Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis

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Abstract. Empirical tests of the resource dispersion hypothesis (RDH), a theory to explain group living based on resource heterogeneity, have been complicated by the fact that resource patch dispersion and richness have proved difficult to define and measure in natural systems. Here, we studied the ecology of African lions *Panthera leo* in Hwange National Park, Zimbabwe, where waterholes are prey hotspots, and where dispersion of water sources and abundance of prey at these water sources are quantifiable. We combined a 10-year data set from GPS-collared lions for which information of group composition was available concurrently with data for herbivore abundance at waterholes. The distance between two neighboring waterholes was a strong determinant of lion home range size, which provides strong support for the RDH prediction that territory size increases as resource patches are more dispersed in the landscape. The mean number of herbivore herds using a waterhole, a good proxy of patch richness, determined the maximum lion group biomass an area can support. This finding suggests that patch richness sets a maximum ceiling on lion group size. This study demonstrates that landscape ecology is a major driver of ranging behavior and suggests that aspects of resource dispersion limit group sizes.

Key words: *felid; Hwange National Park, Zimbabwe;* Panthera leo; *sociality; spatial ecology; waterholes.*

Introduction

In natural ecosystems, resources are often heterogeneously distributed and characterized by temporal variability, and animal ecology is mediated by the abundance of resources, their dispersion in the environment, and the predictability with which they are distributed. Home range configuration is affected by overall resource abundance with increases in abundance leading to smaller ranging areas (e.g., Mills and Knowlton 1991), but, when resource availability is heterogeneous, larger areas may be needed to encompass the spatial and temporal variability of these resources (Macdonald and Carr 1989). This may have implications for animal social organization and prompted the formulation of the resource dispersion hypothesis (RDH; Macdonald 1983, Carr and Macdonald 1986, Macdonald and Carr 1989).

The RDH proposes that heterogeneous spatiotemporal distribution of resources can lead to the formation and maintenance of animal groups, even in the absence of obvious functional benefits of group living (e.g.,

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cooperative hunting, predator defense, alloparental care). The basic concept is that, even a single animal using patchy resources will have to defend a large enough area to be sure that at least one rich patch will be available to satisfy its resource requirements. According to the RDH, for a given patch richness and dispersion, this same area defended by the original resident is predicted to have an excess of resources some or all of the time, so that there might often be sufficient resources to sustain additional animals. The RDH predicts that resource dispersion determines territory size, whereas patch richness independently influences group size. It is among the few hypotheses for the evolution of social behavior that explicitly address the role of landscape structure (see also the benefits-of-philopatry hypothesis; Stacey and Ligon 1991).

The RDH is the most frequently used model to explain the sociality of Eurasian badgers *Meles meles* for which there are no obvious direct benefits of group living (Kruuk and Parrish 1987, Johnson et al. 2001). However, its generalization has been questioned and widely debated in the literature (Johnson et al. 2002, Johnson and Macdonald 2003, Revilla 2003*a*, *b*). This is partly because empirical testing of the RDH is complicated by the fact that the pertinent variables

(resource patch dispersion and richness) have proven difficult to define and measure in natural systems (Johnson et al. 2002). Additionally, many species have been shown to benefit directly from group living, and this makes less obvious the role of resource dispersion in shaping their societies.

One strong prerequisite to the RDH is that key habitats holding key resources have a heterogeneous spatial and/or temporal distribution. Few systems allow the empirical testing of RDH predictions with easily identifiable resource patches and even fewer where the dispersion and richness of resource patches are straightforward to measure. Here, we studied the spatial and social ecology of a large social carnivore, the African lion (*Panthera leo*), in Hwange National Park, Zimbabwe, an ecosystem characterized by waterholes that are heterogeneously distributed and constitute key habitat features around which herbivores aggregate in the dry season (Valeix 2011). Lion habitat selection is largely determined by these habitats and this is where most of their hunts occur (Valeix et al. 2009, 2010). This ecosystem provides an unusual opportunity to test the predictions of the RDH in a system where resource patch dispersion (distance between neighboring waterholes) and richness (prey abundance or biomass at waterholes) are characterized by a high variability, and are easy to quantify. Waterhole dispersion is expected to determine territory size, with territory increasing as water sources become more widespread in the landscape (prediction 1), and the richness of water sources (herbivore abundance or biomass) is expected to influence lion group size, with larger groups found in areas where water sources attract the highest herbivore abundance (prediction 2). All three dimensions of prey richness (body size, herd size, and number) clearly influence overall prey abundance/biomass, and hence, have major implications for lion foraging; we investigated these in this study. Lion foraging behavior is likely to also be influenced by prey vulnerability to predation; however, the factors influencing this vulnerability (e.g., herbivore age, body condition, vigilance levels) can be considered homogeneous amongst the different waterholes of the study area (e.g., during a drought, the number of young, and the body condition of one herbivore species are likely to be affected by the dry conditions in a given way, but overall, this influence will exist for the whole population of this species in the study area). Hence, this study focuses on prey abundance only.

Lions are social carnivores and are ideal for studies of social grouping because they live in fission–fusion social units that allow pride members to form subgroups of differing sizes (Schaller 1972). For this species, group living is influenced by numerous benefits such as cooperative hunting (Stander 1992), mutual defense of kills (Cooper 1991), and cooperative defense of territory and young (Packer et al. 1990). However, larger groups

are often found in territories characterized by richer habitats (Mosser 2008, Mosser et al. 2009). For species, such as African lions, for which there are obvious benefits of group formation, group size is not expected to be determined solely by patch richness and we do not expect them to be contractionists (sensu Macdonald 1983, Kruuk and Macdonald 1985). Group size is expected to be influenced by a number of factors, and we do not suggest that the RDH provides an exclusive explanation for observed group size; rather, we hypothesize that patch richness determines the maximum group size an area can support. Hence, in this study, we expected the richness of water sources to set a maximum ceiling on lion group size (prediction 3).

METHODS

Study area

The study area covered ~7000 km² in the northern region of Hwange National Park (Hwange), Zimbabwe. Hwange covers ~15 000 km² of semiarid dystrophic (low-nutrient soil) savanna in northwestern Zimbabwe (19°00′ S, 26°30′ E). The vegetation is primarily woodland and bushland savanna, with plant communities dominated by *Colophospermum mopane*, *Combretum* spp., *Acacia* spp., *Baikiaea plurijuga*, and *Terminalia sericea* (Rogers 1993). The long-term mean annual rainfall is 613 mm, which falls primarily between October and April. Annual rainfall is highly variable (CV = 26%). At the end of the dry season, the only surface water available to animals is found in artificial waterholes, as well as in a few natural waterholes in years of good rainfall. Lion density in the study area is estimated ~2.7 lions/100 km² (Loveridge et al. 2007).

Lion data

From 2002 to 2010, lions were closely monitored in the study area, of which 30 female and 31 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). Animals' locations were available hourly from 18:00 to 07:00 hours, plus fixes at 09:00 and 16:00 hours. 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 masses (±SD) was 199 ± 10 kg for adult males (N = 4) and 143 ± 11 kg for adult females (N = 6). These are consistent with those published for southern African populations (Smuts et al. 1980). Every effort was made to find the collared lions at least once a month to download positional data from the GPS radio collars and record the size and composition of their group at that time.

Waterhole data

Every year at the end of the dry season, Wildlife Environment Zimbabwe (WEZ) conducts 24-hour game

counts at active waterholes during the full moon (26 September ± 8 days). The number of animals coming to drink from midday to midday the next day is recorded for all species. In the study area, an average of 40 waterholes are monitored every year, and aerial surveys at the time of the waterhole monitoring allowed us to estimate that this represents 90% of all active waterholes. This monitoring allowed us to know the total number of herbivores, the number of herds, and the average herd size that visited each waterhole in 24 hours for each large-herbivore species. It also informed us on the composition of the herbivore community at each waterhole. Some herbivores may visit a waterhole several times in 24 hours, and others may not come to drink at all. However, any biases this variability may introduce are likely to be the same for all waterholes. Hence, the data collected are good proxies of the relative abundance of herbivores in the vicinity of the different waterholes.

Influence of waterhole dispersion on lion home range size

We used data from only one collared lion per group at any time. Preliminary analyses revealed that lionesses from the same pride stay together most of the time in Hwange, with females from a pride sighted together in 89.2% ± 7.4% of sightings. Hence, movements of one lioness are considered to be representative of the pride. Lion home ranges were calculated using the local convex hull (LoCoH) nonparametric kernel method (Getz and Wilmers 2004, Getz et al. 2007) with heuristic value $k = \sqrt{n}$ (n is the number of points in the set). For each individual and each year, we calculated the September home range, which corresponds to the peak of the dry season and just preceded and overlapped with the WEZ monitoring. Only September home ranges for which a minimum of 28 days and 300 locations were available were estimated (this represents 57 home ranges from 21 female and 15 male adults). Home range analyses were undertaken using the extension LoCoH v.2.1 for ArcView (version 3.2; ESRI 1999). The dispersion of waterholes was measured using the distance between two neighboring waterholes. For each home range, an index of waterhole dispersion was calculated by averaging the distance between two neighboring waterholes over all waterholes encompassed within the home range. We performed linear mixed-model analyses on lion September home range size with lion identity included as a random factor and the index of waterhole dispersion, sex, and the interaction between these two variables as fixed factors to test prediction 1. Linear mixed models were performed with SAS software (version 8.2; SAS Institute 2002), using the MIXED procedure and restricted maximum likelihood estimation method.

Influence of waterhole richness on lion group size

For each lion group, we calculated the biomass of the group using the composition of each pride and coalition observed during routine data collection. We used field data for adult weight (see details in *Lion data*). For cubs and subadults, we used growth equations from Smuts et al. (1980): body mass (kg) = 4.21 × age (months) + 5.29 for males ($r^2 = 0.98$) and body mass (kg) = 3.31 × age (months) + 6.64 for females ($r^2 = 0.99$). For each waterhole and each year, waterhole richness (approximately prey abundance) was assessed using five measures: total number of herbivores visiting the waterhole in 24 h, total number of herbivore herds visiting the waterhole in 24 h, average herd size, mean herbivore individual biomass, total herbivore biomass at the waterhole in 24 h. Mean herbivore individual biomass and total herbivore biomass were calculated using the unit mass, i.e., the average mass of individuals in a population (Cumming and Cumming 2003). The unit mass implicitly takes into account the composition (age class and sex) of a population. For each lion and dry season, five indices of waterhole richness were calculated by averaging the above measures over all waterholes encompassed within the lion home range. The analyses described further were run five times to explore the role of these five indices of prey availability for lions. Herd size was log-transformed to meet the normality requirement. Only main prey species (Davidson 2009) were included in the analyses: African buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*) four or less years old (frequently recorded as prey during drought years in Hwange; Loveridge et al. 2006), blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus quagga*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), roan antelope (*Hippotragus equines*), sable antelope (*Hippotragus niger*), warthog (*Phacochoerus aethiopicus*), and waterbuck (*Kobus ellipsiprymnus*). We first performed linear mixed-model analyses on lion group biomass with lion identity included as random factor and the index of waterhole richness, sex, and the interaction between these two variables as fixed factors to test prediction 2. Classical linear models estimate the rate of change in the mean of the response variable. Because we were also interested in the rate of change in the maximal values of group biomass, we then used quantile regressions that extend this estimation to any part of the response distribution, i.e., to any selected quantile, with the τth one-sample quantile estimate defined as the value having a proportion τ of the sample observations less than or equal to the estimate (Cade et al. 1999, Koenker 2005). This method allowed us to investigate trends in only a specific range of the data. Here, we investigated the changes in the highest values of lion group size (cf. prediction 3) by performing 0.7, 0.8, and 0.9 quantile regressions to estimate and test slopes along the "edge" of point clouds. Significant levels were assessed using the bootstrapping method (Koenker 2005). These statistical
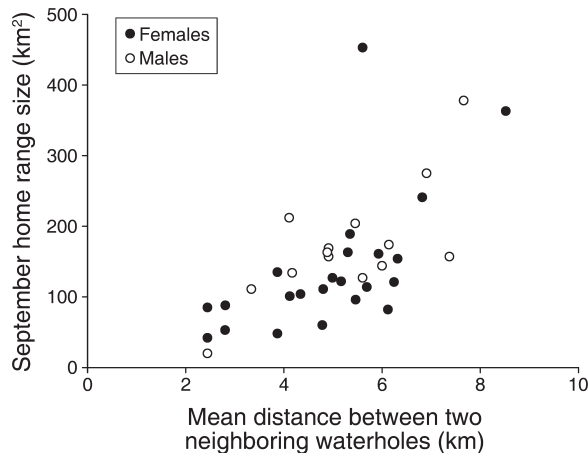
FIG. 1. Relationship between the index of waterhole dispersion and lion (*Panthera leo*) home range size in the dry season in Hwange National Park, Zimbabwe.

analyses were run with R software using the "quantreg" package (R Development Core Team 2011).

RESULTS

Influence of waterhole dispersion on lion home range size

The distance between two neighboring waterholes ranged from 1 km to 10 km (mean ± SD = 4.5 ± 2.2 km). The index of waterhole dispersion significantly influenced the size of September home ranges in lions (estimate ± SE = 0.041 ± 0.008, $F_{1,12}$ = 26.52, P = 0.0002), with larger home ranges in areas where waterholes are more dispersed (Fig. 1). September home range size was not influenced by the interaction between sex and the index of waterhole dispersion ($F_{1,11}$ = 0.001, P = 0.98) or by the sex ($F_{1,12}$ = 0.70, P = 0.42).

Influence of waterhole richness on lion group size

Waterholes varied greatly in their attendance by herbivores: There was a mean of 27 herds visiting a

waterhole in 24 hours (SD = 26, range = 0–220), a mean of 165 individuals visiting a waterhole in 24 hours (SD = 211, range = 0–1988), a mean herd size of 9.7 individuals (SD = 29.9, range = 1–536), a mean individual biomass of 295 kg (SD = 74 kg, range = 135–750 kg), and the mean total herbivore biomass visiting a waterhole in 24 hours was 52 299 kg (SE = 81 485 kg, range = 135–868 040 kg). Linear models revealed that lion group biomass was not influenced by the indices of the mean number of main prey herds or individuals visiting a waterhole in 24 hours ($F_{1,12}$ = 2.00, P = 0.18, and $F_{1,12}$ = 2.59, P = 0.13, respectively), the index of the mean herd size for lion main prey ($F_{1,12}$ = 1.70, P = 0.22), the indices of the mean individual biomass or total biomass of main prey visiting a waterhole in 24 hours ($F_{1,12}$ = 3.24, P = 0.10, and $F_{1,12}$ = 0.02, P = 0.89, respectively). However, the quantile regression analyses revealed that the high values of lion group biomass, i.e., maximum group size, increased as the index of mean number of main prey herds increased (Table 1). Fitting the 0.9th-quantile trend line showed this relationship (Fig. 2). There was no significant effect of other prey richness indices.

DISCUSSION

Our results show that the mean distance between two neighboring waterholes is a strong determinant of lion home range size, and hence, provides strong support to the first prediction of the RDH, which is that territory size increases as resource patches are more dispersed in the landscape (see also Mills 1990, Geffen et al. 1992, Valenzuela and Macdonald 2002 for first empirical support for this prediction in species other than badgers). Lion September home range size varied from 20 km² in areas where the mean distance between neighboring waterholes was 2.4 km to >350 km² in areas where the mean distance between neighboring waterholes was ~8 km. The core concept of the RDH is that animals have to defend a large enough area to be sure that at least one "ripe" patch will be available to

TABLE 1. Slope estimates (±SE) for the selected quantiles and their significance level for lion (*Panthera leo*) group biomass depending on five indices of prey availability in Hwange National Park, Zimbabwe.

Quantile	Number of herds		log(herd size)		Number of individuals		Individual biomass		Total herbivore biomass	
	Slope	P	Slope	P	Slope	P	Slope	P	Slope (×1000)†	P
0.1	0.00 ± 3.62	1.000	0.00 ± 64.36	1.000	0.00 ± 0.17	1.000	0.00 ± 0.43	1.000	0.00 ± 0.00	1.000
0.2	0.00 ± 5.31	1.000	37.06 ± 58.22	0.529	0.23 ± 0.34	0.501	0.00 ± 0.65	1.000	0.00 ± 0.95	1.000
0.3	8.05 ± 5.17	0.128	101.18 ± 51.35	0.097	0.55 ± 0.51	0.289	−0.58 ± 0.75	0.450	0.00 ± 1.29	1.000
0.4	8.35 ± 5.31	0.125	87.83 ± 58.61	0.145	0.53 ± 0.52	0.311	−0.61 ± 0.75	0.418	1.16 ± 1.41	0.417
0.5	9.88 ± 5.03	0.057	76.25 ± 60.86	0.221	0.56 ± 0.56	0.327	0.31 ± 0.88	0.731	1.11 ± 1.41	0.439
0.6	**10.85 ± 4.95**	**0.035**	109.05 ± 77.84	0.172	0.59 ± 0.72	0.419	0.02 ± 1.03	0.988	1.35 ± 1.46	0.364
0.7	**13.38 ± 5.29**	**0.016**	87.17 ± 138.66	0.535	0.66 ± 0.84	0.438	0.99 ± 1.24	0.433	1.06 ± 2.33	0.651
0.8	**15.31 ± 5.63**	**0.010**	−41.34 ± 158.77	0.797	1.13 ± 0.91	0.221	0.83 ± 1.28	0.522	3.47 ± 2.72	0.211
0.9	**12.09 ± 4.39**	**0.009**	−80.29 ± 175.14	0.650	1.20 ± 0.71	0.098	−0.88 ± 2.21	0.694	3.01 ± 2.95	0.314

Note: Quantiles for which trends are significant ($P < 0.05$) are shown in boldface type.
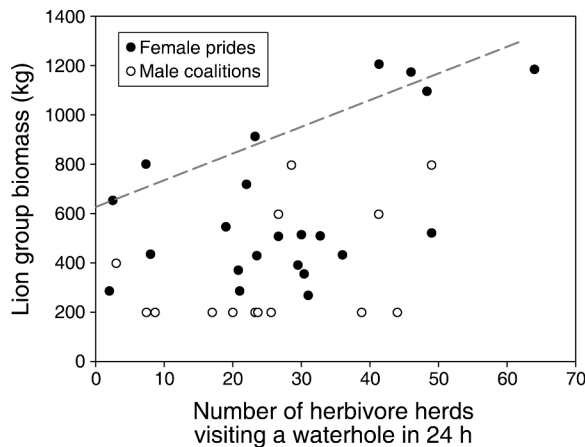† Slope values shown have been multiplied by 1000.

FIG. 2. Relationship between lion group biomass and an index of waterhole richness (mean number of main prey herds encountered at a waterhole in 24 hours) in Hwange National Park, Zimbabwe. The dashed line shows the 0.9th-quantile regression fit.

satisfy its resource requirements. In Hwange, the "ripeness" of a resource patch for a lion can be linked to the ease with which lions can catch a prey in the patch, which is linked not only to prey local abundance, but also to prey catchability (e.g., level of vigilance). Both factors are likely to be characterized by a strong temporal variability associated to the presence or absence of predators. Indeed, herbivores make several behavioral adjustments in the immediate presence of predators to decrease the probabilities of encounter, attack, and capture by the predator (Creel et al. 2005, Valeix et al. 2009, Périquet et al. 2010), a process known as a behavioral resource depression (Kotler 1992). In Hwange, lions make most of their kills in the vicinity of a waterhole (Valeix et al. 2009), but avoid consecutive kills in the same area and in most cases move to a different waterhole after a kill, possibly because of this behavioral resource depression and to allow "recovery" of the resource patch (Valeix et al. 2011). Hence, lions need a home range that encompasses enough waterholes so that at any one time, at least one patch has an adequate level of food security (sensu Carr and Macdonald 1986), and lions can rotate their hunting between different waterholes.

In the Serengeti National Park, Tanzania, river confluences provide all important resources to lions (food, water, and shelter), and hence, represent high-value landscape features associated with a high reproductive success for lions (Mosser et al. 2009). There, territories that encompass several such hotspots support larger groups (Mosser 2008), which provides some support to the second prediction of the RDH (i.e., group size increases as patch richness increases). Predictions relating group size and patch richness per se have rarely been empirically tested because of the

difficulty of measuring patch richness (Johnson et al. 2002). Here, we explored five dimensions of patch richness for a carnivore: an index of prey herd encounter rate, an index of prey individual encounter rate, the average herd size, the average body size of herbivores encountered, and an index of the total herbivore biomass available in the patch. None of these indices dictated lion group biomass. This was not unexpected, as there are several forces driving group formation for lions, from cooperative hunting (Stander 1992) and the mutual defense of kills (Cooper 1991) to cooperative defense of territory and young (Packer et al. 1990). However, we show that, while small groups can be found everywhere, patch richness determines the maximum group size an area can support. In our study, the largest lion groups (biomass >1000 kg) were found only in areas where there were over 40 herbivore herds visiting a waterhole in 24 hours. Prey body size could have been expected to also be important here because, if lions are able to catch larger prey, the patch will be richer than a patch where only small-bodied prey are available. Hwange is a dystrophic savanna, and the herbivore community is dominated by very large-bodied herbivores (e.g., elephant, giraffe, buffalo, zebra; unit biomass >200 kg) compared to other African savannas (Fritz et al. 2011). It is thus possible that a relationship between prey body size and lion group size, which could have been detected in a system characterized by a different herbivore community, was not detected in Hwange, where the average individual prey body size is uniformly large and where frequency of encounters with prey herds may thus be more important. By showing that the mean number of herbivore herds visiting a waterhole in 24 hours, a proxy of prey herd encounter rate by lions and ultimately patch richness, determines the maximum lion group biomass an area can support (prediction 3), our study provides the first empirical evidence that patch richness sets a maximum ceiling on animal group size.

Several sociological or ecological hypotheses have been put forward to explain group formation. For large carnivores, the sociological hypotheses that have received much support are cooperative hunting (Stander 1992), mutual defense of kills (Cooper 1991), and cooperative defense of territory and young (Packer et al. 1990). Several ecological hypotheses other than the RDH have been suggested, such as the resource abundance hypothesis (Wrangham et al. 1993), the prey renewal hypothesis (Waser 1981), the patch size hypothesis (Chapman et al. 1994), or the temporal food availability hypothesis (Malenky and Wrangham 1994). Few of these hypotheses are mutually exclusive. For ecological hypotheses, the RDH, by taking explicitly into account both the spatial and temporal variability of resources, provides the most realistic framework and is integrative of several other ecological hypotheses that

take this variability into account only partially (Johnson et al. 2002). Criticism of the RDH (Revilla 2003*a*, *b*) has prompted the clarification that resource dispersion alone does not favor, but merely facilitates, the evolution of sociality, but, paired with the social advantages of grouping (such as cooperative hunting or territorial defense), resource dispersion and the existence of "spatial groups" pave the way to consistent sociality and may determine the maximum social group size that can be supported in an area. Hence, the RDH is not exclusive of sociological hypotheses to explain group formation; rather, it shows how resource dispersion facilitates the formation of groups on which sociological factors can operate.

The RDH has been pioneering in linking concepts of landscape ecology and animal behavior, and our empirical study provides evidence that strongly encourage such an integration. Here, our study clearly demonstrated that landscape ecology is a major driver of ranging behavior and suggested that aspects of resource dispersion limit group sizes.

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