



## How lions move at night when they hunt?

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Movement patterns of lions (*Panthera leo*) reveal how they hunt large herbivores in heterogeneous landscapes such as the Kruger National Park in South Africa. Large herbivores are distributed differently on the landscape and therefore have different vulnerabilities as prey for lions. For instance, blue wildebeest (*Connochaetes taurinus*) occupy small grazing lawns at night but are difficult for lions to capture because open areas lack cover for stalking. African buffalo (*Syncerus caffer*) aggregate in large herds but are less available because these herds only intermittently enter the home ranges of individual lion prides. Unlike large herds of wildebeest and buffalo, plains zebra (*Equus quagga*) move widely in small herds while browsing greater kudu (*Tragelaphus strepsiceros*) and giraffes (*Giraffa camelopardalis giraffa*) generally occur in lower densities. We used spatial data derived from GPS collars to investigate several hypotheses regarding the movements of three lion prides in response to their prey. We found that lions were most active and moved longer distances during nighttime than during daytime. Lions remained within their core home ranges on 87% of nights and wandered to the outlying areas of the home ranges every second night. Lions visited grazing lawns, that is, area of short grass, where wildebeest herds resided every second night, and moved toward the direction of buffalo herds within 2 km of vicinity. Lions spent more time near riverbanks that provided dense woody cover at night than expected but concentrated only weakly near sites with surface water where herbivores drank in the dry season. Our study contributes to understanding how lions vary their movements in response to the spatial and temporal heterogeneity in the relative availability and vulnerability of multiple prey species.

Key words: independent mixture model, Kruger National Park, landscape of fear, movement behavior, *Panthera leo*, predation

Prey vulnerability and availability influence both the movement and space use patterns of large carnivores (Balme et al. 2007; Davidson et al. 2012; Owen-Smith 2015). As an ambush predator, lions (*Panthera leo*) are generally more successful at stalking and killing their prey in areas with dense woody vegetation or other cover (Hopcraft et al. 2005); however, herbivores that are mostly browsers, that occupy these habitats are often sparsely distributed low densities (Owen-Smith 2008; Thaker et al. 2011; O’Kane et al. 2013). In contrast, that are grazers aggregate in open areas but are less vulnerable to being ambushed because of higher visibility, thus better predator detection (Valeix et al. 2009; Stabach et al. 2016). Overall, African herbivore assemblages present a diverse set of potential prey species of different vulnerability and availability for ambush predators, due to differences in prey body size, densities, and habitat preferences.

Lions preferentially hunt herbivores weighing 100–900 kg, especially blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), and African buffalo (*Syncerus caffer*) (Hayward and Kerley 2005; Owen-Smith and Mills 2008a). Lions hunt mostly at night (Fischhoff et al. 2007; Hayward and Hayward 2007; Hayward and Slotow 2009) and less often during the day (Van Orsdol 1984). Lions rely upon the cover provided by tall grass, dense woody vegetation, or gullies to ambush their prey (Funston et al. 2001; Hopcraft et al. 2005; Loarie et al. 2013; Davies et al. 2016). They may also concentrate their hunting around water sources that draw aggregations of ungulates (Davidson et al. 2012, 2013). For example, in Hwange National Park in Zimbabwe, lions spent more time searching for prey in the vicinity of waterholes by reducing their movement speed and increasing their turning angles (Valeix et al. 2010, 2011).

In west-central Kruger National Park, South Africa, where our study was located, wildebeest herds confine their movements mostly to grazing lawns, that is, short grass areas also having little woody plant cover, which encompass less than 10% of the study area, for most of the wet season and into the early dry season (Yoganand and Owen-Smith 2014; Owen-Smith and Traill 2017). Although the location of these wildebeest is highly predictable to lions, hunting success could be low because of the lack of much vegetation cover for stalking (Davidson et al. 2012; Davies et al. 2016; Martin and Owen-Smith 2016). Buffalo herds range widely, occupying the home ranges of lion prides intermittently. Zebra herds move unpredictably and are wide-ranging (Owen-Smith 2013; Owen-Smith and Martin 2015). Like buffalo and zebras, impala aggregate in large herds and are widespread but are less rewarding to lions due to their small size (Funston and Mills 2006; Owen-Smith and Mills 2008b). During the dry season, water-dependent grazers concentrate around remaining water sources, but generally schedule such visits during daytime when visibility is greatest for detecting nearby predators (Cain et al. 2012). Unlike grazing species, browsing giraffe (*Giraffa camelopardalis giraffa*) and greater kudu (*Tragelaphus strepsiceros*) occupy wooded habitats (du Toit and Owen-Smith 1989) but occur in low densities.

Despite variable prey vulnerability and availability, past study suggests that lions kill these ungulates in proportion to their densities (Martin and Owen-Smith 2016; Cain J.W., unpublished lion kill data). To investigate how lions responded to multiple prey species, primarily at night, we tracked the movements of lions and two of their primary prey species, blue wildebeest and African buffalo. We tested the following hypotheses (Fig. 1) that lions: (1) are primarily active at night; (2)

visited grazing lawns more frequently during the wet season than in the dry season; (3) tended to move toward the direction of the buffalo herd when it was present nearby; (4) spent more time near perennial water sources during the dry season; (5) spent a greater proportion of nights near riverbanks where the vegetation cover was denser than in the surrounding area; and (6) concentrated their movements in core regions of their home ranges and periodically visited outlying regions.

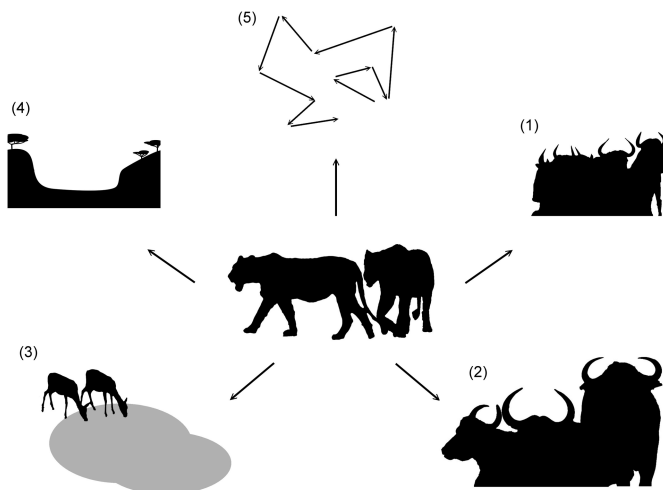
## MATERIALS AND METHODS

**Study area.**—We investigated the movements of GPS-collared animals in the west-central region of Kruger National Park, South Africa, and the adjacent Timbavati Private Nature Reserve and Manyeleti Game Reserve. We defined the extent of the study area (300 km<sup>2</sup>; 24.27°–24.32°S; 31.24°–31.33°E) by the home ranges of three study lion prides collectively (see details about lion data below).

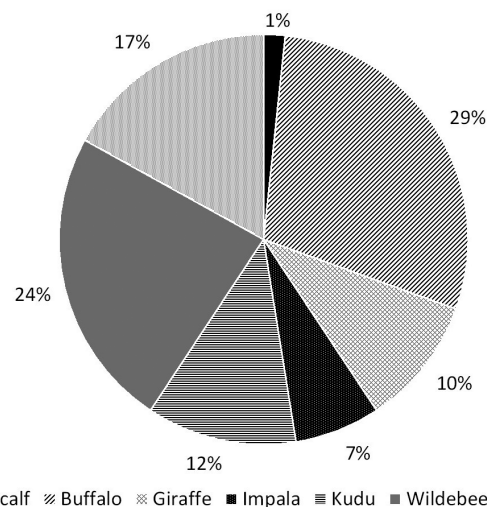
The average annual rainfall in the study area was 540 mm, of which 85% was received during the summer months from November to March (Owen-Smith and Goodall 2014). Two seasonal rivers flowed through the study area during the summer. Although most water sources dried up during the dry winter months, water was available to wildlife in artificial dams, pumped troughs, and pools in riverbeds.

Common large herbivores in the study area were blue wildebeest, plains zebra, African buffalo, giraffe, greater kudu, and impala. Among these species, buffalo constituted 29%, wildebeest 24%, and zebra 17% of the lion kills found in the study area ( $n = 59$ ; Fig. 2; Cain 2010).

**Data use and collection.**—Five lionesses, from three different prides, and two female buffalos, each from different herds, were fitted with GPS collars (Table 1) in June 2009 to November 2010. Collars were fitted by South African National Parks (SANParks) veterinary staff, following SANParks ethical guidelines.



**Fig. 1.**—Illustration of the five alternative hunting tactics of the lions that were postulated (1) lions seek wildebeests by moving to grazing lawns during nighttime, (2) lions approach buffalo herds when these herds are within their home ranges during the night, (3) lions lurk close to perennial water sources during the day in the dry seasons to ambush ungulates coming to drink, (4) lions hang out near riverbanks which provides denser woody vegetation cover from which to pounce on ungulates, (5) lions seek for prey opportunistically by systematically searching different sectors of their home ranges.



**Fig. 2.**—Proportion of prey species in lion kills ( $n = 59$ ) from June 2009 to March 2010.

**Table 1.**—Information on the pride and herd formation of lions and buffalos, and GPS data availabilities in the study area 2009–2010.

Animal ID	Number of individuals
Lion	
Western Pride	One adult male, three adult females, four subadult males, three subadult females, five juveniles
Eastern Pride	Two adult males, three adult females, 5–7 juveniles
Southern Pride	One adult male, one adult female, one subadult female, three subadult of unknown sex
Buffalo	
AG33	200–300
AG34	70–100

Two of the collared lionesses were from the Western Pride (pride size = 19), two from the Eastern Pride (pride size = 10–12), and one from Southern Pride (pride size = 6; Table 1). The time steps between GPS locations varied between 1 and 2 h during nighttime for the Western and the Eastern Pride. The fixed interval around midday was spaced further apart to extend battery life assuming that the lions were likely to be resting then. For the Western Pride, 40% and 48% of the data were recorded at 1-h and 2-h intervals, respectively. For the Eastern Pride, 71% of the data were recorded at 1-h intervals and 23% at 2-h intervals. For the Southern Pride, 96% of the data were recorded at 1-h intervals. The two collared lionesses in the Western Pride were within 250 m of each other for 81% of days and >1 km away from each other in fewer than 7% of days from June 2009 until July 2010 (408 days). We amalgamated the location data from both lionesses in the same pride during this time period to represent the pride movements by retaining only the location of the individual whose collar had the higher GPS fix success. After July 2010 until November 2010 when the two lionesses from the Western Pride remained further apart than 1 km, but still within their shared home range, their movements were considered independent (Western A and Western B; 96 days). The lionesses belonging to the Eastern Pride were within 250 m of each other in 75% of the days and >1 km apart from each other in less than 7% of the days. We thus amalgamated the location data from the two lionesses similar to the Western Pride throughout the study period to represent the pride (545 days). Data were supplied for the Southern Pride only from January 2010 until June 2010 (122 days), when the collar failed. Through the strategic deployment of the five collars, our data set documented almost the complete movements of all of the lion prides inhabiting our 300-km<sup>2</sup> study area on frequently an hourly resolution throughout the day and night, for over a year in the case of two of the prides.

GPS locations were recorded hourly for the collared buffalo (504 days). The two female buffalos were from two separate herds, numbering around 70–100, and 200–300 animals, at the time of collaring. Buffalo herds often split up at times, meaning that there may have been further encounters between lions and buffalo that were not detected due to the absence of the collared females. The collared buffalo females moved beyond the home ranges of the lions both in the west and in the south (Supplementary Data SD1).

GPS data for the lion movements were separated into three seasons based on long-term rainfall patterns: (1) early dry season—April to July; (2) late dry season—August to November; (3) wet season—December to March (Owen-Smith

and Traill 2017). The data were further separated into daytime from 06:00 to 17:59 and nighttime from 18:00 to 05:59 from April to September, and into daytime from 05:00 to 18:59 and nighttime from 19:00 to 04:59 from October to March, based on the times of sunrise and sunset during these times of the year.

Movement data were analyzed separately for each pride and separately for the two Western Pride lionesses after July 2010 (representing one late dry season). Except where stated, data were analyzed for each season and time of the day (i.e., daytime and nighttime) separately. Results from the separated Western Pride lionesses were then amalgamated to represent the Western Pride as a whole for the late dry season. We assumed that the movement responses shown by the lions during successive nights were independent, and hence treated each night (or day) as an independent sample unit. Because the lions could display multiple hunting tactics during the course of a single night if their first hunting attempt was unsuccessful, we assumed that more than one of the hunting tactics could be employed during the same night.

**Hypothesis 1.**—We predicted that the average distance moved by the lions during nighttime was greater than during daytime for all seasons. We calculated the summed distance moved by the lions for each day and night, averaged by season, and tested the effects of season and time of the day on the distance using one-way ANOVA and Bonferroni post hoc *t*-tests. To look for distinctions in hourly movements, we calculated the daily distribution of step displacements, using independent mixture models (IMMs) with gamma distributions following Owen-Smith et al. (2012) and Goodall et al. (2017). We fitted the model with maximum likelihood using Excel Solver, which provided parameter values and their proportional contributions to the gamma distributions. We fitted models with three and four activity states, respectively, and ranked the models based on Akaike information criterion (AIC) values. We classified lion activities into three or four distinct states because models with more than four activity states would be difficult to interpret biologically. Using the model outputs, we calculated the likely proportions of time the animals spent in the different activity states at each hourly interval over 24-h interval, derived from the probabilities of the animals being in each state, during the entire study period.

**Hypothesis 2.**—We expected that the lions spend more nights in grazing lawns during the wet season compared to the dry season, and proportionally more nights compared with the availability of grazing lawns within their home ranges. We first estimated the seasonal home ranges of the lions using kernel density estimation with bandwidth calculated using the least



squares cross-validation method in the Geospatial Modeling Environment V0.7.4.0 (Beyer 2015). We constructed the 50% and 90% isopleths from the kernel densities to represent the core use area and effective home range of the lions, respectively (Lehmann et al. 2008), and mapped them in ArcGIS 10.3.

Building on previous findings of the concentrated use of grazing lawns by 10 wildebeest herds fitted with GPS collars (Yoganand and Owen-Smith 2014; Owen-Smith and Traill 2017), we investigated the proportion of nights, frequencies, and duration of visits to grazing lawns by lions. We merged pixels classified as sodic-lawns (open grassland with short grasses on granite) and gabbro-lawns (open grassland with short grasses on gabbro uplands) that were within 250 m of each other into cohesive grazing lawns using the habitat map created by Yoganand and Owen-Smith (2014), adopting the 250-m radius used by Martin et al. (2015). We then identified lion locations that were situated within grazing lawns and calculated the number and proportions of nights when the lions were present in the lawns for all periods. We calculated the proportional availabilities of grazing lawns within 90% home ranges of the lion prides by dividing the areas of lawns within home ranges by the areas of the home ranges. To establish whether lions visited grazing lawns seasonally, we used a log-linear model with binomial distribution to test the effect of seasons on the proportion of nights at lawns. We constructed the models using season as the independent variable, and presence or absence of a lion as the dependent variable. We then used the Pearson's chi-squared test to test the differences between observed number of nights when lions visited lawns and the expected numbers (calculated by multiplying the total number of nights by proportional availabilities). To understand revisitation patterns by lions to the grazing lawns, we further investigated the frequencies and durations of visits to the lawns. We defined the minimum revisitation interval as 24 h (i.e., locations in lawns within the same night were considered the same visit). We calculated the number of days between each visit and duration of stay in the lawns during each visit, and then tested the effect of season using one-way ANOVA and Bonferroni post hoc *t*-tests.

**Hypothesis 3.**—We expected the lions to move toward the direction of the buffalo herd when the herd became within 2-km radius of the lions during the night, and accordingly lessen the distance between them and the herd in consecutive time steps. We identified and calculated the number and proportion of nights when buffalos were within the home range of each lion pride. We then extracted the locations of the buffalos within the home ranges and calculated the distances between the lions and buffalos using their simultaneous locations during nighttime. Following Martin and Owen-Smith (2016), we identified two measures of encounters: (1) probable encounter, when the distance apart was <1 km, and (2) possible encounter, when the distance was 1–2 km, assuming that the lions might detect the scent and sounds of the large herds of buffalos further than 1 km away. We defined encounters based on the first lion–buffalo location pair that fell within 2 km during each night, with only one encounter defined for the same buffalo herd per night. The number of nights that had resulted in an encounter was calculated separately for each pride. We compared the number of

nights in which an encounter occurred to that when encounters did not occur, when the buffalos were within the home ranges of the lions, by fitting intercept-only log-linear models with binomial distribution. The direction (in azimuth) of the buffalos from the lions at the time of each encounter (*t*) was calculated and compared to the direction of movement by lions from time *t* to time *t* + 1. If the latter fell between –90 and +90 degrees of the direction of the former, we defined the lion response as moving toward the buffalos (see [Supplementary Data SD1](#) for an example). The frequencies of encounters resulting in lions moving toward the buffalos were then calculated and compared to the frequencies of lions moving away from the buffalos using log-linear models with binomial distribution. An intercept-only model was built using the frequencies of moving away and toward buffalos as the dependent variable. We combined the frequencies of probable and possible encounter in the models because of small sample sizes ([Supplementary Data SD1](#)). For those encounters in which lions moved toward the buffalos, we further calculated and compared the distance between the lions and buffalos at time *t* to that between the lions at time *t* + 1 and the buffalos at time *t*.

**Hypothesis 4.**—We predicted that the lions spend proportionately more time, both nighttime and daytime, within 100 m of perennial water sources during the dry season compared with the proportional availability of such localities within their home ranges, with this response being stronger during daytime when herbivores are more likely to come to drink. We calculated the number of days and nights when any of the lion locations was within 100 m from a water source. To define the availability of water sources, we calculated the percentage of the lion home ranges that were within 100 m of the water sources. Log-linear models with binomial distributions were then applied to test the interactions between seasons and time of the day on lion presence in relation to water source. The models were built using the frequencies of the lions being within versus further than 100 m of water as the dependent variables and the seasons and time of the day as independent variables.

**Hypothesis 5.**—We predicted that the lions spend a greater proportion of nights within 100 m of riverbanks, where the vegetation cover was denser, compared to the proportional availability of such localities within their home ranges, year-round. We calculated the number of nights when any of the locations were within 100 m from the riverbanks and used log-linear models with binomial distributions to test the effect of seasons on lion presence in relation to riverbanks during nighttime. In the model, the frequencies of the lions being either within or further than 100 m from the riverbanks were used as dependent variables, and season as independent variable. We also used the Pearson's chi-squared test to test the differences between observed frequencies of presence within 100 m of riverbanks and the expected frequencies (i.e., the proportion of the lion home range that was within 100 m of the riverbank).

**Hypothesis 6.**—We expected that, while the lions spend most of their nights within the core area of their home ranges, they ventured into the outlying regions at regular time intervals and spent similar number of nights among different sectors systematically. We divided the home ranges of each lion pride over the

entire study period into five sectors: the core (50%) area, and the northeast, southeast, southwest, and northwest sectors obtained from dividing the noncore home range by an axis running from north to south and another from east to west (Supplementary Data SD1). We calculated the revisitation intervals, defined as the number of days between each visit, and duration of visits to each home range sector by the lions, averaged by season.

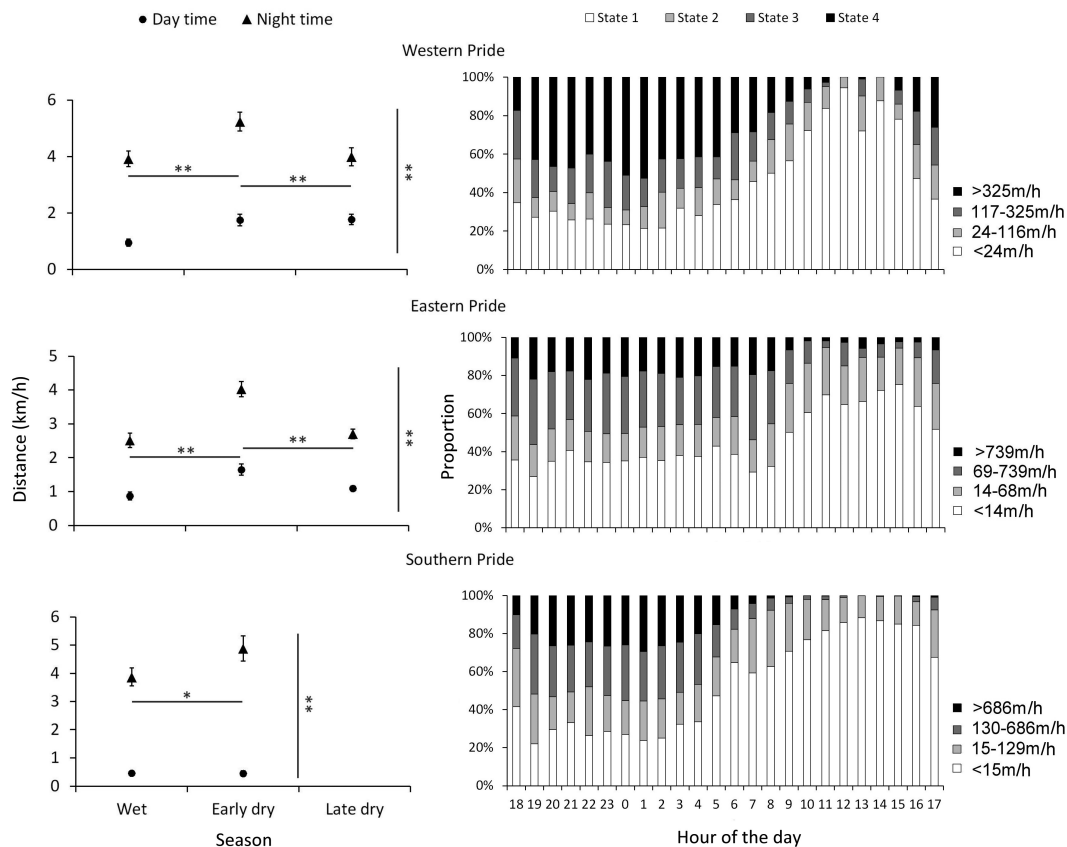
## RESULTS

**Hypothesis 1.**—Lions moved longer distances during nighttime (range: 3.5–5 km per night) compared to day time (range: 1–1.5 km per day), with an increase in distances moved from wet season to early dry season during nighttime (Fig. 3; Western Pride:  $F_{2,398} = 11.57$ ,  $P < 0.001$ ; Eastern Pride:  $F_{2,525} = 18.82$ ,  $P < 0.001$ ; Southern Pride:  $t_{104} = -1.83$ ,  $P < 0.05$ ). The IMMs with four movement states had lower AIC values and explained the movement patterns of lions better than the models with three states (Table 2). The range of movement rates suggests four underlying movement states of lions: (1) stationary, when lions were presumably resting; (2) slow movement, perhaps between resting sites or while socializing; (3) intermediate movement, presumably while searching for or stalking prey; and (4) longer movements indicating persistent travel (Table 2). Activity states distribution was calculated using the four-state model as it had a lower AIC value than the three-state model. The lions spent

more than 40% of time in state 3 (>69 m/h) and state 4 (>300 m/h) during nighttime between 18:00 and 06:00, but less than 20% of time on these states during daytime between 09:00 and 16:00 (Fig. 3). In fact, they spent as much as 90% of time being stationary in state 1 (<30 m/h) during daylight hours (Fig. 3).

**Hypothesis 2.**—The core ranges of the Western Pride and Eastern Pride encompassed more grazing lawn habitat than that of the Southern Pride (Fig. 4). All prides had one stretch of river channel within their core ranges except for the Western Pride during the early dry season. The number of perennial water sources within the Western Pride home range changed from 11 in the wet season to 14 in the early dry season and 12 in the late dry season. Although the two lionesses of the Western Pride had separated during the late dry season of 2010, their home ranges remained within the total home range of the pride established before separation.

The Western Pride lionesses visited grazing lawns on as many as 60% of nights and the Eastern Pride lionesses around 80% of nights during the wet season, which in both cases was significantly higher than in the dry seasons (Table 3 and Supplementary Data SD2). The occupation of grazing lawns by the lionesses at night decreased with the progression from wet to late dry season for all lion prides (Supplementary Data SD2). The lionesses spent a vastly greater proportion of their time within the grazing lawn areas at night than expected from the proportional availabilities of the lawns in all seasons



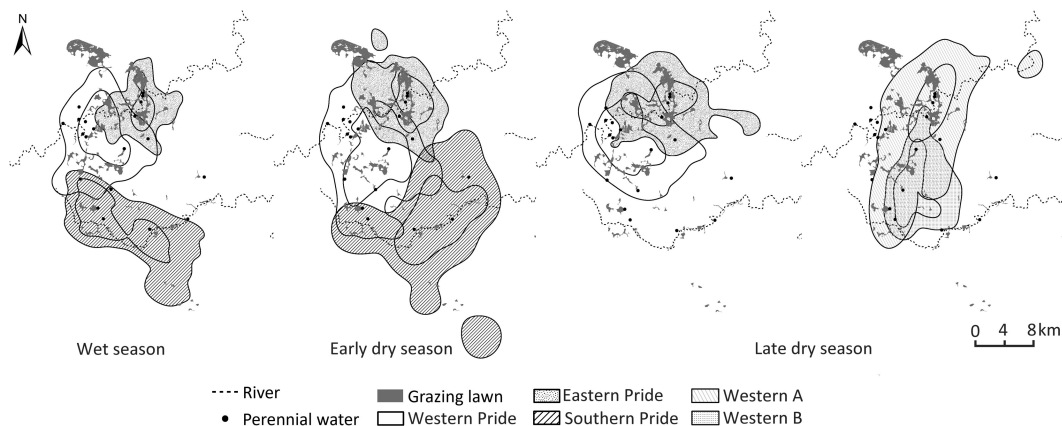
**Fig. 3.**—Left: Summed hourly distance moved by lions in the study area during day time and nighttime distinguished by season (mean  $\pm$  standard error). Asterisks indicate results of post hoc test (\* $P < 0.05$ , \*\* $P < 0.001$ ). Right: Year-round daily movement activities derived from four-state independent mixture models with gamma distribution of the lions.

**Table 2.**—Akaike information criterion (AIC) values of three-state and four-state independent mixture models with gamma distribution fitted to hourly movement rates of lions, and the range of movement rates (m/h) identified from the cross-over points between the gamma distributions of each predominant activity states of the four-states models.

Lion ID	Three states	Four states	ΔAIC
Western Pride	−2084.40	−2088.35	3.95
Eastern Pride	−10762.47	−10924.14	161.67
Southern Pride	−7559.80	−7565.22	5.42

Range of movement	State 1	State 2	State 3	State 4
Western Pride	<24	24–116	117–325	>325
Eastern Pride	<14	14–68	69–739	>739
Southern Pride	<15	15–129	130–686	>686



**Fig. 4.**—Home ranges of all lion prides, defined using kernel density estimation. Inner and outer boundaries represent 50% and 90% isopleths, respectively.

([Supplementary Data SD2](#); Western Pride:  $\chi^2_2 = 1,843.34$ ,  $P < 0.001$ ; Eastern Pride:  $\chi^2_2 = 911.28$ ,  $P < 0.001$ ; Southern Pride:  $\chi^2_1 = 4,348.14$ ,  $P < 0.001$ ). The collared lionesses visited a grazing lawn almost every other night during the wet season and an increase in revisitation intervals was observed for the Western and Eastern Pride from wet season to early dry season ([Table 4](#); Western Pride:  $F_{2,206} = 5.83$ ,  $P < 0.01$ ; Eastern Pride:  $F_{2,300} = 4.19$ ,  $P < 0.05$ ). The durations of stay at the lawns were similar except that the Eastern Pride had a small increase from 1.5 to 2 h in time spent from wet and early dry season to late dry season ([Table 4](#);  $F_{2,310} = 8.54$ ,  $P < 0.001$ ).

**Hypothesis 3.**—The frequencies of nights when collared buffalos were located within lion home ranges varied between prides and seasons ([Table 5](#)). However, the probability of occurrence of encounters was high for all prides when the buffalos were located within the lion home ranges ([Table 3](#)). The proportion of nights with encounters was highest for the Western Pride (>15% for all seasons) and the lowest for the Eastern Pride (<10% for all seasons). We identified a total of 34 probable encounters (average distance apart 700 m for 1-h time steps and 622 m for 2-h time steps), and 107 potential encounters (average distance 1,339 m for 1-h time steps and 1,260 m for 2-h time steps), for all of the lion prides ([Table 5](#)). The lions moved toward the direction of the buffalos for over 60% of the encounters, when we considered all of the lions together. Over 65% of the cases in which lions moved toward buffalos resulted

in a reduction in proximity between both ([Supplementary Data SD2](#) and [Table 3](#)). When individual prides were considered, the high tendency of moving toward buffalo (>50% of encounters) was supported statistically only for the Western Pride and Southern Pride ([Supplementary Data SD2](#)).

**Hypothesis 4.**—The availabilities of areas within 100 m of water were below 5% within all lion home ranges, with the proportions of days and nights when the lions were present within 100 m of the perennial water sources stayed below 10% across seasons and times of the day ([Supplementary Data SD2](#) and [Table 3](#)).

**Hypothesis 5.**—The availabilities of riverbanks were also below 10% across seasons for all lions. The frequencies of nights when lions were present within 100 m of riverbanks were similar between seasons ([Supplementary Data SD2](#) and [Table 3](#)). The utilization proportion was below 30% of nights for all lion prides, but higher than what was available (Western Pride:  $\chi^2_1 = 104.41$ ,  $P < 0.001$ ; Eastern Pride:  $\chi^2_1 = 9.06$ ,  $P = 0.011$ ) except for the Southern Pride ( $\chi^2_1 = 0.92$ ,  $P = 0.338$ ; [Supplementary Data SD2](#)).

**Hypothesis 6.**—Lions revisited an outlying sector every other night, but generally remained within that sector for only a single night ([Supplementary Data SD2](#)). Lions remained within their core ranges on as much as 87% of nights ([Table 6](#)), that is, they centered their movements within the core area but visited a different outlying region every other night.

**Table 3.**—Log-linear model results for the frequencies of presence of lions in relation to grazing lawns, buffalos, perennial water sources, and riverbanks.

	Coefficient	Standard error	z-value	P-value
A. Presence at grazing lawns during nighttime (ref. level: wet season)				
Western Pride				
Early dry season	−0.323	0.187	−1.733	0.083
Late dry season	−0.830	0.225	−3.685	<0.001
Eastern Pride				
Early dry season	−0.679	0.191	−3.563	<0.001
Late dry season	−1.039	0.195	−5.332	<0.001
Southern Pride				
Early dry season	−1.314	0.273	−4.816	<0.001
B. Frequencies of encounters when buffalos were within home ranges during nighttime				
Western Pride	−1.126	0.137	−8.248	<0.001
Eastern Pride	−2.241	0.333	−6.736	<0.001
Southern Pride	−1.649	0.345	−4.775	<0.001
C. Frequencies in moving toward buffalos when probable (<1 km) and potential (<2 km) encounters occurred during nighttime				
Western Pride	0.458	0.195	2.352	0.019
Eastern Pride	0.357	0.493	0.724	0.469
Southern Pride	1.609	0.775	2.078	0.038
D. Presence within 100 m from perennial water sources (ref. level: wet season and day time)				
Western Pride				
Early dry season	−0.613	0.773	−0.793	0.428
Late dry season	0.855	0.615	1.389	0.165
Nighttime	0.053	0.719	0.073	0.942
Early dry season x nighttime	1.215	0.982	1.238	0.216
Late dry season x nighttime	−0.027	0.879	−0.030	0.976
Eastern Pride				
Early dry season	−0.537	1.008	−0.533	0.594
Late dry season	−0.135	0.874	−0.154	0.877
Nighttime	0.573	0.924	0.619	0.536
Early dry season x nighttime	−0.527	1.366	−0.385	0.700
Late dry season x nighttime	−0.981	1.271	−0.772	0.440
Southern Pride				
Early dry season	0.573	0.931	0.615	0.539
Nighttime	−0.045	1.015	−0.044	0.965
Early dry season x nighttime	−0.360	1.378	−0.261	0.794
E. Presence within 100 m from perennial water sources during day time (ref. level: wet season)				
Western Pride				
Early dry season	−0.613	0.773	−0.793	0.428
Late dry season	0.855	0.615	1.389	0.165
Eastern Pride				
Early dry season	−0.537	1.008	−0.533	0.594
Late dry season	−0.135	0.874	−0.154	0.877
Southern Pride				
Early dry season	0.573	0.931	0.615	0.539
F. Presence within 100 m from perennial water sources during nighttime (ref. level: wet season)				
Western Pride				
Early dry season	0.602	0.605	0.996	0.319
Late dry season	0.828	0.628	1.319	0.187
Eastern Pride				
Early dry season	−1.064	0.922	−1.154	0.249
Late dry season	−1.116	0.922	−1.210	0.226
Southern Pride				
Early dry season	0.212	1.016	0.209	0.835
G. Presence within 100 m from riverbanks during nighttime				
Western Pride	−2.282	0.177	−12.86	<0.001
Eastern Pride	−2.986	0.224	−13.35	<0.001
Southern Pride	−3.689	0.585	−6.311	<0.001

## DISCUSSION

Lions were more active and moved longer distances during nighttime than during daytime in all seasons. The core home ranges of the lion prides were located where grazing lawn patches were present. Lions focused their movements strongly on the grazing lawns where they could expect to find wildebeest

herds (Yoganand and Owen-Smith 2014; Martin and Owen-Smith 2016) and occupied the lawns less frequently during the dry season when many of the wildebeest herds had moved elsewhere (Yoganand and Owen-Smith 2014). Following encounters with lions, wildebeest seemed to dodge the lions and then return to the grazing lawns after the lions moved away



**Table 4.**—The average revisitation intervals and duration of each visit to grazing lawns by the lions during nighttime (mean  $\pm$  standard deviation); different letters in square brackets represent significant differences at  $P < 0.05$  for the same pride across seasons.

Season	Wet	Early dry	Late dry
Revisitation intervals (no. of nights between visits)			
Western Pride	1.53 $\pm$ 0.91 [a]	1.89 $\pm$ 1.54 [b]	2.57 $\pm$ 2.54 [b]
Eastern Pride	2.99 $\pm$ 1.80 [a]	3.95 $\pm$ 3.05 [b]	2.64 $\pm$ 2.27 [a]
Southern Pride	2.16 $\pm$ 2.61 [a]	2.33 $\pm$ 2.13 [a]	
Duration of visits (hour)			
Western Pride	2.39 $\pm$ 2.02 [a]	2.41 $\pm$ 2.09 [a]	2.55 $\pm$ 2.66 [a]
Eastern Pride	1.48 $\pm$ 1.88 [a]	1.48 $\pm$ 1.15 [a]	2.04 $\pm$ 1.78 [b]
Southern Pride	2.03 $\pm$ 1.53 [a]	2.48 $\pm$ 2.01 [a]	

**Table 5.**—Number of nights when buffalos were within the home ranges (HR) of the lions and when either probable encounter (<1 km proximities) or potential encounter (<2 km proximities) had occurred.

	Wet		Early dry		Late dry	
	Within HR	Encounter	Within HR	Encounter	Within HR	Encounter
Western Pride	86	38	112	45	92	14
Western A					13	1
Western B					26	7
Eastern Pride	30	2	28	5	46	10
Southern Pride	46	6	16	6		

**Table 6.**—Percentage of nights in visiting the core home range and more than one home range areas by the lions.

	Core	>1 area
Western Pride		
Wet	0.80	0.39
Early dry	0.69	0.52
Late dry	0.66	0.40
Eastern Pride		
Wet	0.86	0.31
Early dry	0.69	0.48
Late dry	0.70	0.41
Southern Pride		
Wet	0.87	0.35
Early dry	0.64	0.36

indicating unsuccessful capture attempts (Martin and Owen-Smith 2016). During the dry season when wildebeest herds were absent from the lawns, the lions still had opportunities to capture impala or zebra, which also seem to concentrate in the open lawn habitat during nighttime (Burkpile et al. 2013).

The Western Pride encountered herds containing collared buffalo more frequently than the Eastern and Southern Prides, because the home ranges of the two buffalo herds were located toward the west. As we postulated, the lions did orientate their movements toward buffalo herds when these buffalos entered their home ranges. However, when we considered only the Western Pride, which has the largest sample size of encounters, the lions seemed to approach the buffalo only following possible encounters within 2 km, while approaches were less consistently in the direction of the buffalo herd for probable encounters within 1 km. This could be explained if the buffalos were also responding to the lions by moving away from the lions. Encounters within 1 km thus probably involved interactive changes in the directions of movement of the lions and the buffalos.

The core areas of lion home ranges encompassed the courses of seasonal rivers and collared lion prides did concentrate near

riverbanks at night while presumably hunting. Lions made more kills close to rivers than expected from a random distribution in Klaserie Private Nature Reserve (de Boer et al. 2010), which is close to our study area. This was explained by the concentration of water-dependent prey around the rivers (de Boer et al. 2010). Similar to observations in Serengeti National Park, our collared lionesses selectively tended to favor river embankments providing greater concealment for ambushing opportunities (Kittle et al. 2016). While zebra tend to avoid denser vegetation, kudu and giraffe may be drawn to the greater availability of browse along water courses in Kruger National Park (Smit et al. 2007).

Contrary to observations in Hwange and Serengeti national parks (Hopcraft et al. 2005; Valeix et al. 2010; Davidson et al. 2012), lions in our study area did not spend much time around perennial water sources drawing high prey concentrations. This is probably because perennial water sources were numerous and widely distributed within our study area, with 20 water sources present within 300 km<sup>2</sup> in comparison to about 55 waterholes in 15,000 km<sup>2</sup> in the Hwange National Park (Valeix et al. 2010). Prey distribution was therefore unlikely to be concentrated around any particular waterhole during the dry season, reducing the expected value of a sit and wait tactic in our study area.

Because wildebeest remained mostly within open habitat patches offering little cover for stalking lions, and buffalos were only intermittently encountered, lions needed to search opportunistically for zebra or other large herbivores on most nights. The mobile zebra herds incurred encounters with lions almost as frequently as the sedentary wildebeests, but reacted more strongly than wildebeest by moving away from vicinity of the encounter more frequently (Martin and Owen-Smith 2016). Lions visited an outlying sector of their home ranges every night and seldom stayed in the same outlying region for more than one night, thereby allowing time for disturbed zebra or other potential prey to return. Lions in the Hwange National Park moved at least 5 km away from kill sites within 2 days and revisited the same area only after 25 days (Valeix et al. 2011).



To conclude, lions showed variable movement behavior while hunting to accommodate spatial distinctions in the availability of various prey species. While they did tend to focus their movements on the places where wildebeest, typically their most favored prey, were located, on most nights, they moved more widely seeking opportunistic encounters with other large herbivore species. Unlike the Hwange lions (Valeix et al. 2010; Davidson et al. 2012), they did not concentrate their hunting near waterholes in our circumstances where water sources were widely available to water-dependent herbivores. They generally hunted actively rather than lurking in ambush in places providing cover. Thus, the three lion prides employed a diversity of movements to accommodate the differing availability and vulnerability of the prey species that they hunted.

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### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Locations of the collared buffalos in the study area, and examples showing how the direction and distance of movement of lions were calculated after encountering a buffalo herds, and how a lion home range was divided into five different sectors.

**Supplementary Data SD2.**—Lion movement in relation to grazing lawn, perennial water sources, and riverbanks, and results of lion–buffalo analyses.

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