Journal of Applied Ecology

Journal of Applied Ecology 2016 doi: 10.1111/1365-2664.12714

REVIEW

Does wildlife resource selection accurately inform corridor conservation?

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Summary

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 16 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.

Key-words: behavioural state, conservation planning, corridor ecology, dispersal, landscape connectivity, landscape resistance, movement ecology, resource selection, step selection

Introduction

Connectivity, that is 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

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(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, that is land allowing movement of focal species between two or more habitat areas (Beier, Majka and Spencer 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 16 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 (Graves, Beier & Royle 2013; Reding *et al.* 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 *et al.* 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.* 2015).

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 *et al.* (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 *et al.* (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 (i) evaluate the extent to which these efforts have incorporated movement behaviour and (ii) 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 towards 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 keywords: 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 (i) the source of biological data (study species and data collection method), (ii) type of RSF employed (e.g. point selection, step selection), (iii) whether movement behaviour was explicitly considered in developing connectivity models and (iv) 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.* 2015). 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: travelling, 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 travelling data set (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.* 2015; 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

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

Study	Species	Data collected	RSF type	Consideration of movement behaviour	Validation of connectivity predictions with independent movement data
Braaker *et al.* (2014)	*Erinaceus europaeus*	Relocation – GPS	PSF	None	None
Brodie *et al.* (2014)	*Hemigalus derbyanus; Helarctos malayanus; Neofelis diardi; Rusa unicolor; Macaca nemestrina*	Detection – Camera trap	PSF	None	None
Carvalho *et al.* (2015)	*Genetta genetta*	Relocation – VHF	PathSF	None	None
Chetkiewicz & Boyce (2009)	*Ursus arctos; Puma concolor*	Relocation – GPS	PSF	None	None
Clark *et al.* (2015)	*Ursus americanus luteolus*	Relocation – GPS	SSF	Removed relocations <100 m apart	None
Cushman & Lewis (2010)	*Ursus americanus*	Relocation – GPS	PathSF	None	None
Elliot *et al.* (2014)	*Panthera leo*	Relocation – GPS	PathSF	Resource selection of dispersing individuals	None
Harju *et al.* (2013)	*Centrocercus urophasianus*	Relocation – GPS	SSF	Resource selection during travelling and relocating states	Validated with independent GPS data in travelling and relocating states
Kautz *et al.* (2006)	*Puma concolor coryi*	Relocation – VHF	PSF	None	None
Kindall & Manen (2007)	*Ursus americanus*	Relocation – VHF	PSF	None	None
LaPoint *et al.* (2013)	*Martes pennanti*	Relocation – GPS	PSF	None	Validated with 'animal-defined' corridors based on rate of fast, linear movement
Mateo-Sánchez, Cushman & Saura (2014)	*Ursus arctos*	Detection – Sign	PSF	None	None
McClure, Hansen & Inman (2016)	*Cervus elaphus; Gulo gulo*	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)	*Rangifer tarandus caribou*	Relocation – GPS	PSF	None	None
Proctor *et al.* (2015)	*Ursus arctos*	Relocation – GPS	PSF	None	None
Pullinger & Johnson (2010)	*Rangifer tarandus caribou*	Relocation – GPS	SSF	Resource selection during large-scale movements	Validated with independent GPS data identified as long-distance movement
Reding *et al.* (2013)	*Lynx rufus*	Relocation – VHF	PathSF	None	None
Richard & Armstrong (2010)	*Petroica longipes*	Relocation – VHF	SSF	Resource selection of dispersing individuals	None
Roever, van Aarde & Leggett (2013)	*Loxodonta africana*	Relocation – GPS	PSF	None	None
Squires *et al.* (2013)	*Lynx canadensis*	Relocation – GPS	SSF	Resource selection during movement state	None
Sutcliffe *et al.* (2003)	*Aphantopus hyperantus; Heodes virgaureae*	Relocation – Mark–recapture	MSF	Resource selection for matrix with highest passage rates	None
Thatcher, van Manen & Clark (2009)	*Puma concolor coryi*	Relocation – VHF	HSF	None	None
Trainor *et al.* (2013)	*Picoides borealis*	Relocation – VHF	PSF	Resource selection of dispersing individuals	Validated with frequency of dispersal events within predicted corridors
Verbeylen *et al.* (2003)	*Sciurus vulgaris*	Detection – Sign	MSF	None	None
Walpole *et al.* (2012)	*Lynx canadensis*	Detection – Sign	PSF	None	None
Wang *et al.* (2014)	*Ailuropoda melanoleuca*	Detection – Camera trap	PSF	None	None
Zeller *et al.* (2014)	*Puma concolor*	Relocation – GPS	PSF	Resource selection during movement state	None
Zeller *et al.* (2015)	*Puma concolor*	Relocation – GPS	SSF, PathSF	Removed relocations <200 m apart	None

PSF, 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, McGarigal and Whiteley 2012).

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

Category	Variable name	Description	Source
Habitat cover	Swamp	Moist and seasonally flooded floodplains	Broekhuis *et al.* (2013)
	Grassland	Former floodplains characterized by shrubbed grassland	
	Woodland	Mixed woodland dominated by *Acacia* spp.	
	Mopane	Woodland composed primarily of *Colophospermum mopane* 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 Management 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	

width for African wild dogs (8 km; 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). First, 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 (Supporting information) 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 *et al.* (2013) found that connectivity estimates based on resource selection during travelling 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 data set 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 towards generating management strategies. As showcased by several such

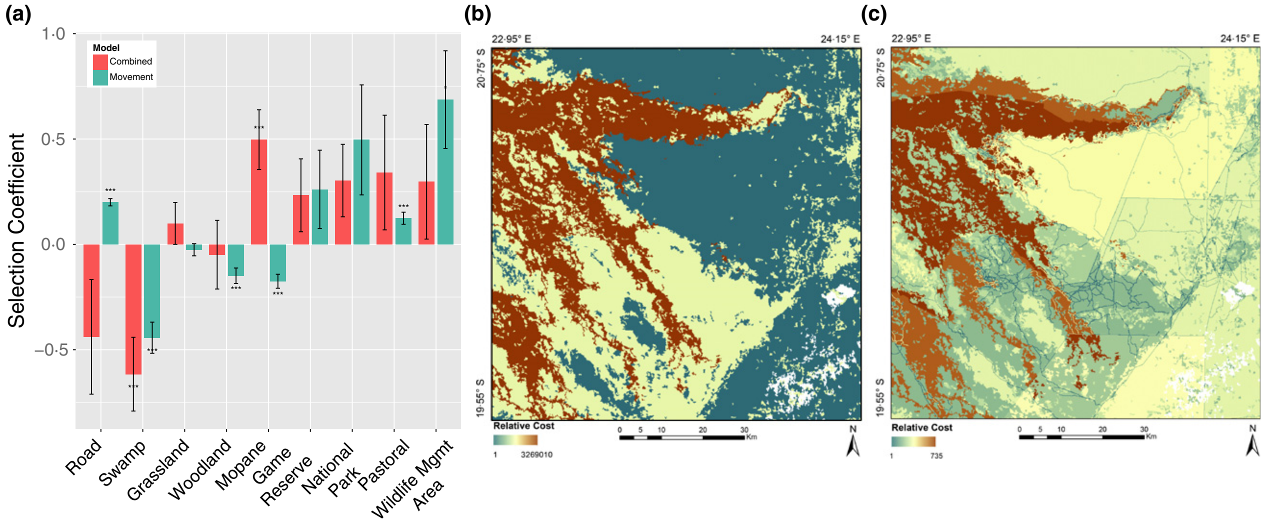

Fig. 1. (a) Comparison of step selection parameter estimates and standard errors for the combined model, measuring resource selection for all location data independent of behavioural state, and the movement model, measuring resource selection only when wild dogs were in a 'travelling' behavioural state (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 ($P < 0{\cdot}05$) in the combined model. Resistance values were calculated as the inverse of scaled 'probability of use' values $w(x) = \exp(\text{ß}_1 x_1 + \text{ß}_2 x_2 + \ldots.)$ where ß_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.

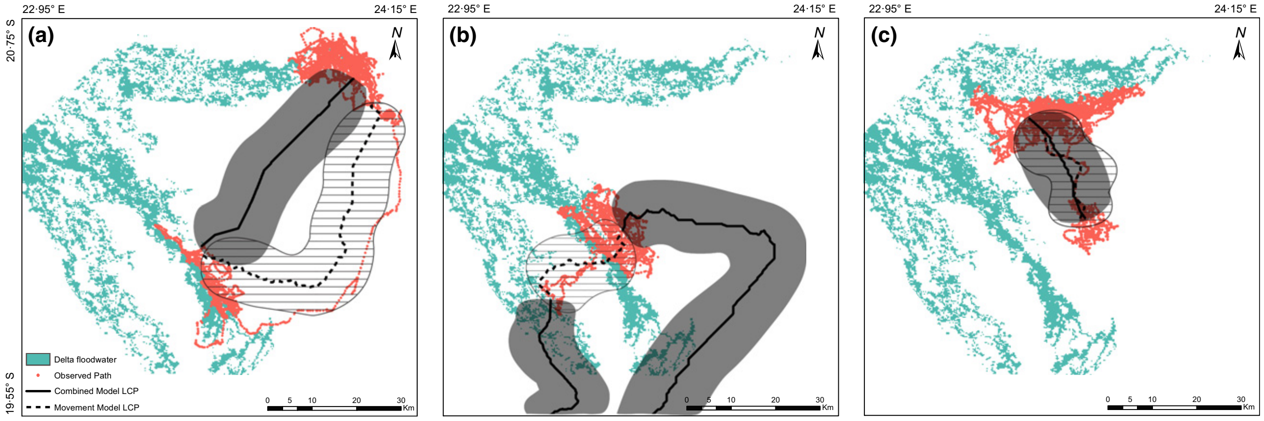

Fig. 2. Comparison between least-cost corridors derived from combined model (solid black lines), movement model (dashed black lines) and GPS-captured paths (orange dots) from three distinct dispersal events in (a) October 2014, (b) August 2013 and (c) January 2012 (Table S1). Okavango Delta floodwaters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

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

		Path deviation		
Model	LCC overlap %	Mean (km)	SD	*P*
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	0·34	0·75	0·07
Path 3 – Combined	100	1·93	1·55	

studies, multiple data collection, and 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 (i) 'travelling', 'relocating' or

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

Approach	Description	No. of Studies	Example studies
Behavioural	Use localities when the individual is in a travelling/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 & Lewis (2010), Roever *et al.* (2013), Walpole *et al.* (2012)

'moving' based on step-length distributions (Harju *et al.* 2013; Zeller *et al.* 2014); (ii) 'large-scale movements' delimited by a threshold for movement rate (Pullinger & Johnson 2010); and (iii) 'active' vs. '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 vs. long-distance movement for caribou *Rangifer tarandus* by examining movement rate between 3-h 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 necessitates 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 (Nathan *et al.* 2008; Schick *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 and 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 photographs 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 'travelling' 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 travelling 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 *et al.* 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

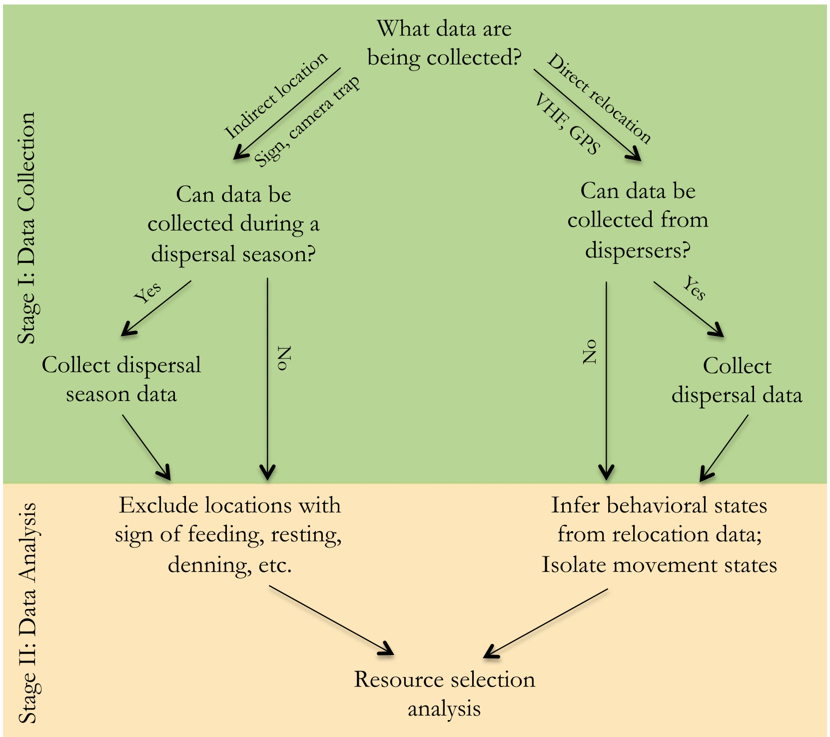

Fig. 3. A decision tree for focusing resource selection analyses on animal movement for connectivity planning. At the data collection stage, decisions are made as to the type of data that can be collected and whether collection can be targeted towards dispersal seasonally or demographically. At the data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

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 4-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

We thank the Botswana Ministry of Environment for permission to conduct this research (EWT 8/36/4 XXIV). This material is based upon work supported by the National Science Foundation (Grant No. 325 DGE1106400), the Riverbanks Zoo and The Explorers Club. We thank J. Lowe and S. Amos for fabricating collars and the EPSRC (EP/H013016/1), BBSRC (BB/J018007/1) and ERC (323041) for funding the collaring programme. We thank K. Golabek and BPCT research assistants for valuable field contributions, B. Reineking, C. Harris and M. Tsalyuk for assistance with analyses and W. Getz, E. Lacey, A. Merenlender and the Brashares Group for helpful comments. We are grateful to N. Balkenhol, P. Beier and an anonymous reviewer for providing feedback that greatly strengthened this manuscript.

Data accessibility

African wild dog dispersal path data are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.66kc7 (Abrahms *et al.* 2016).

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Received 14 March 2016; accepted 3 June 2016
Handling Editor: Matt Hayward

Supporting Information

Additional Supporting Information may be found in the online version of this article.

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

Table S2. AIC model selection results for step selection functions.

Table S3. Step selection parameter estimates.

Table S4. Results of sensitivity analysis for 1-h fix intervals.

Appendix S1. Detailed methods for African wild dog case study.