

Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna

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Within-population studies are needed to investigate the extent of, and the factors underlying, intraspecific variation in home range size. We used data from 12 female and 8 male adult lions instrumented with GPS radio-collars to describe the ranging behaviour of lions in a population from a dystrophic semi-arid savanna, Hwange National Park, Zimbabwe. We measured prey availability at the home range scale in 2003, 2004, and 2005. For females, home range size increased as pride biomass increased, which is strongly suggestive of expansionism. Once controlled for pride biomass, home range size decreased as prey biomass increased. Pride ranges responded to changes in food abundance on an annual timescale rather than on a seasonal timescale. Female home range size was influenced by the abundance of kudu in the early dry season, whereas it was influenced by buffalo and young elephant abundance in the late dry season. This study shows that female home range size is mainly driven by the size of the pride, but also by prey abundance. Furthermore, female seasonal home range size may be determined, not only by prey abundance, but also by prey dispersion in the landscape. Home range size of males was driven by both prey biomass and the density of female prides.

Home range (*sensu* Burt 1943) behaviour is a common pattern of space use and understanding variation in animal home range size, and identifying the factors that underlie this variation, are fundamental to understanding the distribution and abundance of animals, and ultimately their population regulation (Wang and Grimm 2007), habitat selection (Rhodes et al. 2005), community structure (Fagan et al. 2007), and for management and conservation of ecosystems (Woodroffe and Ginsberg 2000). Interspecific variation in home range size has been thoroughly explored, particularly in terms of allometric relationships (McNab 1963, Kelt and Van Vuren 2001). At the intraspecific level, there has been considerable work on variation in home range size (Kruuk and Parish 1987, Geffen et al. 1992, Patterson and Messier 2001, Said et al. 2005) but the extent of, and mechanisms underlying, intraspecific variation are less well understood (but see Börger et al. 2006a, 2008). The ranging behaviour of animals is likely to be affected by a number of ecological (for food see McLoughlin and Ferguson 2000, for landscape structure see Said and Servanty 2005), demographic (for population density see Benson et al. 2006), and behavioural factors (for competition for territories see Rohner and Krebs 1998). Furthermore, mammals frequently exhibit distinct

inter-sexual differences in ranging behaviour. These differences are manifestations of separate selection pressures: female reproductive success is closely tied to an ability to exploit resources, whereas male reproductive success is coupled with an ability to find and mate with females (Clutton-Brock 1989). Thus, female ranging behaviour is expected to be configured around the distribution of resources while that of males is expected to be largely influenced by the distribution of females.

An animal's home range is often considered to be mediated by the abundance of resources, as well as by their dispersion, and the predictability with which they are available (Macdonald and Carr 1989). Indeed, increases in overall resource abundance may lead to smaller ranging areas (Mills and Knowlton 1991) but, when resource availability is heterogeneous, larger areas may still be needed to encompass the spatial variability (e.g. patches of high habitat quality) and temporal variability (e.g. grass renewal, birth peaks, arrival of migratory prey) of these resources (Macdonald and Carr 1989). The quantity, quality, and distribution of resources in African savanna ecosystems show wide variation in space and time, and are influenced by the interaction between rainfall and soil characteristics (Bell 1982, East 1984, Fritz and Duncan 1994). This

influences both herbivore biomass (Coe et al. 1976) and herbivore community structure (East 1984, Fritz and Duncan 1994), and therefore indirectly carnivore numbers (East 1984, Grange and Duncan 2006) and potentially carnivore home ranges.

While access to resources (food, females) is thought to be a key determinant of home range size, in social species ranging behaviour may also be influenced by social factors. For instance, various relationships between group size and home range size exist (Macdonald 1983). Kruuk and Macdonald (1985) predict that home range behaviour in group living species should conform to one of two strategies. They should either expand their range to encompass sufficient additional resources to support more group members (expansionism) or increase group size only up to the size that can be sustained on the resources within the smallest economically defensible range needed to support the minimum social unit (contractionism). Expansionism is likely to occur where the sociological benefits of a larger group outweigh the costs of securing and maintaining the larger range needed to sustain it. The dispersion of resources will surely influence the costs of expansionism, and thus the net marginal advantage of recruiting additional group members (Macdonald and Carr 1989). The goal of this study is to assess the role of ecological and social factors in shaping the size of home ranges using the example of a social large carnivore, the African lion *Panthera leo*.

Intraspecific variation in home range size has been reported for lions and home range size varies markedly between populations across a spectrum of ecosystems (from 20 to 404 km² – van Orsdol et al. 1985, Stander 1991, Hanby et al. 1995, Funston and Mills 2006). Lion social group size also varies markedly (from 2 to 35 – Schaller 1972, van Orsdol et al. 1985) and there has been debate as to the contributions of various selective pressures favouring their sociality (for communal hunting see van Orsdol 1981 and Cooper 1991; for advantages in territoriality and cooperative cub defence see Packer et al. 1990). Macdonald (1983) drew attention to evidence of expansionism in the relationship between the size of lion groups and the home ranges they occupied. However, an inter-population comparison suggested that lion pride home range size was not correlated with group size, but was negatively correlated with lean season prey abundance (van Orsdol et al. 1985). Furthermore, lions are opportunistic predators and seasonal shifts in prey selection have recently been demonstrated (Owen-Smith 2008). It is therefore possible that home range size may respond to different factors at different timescales. Ranging behaviour in lions is expected to differ between the sexes as it has been suggested that male ranges are more likely to depend on both food resources and the need to defend and access female prides, while female ranges are configured around access to resources (Schaller 1972). The high variability in prey abundance across African savannas may add to the difficulty in comparing systems, and most behavioural studies of lions have been undertaken in eutrophic savannas (high nutrient soil quality) such as the Serengeti-Mara ecosystem, Tanzania-Kenya (Schaller 1972, Packer et al. 1990, Hanby et al. 1995), and to a lesser extent in mesotrophic savannas (medium nutrient soil quality) such as the Kruger National

Park, South Africa (Funston and Mills 2006). Less is known about lion populations in dystrophic savannas (low nutrient soil quality) (but see Stander 1991) where the low nutrient soil content leads to a low density herbivore community dominated by large (African buffalo *Syncerus caffer*) to very large (giraffe *Giraffa camelopardalis* and African elephant *Loxodonta africana*) herbivores (Fritz et al. 2002).

We investigated the impact of group social structure and spatial and temporal variation in food resources (prey biomass) on lion home range size within a single population. We developed a large and detailed data set of both lion movements and the seasonal variation in abundance of their ungulate prey in a semi-arid dystrophic savanna, Hwange National Park, Zimbabwe, to: 1) explore the effects of group size and prey biomass on social carnivore home range size; 2) provide insights into the role of annual and seasonal variation in prey biomass; 3) assess whether some prey species have a greater seasonal influence on home range size than do others; 4) assess whether male home range size is related to prey biomass or the need to defend access to females. Through this study, we aim at identifying whether either or both social factors (group size) or ecological factors (prey biomass) determine home range size in social carnivores.

Materials and methods

Study site

The study was carried out in the northern part of Hwange National Park (HNP). HNP covers ca 15 000 km² 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. No surface water remains in the southern area of the park during the dry season, except in years of exceptionally high rainfall. In the northern area of the park, water is artificially supplied to some waterholes (ca 50) during the dry season. HNP research staff recorded rainfall data daily. The long-term (1928–2005) mean annual rainfall is 606 mm but is highly variable (CV ≈ 30%). Annual rainfall was calculated as the rainfall that fell between October and September the following year. Annual rainfall was 362.6 mm in 2003, 695.8 mm in 2004 and 287 mm in 2005, which are the years corresponding to our study. Even though annual rainfall was higher in 2003 than in 2005, 2003 endured a more severe drought (it was the second of two consecutive dry years; 2002 received 476 mm). Three seasons are distinguished in this study: wet season (November–February), early dry season (March–June), and late dry season (July–October). The wet season of year Y corresponds to the period between November of year Y–1 and February of year Y. Lion density was ca 2.7 lions 100 km⁻² in the northern region of HNP (Loveridge et al. 2007a).

Lion data

From 2002 to 2005, female prides and male coalitions were closely monitored in the northern part of HNP

(ca 7000 km²). We captured and instrumented 17 female and 10 male adults with GPS Simplex radio-collars (female: 900 g, male: 950 g; Televilt Positioning, Lindesberg, Sweden; see Loveridge et al. 2007a for details). Only data from 12 female and 8 male adults fitted with GPS Simplex radio-collars were used either because data were not available for a whole 4-month study season (the difficulty of recapturing individuals to replace telemetry equipment combined with a high mortality rate (cf. Loveridge et al. 2007a) led to incomplete data for some individuals) or to avoid pseudo-replication when two females had been collared within the same pride. Captured lions were, where possible, weighed using a canvas stretcher attached to a scale, suspended from poles attached to the front of a 4 × 4 vehicle. Mean weight (\pm SD) was 199 ± 10 kg for adult males ($n = 4$) and 143 ± 11 kg for adult females ($n = 6$). These weights are consistent with those published for southern African populations (Smuts et al. 1980). Positional data from the GPS Simplex radio-collars were downloaded regularly (for each individual, one location was available hourly from 18:00 to 7:00), and animals' locations were available from November 2002 to October 2005. Preliminary analyses revealed that lionesses from the same pride stay together most of the time in HNP, with females from a pride sighted together in $89.2 \pm 7.4\%$ of sightings. Consequently, we assume that individual ranges do generally represent pride ranges. We calculated pride biomass using the composition of each pride based on monthly observation. We used field data for adult weight (see details above). For cubs and sub-adults, we used growth equations from Smuts et al. (1980): body mass (kg) = $4.21 \times \text{age (months)} + 5.29$ for males ($r^2 = 0.98$) and body mass (kg) = $3.31 \times \text{age (months)} + 6.64$ for females ($r^2 = 0.99$).

Analysis of home ranges

We defined home ranges and cores (sensu Powell 2000) as the 90% (recommended by Börger et al. 2006b) and 50% probability contour of location distribution using the fixed 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 and Börger et al. 2006a). Home range estimates are subject to many uncertainties. We consequently calculated home ranges using an alternative method: the local convex hull (LoCoH) nonparametric kernel method (Getz and Wilmsers 2004, Getz et al. 2007) with the heuristic value $k = \sqrt{n}$ (n is the number of points in the set). All subsequent analyses were carried out with the two home range estimators but when LoCoH is not specified, home range is taken to mean the 90% kernel home range. We investigated home range size for wet, early dry, and late dry season. We preliminarily found a very strong correlation between the home range estimates based on all available fixes per day and those using only one fix per day ($F_{1, 41} = 2579.1$; $p < 0.0001$; $r^2 = 0.985$). Consequently, in all subsequent home range size analyses, we arbitrarily used the locations taken at 00:00 h or the GPS location taken closest to 00:00 h on that night to compare home range estimates based rigorously on the same number of locations

(we used the same number of points, ca 120 fixes $- 1 \text{ fix d}^{-1}$ for 4 months $-$ to construct each seasonal home range). Only animals whose GPS receiver was operational during a whole season were used in the analyses. Home-range analyses were undertaken using Ranges 7 (ver. 0.811, South and Kenward 2006) for the kernel density estimator and using the extension LoCoH v.2.1 for ArcView (ver. 3.2, Environmental Systems Research Inst., Redlands, USA) for the LoCoH estimator.

Prey abundance data

Many studies resorted to using habitat types as surrogate proxies for resource availability; in contrast, we measured, where possible, prey availability directly at the home range scale. Given the opportunistic foraging behaviour of lions in HNP (Loveridge et al. 2006, van Kesteren 2006), all large herbivore species present in the study area were included in our analysis, including elephants ≤ 4 yr-old (frequently recorded as prey during drought years in HNP, Loveridge et al. 2006). Species included are: African buffalo, African elephant, blue wildebeest *Connochaetes taurinus*, Burchell's zebra *Equus quagga*, eland *Taurotragus oryx*, giraffe, greater kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus*, roan antelope *Hippotragus equines*, sable antelope *Hippotragus niger*, warthog *Phacochoerus aethiopicus*, and water-buck *Kobus ellipsiprymnus*. The abundance of herbivores in the northern part of HNP has been monitored since December 2002 with road counts (see transect coverage in Fig. 1). Monitoring sessions were carried out in December (wet season), May–June (early dry season) and September–October (late dry season). The Main Camp area was monitored in the three seasons, the Sinamatella area in the early and late dry season, and the Ngamo area in the late dry season (see areas in Fig. 1).

Calculation of prey kilometric biomass

We calculated the kilometric abundance index for each prey species (Vincent et al. 1991, Maillard et al. 2001), which represents an encounter rate per kilometre of road driven and was taken as a proxy for the rate at which lions encounter individuals of each species of prey. We then converted the kilometric abundance index into kilometric biomass by multiplying the unit mass (i.e. the average mass of individuals in a population (Cumming and Cumming 2003)) by kilometric abundance for each of the prey species. We also calculated the total prey kilometric biomass by adding the kilometric biomasses of all the species encountered (this measure of prey abundance is referred to as the prey kilometric biomass hereafter). For most home ranges (65%), we used the data from line transects encompassed by their home ranges. However, some home ranges included insufficient transect coverage (e.g. lionesses F6 and F8 in Fig. 1), or corresponded to periods when no road count data were collected (e.g. in May for animals in the Ngamo area). For these seasonal home ranges ($n = 14$ for females and 9 for males), we calculated the mean prey biomass of each habitat type, and then extrapolated the prey kilometric biomass for each home range based on the habitat composition of the range. Habitat composition was

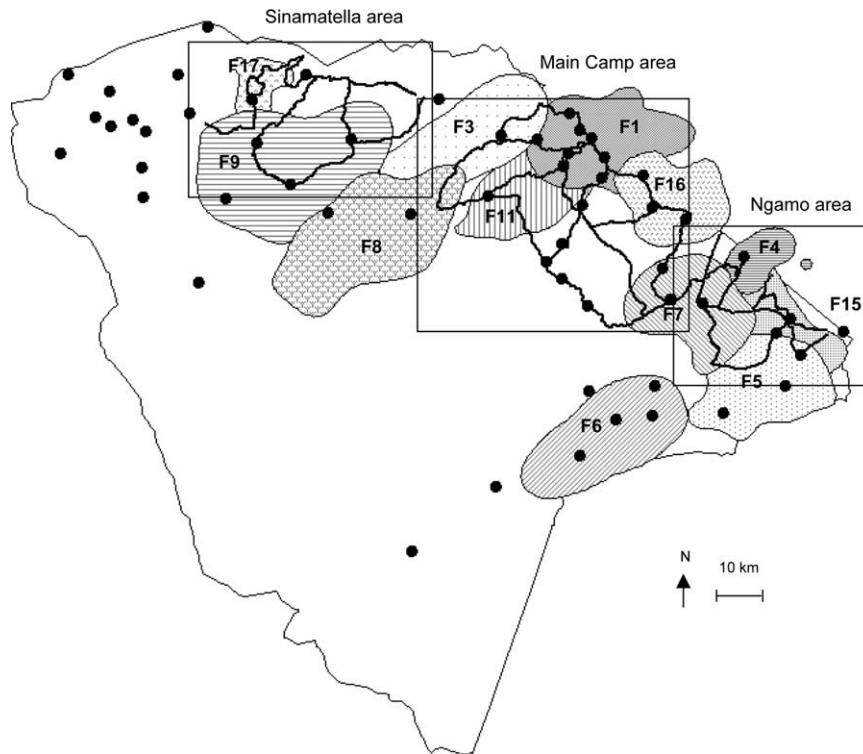


Figure 1. Map of the location of the mean seasonal home range for females (each shaded area represents one mean seasonal home range for one female and labels indicate the identity of the female). Black lines represent the transects along which prey abundance was monitored. Black dots represent pumped waterholes.

extracted from the vegetation map layer (Rogers 1993) using ArcView 3.2. This approach was validated by comparing the calculated prey kilometric biomasses measured by direct transects and those estimated by using habitat type as a surrogate. In home ranges for which both measures were made, they were positively correlated ($F_{1,26} = 50.78$; $p < 0.0001$; $r^2 = 0.67$). No seasonal home range overlap occurred between the marked males but some home range overlap occurred between marked females (21 of 42 seasonal home ranges concerned; mean \pm SE = $17 \pm 3\%$; range = 3–42%). We considered that resource availability in areas of overlap was inversely proportional to the number of prides using the area. We therefore took into account depletion of resources by competing female groups in the analyses by dividing the prey kilometric biomass in the area of overlap by the number of prides potentially in competition.

Analysis of home range size variation

Data gathered on males and females were analysed separately. For females, we fitted a mixed linear model with restricted maximum likelihood estimation, using seasonal home range size as the dependent variable and individual identity as a random factor. Explanatory variables were pride biomass (log-transformed for linearity), prey kilometric biomass, and the interaction between these two variables. We selected the most likely model using AICc (Akaike information criteria corrected for small sample size) (Burnham and Anderson 2002). Relative strength of evidence of each model was assessed using Akaike weights (referred to as w and calculated

as $\exp(-0.5\Delta\text{AICc})$; models giving relative strength of evidence of 0.5 or greater can be considered as strong contenders for the model providing the best fit). In addition, we report R^2 values, which provide the proportion of variance explained by the model (fixed + random effects). The effect of pride biomass had to be controlled before testing for the effect of other variables so we used a type 1 approach and pride biomass was the first covariate to be entered. We further regressed female seasonal home range size against the density of waterholes to gain insights into the influence of such key habitat feature. To investigate the influence of each prey species on home range size per season, we could not justifiably perform a mixed-model procedure because of the low number of degrees of freedom, so we regressed female mean seasonal home range size against the mean kilometric biomass of each prey species.

For males, due to the smaller sample size, we also regressed the mean seasonal home range size separately against 1) the mean number of males in the coalition, 2) the mean prey kilometric biomass, 3) the mean density of waterholes in the home range, and variables linked to females such as 4) the mean number of prides of females encompassed, 5) the mean number of females encompassed, 6) the mean density of prides of females within the male home range (= number of prides encompassed/male home range size), and 7) the mean density of females within the male home range (= number of females encompassed/male home range size). When we examined the influence of females, 8 male seasonal home ranges were excluded from the analysis because no corresponding information was available for females. Statistical analyses were performed with SAS software (ver. 8.2) (SAS Inst. 1999), using REG

and MIXED procedure for normally distributed data (Kolmogorov-Smirnov: $D = 0.11$; $p = 0.15$).

Results

Prey biomass

The mean total prey biomass density for the whole northern part of HNP in October was 2312 kg km^{-2} (95% CI: $1759\text{--}3119 \text{ kg km}^{-2}$). It is noteworthy that prey abundance was constant in the wet season, but prey abundance in the study area increased in the late dry season as annual rainfall decreased (Fig. 2a). Prey abundance was consistently higher in the late dry season for a given year, particularly for a dry year (Fig. 2a).

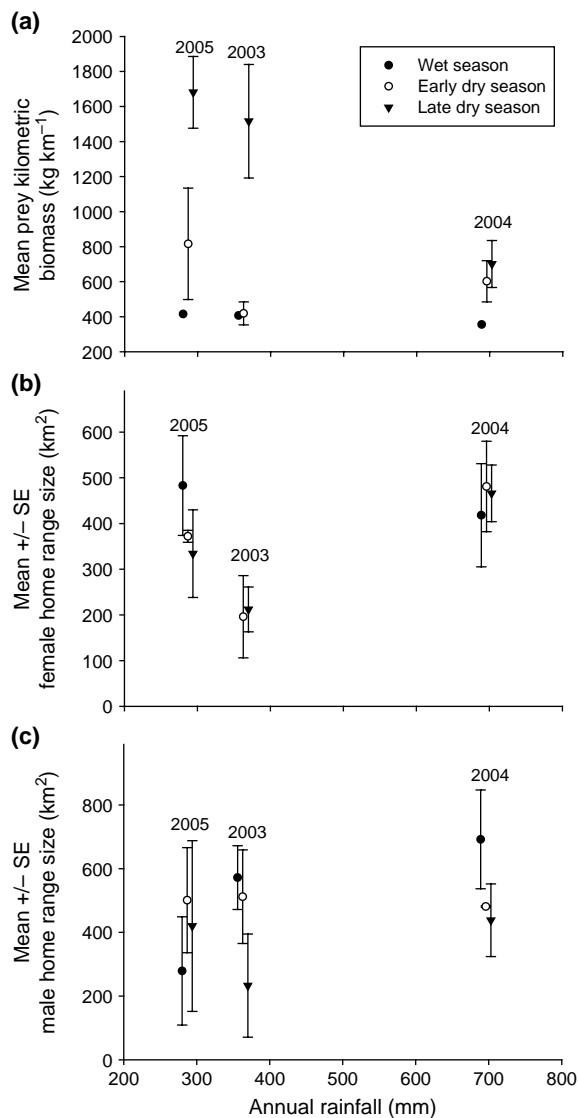


Figure 2. Relationship between annual rainfall and (a) mean prey kilometric biomass; (b) mean female seasonal home range size (no information is provided for the wet season 2003 because positional data from the GPS Simplex radio-collars for female began in February 2003); (c) mean male seasonal home range size.

Home ranges

Mean seasonal home range size was 388 km^2 for females (SE = 35 km^2 ; range = $35\text{--}981 \text{ km}^2$; Table 1 for details) and 478 km^2 for males (SE = 50 km^2 ; range = $71\text{--}1002 \text{ km}^2$; Table 1 for details). Home range size did not change significantly between seasons of the same year for either sex (paired-sampled Friedman test: females: $Q = 0.25$; $p = 0.88$; males: $Q = 0.67$; $p = 0.72$; Fig. 2b, c). Our data were sufficient to assess the effect of year on home range size for only 6 females for which seasonal home ranges were averaged and compared between 2003 and 2004. Home range size for these females was significantly larger in 2004 than in 2003 (Paired sample Wilcoxon test $S = 6$; $p = 0.014$; Fig. 2b). LoCoH seasonal home range size was 396 km^2 for females (SE = 33 km^2 ; range = $101\text{--}925 \text{ km}^2$) and 534 km^2 for males (SE = 51 km^2 ; range = $109\text{--}1156 \text{ km}^2$). Mean seasonal core size was 153 km^2 for females (SE = 15 km^2 ; range = $13\text{--}384 \text{ km}^2$) and 182 km^2 for males (SE = 24 km^2 ; range = $20\text{--}426 \text{ km}^2$). The size of LoCoH home ranges and 50% kernel cores showed the same pattern of annual and seasonal variations as the size of 90% kernel home ranges.

Female home range size variation

The confrontation of alternative models (Table 2) did not clearly allow us to identify whether the “pride” model or the additive model “pride + prey” was the most likely to explain seasonal home range size ($\Delta\text{AICc} \leq 2$ and $w > 0.5$). Parsimony would dictate consideration of the “pride” model as the best model to explain seasonal home range size. The relationship between pride biomass and home range size was indeed very strong, in particular for prides for which total pride biomass is $\leq 800 \text{ kg}$ (the weakened relationship for prides $> 800 \text{ kg}$ is attributable largely to the behaviour of one female F7 and to the possible existence of a threshold at higher values of pride biomass) (Fig. 3a). However, once controlled for pride biomass, prey kilometric biomass had a significant effect on seasonal home range size (estimate \pm SE = -0.099 ± 0.036 ; $F_{1,27} = 11.15$; $p = 0.0025$). Hence, even though pride biomass had the strongest effect on seasonal home range size, we considered an additive model with a positive relationship with pride biomass (Fig. 3a), and a negative relationship with prey kilometric biomass (Fig. 3b). Because different females were sampled in different years, our conclusions regarding “year” effects can only be tentative, but it is noteworthy that 1) slopes of the relationship between seasonal prey biomass and seasonal home range size differed between wet years (2004) and dry years (2003 and 2005), and 2) for a given prey biomass, home range size differed between years (Fig. 4b). Seasonal home range size was negatively related to the density of waterholes in the seasonal home range ($F_{1,27} = 14.43$; $p = 0.0007$; $r^2 = 0.67$). We found similar results for seasonal LoCoH home ranges and 50% cores (Table 2), which also increased as the pride biomass increased ($F_{1,27} = 24.70$; $p < 0.0001$; and $F_{1,27} = 22.60$; $p < 0.0001$ respectively) and decreased as the prey kilometric biomass increased ($F_{1,27} = 8.83$; $p = 0.0062$; and $F_{1,27} = 6.99$; $p = 0.0135$ respectively). F3 and F17 have only a single record, so we checked that this did not bias the

Table 1. Seasonal home range size for African lions in Hwange National Park, Zimbabwe.

Individual	90% kernel home range size (km ²)								
	2003			2004			2005		
	wet	early dry	late dry	wet	early dry	late dry	wet	early dry	late dry
Females									
F1		115	292			287	450	384	522
F3		376							
F4		96	79	145	35				
F5			91	171	392	509	673		
F6			283	789	778				
F7			159	426	366	276	189	385	450
F8			369	467	742	689			
F9				981	836	656			
F11				240	429	406			
F15							620	347	267
F16					268	442			
F17									96
Males									
M1	541	785							
M2				519		673		666	152
M4	833	280							
M5	566	470							
M6			71	1002	478	584	449		
M7	346		395	554	483	187			
M8						306			
M9							109	336	687

results of the mixed model; the model excluding data from these two females provided the same results.

A focus on prey species

Mean female home range size was clearly associated with the mean kilometric biomass of kudu ($F_{1,10} = 10.02$; $p = 0.012$; $r^2 = 0.53$) in the early dry season, whereas it was influenced by the mean kilometric biomass of buffalo ($F_{1,10} = 7.89$; $p = 0.020$; $r^2 = 0.47$) and juvenile elephant (<4 yr-old) ($F_{1,10} = 5.69$; $p = 0.041$; $r^2 = 0.16$) in the late dry season; for all other species: $p > 0.05$. There was no significant relationship between female mean home range

size and the mean kilometric biomass of any particular prey species in the wet season (all $p \geq 0.05$).

Male home range size variation

Mean seasonal home range size for males was not influenced by the number of males in the coalition but the relationship approached statistical significance ($F_{1,6} = 4.05$; $p = 0.09$). There was a negative relationship between mean seasonal home range size and mean prey kilometric biomass ($F_{1,6} = 10.52$; $p = 0.0176$; $r^2 = 0.64$; Fig. 4a). There was no significant relationship between mean seasonal home range size and mean kilometric biomass of any particular prey species (all $p \geq 0.05$). Mean seasonal home range size was not influenced by the density of waterholes ($F_{1,6} = 0.66$; $p = 0.45$). When we examined the influence of females on male mean seasonal home range size, we found that the home range size decreased as the density of prides encompassed within the male home range increased ($F_{1,4} = 12.87$; $p = 0.0230$; $r^2 = 0.76$; Fig. 4b).

Table 2. Summary statistics for models of seasonal home range size for female African lions in Hwange National Park, Zimbabwe.

	AICc	Δ AICc	w	R ²
90% kernel home range				
Pride	532.0	0.9	0.64	0.68
Prey	560.4	29.3	0.00	0.59
Pride+prey	531.1	0	1.00	0.66
Pride+prey+(prey × year)	533.6	2.5	0.29	0.64
LoCoH home range				
Pride	534.2	0.6	0.74	0.62
Prey	558.2	24.6	0.00	0.52
Pride+prey	533.6	0	1.00	0.62
Pride+prey+(prey × year)	535.5	1.9	0.39	0.62
50% kernel core				
Pride	468.9	0	1.00	0.66
Prey	495.5	26.6	0.00	0.54
Pride+prey	470.9	2	0.37	0.62
Pride+prey+(prey × year)	475.9	7	0.03	0.61

Pride = log(pride biomass).
Prey = prey kilometric biomass.

Discussion

Our results strongly suggest that pride biomass is the main determinant of pride seasonal home range size. This is very strongly suggestive of expansionism, with larger prides inhabiting larger home ranges (Macdonald 1983, Kruuk and Macdonald 1985). Because spatial and temporal distribution of resources in semi-arid savannas is often unpredictable, it is possible that species which form social groups may, in these environments, adopt an expansionist strategy. It is noteworthy that the relationship between lion pride biomass and home range size is especially strong for prides whose biomass is ≤ 800 kg. This relationship

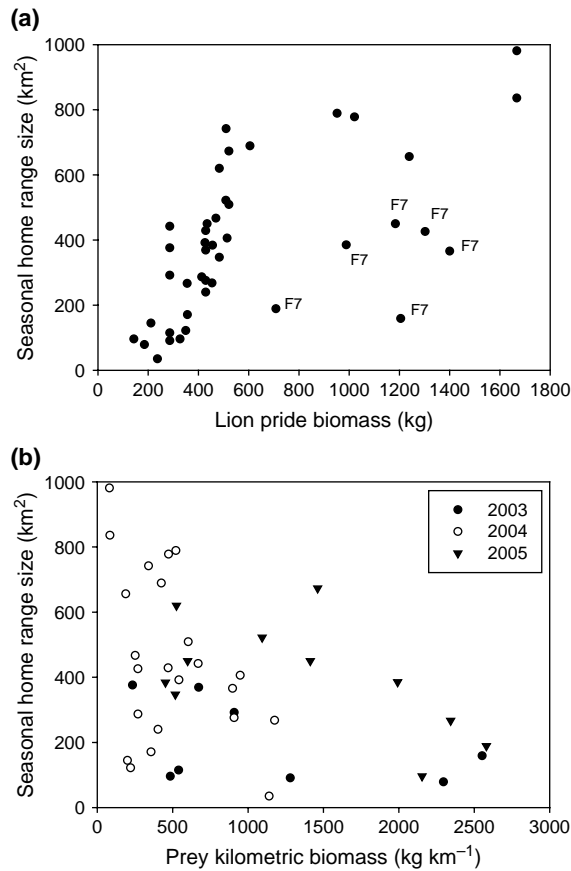


Figure 3. (a) Relationship between lion pride biomass and female home range size. F7 is indicated as we believe this female can be regarded as an outlier. (b) Relationship between prey kilometric biomass and female home range size (see Table 3 for model details).

appears to reach a threshold at pride biomass equivalent to 800 kg (~ 4 adult females). There are two possible reasons for this: one is that the benefits of larger prides (e.g. for communal hunting see van Orsdol 1981 and Cooper 1991; for advantages in territoriality and cooperative cub defence see Packer et al. 1990) outweigh the costs of home range expansion up to prides of 4 adult females, but less so thereafter, and the other is that patrolling a range of greater than 800 km² becomes disadvantageous in terms of defence, energy and maintenance of local knowledge.

Having controlled for pride biomass, pride seasonal home range size was inversely related to prey biomass within each home range, mirroring the general relationship previously reported between ecosystems (van Orsdol et al. 1985). Our results further demonstrate that female seasonal home range size was mainly determined by the abundance of kudu in the early dry season, and of buffalo and young elephant (< 4 yr-old) in the late dry season. These findings corroborate recent evidence showing seasonality in prey consumed in Kruger National Park, South Africa (Owen-Smith 2008). Buffalo and kudu are the two main prey species in HNP (Loveridge et al. 2007b) and young elephants make up an unusually large proportion of lion prey in HNP in the dry season of years of low rainfall (Loveridge et al. 2006). Both buffalo and young elephant are dangerous species for lions to hunt. However, both are

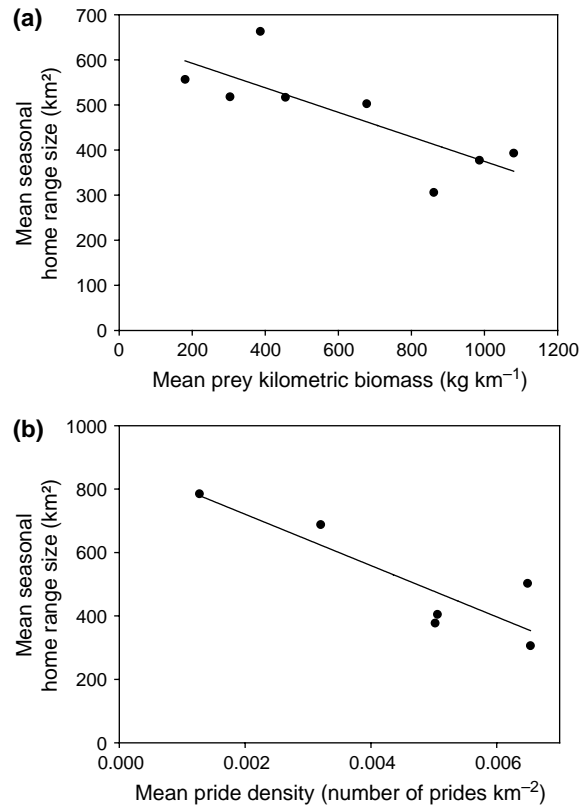


Figure 4. Regression of the mean male seasonal home range size against (a) the mean prey kilometric biomass and (b) the mean pride density encompassed within the male home range.

more vulnerable to predation in the late dry season when nutritional and water deprivation further weaken susceptible individuals (young and old). Furthermore, both elephant and buffalo aggregate in the vicinity of waterholes during the late dry season, but disperse widely when water is available throughout the park. Thus in the late dry season, buffalo and young elephant can be predictably found near waterholes and thus lions configure their ranges to ensure access to these areas. In the wet season, when buffalo and elephant herds have dispersed, lions must rely on more sedentary species such as kudu, which although resident year round are less predictably distributed, forcing lions to alter their foraging patterns and home range use during these periods of less predictable resource abundance.

When resources vary in availability over both the short and the long term, it poses difficult decisions for long-lived, territorial species whose ranges persist for longer than the periodicity of changes in resource availability. In arid and semi-arid savannas, such as HNP, the distribution of herbivores in the landscape is constrained by the distribution of surface water (Redfern et al. 2003, Valeix et al. 2009), which is largely influenced, seasonally and annually, by annual rainfall (Chamaillé-Jammes et al. 2007, 2008). In HNP, changes in local herbivore abundance are likely to arise from movements of some herbivore species between the southern sector of HNP where there is nearly no surface water under dry conditions, but where water is widely available in the wet season, and the northern sector of HNP where artificially supplied waterholes ensure provision of water throughout the year. This may explain why herbivore

abundance in the ca 7000 km² study area was higher during late dry seasons of years of low rainfall, and, within each year, herbivore abundance was higher in the late dry season than in the wet and early dry seasons. There was no consistent seasonal difference in female home range size but home ranges were smaller when annual rainfall was lower. It is likely that in wet years, larger home ranges will lead to larger overlaps between pride seasonal home ranges. These results suggest that pride ranges respond to changes in food abundance between years, but in the shorter term, they remain constant between seasons, adapted perhaps to the worst of recent conditions. Over short time-scales, it may be too energetically costly to adapt home ranges to short-term variations in resource availability (Macdonald and Carr 1989). Additionally, there are fewer waterholes retaining water during the dry season in dry years than in wet years in HNP (Chamaillé-Jammes et al. 2007, 2008). Under dry conditions, herbivores tend to aggregate around the few scarce water sources (Thrash et al. 1995), where predators have a greater chance of encountering their prey. Thus, through its influence on surface water availability, annual rainfall influences not only the abundance of herbivores, but also their dispersion and the predictability with which lions encounter them around waterholes, and ultimately ranging behaviour of carnivores. In the case of lions in HNP, the fact that slopes of the relationship between prey biomass and seasonal home range size tended to differ between years and that for a given prey biomass, home range size tended to differ between years, suggested that the variation cannot be attributed solely to variation in herbivore abundance. Our findings corroborate those from previous studies that showed that climatic variability explains variance around the seasonal pattern in home range size (Fisher and Owens 2000, Börger et al. 2006a, b). For carnivores, the effect of rainfall on home range size appears to be indirect through prey abundance and dispersion (Marker and Dickman 2005).

As suggested in this study, pride biomass is likely to be the main determinant of seasonal home range size, and the abundance, distribution and dispersion of herbivores (and particularly of kudu in the early dry season, and of buffalo and young elephant in the late dry season) within the landscape, primarily determined by the distribution of waterholes, may also significantly influence the configuration of home ranges. However, it is likely that home range size is not only determined by intra-group and ecological factors, but also by interactions with con-specifics and intraspecific competition for space. For instance many studies have demonstrated that home range size in territorial species appears to scale inversely with population density (Krebs 1971, Erlinge et al. 1990, Makarieva et al. 2005, Marker and Dickman 2005). Since lions are exclusively territorial and, males particularly, will not tolerate the presence of non-members in their territories (McComb et al. 1994, Heinsohn 1997), it is highly likely that the location and size of home ranges is influenced by the interactions of resident groups with their neighbours, and home range size is expected to be inversely related to population density. Unfortunately, we could not investigate these patterns in this study since most home ranges bordered unstudied areas. However, if interactions with conspecifics had an effect on home ranges, we suspect that

this effect was not strong because the study was carried out in a low density lion population.

It is noteworthy that male lion density was artificially low because of trophy hunting off-take over the study period (Loveridge et al. 2007a), which might have allowed males to range further in the absence of intra-sexual competition. Still, our results showed that males differed from females in their ranging behaviour as previously demonstrated in several carnivore studies (Dillon and Kelly 2008). Male home range size was larger than that of females and appeared to be affected by both prey abundance and pride density. It is likely that home range sizes of males were determined indirectly by prey abundance, through association with female prides, and larger ranges are a male reproductive strategy because they configure their home ranges not only to secure food but also to acquire and defend access to females (Schaller 1972, Bygott et al. 1979). This is corroborated by the fact that males have larger home ranges when the density of female prides is lower, suggesting that male lions extend their home range to cover a minimum number of prides.

Our study clearly shows that home range size in social carnivores is primarily influenced by social factors, such as group size which is intrinsically linked to the group metabolic needs. It also emphasizes the role of ecological factors, and more particularly the interaction between prey abundance and distribution, which may further explain home range size, shedding light on the ecological algebra of intraspecific variation in home range size.

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References

- Bell, R. H. V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. – In: Huntley, B. J. and Walker, B. H. (eds), *Ecology of tropical savannas*. Springer, pp. 193–216.
- Benson, J. F. et al. 2006. Regulation of space use in a solitary felid: population density or prey availability? – *Anim. Behav.* 71: 685–693.

- Börger, L. et al. 2006a. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. – *Am. Nat.* 168: 471–485.
- Börger, L. et al. 2006b. Effects of sampling regime on the mean and variance of home range size estimates. – *J. Anim. Ecol.* 75: 1393–1405.
- Börger, L. et al. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. – *Ecol. Lett.* 11: 637–650.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretical approach. – Springer.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. – *J. Mammal.* 24: 346–352.
- Bygott, J. D. et al. 1979. Male coalitions in large coalitions gain reproductive advantages. – *Nature* 282: 839–841.
- Chamaillé-Jammes, S. et al. 2007. Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: potential implications for herbivore dynamics. – *Austral Ecol.* 32: 740–748.
- Chamaillé-Jammes, S. et al. 2008. Resource variability, aggregation and direct density-dependence in an open context: the local regulation of an African elephant population. – *J. Anim. Ecol.* 77: 135–144.
- Clutton-Brock, T. H. 1989. Mammalian mating systems. – *Proc. R. Soc. B* 236: 339–372.
- Coe, M. J. et al. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. – *Oecologia* 22: 341–354.
- Cooper, S. M. 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. – *Afr. J. Ecol.* 29: 130–136.
- Cumming, D. H. M. and Cumming, G. S. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. – *Oecologia* 134: 560–568.
- Dillon, A. and Kelly, M. J. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. – *J. Zool.* 275: 391–398.
- East, R. 1984. Rainfall, soil nutrient and biomass of large African savanna mammals. – *Afr. J. Ecol.* 22: 245–270.
- Erlinge, S. et al. 1990. Density related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. – *J. Mammal.* 71: 597–603.
- Fagan, W. F. et al. 2007. Population and community consequences of spatial subsidies derived from central-place foraging. – *Am. Nat.* 170: 902–915.
- Fisher, D. O. and Owens, I. P. F. 2000. Female home range size and the evolution of social organization in macropod marsupials. – *J. Anim. Ecol.* 69: 1083–1098.
- Fritz, H. and Duncan, P. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. – *Proc. R. Soc. B* 256: 77–82.
- Fritz, H. et al. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. – *Oecologia* 131: 620–625.
- Funston, P. and Mills, M. G. L. 2006. Behavioural ecology of lions in Kruger National Park. – In: Loveridge, A. J. et al. (eds), *Lion research conservation – Workshop 3 and 4 – from conflict to socioecology*. Wildlife Conservation Research Unit, Oxford, pp. 54–56.
- Geffen, E. et al. 1992. Habitat selection and home range in the Blandorf's fox, *Vulpes cana*: compatibility with the resource dispersion hypothesis. – *Oecologia* 91: 75–81.
- Getz, W. M. and Wilmers, C. C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. – *Ecography* 27: 489–505.
- Getz, W. M. et al. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. – *PlosOne* 2: e207.
- Grange, S. and Duncan, P. 2006. Bottom-up and top-down processes in African ungulate communities: resources and predation acting on the relative abundance of zebra and grazing bovids. – *Ecography* 29: 899–907.
- Hanby, J. P. et al. 1995. Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains. – In: Sinclair, A. R. E. and Arcese, P. (eds), *Serengeti II: dynamics, management, and conservation of an ecosystem*. Univ. of Chicago Press, pp. 315–331.
- Heinsohn, R. 1997. Group territoriality in two populations of African lions. – *Anim. Behav.* 53: 1143–1147.
- Hemson, G. 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.
- Kelt, D. A. and Van Vuren, D. H. 2001. The ecology and macroecology of mammalian home range area. – *Am. Nat.* 157: 637–645.
- Krebs, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. – *Ecology* 52: 2–22.
- Kruuk, H. and Macdonald, D. W. 1985. Group territories of carnivores: empires and enclaves. – In: Sibly, R. M. and Smith, R. H. (eds), *Behavioural ecology*. Blackwell, pp. 521–536.
- Kruuk, H. H. and Parish, T. 1987. Changes in the size of groups and ranges of the European badger (*Meles meles* L.) in an area in Scotland. – *J. Anim. Ecol.* 56: 351–364.
- Loveridge, A. J. et al. 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. – *J. Zool.* 270: 523–530.
- Loveridge, A. J. et al. 2007a. The impact of sport-hunting on the lion population in a protected area. – *Biol. Conserv.* 134: 548–558.
- Loveridge, A. J. et al. 2007b. Hwange Lion Project Annual Report 2007. – Zimbabwe Parks and Wildlife Management Authority, Zimbabwe.
- Macdonald, D. W. 1983. The ecology of carnivore social behaviour. – *Nature* 301: 379–384.
- Macdonald, D. W. and Carr, G. M. 1989. Food security and the rewards of tolerance. – In: Standen, V. and Folley, R. A. (eds), *Comparative socioecology: the behavioural ecology of humans and other mammals*. Blackwell, pp. 75–99.
- Maillard, D. et al. 2001. The kilometeric index as a monitoring tool for population of large terrestrial animals: a feasibility test in Zakouma National Park, Chad. – *Afr. J. Ecol.* 39: 306–309.
- Makarieva, A. N. et al. 2005. Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability. – *Ecol. Complex.* 2: 259–271.
- Marker, L. L. and Dickman, A. J. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. – *S. Afr. J. Wildl. Res.* 35: 105–115.
- McComb, K. et al. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. – *Anim. Behav.* 47: 379–387.
- McLoughlin, P. D. and Ferguson, S. H. 2000. A hierarchical sequence of limiting factors may help explain variation in home range size. – *Ecoscience* 7: 123–130.
- McNab, B. K. 1963. Bioenergetics and the determination of home range size. – *Am. Nat.* 97: 133–140.
- Mills, L. S. and Knowlton, F. F. 1991. Coyote space use in relation to prey abundance. – *Can. J. Zool.* 69: 1516–1521.
- Owen-Smith, N. 2008. Changing vulnerability to predation related to season and sex in an African ungulate assemblage. – *Oikos* 117: 602–610.
- Packer, C. et al. 1990. Why lions form groups: food is not enough. – *Am. Nat.* 136: 1–19.

- Patterson, B. R. and Messier, F. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. – *J. Mammal.* 82: 463–477.
- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. – In: Boitani, L. and Fuller, T. K. (eds), *Research techniques in animal ecology – controversies and consequences*. Columbia Univ. Press, pp. 65–110.
- Redfern, J. V. et al. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. – *Ecology* 84: 2092–2107.
- Rhodes, J. R. et al. 2005. A spatially explicit habitat selection model incorporating home range behavior. – *Ecology* 86: 1199–1205.
- Rogers, C. M. L. 1993. A woody vegetation survey of Hwange National Park. – Dept of National Parks and Wildlife Management, Zimbabwe.
- Rohner, C. and Krebs, C. J. 1998. Response of great horned owls to experimental “hot spots” of snowshoe hare density. – *Auk* 115: 694–705.
- Said, S. and Servanty, S. 2005. The influence of landscape structure on female roe deer home-range size. – *Landscape Ecol.* 20: 1003–1012.
- Said, S. et al. 2005. Ecological correlates of home-range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. – *J. Zool.* 267: 301–308.
- SAS Inst. 1999. SAS/STAT software, ver. 8. – Carey, NC.
- Schaller, G. B. 1972. *The Serengeti lion: a study of predator prey relations*. – Chicago Univ. Press.
- Smuts, G. L. et al. 1980. Comparative growth of wild male and female lions (*Panthera leo*). – *J. Zool.* 190: 365–373.
- South, A. B. and Kenward, R. E. 2006. Ranges7 v1.0: for the analysis of tracking and location data. – Anatrack, Wareham, UK.
- Stander, P. E. 1991. Demography of lions in the Etosha National Park, Namibia. – *Madoqua* 18: 1–9.
- Thrash, I. et al. 1995. Dry season herbivore densities around drinking troughs in the Kruger National Park. – *J. Arid Environ.* 29: 213–219.
- Valeix, M. et al. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. – *Ecology* 90: 23–30.
- van Kesteren, F. 2006. Analysis of the diet of African lions (*Panthera leo*) in Hwange National Park, Zimbabwe. – M.Sc. thesis, Univ. of Oxford.
- van Orsdol, K. G. 1981. Lion predation in Rwenzori National Park, Uganda. – Ph.D. thesis, Univ. of Cambridge.
- van Orsdol, K. G. et al. 1985. Ecological correlates of lion social organization (*Panthera leo*). – *J. Zool.* 206: 97–112.
- Vincent, J. P. et al. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. – *Acta Theriol.* 36: 315–328.
- Wang, M. and Grimm, V. 2007. Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. – *Ecol. Model.* 205: 397–409.
- Woodroffe, R. and Ginsberg, J. R. 2000. Ranging behaviour and vulnerability to extinction in carnivores. – In: Gosling, L. M. and Sutherland, W. J. (eds), *Behaviour and conservation*. Cambridge Univ. Press, pp. 125–140.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. – *Ecology* 70: 164–168.