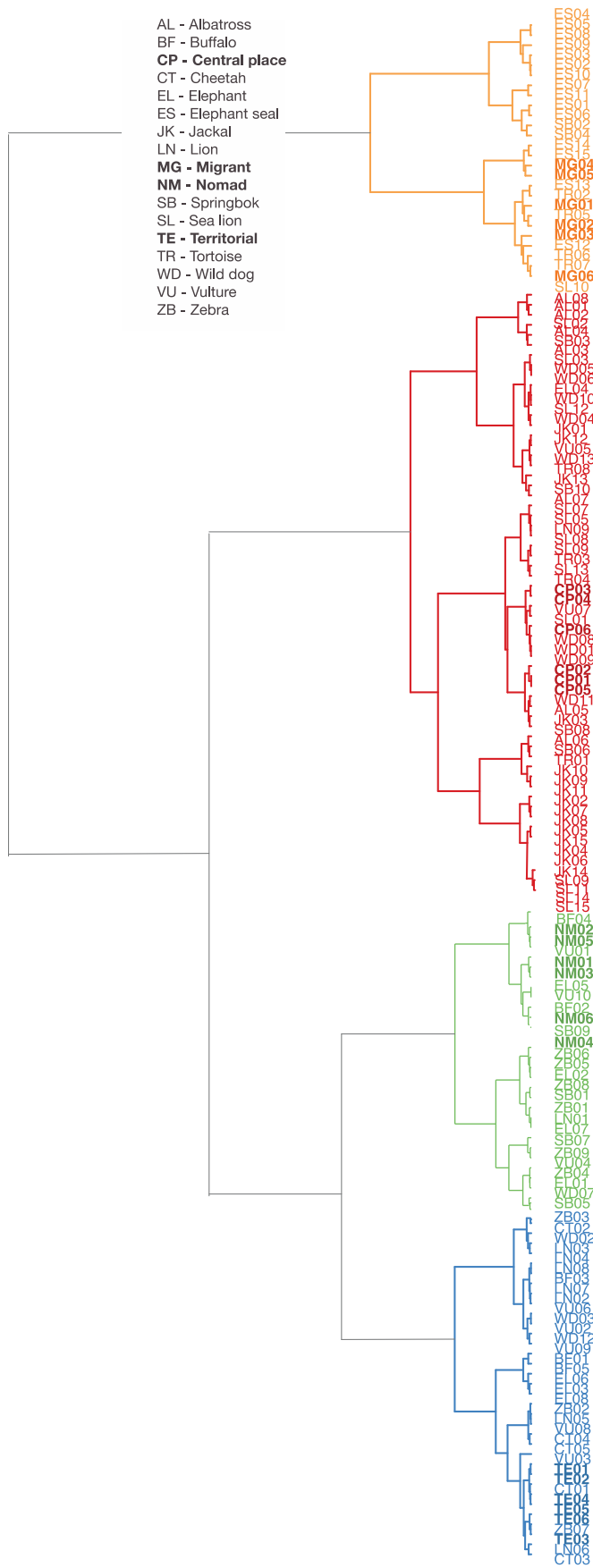


Figure S1. Full dendrogram displaying results of Ward hierarchical cluster analysis of all individuals based on PC1 and PC2 values. All individuals organize into four clusters, which can be considered movement syndromes. Simulated individuals are highlighted in bold.

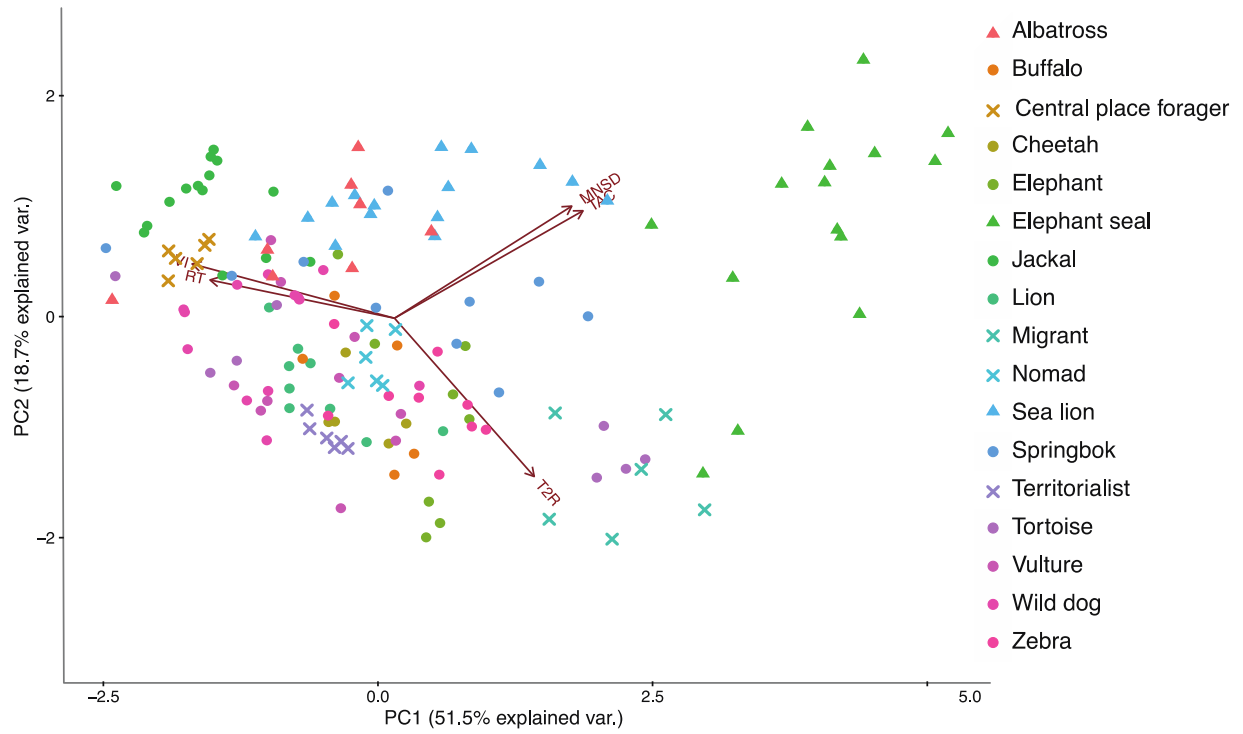


Figure S2. Scatterplot of individuals based on PCA-defined axes. Simulated individuals are plotted for reference, although not included in the PCA.

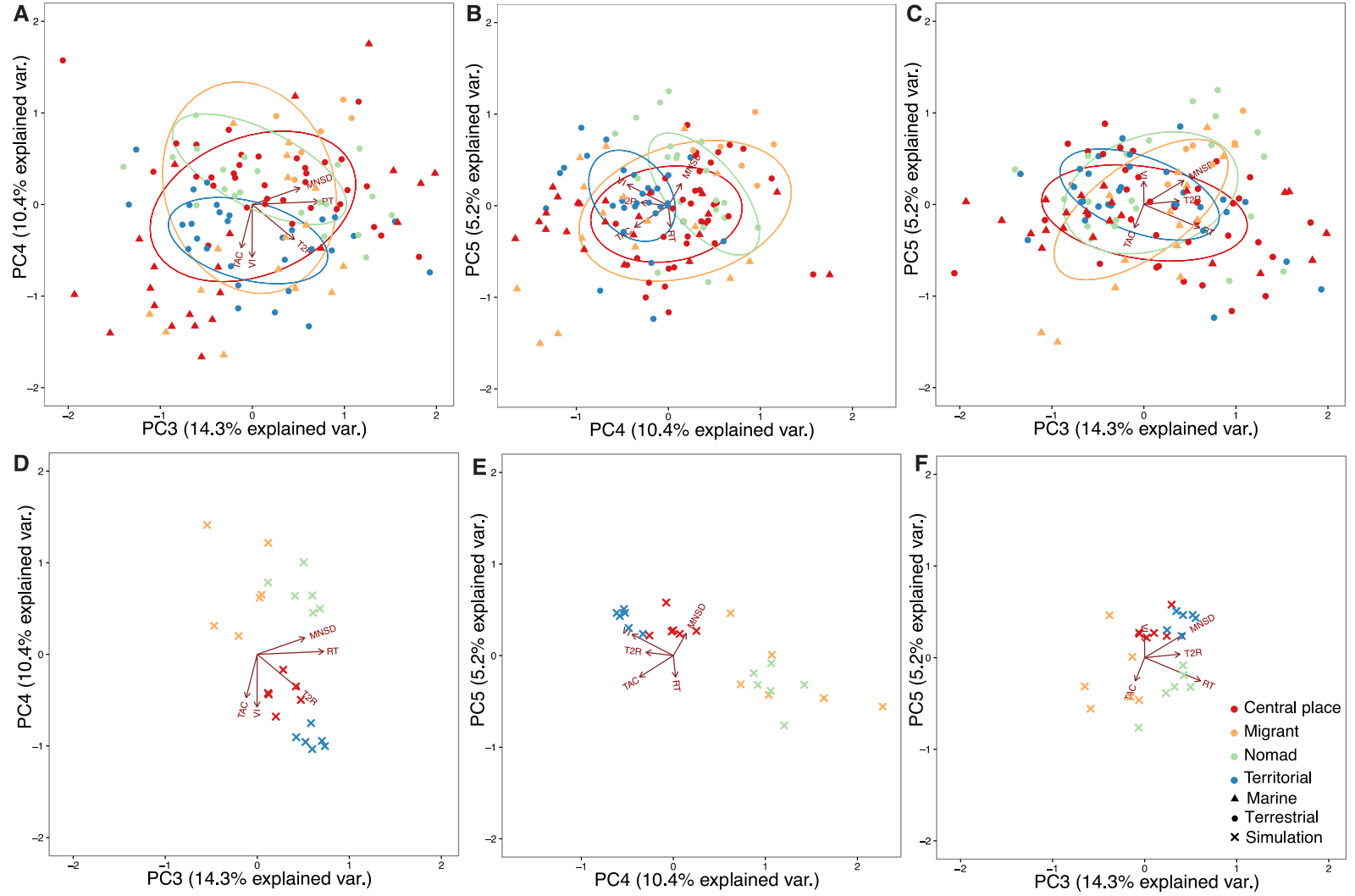


Figure S3. Scatterplot of classified empirical (panels A-C) and simulated (panels D-F) individuals based on minor PC axes (PCs 3, 4, and 5). Ellipses represent the 50% probability contour for cluster classifications based on PC1 and PC2.

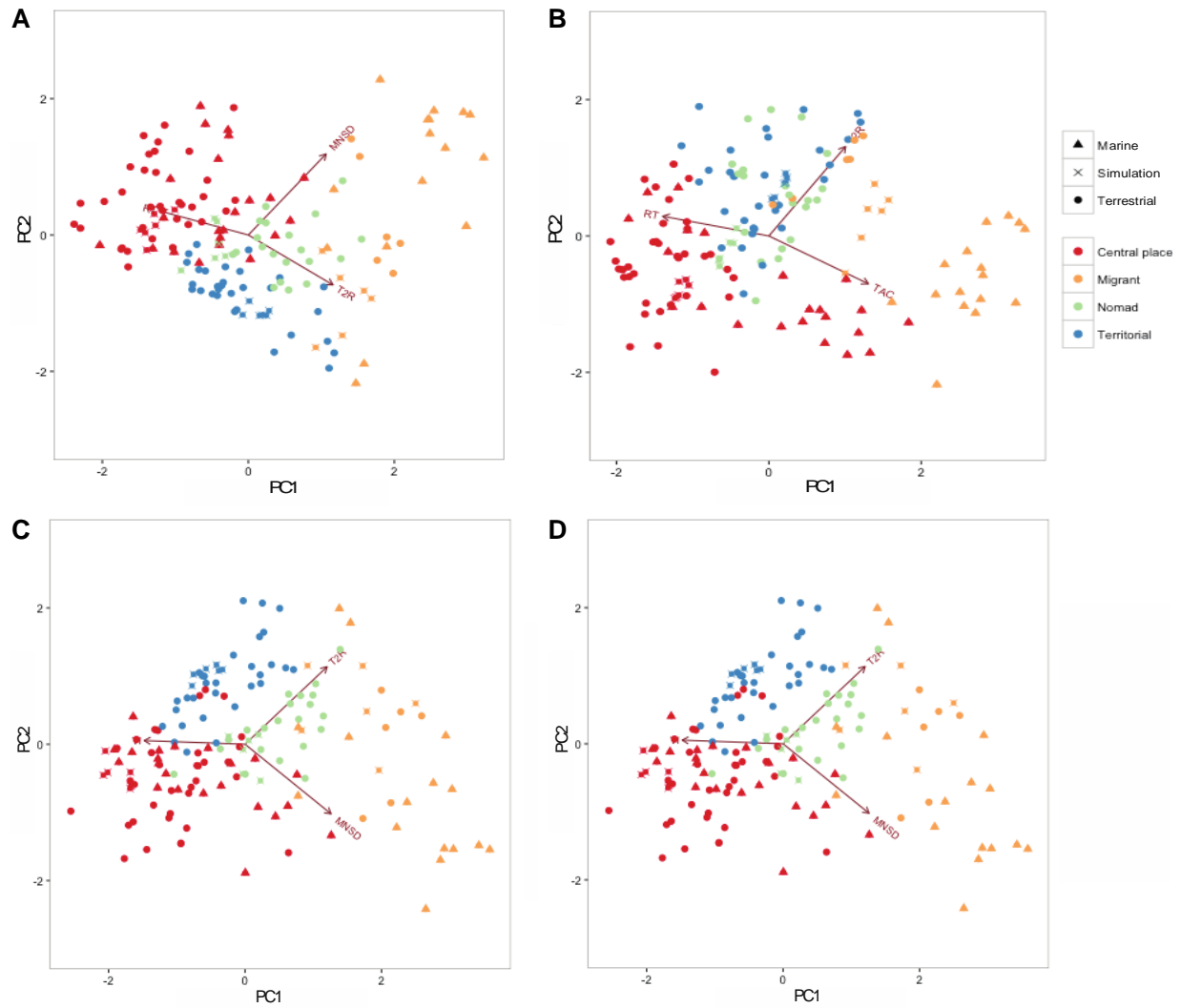


Figure S4. Scatterplots of classified individuals in PCA-defined axes based on a reduced set of three metrics to explore effects of collinearity between metrics: A) Residence Time (RT), Time-to-Return (T2R), and Maximum Net Squared Displacement (MNSD); B) RT, T2R, and Turn Angle Correlation (TAC); C) Volume of Intersection (VI), T2R, MNSD; and D) VI, T2R, and MNSD. Colors refer to cluster classifications based on the full set of five metrics for comparison.

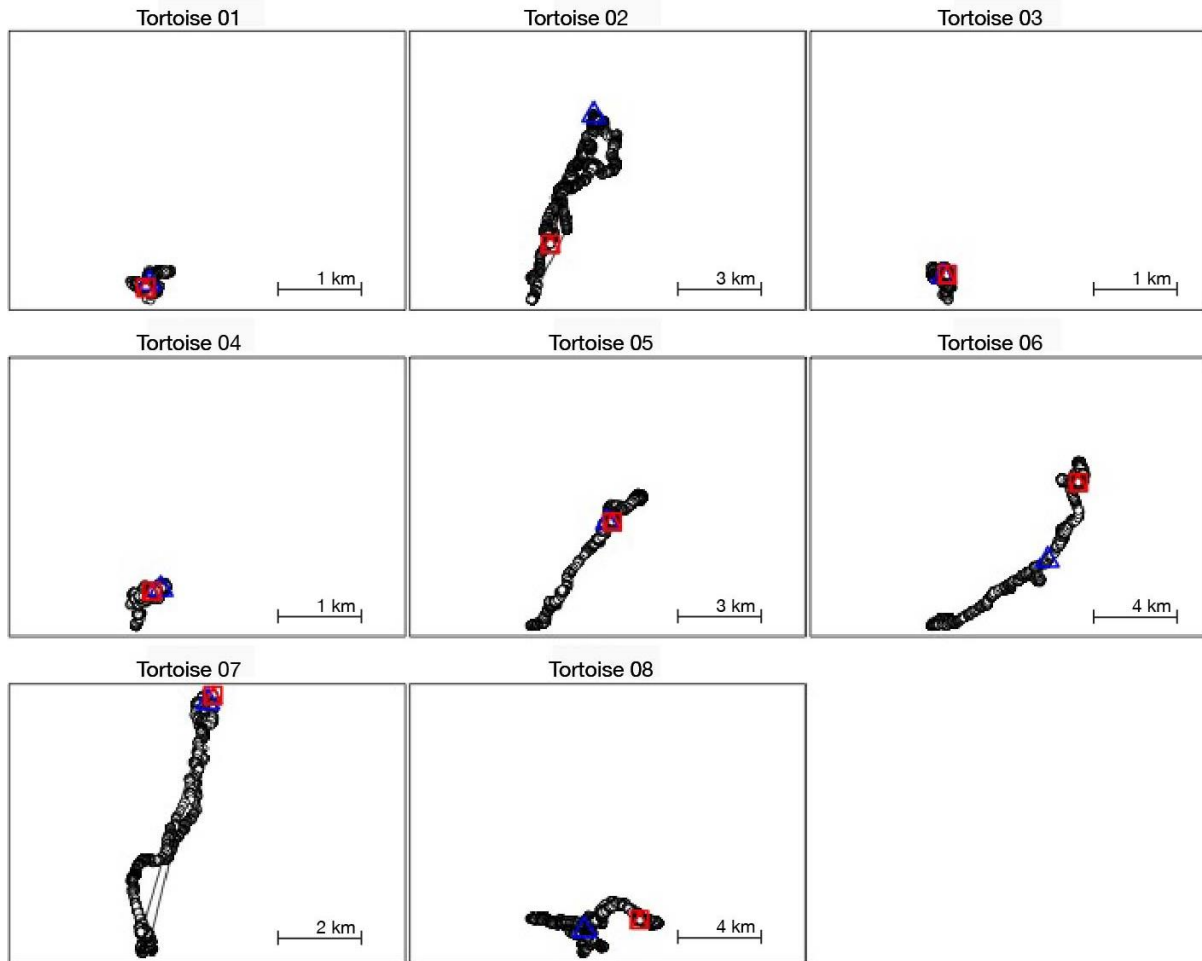


Figure S5. Movement paths of GPS-tracked resident (Tortoise 01, 03, 04, 08) and migratory Galapagos tortoises (Tortoise 02, 05-07). Movement paths begin at the blue triangle and end at the red square.

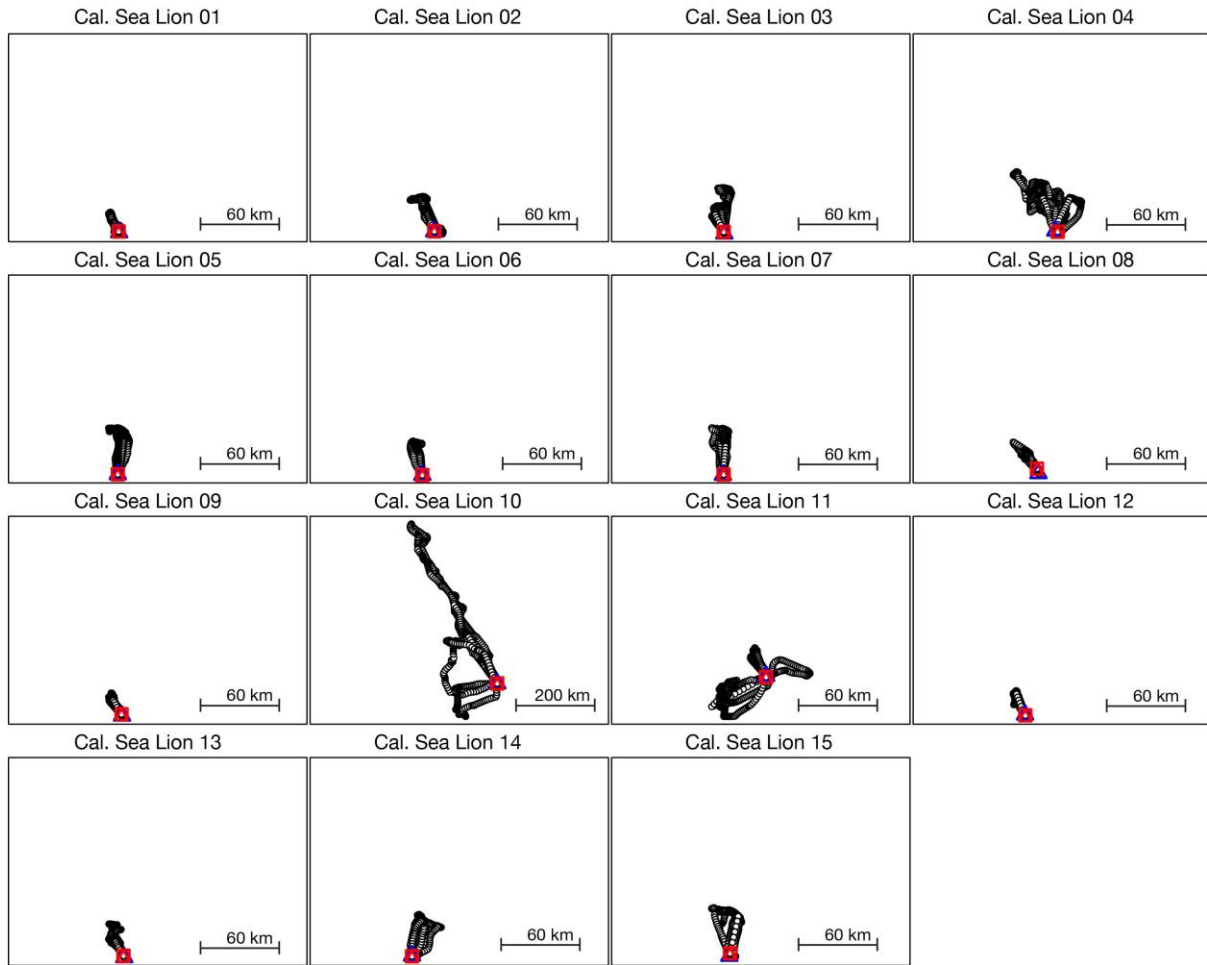


Figure S6. Movement paths of GPS-tracked California sea lions. Data were collected from females over a 3-month breeding period between November-February during which they exhibited central place foraging from the breeding colony. All individuals were appropriately classified as central place foragers except Sea Lion 10, which was classified as a migrant. Movement paths begin at the blue triangle and end at the red square.

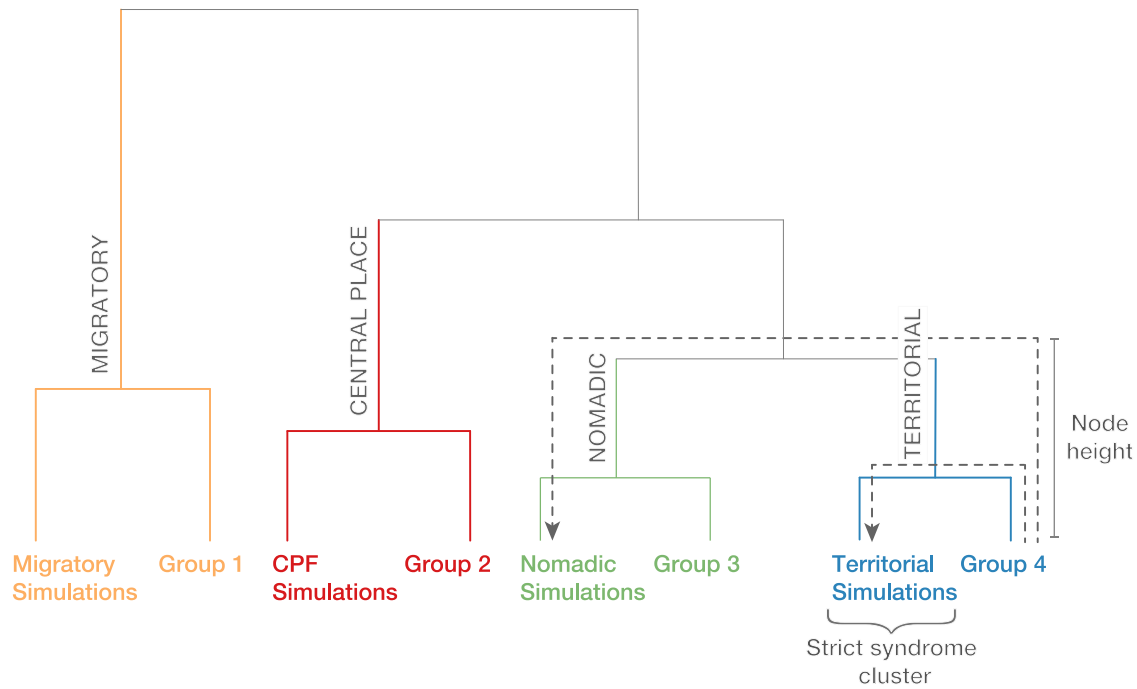


Figure S7. Illustration of method for quantifying the degree of intermediacy among movement syndromes for a given trajectory in a hypothetical dendrogram. The “strict syndrome cluster” is defined as the lowest cluster that contains all the simulations from a single syndrome. If a given trajectory is contained within the strict syndrome cluster then it is classified as being that syndrome *sensu stricto*. If a trajectory falls outside the strict syndrome cluster but within the greater syndrome cluster, then it is classified as being that syndrome *sensu lato*. In this diagram, a trajectory in Group 4 would be considered Territorial in *sensu lato*. Its degree of intermediacy between Territorial and Nomadic syndromes would be the ratio between its distance in terms of node heights to the strict Nomadic syndrome cluster and its distance to the strict Territorial syndrome cluster (gray hashed arrows).

5. Conclusions

Key Findings

At a global scale, conservation efforts in response to habitat alteration are arguably the most critical element of any strategy for protecting biodiversity. Therefore, research advancing our understanding of animal movement and landscape connectivity is imperative. The body of work presented in this dissertation provides several new approaches for increasing our understanding of the ecology and conservation of wildlife movement, and in particular for measuring wildlife responses to environmental change. Moreover, understanding the nature and drivers of behavioral modification in response to human disturbance is important for predicting how increased human activity will affect species.

My second chapter clearly showed that how animals respond to features in their environment (e.g., resource patches, anthropogenic features) can greatly depend on their behavioral state during which the landscape feature is encountered. My analyses using GPS and accelerometer data from thirteen African wild dogs showed revealed strong patterns of road selection when traveling, ignoring roads when high-speed running, and road avoidance when resting. Yet a key finding from this study was that these distinctions were not evident when analyzing all movement data in a single resource selection function, which is the status quo in resource selection studies. Thus, to fully understand how an anthropogenic landscape feature affects movements of wildlife populations, patterns of resource selection should be explicitly linked with behavioral states.

In my third chapter, I extended these findings to show how behaviorally-mediated patterns of resource selection play out in a landscape connectivity modeling context. I tested behavior-specific predictions of connectivity with long-distance dispersal movements of African wild dogs, which demonstrated that including only directed-movement behavior when measuring resource selection reveals far more accurate patterns of landscape connectivity than a model measuring resource selection independent of behavioral state. Results from this work can be directly applied in Botswana to make conservation recommendations to mitigate existing movement barriers or to protect key areas for landscape connectivity against future development for African wild dogs. I also conducted a systematic review of connectivity literature that revealed that most of the research done to date has superficially considered all animal location data as representative of resource selection patterns, despite the fact that an animal's behavioral state has been shown to be an important component of resource selection and space use. A key conclusion from this work is that researchers and conservation practitioners should be aware resource selection within an animal's home range is not always a suitable proxy for movement preference during dispersal, and failure to recognize this distinction may have important consequences for preserving landscape connectivity. Together, my second and third chapters highlight the value of incorporating behavioral information into conservation planning, and provide approaches for better linking behavior with resource selection and connectivity analyses in future efforts.

My fourth chapter identifies a framework for classifying individual animals by broad-scale movement patterns. For this I combined GPS movement data from 13 species in three taxonomic

classes with computer-simulated idealized movement paths. A central finding from this work is that a simple set of metrics can reliably classify broad-scale movement patterns like migration, nomadism, or territoriality across a wide range of vertebrate taxa in both terrestrial and marine environments. This classification scheme can inform predictions in multiple areas of ecological research. For example, an individual or species' movement classification can inform predictions on how it will respond to climate change or its invasion potential in an exotic environment. In addition, this work provides researchers with a standardized set of metrics for expediently analyzing animal trajectories of any species over time to detect any changes in movement pattern that may be indicative of environmental change.

Taken together, my dissertation sheds light on the processes shaping animal movement patterns, with applications to landscape connectivity science and predicting impacts of human-driven environmental changes.

Future Research

A few directions for future research emerge from the results of this work, while at the same time advances in monitoring technology are fostering new opportunities to study animal movement that promise to enhance biodiversity conservation. First, a significant challenge to current approaches in connectivity modeling that my dissertation did not address is the static treatment of the landscapes considered in the modeling process. Current trends in characterizations of animal space use and connectivity science do not account for dynamic fluctuations in the environment at multiple temporal scales, such as seasonal changes in vegetation or species distributions, or long-term changes in land-use and/or climate, because this is computationally challenging (Roshier & Reid 2003; Zeller, McGarigal & Whiteley 2012). Connectivity methods rely instead on stationary images of remotely sensed landscapes, despite recognition that few landscapes are static through time (Beier *et al.* 2011; Rudnick *et al.* 2012). This challenge is exemplified in my study system, the Okavango Delta, where dramatic seasonal fluctuations in hydrography influence the permeability of the landscape to wildlife populations. The seasonal Delta flood has been shown to create a temporarily impermeable barrier for all large carnivore species except lions from June to September (Cozzi *et al.* 2013). Geophysical constraints due to the flood system may therefore seasonally restrict both home range extents and dispersal paths. Thus, assuming that environments are static may result in a limited or even spurious understanding of animal space use. When applied to connectivity planning, assumptions of static environments may lead to inaccurate designation of wildlife corridors or corridors that only provide temporary windows of connectivity (Zeigler & Fagan 2014). Development of methods to overcome this limitation, such as dynamic resistance surfaces that can identify regions on a landscape where planners may expect high variability in contributions to connectivity, is an important next step.

Similarly, accounting for spatiotemporal variation not only in the physical environment, but also in the effects of interspecific interactions, could help inform a more biologically relevant framework for modeling animal movement and landscape connectivity. Resistance surface modeling seeks to bridge classic metrics of structural landscape connectivity with functional connectivity by including species-specific ecological information such as dispersal ability (Rudnick *et al.* 2012). However, many ecological processes that likely affect movement choices

are often omitted from models as they are difficult to quantify and map, and linking behavioral ecology with connectivity science is recognized as a need for future research (Rudnick *et al.* 2012). In particular, interspecific competition and predation significantly alter animal behavior and movement over multiple spatial scales (Fortin *et al.* 2005; Broekhuis *et al.* 2013). This understanding has been conceptualized as a “landscape of fear”, in which relative levels of predation risk are represented as “peaks and valleys that reflect the level of fear of predation a prey experiences in different parts of its area of use” (Laundré, Hernández & Ripple 2010). In my study system, African wild dogs are limited by direct predation and competition by lions and hyenas, and are known to avoid these sympatric predators when there is immediate risk of encounters (Webster, McNutt, and McComb 2012). Future research should explore the utility of a marriage between landscape of fear and connectivity approaches to assess the effects of including interspecific interactions in resistance surface modeling predictions.

Finally, scientific culture and practices from the disciplines of landscape ecology and marine, or ‘seascape’, ecology could undoubtedly better speak to and inform one another. Methods for dealing with the extreme dynamism inherent in seascape ecology, such as the pairing of animal locations with real-time oceanographic conditions (Block *et al.* 2011) and the development of dynamic ocean management (Lewison *et al.* 2015), could aid in the development of dynamic landscape connectivity modeling as described above. On the other hand, most analyses of connectivity in marine environments rely on estimates of genetic distances between populations that supply a low-resolution understanding of seascape connectivity (Thomas *et al.* 2015). Resistance surface modeling borrowed from landscape ecology could offer a more detailed and management-relevant understanding of connectivity between marine populations or oceanographic features (Caldwell & Gergel 2013). Studies bridging the disciplines of landscape and seascape ecology are rare, and further investigation is needed on what can and cannot translate between fields (Manderson 2016), but strengthening their cross pollination holds promise in improving both terrestrial and marine spatial planning for the conservation of biodiversity.

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