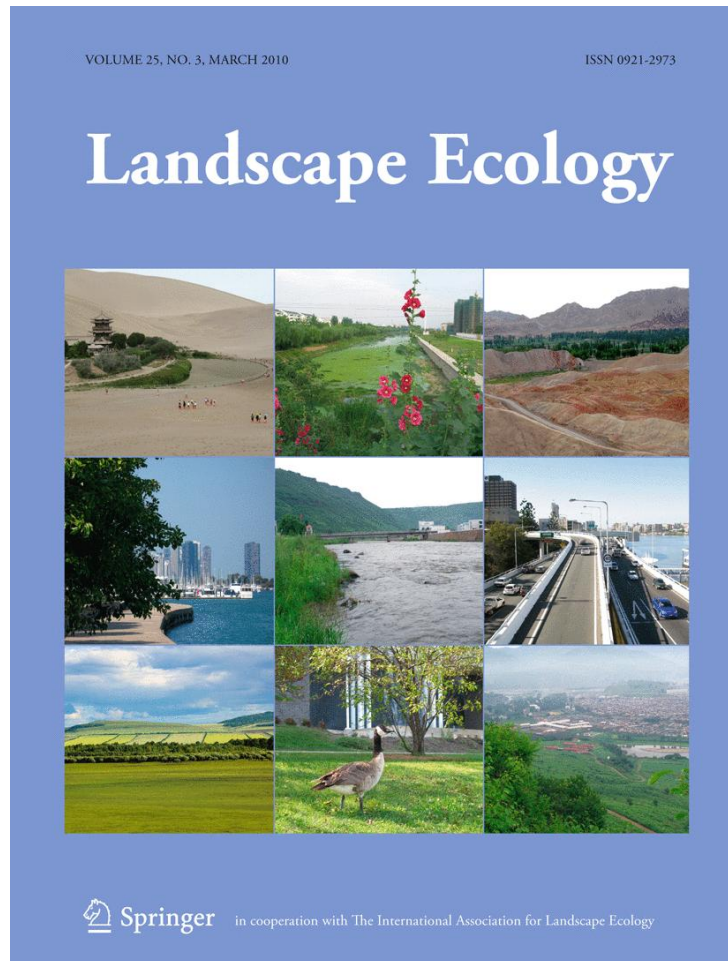


**ISSN 0921-2973, Volume 25, Number 3**



**This article was published in the above mentioned Springer issue.  
The material, including all portions thereof, is protected by copyright;  
all rights are held exclusively by Springer Science + Business Media.  
The material is for personal use only;  
commercial use is not permitted.  
Unauthorized reproduction, transfer and/or use  
may be a violation of criminal as well as civil law.**

# How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe

Marion Valeix · Andrew J. Loveridge ·  
Zeke Davidson · Hillary Madzikanda ·  
Hervé Fritz · David W. Macdonald

Received: 1 May 2009 / Accepted: 28 October 2009 / Published online: 12 November 2009  
© Springer Science+Business Media B.V. 2009

**Abstract** Within a landscape where prey has an aggregated distribution, predators can take advantage of the spatial autocorrelation of prey density and intensify their search effort in areas of high prey density by using area-restricted search behaviour. In African arid and semi-arid savannas, large herbivores tend to aggregate around scarce water sources. We tested the hypothesis that water sources are a key determinant of habitat selection and movement patterns of large free-ranging predators in such savannas, using the example of the African lion. We used data from 19 GPS radio-collared lions in Hwange National Park, Zimbabwe. Maps of lions' trajectories showed that waterholes are key loci

on the lions' route-maps. Compositional analyses revealed that lions significantly selected for areas located within 2 km of a waterhole. In addition, analysis of lions' night paths showed that when lions are close to a waterhole (<2 km), they move at lower speed, cover shorter distances per night (both path length and net displacement) and follow a more tortuous path (higher turning angle, lower straightness index and higher fractal dimension) than when they are further from a waterhole. Hence, our results strongly suggest that lions adopt area-restricted searching in the vicinity of waterholes, and reduce their search effort to minimize the time spent far from a waterhole. They provide an illustration of how key habitat features that determine the dispersion of prey (e.g. waterholes in this study) have an influence on the spatial ecology and movement patterns of terrestrial predators.

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10980-009-9425-x](https://doi.org/10.1007/s10980-009-9425-x)) contains supplementary material, which is available to authorized users.

M. Valeix (✉) · A. J. Loveridge · Z. Davidson ·  
D. W. Macdonald  
Wildlife Conservation Research Unit, Zoology  
Department, Oxford University, Tubney House,  
Abingdon OX135QL, United Kingdom  
e-mail: mvaleix@yahoo.fr

M. Valeix · H. Fritz  
Laboratory of Evolutionary Biometry and Biology,  
University of Lyon, CNRS University Claude Bernard  
Lyon 1 UMR 5558, Bât Gregor Mendel, 43 Bd du  
11 novembre 1918, 69622 Villeurbanne cedex, France

H. Madzikanda  
Zimbabwe Parks and Wildlife Management Authority,  
PO Box CY140, Causeway, Harare, Zimbabwe

**Keywords** Area-restricted search · Compositional analysis · Fractals · Habitat selection · Hwange National Park · Landscape structure · *Panthera leo* · Path tortuosity

## Introduction

Landscapes are characterized by spatial heterogeneity (Kotliar and Wiens 1990) and the interaction between animal movement and landscape structure is a key process in a large spectrum of fundamental behavioural and ecological processes such as foraging behaviour

(e.g. Etzenhouser et al. 1998; Bailey and Thompson 2006), spatial distribution of animals (Turchin 1991), migration and dispersal (Gustafson and Gardner 1996). The characteristics of an animal's movements reflect its relationships with diverse abiotic and biotic factors and may be influenced by habitat characteristics (e.g. Bélisle et al. 2001), resource abundance and distribution (Fauchald 1999), predation risk (e.g. Fortin et al. 2005; Frair et al. 2005), and other complex behavioural processes (e.g. Roshier et al. 2008). However, it is commonly accepted that, all else being equal, animals should spend more time, and move differently, in areas where resources are abundant than in areas where they are scarce.

Within a landscape where prey has an aggregated distribution, predators can take advantage of the spatial autocorrelation of prey density and intensify their search effort in areas of high prey density by using area-restricted search behaviour, i.e. lowering speed and increasing turning rate in response to increased resource abundance (Smith 1974a, b; Kareiva and Odell 1987). In areas of lower prey density, an extensive search mode is expected, where rapid, straight-line travel minimizes the time spent between rich patches and reduces search effort (Zollner and Lima 1999). Besides, animals can use their navigation capacity, i.e. their ability to choose a heading destination and know their location relative to their destination, to adopt oriented movement and travel by orienting themselves towards a given goal (Nams 2006). This is very likely to be the case when patches of resources are clearly identified in the landscape. Consequently, perception of prey abundance and distribution can dictate directly which mode of search behaviour is employed, and may have an important effect on the movement patterns of predators. The development of radio- and satellite-telemetry now facilitates a finer understanding of how animals travel at large spatial or temporal scales and the recent combined use of such data with Geographic Information System (GIS) has become a powerful tool to investigate the interaction between animal movement and their environment. The relationship between search patterns and the distribution of prey has been documented for large free-ranging predators in marine ecosystems (e.g. Pinaud and Weimerskirch 2005; Bailey and Thompson 2006) but extremely little is known for large free-ranging

predators in terrestrial ecosystems (but see Atkinson et al. 2002).

Animal movement has been the focus of much theoretical and empirical work over the past 25 years, and the methods used have been very diverse including correlated random walk (Kareiva and Shigesada 1983), fractal analysis (With 1994; Nams 2005; e.g. Fritz et al. 2003), first passage time (Fauchald and Tveraa 2003), Lévy flights (Viswanathan et al. 1996), and state-space models (Jonsen et al. 2003). Often, the approaches are aimed at (1) determining the scale at which the animal uses area-restricted search behaviour, (2) identifying the areas where the animal uses area-restricted search behaviour and ultimately (3) assessing the habitat variables that characterizes such areas (e.g. Pinaud and Weimerskirch 2005). Here we propose a new hypothesis-testing approach. In arid and semi-arid savannas, large herbivores tend to aggregate around scarce water sources (Thrash et al. 1995; Redfern et al. 2003). Hence, we tested the hypothesis that water sources are a key determinant of movement patterns of large carnivores in arid and semi-arid savannas. In particular, predators should adopt area-restricted search behaviour in areas located in the vicinity of a waterhole, where their encounter rate with potential prey is very likely to be higher.

We used data from 19 GPS radio-collared African lions (*Panthera leo*) in Hwange National Park, Zimbabwe, where ungulate habitat selection is strongly influenced by the distance to waterholes (Valeix et al. 2009). We tested the hypotheses that (1) waterholes attract lions resulting in selection for habitats in the vicinity of waterholes, and (2) lion movement characteristics are influenced by the distance to a waterhole. More particularly, we tested whether lions show area-restricted search behaviour in the vicinity of waterholes (characterized by increased turning rate and lower speed) and move faster and in straighter lines further from waterholes. In addition, we hypothesize that seasonality in semi-arid systems has an important effect on lion movement patterns with waterholes having a greater influence on lion movements under drier conditions (with area-restricted search being more pronounced as the dry season progresses) since prey are expected to be more aggregated around waterholes when water sources are scarcer.

## Methods

### Study site and animals

The study was carried out in the northern part of Hwange National Park (HNP). HNP covers c. 15,000 km<sup>2</sup> of dystrophic savanna in north-western Zimbabwe (19°00' S, 26°30' E). Altitude varies from 800 to 1100 m. The vegetation is primarily woodland and bushland savanna (64%) and vegetation communities are dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga* and *Terminalia sericea* (Rogers 1993). HNP is a semi-arid ecosystem with a mean annual rainfall of 606 mm and where annual rainfall is highly variable (CV  $\approx$  30%). Most rain falls between November and February. Three seasons are distinguished in this study: wet season (November–February), early dry season (March–June) and late dry season (July–October). The surface water available to animals is largely dependent on rainwater collected in natural depressions that are generally dry at the end of the dry season, and artificial permanent dams or waterholes, which are pumped during the dry season (~55 waterholes). A GIS layer of all main waterholes (all pumped waterholes and the largest natural ones that retain water throughout the dry season in most years) was available.

Since 2002, lions were closely monitored in the study area, of which 11 female and 8 male adults were fitted with GPS Simplex radio-collars (female: 900 g, male: 950 g; Televilt Positioning AB, Lindesberg, Sweden; see Loveridge et al. 2007 for details) and provided regular and continuous data over long periods. For each animal, one location was available hourly from 1800 to 700 hours. We extracted the distance to the closest waterhole for each location using ESRI ArcMap 9.2.

### Site selection analyses

We performed compositional analyses (Aebischer et al. 1993), a method that uses individuals as sampling units, using the package “adehabitat” for R software (Calenge 2006) to examine whether lions preferentially used areas close to waterholes. Distance to water was categorized into five classes: 0–2, 2–4, 4–6, 6–8 and >8 km. For each animal, we calculated the proportion of locations within each distance-to-water

class (representative of site use) and the proportion of each distance-to-water class in the animal's home range (representative of site availability). Home ranges were calculated using the 95% probability contour of all locations distribution using the kernel density estimator, a method with recognized strengths (Worton 1989; Powell 2000), and the reference smoothing factor  $h_{ref}$  (recommended by Hemson et al. 2005; Börger et al. 2006). Home range analyses were undertaken using Ranges 7 software (South and Kenward 2006). Site preferences were represented by the Manly-Chesson selection index (Manly et al. 1972; Chesson 1978), which is the proportional use divided by the proportional availability of distance-to-water class. This index value is <1 or >1 if the area is, respectively avoided or selected.

### Night path characteristics

Because lions are largely nocturnal and their activity peaks are after 1700 hours and before 0800 hours (Schaller 1972), and our data are continuous (one location every hour) between 1800 and 700 hours the following morning, we considered the night path (as defined below) as the scale of interest. We defined the straight-line segment linking two successive locations taken at 1 h intervals as the step, and the combination of all steps from one night (from 1800 to 700 hours) as the sampling unit for the night path. Only nights for which all locations were available were used in the analyses of path characteristics (Table 1).

We used Hawth's tools for ESRI ArcMap 9.2 (Beyer 2007) to extract movement characteristics (SL = step length (m),  $\theta$  = turning angle (°)) between two consecutive locations (1 h), and we then calculated the following night path characteristics:

PL = total path length travelled per night (m).

ND = net displacement = distance between the starting and ending points of the night path (m).

S = Speed. It was either equal to SL when considering step length as one step length corresponds to 1 h or proportional to PL as one night corresponds to 13 h, hence  $S = PL/13$  (m/h).

The tortuosity (i.e. the convoluted aspect) of an animal's path is a key parameter which integrates distances travelled and turning angles and provides further information on how the animal has covered an area. We calculated two indices of tortuosity:

**Table 1** Number of nights for which all locations (every hour from 1800 to 0700 hours) were available for each marked individual lion in Hwange National Park, Zimbabwe

Year	Month	Females												Males										
		F1	F4	F5	F6	F7	F8	F9	F11	F14	F15	F16	M1	M2	M4	M5	M6	M7	M9	M11				
2002	June															17								
	July															30								
	August															30						16		
	September															27						24		
	October															30						30		
	November															28						27		
	December															31						26		
	January															28						27		
	February		3	2												26						13		
	March		22	20												30						27		
	April		12	25	19											28						30		
	May		21	16	12	28	9	2								31						9		
June		22	11	30	27	27	24								26						28			
July		24	14	26	28	29	29								29						30			
August		23	18	28	26	30	31	21							14						22			
September		22	20	29	26	29	26	25	5						28						27			
October		20	22	30	30	30	29	29	30						25						31			
November		23	18	30	27	29	29	30	27						26						28			
December		14	18	28	27	26	31	25	25						28						26			
2004	January		7	16	23	27	26	24	14						28						28			
	February		4	15	23	26	19	16	19						25						25			
	March		18	24	23	18	17	22	22						21						3			
	April		24	26	23	24	25	21	24						16						14			
	May		12	26	28	25	25	28	21						27						19			
	June			25	23	22	26	28	14						27						30			
	July		15	28		28	30	28	21						29						28			
	August		19	22	22	11	30	30	25						30						19			
	September		21	25	25	20	28	24	23						29						26			
	October		27	26	26	15	22	23	12						16						30			
	November		20	28	28	21	19	13							27						29			
	December		15	30	30	16	17								25						16			



Table 1 continued

Year	Month	Males																		
		Females						Males												
		F1	F4	F5	F6	F7	F8	F9	F11	F14	F15	F16	M1	M2	M4	M5	M6	M7	M9	M11
	August									28	11			13						
	September									28				19						
	October									31				15						
	November									13				4						

SI = straightness index =  $ND/PL$  (Batschelet 1981). SI ranges between 0 (very convoluted path) and 1 (straight line).

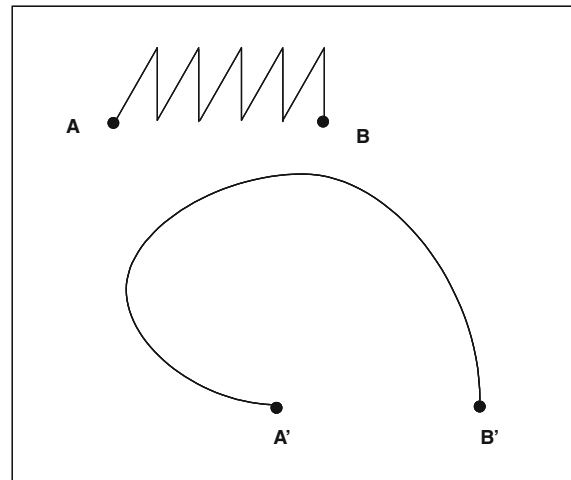
$D$  = fractal mean dimension developed by Nams (Nams 2005; available at <http://www.nsac.ns.ca/envsci/staff/vnams/fractal.htm>).  $D$  ranges between 1 (straight line) and 2 (path is so tortuous as to cover a plane).

SI and  $D$  are different measures of path tortuosity which are not redundant and capture different characteristics of trajectories. Whereas SI tend to capture the straightness of a path,  $D$  captures how well the potential area within which the path is located is covered by the animal (Fig. 1).

We predicted that in the vicinity of waterholes SL and PL should be smaller (i.e.  $S$  should be smaller),  $\theta$  should be higher, ND should be smaller, and that the tortuosity of the path should be higher (i.e. SI smaller and  $D$  higher) than in areas far from a waterhole.

#### Analysis of night path characteristics

For the following analyses, we divided the landscape into 3 classes of distance to water: 0–2 km (close), 2–6 km (intermediate), and 6–10 km (far). Because males and females are likely to exhibit different



**Fig. 1** This figure illustrates how different tortuosity measures may measure different aspects of a trajectory. For the same net displacement, an animal may choose to move following a path of type A–B or of type A'–B'. Even though the straightness index may be very similar in the 2 situations, the fractal dimension will be significantly higher for the path of type A–B than for the path of type A'–B'



spatial behaviour, data gathered on males and females were analysed separately. We performed 2 sets of analyses. (a) We first performed a covariance analysis on step characteristics (SL (i.e.  $S$ ) and  $\theta$ ) with lion identity and night identity as random effects and with two fixed class variables: distance-to-water and season. We also tested the interaction between distance-to-water and season as we expected the differences between movements characteristics to be higher in the late dry season than in the early dry season and in the wet season. For analysis of  $\theta$ , we considered the absolute values of turning angles, hence turning angles ranged from  $0^\circ$  to  $180^\circ$  and we used linear statistics in analysis of turning angles. As temporal serial autocorrelation may affect the data from a same night, we checked whether autocorrelation was present and accounted for it using a first-order autoregressive covariance structure. (b) Then, each night path was assigned to one of the 3 classes of distance to water (if all locations belonged to one class) or removed from the analyses when it covered several classes (e.g. a night path starting close to a waterhole and finishing at 8 km from a waterhole). This allowed us to compare night paths in contrasted areas of the landscape. To rigorously test our hypotheses, we also needed to avoid any bias linked to the surface and/or edge effect due to our landscape sampling design. Because ND in the 0–2 km class from a waterhole are likely to be smaller than ND in the other classes (the maximum distance between two points in the 0–2 km class is 4 km whereas it can be as long as 12 km in the 2–6 km class and 20 km in the 6–10 km class), we considered night paths with  $ND \leq 4$  km only in the following analyses (see also Appendix—electronic supplementary material). We performed a covariance analysis on each night path characteristic (PL (i.e.  $S$ ), ND, SI and  $D$ ) with lion identity as random effect and with distance-to-water, season, and the interaction between both as fixed effects. Statistical analyses were performed with SAS software (version 8.2), using MIXED procedure.

## Results

The mapping of lion trajectories clearly showed that waterholes play a key role in shaping movement patterns and influencing lion spatial ecology (Fig. 2).

### Site selection

Lions of both sexes showed significant selection for sites located within 2 km of a waterhole (female<sub>all seasons</sub>:  $\lambda = 0.148$ ,  $P = 0.002$ ; male<sub>all seasons</sub>:  $\lambda = 0.027$ ,  $P = 0.012$ ; Table 2). The pattern of selection was similar for all seasons (Fig. 3) with both sexes significantly selecting for areas located within 2 km of a waterhole during each season (all  $P < 0.05$ ) except for females in the early dry season for which site selection fell just short of significance (female<sub>early dry season</sub>:  $\lambda = 0.315$ ,  $P = 0.064$ ).

### Night path characteristics

Characteristics of lion movement appeared to differ in the different classes of distance to a waterhole (Table 3).

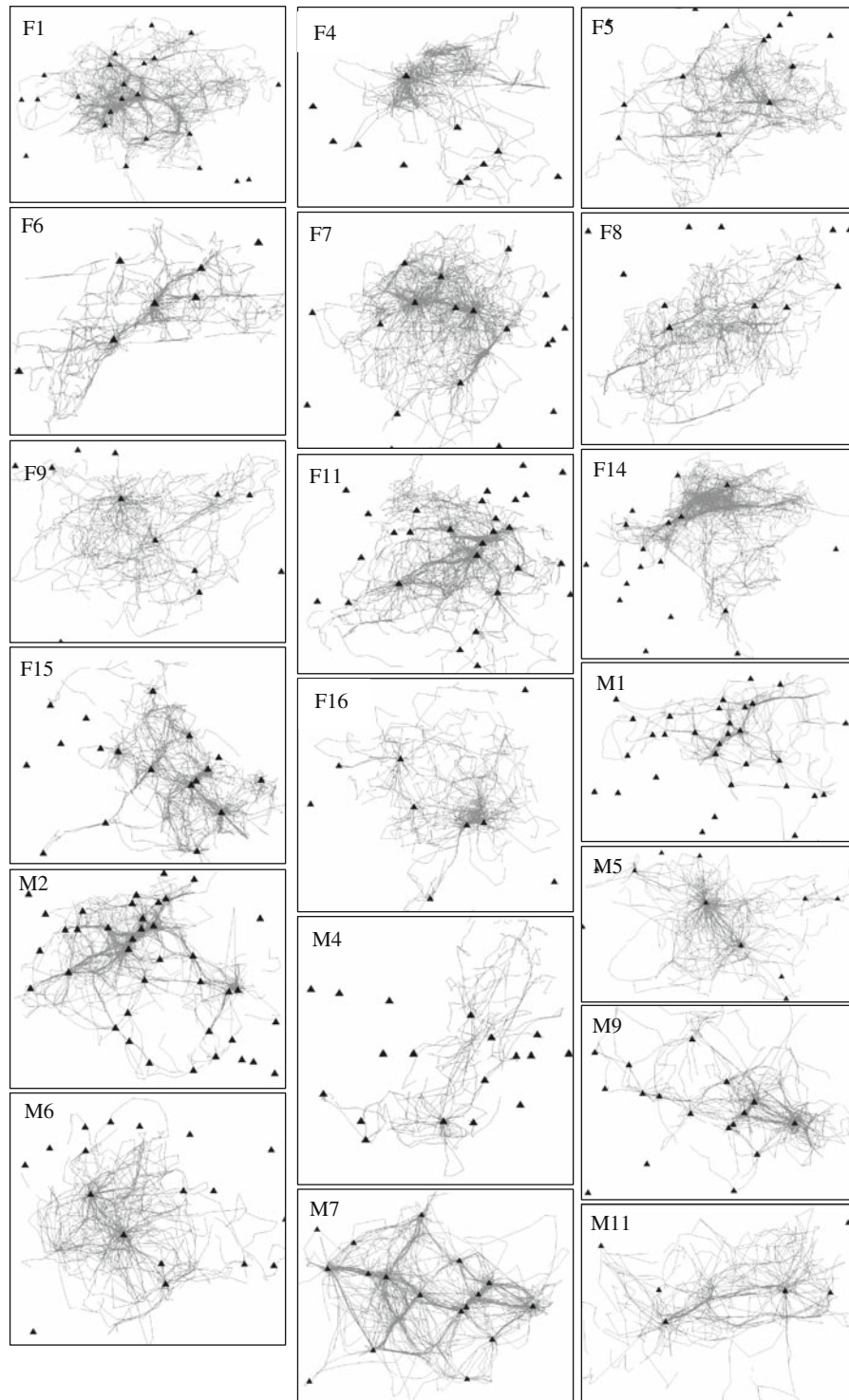
#### *Influence of the interaction between distance-to-water and season*

For females, the interaction between distance-to-water and season had no significant influence on night path characteristics (all  $P > 0.05$ ). However, both season and distance-to-water independently influenced night path characteristics, with distance-to-water having the most significant effect (Fig. 4; Table 4; see below for more details). For males, this interaction influenced path length (Table 5) with the most pronounced differences in the late dry season (Fig. 5c).

#### *Influence of distance-to-water*

Lions of both sexes moved significantly slower in areas close to a waterhole (Tables 4 and 5; Figs. 4a and 5a). On average, female lions travelled 20% quicker when they were far from a waterhole than when they were close, and male lions more than 50% quicker (Table 3). The mean path length travelled by a female lion per night and the net displacement were significantly longer in areas far and at intermediate distances from a waterhole than in areas close to a waterhole (Table 4; Fig. 4c and d). On average, female lions travelled  $\sim 1.5$  km more per night when they were far from a waterhole than when they were close, and covered a net displacement approximately one-third longer (Table 3). For males, the difference





**Fig. 2** Maps showing trajectories for each study lion (e.g. F1 is the map for female 1, M1 is the map for male 1). *Black triangle* symbols represent main waterholes in the study area

**Table 2** Site selection at different distances from water for lions in Hwange National Park, Zimbabwe

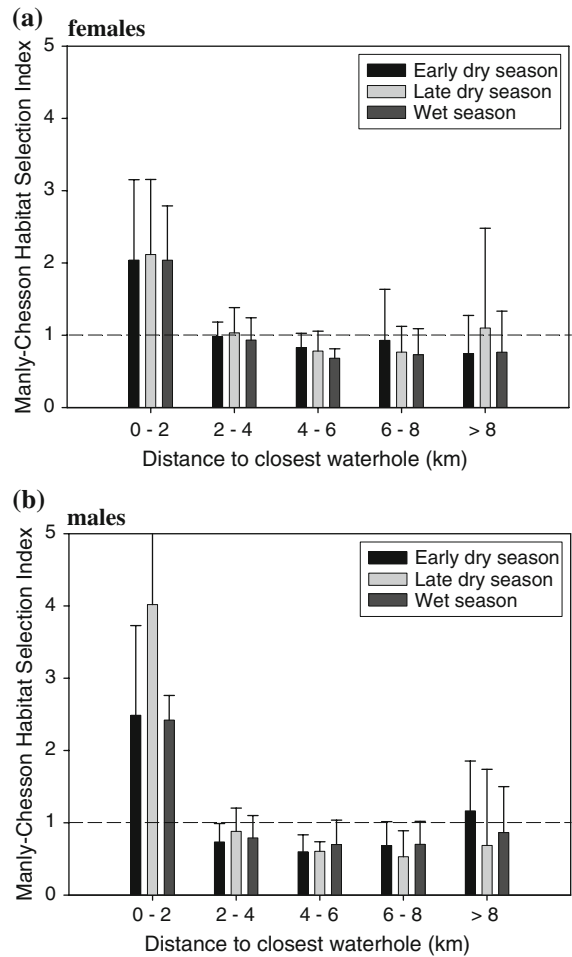
	0–2 km	2–4 km	4–6 km	6–8 km	>8 km
<b>Females</b>					
0–2 km	0	+++	+++	+++	+++
2–4 km	---	0	+++	+	+
4–6 km	---	---	0	+	+
6–8 km	---	-	-	0	+
>8 km	---	-	-	-	0
<b>Males</b>					
0–2 km	0	+++	+++	+++	+++
2–4 km	---	0	+	+	-
4–6 km	---	-	0	+	-
6–8 km	---	-	-	0	-
>8 km	---	+	+	+	0

The results presented are from a compositional analysis. At the intersection of a row and a column, there is a “+” when the row class is more used than the column class, and “-” otherwise. When the difference is significant, the sign is tripled

in path length only held in the late dry season (Fig. 5c) and net displacement was significantly different only between the 0–2 km and 2–6 km distance-to-water classes (Table 5; Fig. 5d—it is likely that there was no difference with the 6–10 km class because of the wet season pattern only). Mean turning angle was significantly higher in areas close to a waterhole than in other areas for both sexes (Tables 4 and 5). Lions appeared to have a tendency to move straighter (lower mean turning angle) when they were not close to a waterhole, and this pattern was consistent across seasons, but the differences in mean turning angle were not large (Table 3; Figs. 4b and 5b). This is consistent with results for tortuosity. First, for females the straightness index was significantly lower, i.e. indicated a more convoluted path, in areas close to a waterhole than in areas at intermediate distances and far from a waterhole (Table 4; Fig. 4e). Second, the fractal dimension of lion night paths was significantly higher, i.e. also indicated a more convoluted path, in areas close to a waterhole for both sexes (Tables 4 and 5; Figs. 4f and 5f).

*Influence of season*

Season did not strongly influence night path characteristics. However, females showed a significantly



**Fig. 3** Manly-Chesson selection index for each distance-to-water class and each season for (a) females and (b) males. Values above 1 indicate preference, values below 1 indicate avoidance and values equal to 1 indicate use in proportion of availability. Error bars represent the standard errors

higher straightness index, i.e. indicated a straighter path, in the early dry season (Table 4; Fig. 4e). Additionally, males covered larger net displacement per night in the early dry season (Table 5; Fig. 5d).

**Discussion**

First, our results clearly show that waterholes are key loci on the lions’ route-maps and that lions make use of several waterholes (see Fig. 2). They may need to monopolise a sufficient number of waterholes to rotate their hunting areas between several to avoid prey predicting their whereabouts. Our results also

**Table 3** Estimate  $\pm$  SE of night path movement characteristics for African lions in Hwange National Park, Zimbabwe, at different distances from water

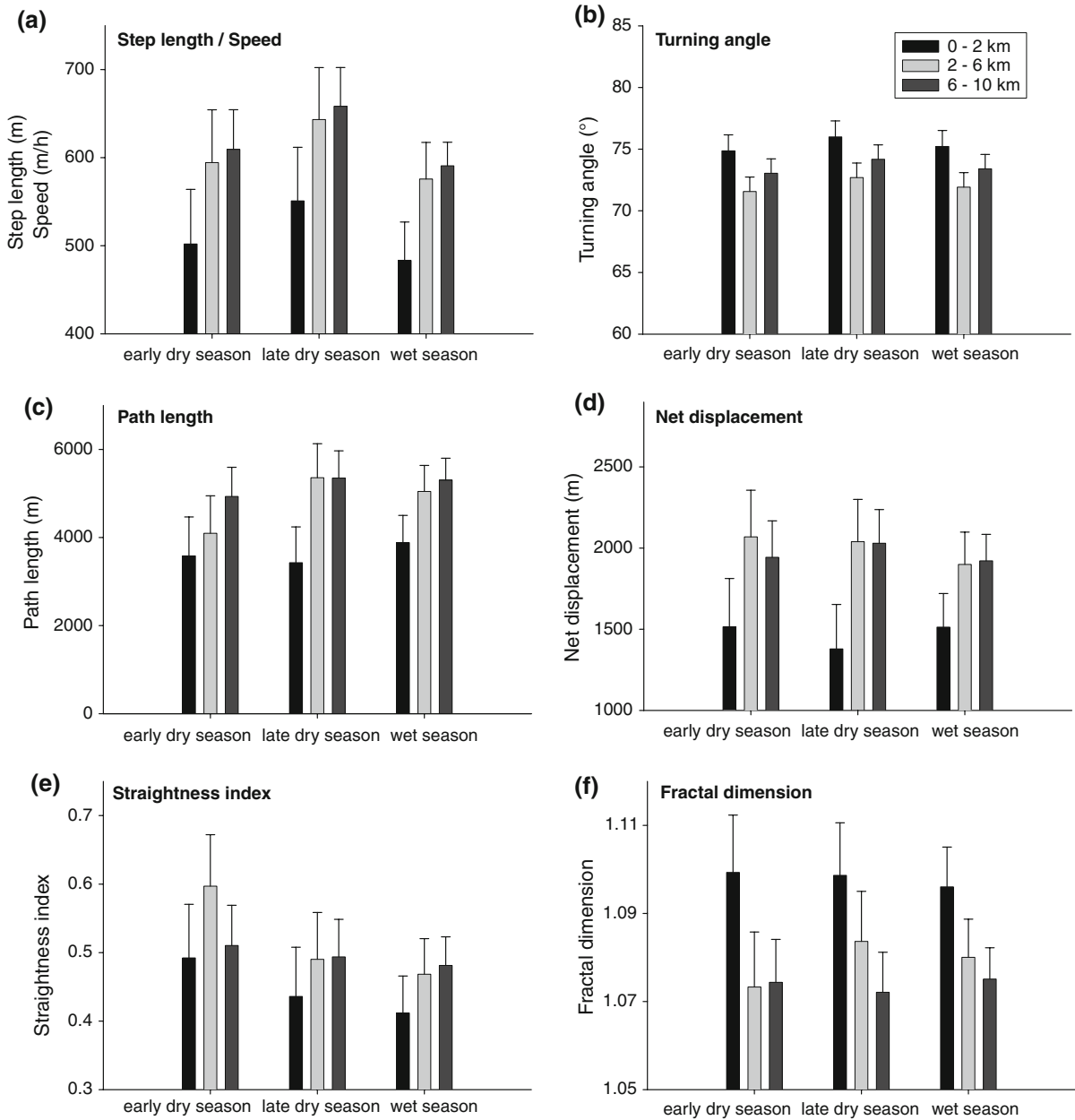
	Distance to a waterhole			Distance to a waterhole		
	Females			Males		
	0–2 km	2–6 km	6–10 km	0–2 km	2–6 km	6–10 km
Step length SL (m) or speed $S$ (m/h)	518 $\pm$ 14	611 $\pm$ 12	625 $\pm$ 27	623 $\pm$ 25	955 $\pm$ 24	952 $\pm$ 52
Turning angle $\theta$ ( $^\circ$ )	75 $\pm$ 1	72 $\pm$ 1	73 $\pm$ 2	72 $\pm$ 1	60 $\pm$ 1	62 $\pm$ 2
Path length PL (m)	3773 $\pm$ 373	5074 $\pm$ 342	5369 $\pm$ 386	3367 $\pm$ 497	3881 $\pm$ 558	4143 $\pm$ 504
Net displacement ND (m)	1425 $\pm$ 124	1971 $\pm$ 114	1936 $\pm$ 123	1392 $\pm$ 181	1720 $\pm$ 207	1531 $\pm$ 182
Straightness index SI	0.41 $\pm$ 0.03	0.48 $\pm$ 0.03	0.46 $\pm$ 0.03	0.45 $\pm$ 0.05	0.50 $\pm$ 0.05	0.48 $\pm$ 0.05
Fractal dimension $D$	1.10 $\pm$ 0.01	1.08 $\pm$ 0.01	1.07 $\pm$ 0.01	1.11 $\pm$ 0.01	1.09 $\pm$ 0.01	1.09 $\pm$ 0.01

clearly show that waterholes are a key determinant of lion habitat selection in arid and semi-arid savannas, such as HNP, where water sources are scarce and patchily distributed. Because the distribution of herbivores in such ecosystems is largely influenced by the distribution of surface water (Redfern et al. 2003; Valeix et al. 2009), lions have a greater chance of encountering their prey in areas surrounding waterholes, and our results showed that lions tend to spend most time in such areas. Our results are therefore consistent with the idea that animals should spend more time in areas where resources are plentiful than in areas where they are scarce. Water sources have already been considered as crucial in lion habitat selection in the Serengeti (Mosser 2008). Through their influence on habitat selection, waterholes are likely to affect both lion home range size and configuration. This is the case in HNP where Loveridge et al. (2009) showed that home range size is partly determined by the density of waterholes, suggesting that the dispersion of waterholes across the landscape determines potential lion territories.

Second, our results indicate that lions of both sexes adopt different movement patterns in areas close to and far from waterholes. The results are clear-cut for female lions and consistently distinguish night path characteristics between areas close to waterholes (<2 km) and those further afield. Male lions also showed different movement patterns in these two categories of areas, but the statistical significance of these differences is less consistent than for females, probably owing to the males' need to patrol their home ranges. When lions are close to a waterhole

(<2 km), they move at lower speed, cover shorter distances (both path length and net displacement) and follow a more tortuous path (higher turning angle, lower straightness index and higher fractal dimension) than when they are further from a waterhole. This may indicate that, by lowering their speed and increasing their turning rate, lions tend to concentrate their search activity in areas surrounding waterholes, i.e. of potential high prey density. In short, our results strongly suggest that lions adopt area-restricted search patterns in the vicinity of waterholes. When lions are far from a waterhole (>6 km), our results show that they adopt rapid and more straight line movements. This may indicate that they reduce their search effort and tend to minimize the time spent far from a waterhole, i.e. in areas of lower prey density. This is consistent with an extensive search mode between rich patches (Zollner and Lima 1999). The dramatically biased distributions of lion locations (see Fig. 2) may not be solely explained in the framework of area-restricted search behaviour. Navigation capacity (the ability of animals to orient and navigate), which has been under-studied in movement models (Holyoak et al. 2008), may also greatly contribute to the web-like pattern shown (Fig. 2). The tendency for directed movements by lions to waterholes may, together with more convoluted paths in the vicinity of waterholes, be key in understanding the spatial patterns of lion behaviour.

Prey are expected to be crowded around a very small number of waterholes in the late dry season and to be more homogeneously dispersed in the wet season. Hence, we expected lions to (1) adopt contrasting movement patterns in the late dry season,



**Fig. 4** Representation of female African lions night path movement characteristics (estimate + SE) for each distance-to-water class and each season in Hwange National Park, Zimbabwe. The following night path characteristics are

with area-restricted search behaviour close to waterholes and extensive search mode when far from them, and (2) adopt a more homogeneous movement pattern in the wet season, when prey are more dispersed. However, the interaction between season and distance-to-water did not play a significant role in lion

displayed: **a** step length (it also equals speed since step length is the distance travelled during 1 h), **b** turning angle, **c** path length, **d** net displacement, **e** straightness index, and **f** fractal dimension

habitat selection and for most lion night path characteristics. But seasonality did play some role in lion movement patterns. Interestingly, the straightness index for females was significantly higher (i.e. indicating a straighter path) in the early dry season, and males had larger net displacements per night in

**Table 4** Summary statistics for mixed models of night path movement characteristics for female African lions in Hwange National Park, Zimbabwe

	Variables	<i>df</i>	<i>F</i>	<i>P</i>	
Step length SL (m) or	Season	2, 30380	8.66	0.0002	Late > early & wet
Speed <i>S</i> (m/h)	Distance-to-water	2, 30380	34.09	<0.0001	I < II & III
Turning angle $\theta$ (°)	Season	2, 24771	0.48	0.6178	
	Distance-to-water	2, 24771	6.22	0.0020	I > II & III
Path length PL (m)	Season	2, 615	2.17	0.1152	
	Distance-to-water	2, 615	12.24	<0.0001	I < II & III
Net displacement ND (m)	Season	2, 615	0.21	0.8084	
	Distance-to-water	2, 615	15.87	<0.0001	I < II & III
Straightness index SI	Season	2, 615	4.77	0.0088	Early > late & wet
	Distance-to-water	2, 615	3.44	0.0327	I < II & III
Fractal dimension <i>D</i>	Season	2, 615	0.35	0.7059	
	Distance-to-water	2, 615	12.37	<0.0001	I > II & III

The last column provides qualitative information on the results, with symbols indicating significance between classes at the *P* level of 0.05. I, II and III represent the 3 classes of distance to water: 0–2 km (close), 2–6 km (intermediate), and 6–10 km (far), respectively. Early, late and dry represent the early dry season, the late dry season and the wet season, respectively. See Fig. 4 for the graphical representation of the results. The interaction season\*distance-to-water is not represented in this table because its effect was non significant at the *P* level of 0.05 for all night path characteristics

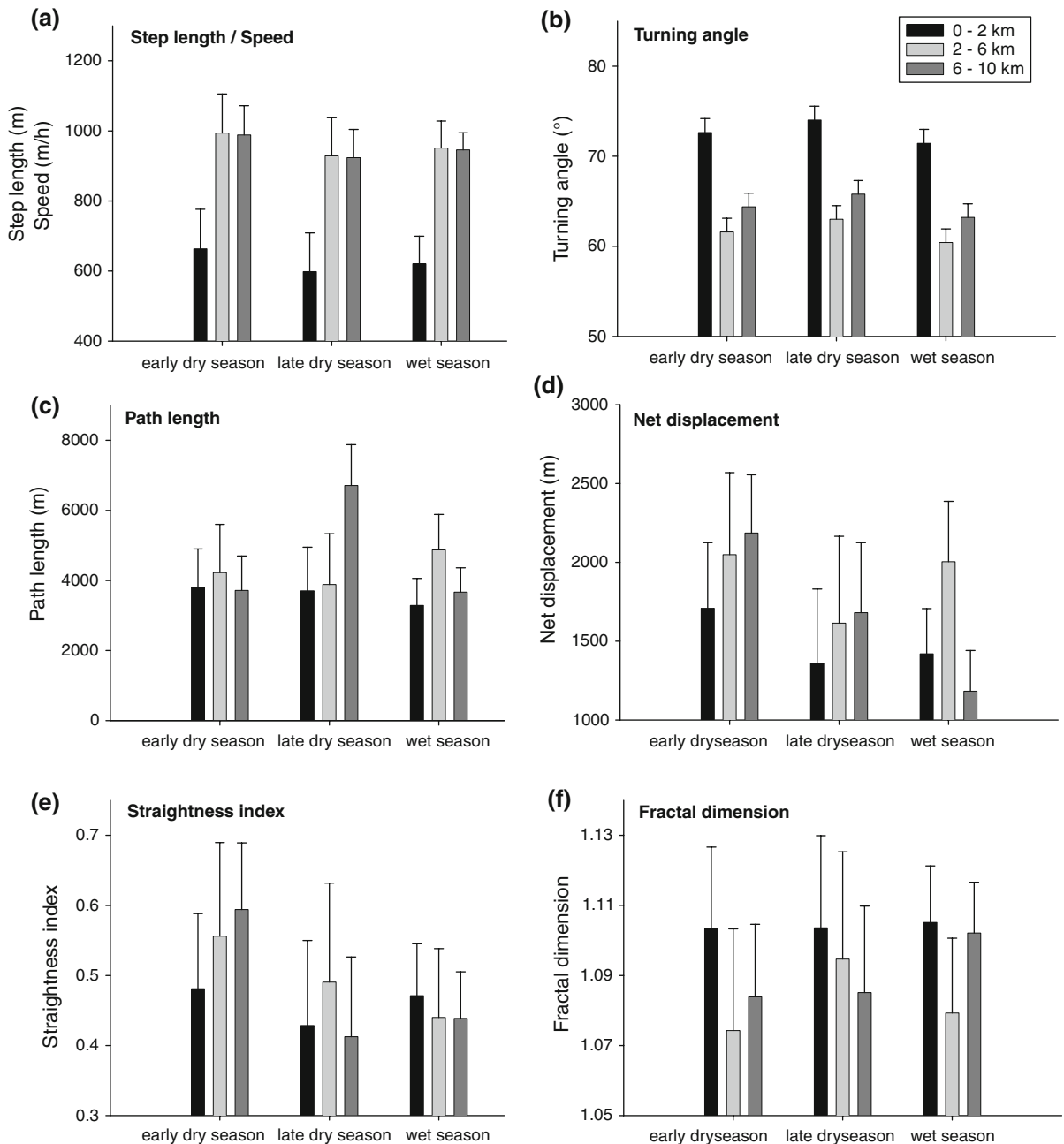
**Table 5** Summary statistics for mixed models of night path movement characteristics for male African lions in Hwange National Park, Zimbabwe

	Variables	<i>df</i>	<i>F</i>	<i>P</i>	
Step Length SL (m) or	Season	2, 22759	2.17	0.1139	
Speed <i>S</i> (m/h)	Distance-to-water	2, 22759	180.49	<0.0001	I < II & III
Turning angle $\theta$ (°)	Season	2, 18864	1.79	0.1673	
	Distance-to-water	2, 18864	64.26	<0.0001	I > II & III
Path length PL (m)	Season	2, 322	1.89	0.1535	
	Distance-to-water	2, 322	3.35	0.0364	
	Interaction	4, 322	2.40	0.0501	See Fig. 5
Net displacement ND (m)	Season	2, 326	5.05	0.0069	Early > late & dry
	Distance-to-water	2, 326	2.87	0.0584	I < II
Straightness index SI	Season	2, 326	2.01	0.1361	
	Distance-to-water	2, 326	0.87	0.4179	
Fractal dimension <i>D</i>	Season	2, 326	0.38	0.6854	
	Distance-to-water	2, 326	2.73	0.0665	I > II & III

The last column provides qualitative information on the results, with symbols indicating significance between classes at the *P* level of 0.05. I, II and III represent the 3 classes of distance to water: 0–2 km (close), 2–6 km (intermediate), and 6–10 km (far), respectively. Early, late and dry represent the early dry season, the late dry season and the wet season, respectively. See Fig. 5 for the graphical representation of the results. The interaction is represented when the effect was significant at the *P* level 0.05 only

the early dry season. One possible explanation resides in the fact that even though lions are opportunistic predators seasonal shifts in prey selection appear to occur in seasonal environments (Owen-Smith 2008). In HNP, it is likely that lions mainly rely on greater kudu (*Tragelaphus strepsiceros*) in the early dry

season (*unpublished data*), and lioness home range size is influenced by the abundance of kudu in the early dry season (Loveridge et al. 2009). Kudus are browsers and most of the park is covered by woodland and bushland (Rogers 1993), and they are less water-dependent than other prey species (often



**Fig. 5** Representation of male African lions night path movement characteristics (estimate + SE) for each distance-to-water class and each season in Hwange National Park, Zimbabwe. The following night path characteristics are

grazers). They are consequently less predictably distributed than other prey species.

In summary, our results are in line with a scenario whereby, throughout the year, lions (1) use several waterholes, (2) spend most of their time in areas

displayed: **a** step length (it also equals speed since step length is the distance travelled during 1 h), **b** turning angle, **c** path length, **d** net displacement, **e** straightness index, and **f** fractal dimension

surrounding these waterholes, (3) adopt area-restricted search behaviour in these areas, and (4) travel quickly using straight lines when they move from one waterhole area to another, hence spending the least possible time far from waterholes where



potential prey are scarce. In arid and semi-arid savannas, large herbivores are more abundant in the vicinity of waterholes (Redfern et al. 2003; Valeix et al. 2009) where they have to go and drink regularly, and are accessible and vulnerable to predation by lions in the vegetation surrounding these water sources (Hopcraft et al. 2005). Hence, it is very likely that the underlying mechanism of the patterns revealed here is that lions spend more time in the vicinity of waterholes and explore these areas thoroughly to maximise their encounter rate with potential prey in areas where prey are relatively more abundant and accessible. Our study corroborates previous findings on large free-ranging predators in marine ecosystems (e.g. Pinaud and Weimerskirch 2005; Bailey and Thompson 2006) which demonstrated that predators use area-restricted search behaviour in areas of high resource abundance. Our results further provide an illustration of how key habitat features (e.g. waterholes in this study), which determine the dispersion of prey, may have a determining influence on predator spatial ecology and movement patterns. Suitable habitats are dictated by the dispersion of these key habitat features. Additionally, predators move differently when they are close to or far from these key habitat features.

**Acknowledgments** The Director General of the Zimbabwe Parks and Wildlife Management Authority is acknowledged for providing the opportunity to carry out this research and for permission to publish this manuscript. This work was made possible with grants from the ANR Biodiversité “BioFun” (ANR-05-BDIV-013-01), the ANR “Fear” (ANR-08-BLAN-0022), the Darwin Initiative for Biodiversity Grant 162/09/015, The Eppley Foundation, Disney Foundation, Marwell Preservation Trust, Regina B. Frankenburg Foundation, Panthera Foundation, and the generosity of Joan and Riv Winant. We thank all the people that participated in the fieldwork, particularly Jane Hunt. We thank Simon Chamaillé-Jammes for his fruitful advice during the construction of this manuscript.

## References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325

Atkinson RPD, Rhodes CJ, Macdonald DW et al (2002) Scale-free dynamics in the movement patterns of jackals. *Oikos* 98:134–140

Bailey H, Thompson P (2006) Quantitative analysis of bottlenose dolphin movement patterns and their relationships with foraging. *J Anim Ecol* 75:456–465

Batschelet E (1981) Circular statistics in biology. Academic Press, London

Bélisle M, Desrichers A, Fortin MJ (2001) Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82:1893–1904

Beyer HL (2007) Hawth's analysis tools for ArcGIS, version 3.27. Available from <http://www.spatial-ecology.com/htools>

Börger L, Franconi N, Ferretti F et al (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am Nat* 168:471–485

Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519

Chesson J (1978) Measuring preference in selective predation. *Ecology* 59:211–215

Etzenhouser MJ, Owens MK, Spalinger DE et al (1998) Foraging behavior of browsing ruminants in a heterogeneous landscape. *Landscape Ecol* 13:55–64

Fauchald P (1999) Foraging in a hierarchical patch system. *Am Nat* 153:603–613

Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288

Fortin D, Beyer HL, Boyce MS et al (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330

Frair JL, Merrill EH, Visscher DR et al (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecol* 20:273–287

Fritz H, Said S, Weimerskirch H (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proc Roy Soc Lond B* 270:1143–1148

Gustafson EJ, Gardner RH (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77:94–107

Hemson G, Johnson P, South A et al (2005) Are kernel the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J Anim Ecol* 74:455–463

Holyoak M, Casagrandi R, Nathan R et al (2008) Trends and missing parts in the study of movement ecology. *PNAS* 105:19060–19065

Hopcraft GJC, Sinclair ARE, Packer C (2005) Planning for success: serengeti lions seek prey accessibility rather than abundance. *J Anim Ecol* 74:559–566

Jonsen ID, Myers RA, Flemming JM (2003) Meta-analysis of animal movement using state-space models. *Ecology* 84:3055–3063

Kareiva PM, Odell G (1987) Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *Am Nat* 130:233–270

Kareiva PM, Shigesada N (1983) Analyzing insect movement as a correlated random walk. *Oecologia* 56:234–238

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260

Loveridge AJ, Searle AW, Murindagomo F et al (2007) The impact of sport-hunting on the lion population in a protected area. *Biol Conserv* 134:548–558



- Loveridge AJ, Valeix M, Davidson Z et al. (2009) Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography Early View* (doi: [10.1111/j.0906-7590.2009.05745.x](https://doi.org/10.1111/j.0906-7590.2009.05745.x))
- Manly BFJ, Miller P, Cook LM (1972) Analysis of a selective predation experiment. *Am Nat* 106:719–736
- Mosser A (2008) Group territoriality of the African lion: behavioural adaptation in a heterogeneous landscape. PhD Dissertation, University of Minnesota
- Nams VO (2005) Using animal movement paths to measure response to spatial scale. *Oecologia* 143:179–188
- Nams VO (2006) Detecting oriented movement of animals. *Anim Behav* 72:1197–1203
- Owen-Smith N (2008) Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos* 117:602–610
- Pinaud D, Weimerskirch H (2005) Scale-dependent habitat use in a long ranging central place predator. *J Anim Ecol* 74:852–863
- Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) *Research techniques in animal ecology—Controversies and consequences*. Columbia University Press, New York, pp 65–110
- Redfern JV, Grant R, Biggs H et al (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84:2092–2107
- Rogers CML (1993) A woody vegetation survey of Hwange national park. Department of National Parks and Wildlife Management, Harare
- Roshier DA, Doerr VAJ, Doerr ED (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia* 156: 465–477
- Schaller GB (1972) *The Serengeti lion: a study of predator prey relations*. Chicago University Press, Chicago
- Smith JNM (1974a) The food searching behaviour of two European thrushes. I: Description and analysis of search paths. *Behaviour* 48:276–302
- Smith JNM (1974b) The food searching behaviour of two European thrushes. II: the adaptiveness of the search patterns. *Behaviour* 49:1–61
- South AB, Kenward RE (2006) *Ranges7 v1.0: for the analysis of tracking and location data*. Anatrack Ltd, Wareham
- Thrash I, Theron GK, Bothma JP (1995) Dry season herbivore densities around drinking troughs in the Kruger National Park. *J Arid Environ* 29:213–219
- Turchin P (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72:1253–1266
- Valeix M, Loveridge AJ, Chamaillé-Jammes S et al (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90:23–30
- Viswanathan GM, Afanasyev V, Buldyrev SV et al (1996) Lévy flight search patterns of wandering albatrosses. *Nature* 381:413–415
- With KA (1994) Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecol* 9:25–36
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168
- Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030