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

Short Title: Integrating behaviour and resource selection

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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.

Key-words

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 (*Orcinas 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 km^2; 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/s^2). 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, $|\beta| = 1.05e\text{-}04$; grassland, $|\beta| = 1.4e\text{-}04$), and increased with increasing habitat density (woodland, $|\beta| = 1.95e\text{-}04$; mopane, $|\beta| = 2.56e\text{-}04$), although road selection was only moderate in the densest habitat category, riparian ($|\beta| = 1.65e\text{-}04$). 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 $\beta = 2.18e\text{-}05$). A second peak in road selection occurred in June-August (min $\beta = -1.04e\text{-}04$), 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.

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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**	***p***
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

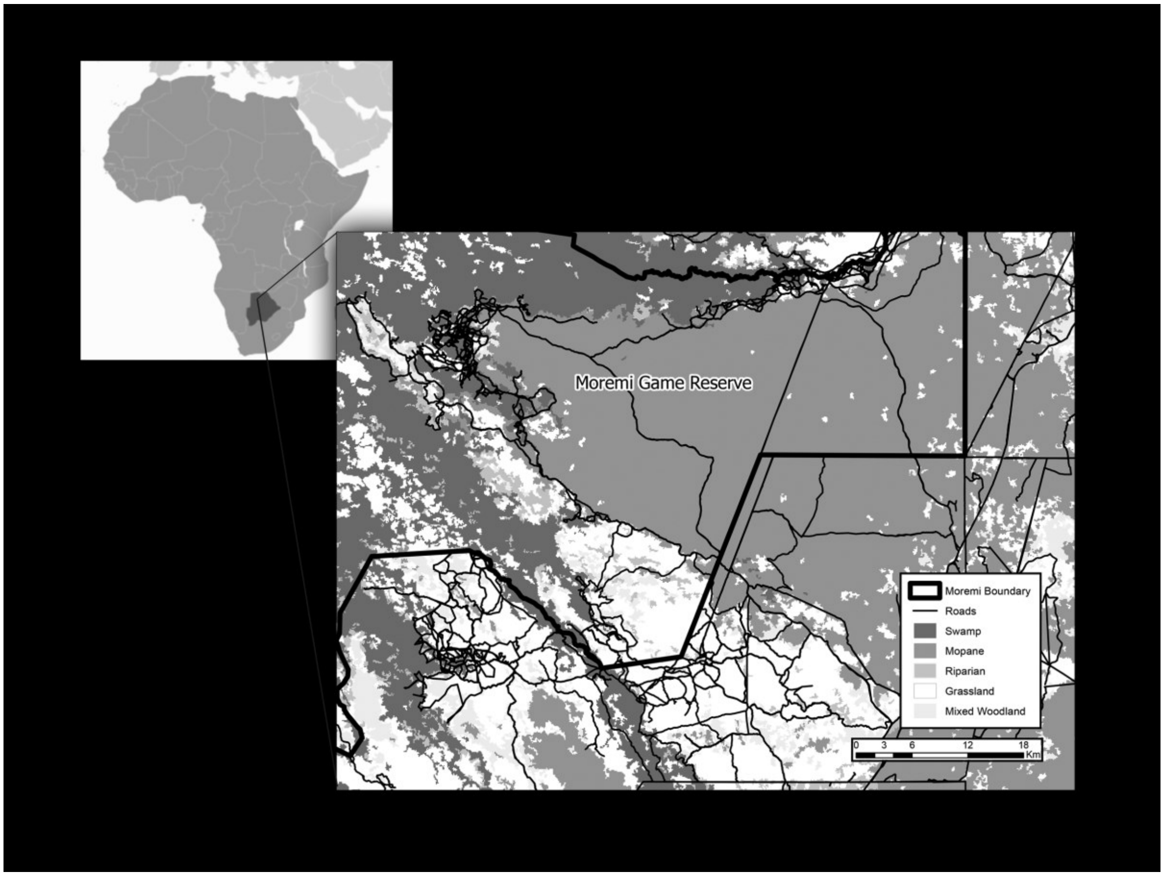
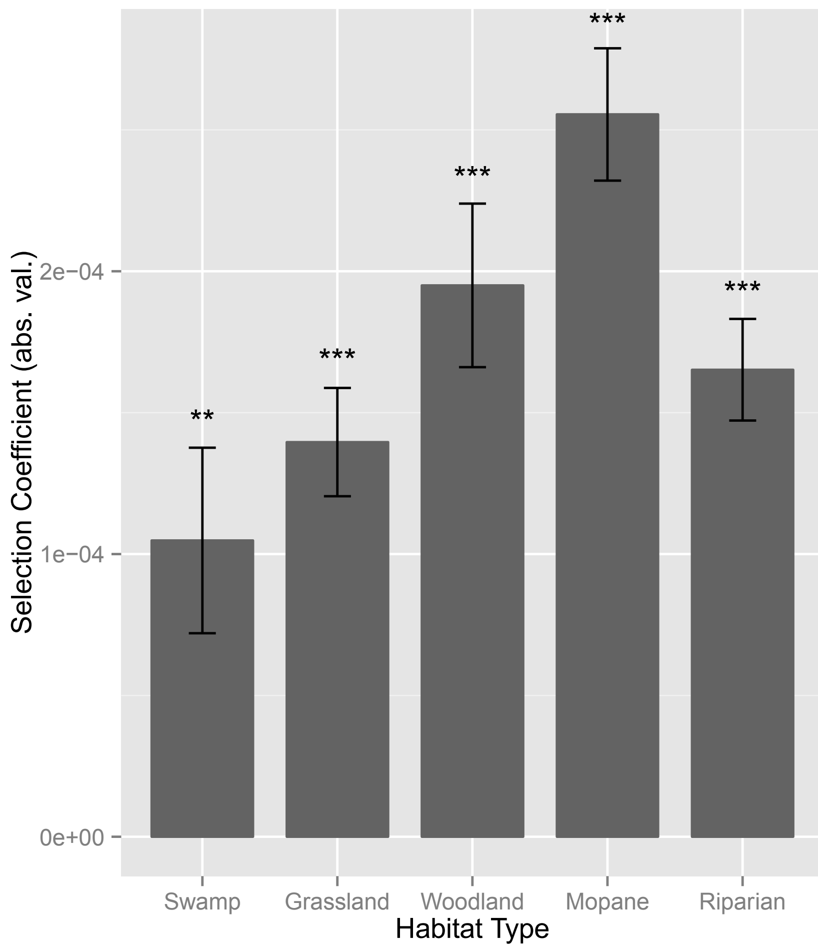

Moremi Game Reserve
Moremi Boundary
Roads
Swamp
Mopane
Riparian
Grassland
Mixed Woodland
0 3 6 12 18
Km

Figure 2

Figure 3



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2e−04
1e−04
0e+00
Selection Coefficient (abs. val.)
Swamp
Grassland
Woodland
Mopane
Riparian
Habitat Type

Figure 4

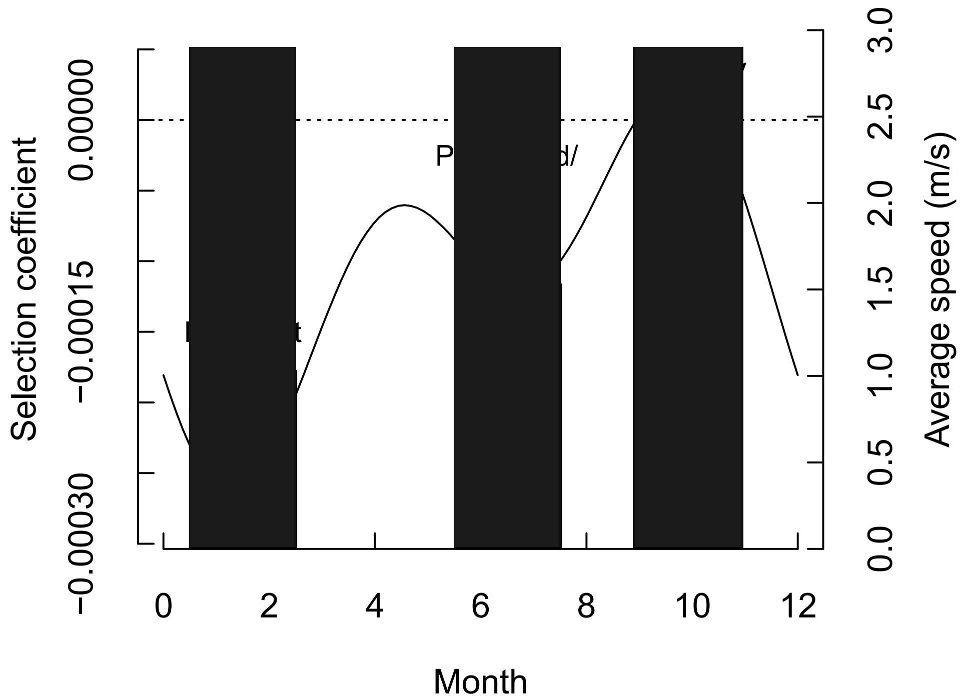
Selection coefficient
0.00000
−0.00015
−0.00030
Average speed (m/s)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
2
4
6
8
10
12
Month

Figure 5

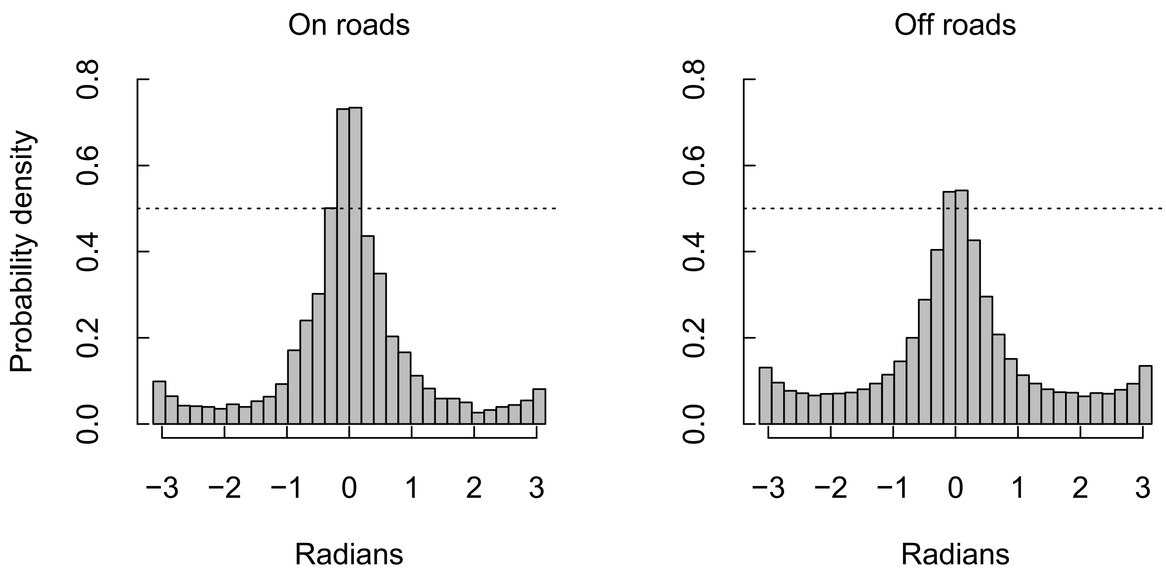
On roads
Off roads
Probability density
0.0
0.2
0.4
0.6
0.8
−3
−2
−1
0
1
2
3
Radians

Figure Captions

Figure 1. Map of study area (*c.* 2700 km^2; 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

The following Supplementary Material is available for this article online.

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.

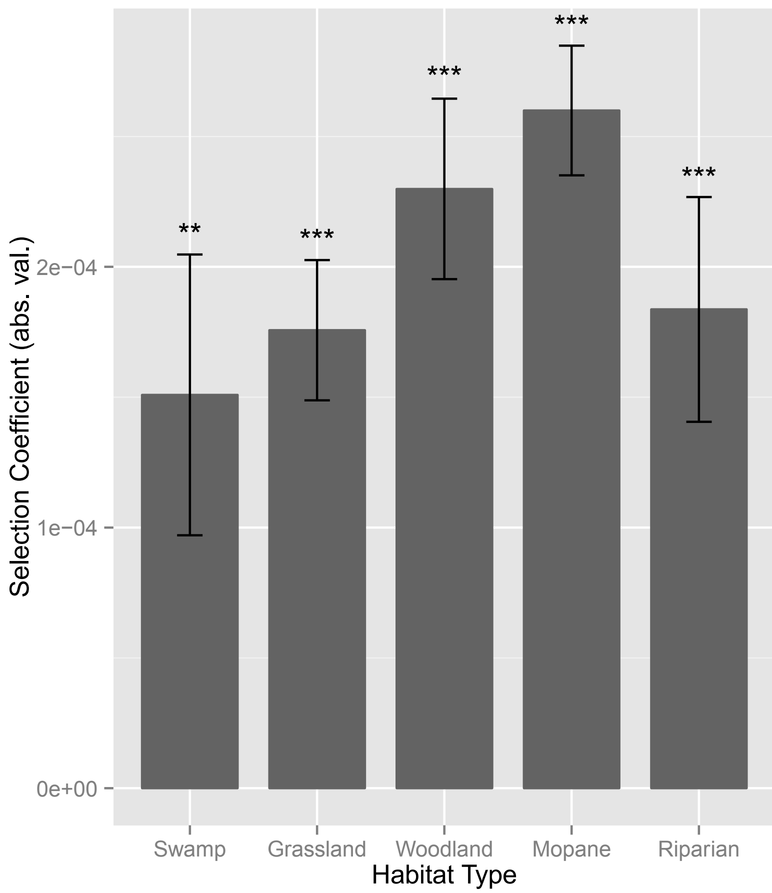

Figure S2. Variation in road selection over time of year (black line) when African wild dogs were moving consistently, excluding multiple individuals from the same pack (“traveling”; $n = 6$ individuals, 25601 steps), and corresponding travel speeds averaged within each season (light grey bars = average 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.