

## Spatiotemporal patterns of lion space use in a human-dominated landscape



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### ARTICLE INFO

#### Article history:

Received 22 June 2014

Initial acceptance 4 August 2014

Final acceptance 7 November 2014

Published online

MS. number: 14-00512R

#### Keywords:

behaviour  
coexistence  
fear  
foraging  
humans  
lions  
movement

The African lion, *Panthera leo*, is threatened throughout much of its remaining range by human impacts such as loss of prey, habitat fragmentation and direct human-caused mortality, often in response to livestock predation. Lions' ability to adjust their behaviour to reduce direct contact with humans may affect their survival. We used fine-scale GPS data to measure lions' response to humans at two scales: between land use types (commercial ranches versus pastoral lands) and with proximity to human-occupied locations (i.e. livestock enclosures: 'bomas') within commercial ranch land. Study lions on commercial ranches reacted to the location and activity levels of humans on the local scale, showing no overall spatial avoidance but fine-scale temporal partitioning in their use of areas in close proximity to bomas, being closest at times when human activity was lowest (i.e. between 2300 and 0500 hours). At the land use scale, however, lions showed significant (but not total) spatial avoidance of pastoral land, despite similar prey densities and habitat structure on both land use types, indicating that lions' ability to utilize pastoral land was limited by pastoral people. When lions did utilize pastoral land, they were more likely to do so during the dark hours, when people were confined to bomas, than during the daylight hours. Lions moved faster and straighter in pastoral lands and when close to bomas, indicating that they adjust 'how' they move in response to humans. They were found closer to bomas with increasing rainfall and decreasing moonlight. Overall, lion movements suggested an ability to partition their activities spatiotemporally with those of humans such that risk of human-caused mortality was minimized while use of a human-dominated landscape was maximized.

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Persecution by humans as a result of livestock predation is a major cause of mortality among large carnivores and may threaten the viability of many populations (Macdonald & Willis, 2013; Woodroffe, 2000). Variations in human densities, distribution, land use, behaviours and attitudes towards conservation in general, and carnivores in particular, create spatial variation in the likelihood of human-caused mortality. The resultant complex peaks and troughs of spatiotemporal variation in human-caused mortality risk in which large carnivores exist is here referred to as the 'Landscape of Coexistence', and is similar to the 'Landscape of Fear' experienced by prey under threat of predation (Laundré, Hernández, & Altendorf, 2001). Large carnivores sharing the landscape with people may thus attempt to trade off activities that enhance their fitness, such as foraging near humans, against risk of human-

caused mortality, ultimately resulting in a variety of heterogeneously distributed behavioural responses of large carnivores to the threat posed by people.

In this context, studies have predominantly focused on spatial avoidance of people by large carnivores (Boydston, Kapheim, Watts, Szykman, & Holekamp, 2003; Mattson, 1990; Schuette, Creel, & Christianson, 2013; Schuette, Wagner, Wagner, & Creel, 2013; Van Dyke et al., 1986). A carnivore's response to people, however, may not be as simple as straightforward avoidance of human-occupied areas (Kolowski & Holekamp, 2009). Such areas may contain valuable resources (e.g. livestock) or access to a limited resource (e.g. dry season water sources; Schuette, Creel, et al., 2013) such that complete avoidance would result in substantial foraging costs. Hence, large carnivores in Landscapes of Coexistence may use such human-occupied areas and behave adaptively by following strategies that optimize resource acquisition while minimizing contact with people, and hence the risk of human-caused mortality (Macdonald, Loveridge, & Rabinowitz, 2010).

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Behavioural responses to predation risk shown by herbivores and mesocarnivores suggest temporal partitioning of habitats and resources can be a strategy to reduce predation risk (Durant, 1998; Harrington et al., 2009; Kronfeld-Schor & Dayan, 2003; Linnell & Strand, 2000; Valeix et al., 2009). Large carnivores can become more nocturnal in human-occupied areas (e.g. all carnivores: Frank & Woodroffe, 2001; mountain lions, *Felis concolor*: Van Dyke et al., 1986; spotted hyaena, *Crocuta crocuta*: Boydston et al., 2003; Holekamp & Dloniak, 2010; African wild dog, *Lycaon pictus*: Rasmussen & Macdonald, 2012; tiger, *Panthera tigris*: Carter, Shrestha, Karki, Babu Pradhan, & Liu, 2012). Responding to human activity levels, rather than just their physical location through spatiotemporal avoidance, may 'fine-tune' a large carnivore's avoidance of people to allow use of human-occupied areas at times when risk of detection is lowest.

Additionally, the spatiotemporal partitioning of activities across Landscapes of Coexistence may allow carnivores to utilize areas in closer proximity to people in ways that reduce their risk of detection. Foraging, for example, may be associated with a higher risk of detection by people than moving quickly through an area (see Douglas-Hamilton, Krink, & Volrath, 2005; Graham, Douglas-Hamilton, Adams, & Lee, 2009; Wall, Wittemyer, Klinkenberg, LeMay, & Douglas-Hamilton, 2013 for examples in African elephant, *Loxodonta africana*). Carnivores may, therefore, be expected to take straighter, faster movement paths in human-occupied areas (Dickson, Jennes, & Beier, 2005; Elliot, Cushman, Macdonald, & Loveridge, 2014). The characteristics of an animal's movement path can reveal where, for how long and also 'how' an animal spends its time (Valeix et al., 2010). Movement parameters may thus allow measurement of changes in an animal's behaviour in response to people and livestock (e.g. Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012). Finally, environmental variables that affect success at hunting wild prey, such as light levels and rainfall, which in turn affect visibility, vegetation cover, prey densities and vigour (Funston, Mills, & Biggs, 2001; Packer, Swanson, Ikanda, & Kushnir, 2011; Patterson, Kasiki, Selempo, & Kays, 2004; Van Orsdol, 1984) may affect the trade-off between the costs and benefits of killing livestock for large carnivores, thus limiting their spatiotemporal avoidance of people and livestock (see Theuerkauf, 2009).

The African lion, *Panthera leo*, is particularly vulnerable to direct persecution by people and is often the first large carnivore species to be eradicated when living alongside people and livestock (Woodroffe, 2001). Lions are, therefore, a revealing model for testing whether behaviour is adjusted as a result of human-caused mortality risk. We expect behavioural adjustment particularly among breeding female groups (prides; see Whitman, 2006), as they exhibit the strongest behavioural responses to predation risk in other species (e.g. Caro, 1987; Childress & Lung, 2003; Liley & Creel, 2007; Pangle & Holekamp, 2010a, 2010b). The spatiotemporal scales at which lions respond to the presence of people may determine the extent and cost of behavioural adjustments. In this study, we used movement data derived from GPS radiocollar data to compare the spatiotemporal behaviour of lions at two scales in the study area: a landscape scale response to land use and a local-scale response to actual locations of people and livestock. In particular, we predicted that lions should behave similarly to less dominant carnivores in response to predation threat by larger carnivores (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013) and respond to human activity by avoiding areas with high risk of human-caused mortality at times when risk of detection by people is high but utilizing these areas during periods when risk of detection is low. Movement parameters were also analysed at the two scales to test the prediction that lions would move faster and straighter in areas where the risk of human-caused mortality is

high. Finally, we predicted that lions' behavioural adjustments in response to people and livestock should be influenced by environmental conditions that affect their hunting success of wild prey and detection by people (Funston et al. 2001; Patterson et al. 2004; Schaller, 1972; Van Orsdol, 1984; Woodroffe & Frank, 2005). We thus explored the influence of rainfall and moonlight levels on spatiotemporal variations in the behaviour of lions in a human-dominated landscape.

## METHODS

### Study Site

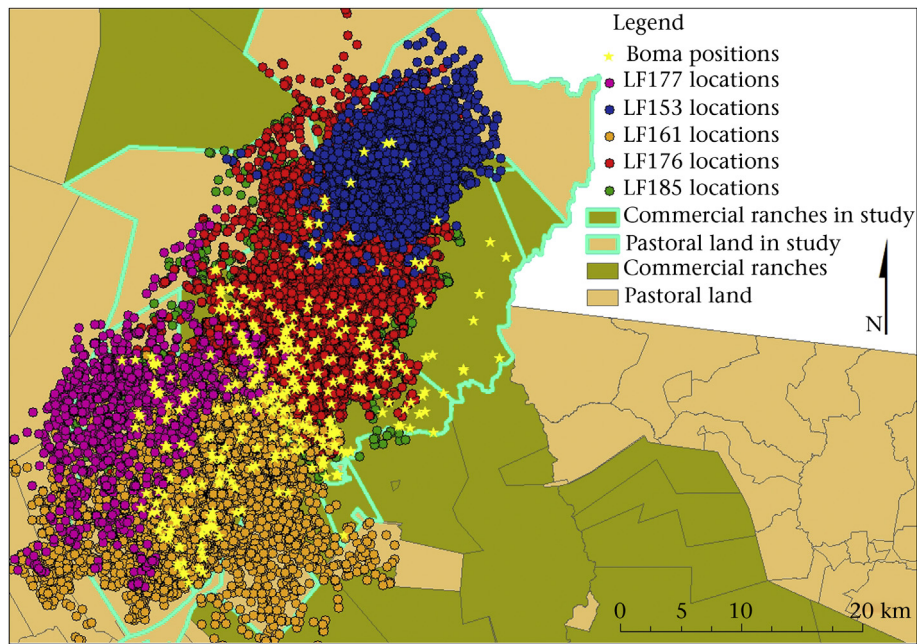
This study was carried out in Laikipia County, Kenya. The area comprises a mosaic of different land use types and is a place where people, livestock, wild ungulates and all the local large carnivore species share the landscape (Georgiadis, Nasser Olweroa, Ojwang', & Románach, 2007; Woodroffe & Frank, 2005). We selected a 2800 km<sup>2</sup> area in the north of the study area which included two land use types, livestock being the main source of income for both: (1) commercial ranches and (2) pastoral land. We selected pastoral areas where population densities of wild prey, and habitat structure, were similar to those on the privately owned commercial ranches with which we made comparisons, based on long-term aerial census data (Georgiadis et al., 2007). Both commercial ranchers and pastoralists used traditional livestock husbandry techniques: livestock was herded into bomas (i.e. livestock enclosures) at night for protection against thieves and large carnivores, and moved out to graze by day, guarded by herders (Frank, 2011; Ogada, Woodroffe, Ouge, & Frank, 2003; Woodroffe, Frank, Lindsey, Ole Ranah, & Románach, 2006). In recent years, boma construction on commercial ranches has advanced from the traditional thorn walls to include some stronger materials such as metal and stone. Additionally, only adult herders accompany livestock during the day on commercial ranches, whereas children are sometimes used to guard grazing livestock on pastoral land (Woodroffe et al. 2006). These differences in livestock husbandry standards, coupled with higher densities of livestock and people on the pastoral lands (Georgiadis et al., 2007), results in a higher potential for human–lion conflict over livestock predation where lions exist on pastoral land, although a lack of reporting in pastoral parts of the study area meant an actual comparison of human–lion conflict levels on the different land use types was not meaningful.

While there is no legal (trophy) hunting of lions in the study area, lions regularly attack livestock, and are killed by people in response, on both land use types (Frank, 2011; Ogada et al., 2003; Woodroffe & Frank, 2005). A 19.4% mortality rate for collared lions in the study area was recorded between 1998 and 2004, with 17 of 18 deaths of collared lions due to retaliatory killing by humans after predation on livestock (Woodroffe & Frank, 2005). During our study period (2009–2012), 17 collared lions were known to be killed by people, while two collared lions died of other causes. People, therefore, represent the main mortality risk to adult lions in the study area.

### Data Collection

#### Lion movements

Five female lions from different prides using both land use types in the study area (Fig. 1) were equipped with a GPS Plus radiocollar (Vectronics Aerospace GmbH). Collared lions were all multiparous females that were members of a pride. We acknowledge that the sample size used in this study was small. Studies on pinnacle carnivores such as lions often suffer from small sample sizes as these species normally occur in low densities. This was further



**Figure 1.** Map showing the two land use types making up the study area (highlighted in blue) and all lion and boma locations collected during the study period. Lion (LF) locations represent the movements of five different pride females, each female being a member of a different pride and using both land use types. Boma movements were only collected on commercial ranches within the core study area and so analyses using the variable 'distance to nearest boma' excluded lion locations falling on pastoral land or on commercial ranch land outside of the core study area. There were no hard boundaries (e.g. fences, busy roads or rivers) between any of the properties in the core study area during the study period.

exacerbated by the fact that this study was carried out in a human-dominated rangeland, where conflict with humans means even lower densities than found in protected areas. As lions form cohesive groups, which often move together (Schaller, 1972), only one individual from each pride was collared to avoid pseudoreplication. Robust statistical analyses were used in order to minimize the chance of any type 1 error. Approval for capture and collaring was received from the Kenya Wildlife Services and research authorization given by the Kenyan National Council for Science and Technology (Ref: NCST/5/002/R/334/4). All capture and animal care followed University of California Animal Care and Use Protocol R191 using methodology described by Frank, Simpson, and Woodroffe (2003). A Dan-inject CO<sub>2</sub> rifle system (Dan-inject RSA, Skukuza, South Africa) was used to dart lions from a car parked at a distance of 10–30 m with a 2 ml dart containing ketamine (NMDA receptor antagonist; dosage: 0.2 mg/kg) and medetomidine (alpha 2 adrenergic agonist; dosage 0.03 mg/kg), administered by intra-muscular injection (shoulder or rump). The darting and administration of drugs was done by A.O.C., who has been trained and qualified in the chemical and physical capture and restraint of wild animals by the Zimbabwe Veterinary Association Wildlife Group, under supervision from the Kenya Wildlife Service's veterinary department. No short-term or long-term adverse effects from the drug combination used were recorded (the following aspects were monitored: breathing rate, heart rate, skeletal muscle movement or spasms, excessive salivation and signs of hallucinogenic effects, i.e. self-harming or other odd behaviour during the induction or recovery phases), nor have there been any adverse effects reported in the literature. Animals were under complete chemical anaesthesia during the marking and handling process and stimuli/stress was minimized by covering the eyes and ears during handling. An injectable long-acting, broad-spectrum antibiotic was administered and topical antibiotic spray used to make sure no infection was introduced by the dart. Ketamine was metabolized and the medetomidine reversed using atipamezole (alpha 2 adrenergic antagonist; dosage 0.17 mg/kg) when signs of increased

responsiveness in the lion were observed (after approximately 1 h). The lion was then observed until able to walk without difficulty and rejoined other pride members. The main purpose for any immobilization carried out for this study was to fit the GPS or VHF collar. All collars used weighed <1% of the animal's body weight, and were removed at the end of the study, or when the batteries went flat or collars malfunctioned. All study animals were monitored regularly to ensure correct fitment and condition of collars. No lion was ever seen to show any sign of noticing that they were wearing a collar, and never attempted to remove the collar during observation. No loss of condition was observed in any collared animals during the study period. On removal of collars, no signs of neck damage (not even minor abrasions or significant hair loss) were observed.

GPS data were downloaded by UHF link at regular intervals between 2009 and 2012; the mean data collection period per female was 26 months, range 4.5–50 months. GPS collars recorded hourly fixes between 1800 and 0700 hours plus one midday fix. Data were cleaned before storage in preparation for analysis; spurious GPS fixes were identified and removed from the data set by initially mapping the hourly locations and deleting any that fell outside of the study area. A second level of filtering erroneous fixes was achieved by attributing a speed value to each location, and setting parameters for a biologically reasonable maximum travel speed for a lion (in this case we used 10 km/h). Any locations with a speed value above that threshold were discarded. All spatial data were imported into ArcMap (ESRI, Redlands, CA, U.S.A.) and projected to the Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37° N). Hawth's tools for ESRI ArcMap 9.2 (Beyer, 2004) were used to extract travel speed and turn angle for each lion location. Lion locations on pastoral land, where boma movements were not recorded, were excluded from the analyses including the variable 'distance to nearest boma'.

'Clusters' in the lion GPS data, i.e. two or more consecutive locations falling within a 50 m radius of each other, were located using an algorithm adapted from the Warren–Cougar algorithm (Knopff, Knopff, Warren, & Boyce, 2009). Clusters might represent



sites where the lions either rested or made a kill, and are referred to collectively as 'stop sites'. The time spent at a stop site is referred to as the 'stop duration'.

#### *Human distribution and activities*

Each lion location was assigned a land use type using 'Intersect point', Hawth's Tools, in ArcGIS 9.3. The two different land use types were assessed based on a GIS layer created by the Centre for Training and Integrated Research in ASAL Development (<http://www.cetrarad.org>), showing different land use types in the study area. This GIS layer was simplified such that the different pastoral land tenure systems were combined and classed as 'pastoral land' to reflect the similar human, livestock and habitat characteristics lions would encounter in these areas. Human locations on both land use types were closely associated with livestock movements; people stay within bomas from just before sunset to shortly after sunrise (1800–0700 hours) but leave the bomas to herd cattle during the day (Frank, 2011; Ogada et al., 2003; Woodroffe et al., 2006). Boma locations were, therefore, a good proxy for human locations at night, and by day the probability of encountering humans was assumed to decline as distance to the nearest boma increased. Owing to poor reporting of lions killed by pastoral people, we did not measure the relative risk of human-caused mortality on one land use type compared to the other but we assumed it to be higher on pastoral land where people are less tolerant of loss of livestock to predators (Romañach, Lindsey, & Woodroffe, 2007). For the purpose of this study, pastoral land and areas in close proximity to bomas (<1.5 km) on commercial ranch land were classed as having high human-caused mortality risk and are termed 'high-risk areas'.

Frequent movements made by pastoral people and the use of temporary bomas exacerbated by tribal insecurity in the pastoral areas meant that the recording of boma locations was restricted to commercial ranch land. Analyses investigating lion responses to human and livestock locations (bomas) were, therefore, carried out on this one land use type. Bomas on the commercial ranches were moved to maximize grazing at intervals of 2–12 weeks, and their locations were recorded over the study period. We calculated the distance from each lion location to the nearest active boma using R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>).

Lion movement data were assigned a human activity category: (1) high activity (0800–1800 hours), when people were awake and moving about on the landscape; (2) medium activity (1900–2200 hours and 0600–0700 hours), when people were inside bomas but likely to be awake; and (3) low activity (2300–0500 hours) when people were inside bomas and likely to be asleep (personal observation).

#### *Environmental data*

Daily rainfall data were available from Mpala Research Centre meteorological station on the southern border of the study area, which was assumed to be representative of the area. Daily rainfall was averaged over monthly periods to give a mean daily rainfall value used for each month. Owing to a lack of clear seasons during the study period, we contrasted the 11 driest months (mean daily rainfall range 0–0.65 mm) and the 11 wettest months (mean daily rainfall range 2.4–7.3 mm).

A moonlight index was calculated for each lion location using the moon phase and moon rise and set times available at the NASA website <http://aa.usno.navy.mil/data/docs/MoonFraction.php>. A moonlight index corresponding to the daily moon phase (i.e. the fraction of the moon showing ranging from 0, which corresponds to new moon, to 1, which corresponds to full moon) was given to each lion GPS data point collected between moonrise and moonset. A

moonlight index of '0' was assigned to any lion GPS data point collected at night between sunset and moonrise or moonset and sunrise, thus accounting for dark periods on otherwise moonlit nights. Dark periods were defined as the nights between new moon and first quarter waxing, and last quarter waning and new moon, and hours when the moon is below the horizon on other nights. Light periods were defined as the nights between first quarter waxing and last quarter waning moon.

#### *Data Analysis*

##### *Spatiotemporal avoidance*

To assess whether lions avoided high-risk areas overall, habitat use (estimated from lion GPS locations) was compared to habitat availability (estimated from randomly sampled locations) by developing resource selection functions (RSF) to estimate the relative probability of use of high-risk areas as presented in Manly, McDonald, Thomas, McDonald, and Erickson (2002) and Johnson, Nielson, Merrill, McDonald, and Boyce (2006). This was done by using mixed-effect logistic regression models where the dependent variable was 1 (for used locations) or 0 (for available locations), explanatory variables were 'distance to nearest boma' and 'land use type' (extracted using 'Intersect point', Hawth's Tools, in ArcGIS 9.3), and 'lion identity' was a random effect. Random locations were generated with the 'Generate Random Points' option of Hawth's tools for ESRI ArcGIS 9.2 (Beyer, 2004) within the home range of the respective individuals, and habitat availability was thus represented by an equal number of random points as actual lion locations to achieve a 1:1 ratio of use versus available sites. Lion home range was calculated as a minimum convex polygon (MCP), using the extension Hawth's tools in ArcGIS 9.3. Although MCPs often overestimate space use (Douglas-Hamilton et al., 2005; Macdonald, Ball, & Hough, 1980), they are a better estimate of the total area potentially available to lions when measuring avoidance of certain areas than home range methods that exclude areas that are unused such as kernel density estimates (Graham et al., 2009). Analyses were performed with R 2.14.2 software using the function 'glmer' in the package 'lme4' (Bates et al., 2012). Serial spatiotemporal autocorrelation was minimized by randomly selecting one location per 24 h cycle (Swihart & Slade, 1985a, 1985b). Lion speed (mean 530 m/h; SD 743; range 0–4892 m/h) strongly suggests that it is very possible for study lions to be on either land use type or move the maximum distance away/towards bomas in a 24 h period. Rarefying the data in this way has proven to be highly conservative, albeit resulting in the loss of a large amount of data (McNay, Morgan, & Brunnell, 1994).

To further investigate the relative probability of use of high-risk areas under different environmental or human-related conditions, we repeated RSF analyses on subsections of the data: (1) the 11 wettest months; (2) the 11 driest months (rainfall being a proxy for seasonal changes in vegetation cover and prey body condition); (3) high human activity periods; (4) medium human activity periods; (5) low human activity periods (representing diel changes in human activity levels on the landscape); (6) moonlight index  $\geq 0.75$ ; and (7) moonlight index  $\leq 0.25$  (moonlight index being a proxy for hourly changes in visibility, e.g. Rasmussen & Macdonald, 2012). Serial spatiotemporal autocorrelation was again minimized by randomly selecting one location per 24 h cycle for each subsection of the data set (Swihart & Slade, 1985a, 1985b).

Finally, to reveal any patterns in lions' use of high-risk areas in response to diel variations in human activity, and monthly or seasonal variations in environmental conditions, regardless of whether these high-risk areas are avoided or not, we performed a covariance analysis on 'distance to nearest boma' and 'land use type' (coded 1 = pastoral land and 0 = commercial ranch) with (1) human

activity level, (2) mean daily rainfall and (3) moonlight index as explanatory variables, and 'night identity' nested in 'lion identity' as a random effect. Biologically meaningful interactions were also investigated; in this case mean daily rainfall\*moonlight index and human activity\*moonlight index. Linear mixed-effect models for the dependent variable 'distance to boma' were performed using the function 'lme' in the R package 'nlme', and generalized mixed-effect models for the dependent variable 'land use type' were performed using the function 'glmmPQL' in the R package 'MASS' (Venables & Ripley, 2002). Model selection for the dependent variable 'distance to boma' was performed using Akaike information criteria (AIC; Burnham & Anderson, 2002). Relative strength of evidence of each model was assessed using Akaike weights ( $w$ ). Model selection for the dependent variable 'land use type' was not possible as AIC values are not an output of glmmPQL models. We give  $P$  values for these models instead. As temporal serial autocorrelation affects independence of data recorded during the same night, we first assessed temporal autocorrelation functions (ACF) using the function 'acf' of the package 'MASS', and ultimately accounted for it using a first-order autoregressive covariance structure (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), allowing us to use all lion locations.

#### Movement parameters

To assess whether lions adjusted their movements in response to human and environmental factors, we looked at three movement parameters: (1) speed, measured as a factor of time and distance between consecutive locations; (2) tortuosity, measured as the turn angle between three consecutive locations; and (3) stop duration, measured as the time spent at locations where two or more consecutive locations fell within a 50 m radius of each other. We performed covariance analyses on each of these movement parameters, with (1) 'land use type' or 'distance to nearest boma', (2) mean daily rainfall, (3) moonlight index, (4) human activity period and (5) direction of lion movement i.e. towards or away from the boma (for 'distance to boma' only) as explanatory variables, and 'night identity' nested in 'lion identity' as a random effect. Speed and stop duration were both log transformed to meet normality requirements. Biologically meaningful interactions were also investigated, in this case mean daily rainfall\*moonlight index, human activity\*moonlight index and distance to boma\*direction of lion movement (only in analyses including the variable 'distance to boma'). Temporal serial autocorrelation was again accounted for using a first-order autoregressive covariance structure when needed (Zuur et al., 2009). Linear mixed-effect models for movement parameters were performed with R 2.14.2 software using the function 'lme' in the package 'nlme'. Model selection was performed using Akaike information criteria (AIC; Burnham & Anderson, 2002). Relative strength of evidence of each model was assessed using Akaike weights ( $w$ ).

## RESULTS

#### Spatiotemporal Avoidance

We recorded 403 different boma locations over a total of 34 340 boma nights (nights\*number of bomas). Throughout the study area, the number of boma locations occupied by livestock and people on any one night averaged 28 (range 25–30). Once cleaned and processed, 33 486 usable lion locations from five individuals were analysed. Study lions showed a significant avoidance of pastoral land when all data were included (i.e. the relative probability of lions using pastoral land was significantly lower than that expected from random), and this avoidance remained consistent for all subsections of the data analyses (Appendix Table A1).

Conversely, the relative probability of lions being found at different distances to bomas was no different than expected from random overall. This remained true for all subsections of the data, with the exception of during periods of low human activities, when lions had a higher relative probability of being closer to bomas than expected from random, i.e. appeared to be attracted to bomas (estimate  $\pm$  SE =  $-5.424\text{e-}05 \pm 1.640\text{e-}05$ ; Appendix Table A2).

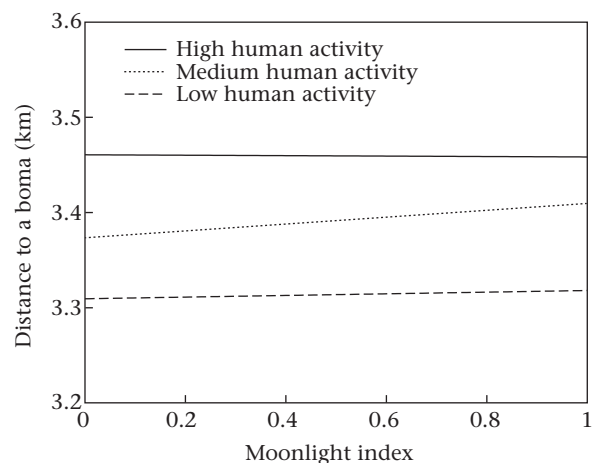
Two explanatory variables significantly affected lions' use of pastoral land; although previous RSF analysis showed pastoral land was avoided overall, when lions did use pastoral land, they did so significantly more during low and medium human activity periods (low: estimate  $\pm$  SE =  $1.128 \pm 0.038$ ;  $P \leq 0.001$ ; medium: estimate  $\pm$  SE =  $0.599 \pm 0.031$ ;  $P \leq 0.001$ ) i.e. when humans were confined to bomas, than they did during periods of high human activity. Use of pastoral land also increased with moonlight levels (estimate  $\pm$  SE =  $0.509 \pm 0.041$ ;  $P \leq 0.001$ ). No significant interactions were found between the explanatory variables.

Distance to nearest boma was best described by the model 'human activity period  $\times$  moonlight index + mean daily rainfall'; this model dominated all comparisons (Appendix Table A3). There was an interaction between human activity period and moonlight index such that moonlight index had very little effect on lion distance to bomas during periods of high human activity (understandable as high human activity was during the daylight hours) and low human activity, but lion distance to bomas declined with decreasing moonlight levels during medium human activity periods, i.e. when people were confined to bomas but still active (Fig. 2). This interaction notwithstanding, lions were significantly closer to bomas when human activity was lowest (2300–0500 hours; estimate  $\pm$  SE =  $-151.251 \pm 12.415$ ), than during other time periods. Lion distance to bomas also declined as rainfall increased (estimate  $\pm$  SE =  $-60.758 \pm 14.241$ ). The relationship between distance to bomas, rainfall and human activity period is further illustrated in Fig. 3. Although the overall diel pattern of boma avoidance remained consistent, the mean distance to the nearest boma for every hour (i.e. the extent of the diel pattern of avoidance) was consistently lower during wet months.

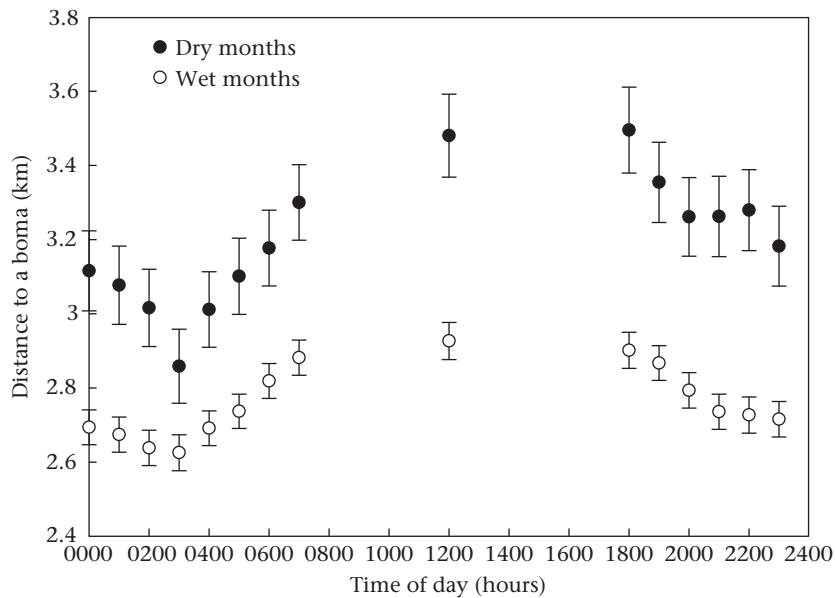
#### Movement Parameters

##### Speed

When considering land use types, lion speed was best described by the model 'moonlight index  $\times$  human activity period + land



**Figure 2.** The interaction between moonlight index (0 = new moon; 1 = full moon) and human activity in the best fit model explaining lion distance to the nearest boma.



**Figure 3.** Distance to a boma (mean  $\pm$  SE) for study lions, depending on the time of day with the effect of rainfall, where wet months (mean daily rainfall  $>2.5$  mm) are contrasted with dry months (mean daily rainfall  $<0.65$  mm). Corresponding human activity periods are as follows: high activity = 0800–1800 hours, medium activity = 1800–2200 hours and 0600–0700 hours, low activity = 2300–0500 hours.

use + mean daily rainfall' (Appendix Table A4). Lion speed was significantly higher on pastoral land (estimate  $\pm$  SE =  $0.203 \pm 0.025$ ) and this was the same in all hours for which data were collected (Fig. 4a). Lion speed decreased with increasing rainfall (estimate  $\pm$  SE =  $-0.035 \pm 0.006$ ). An interaction between moonlight index and human activity period indicated that lion speed decreased with increasing moonlight levels far more during periods of medium human activity than it did during periods of low human activity (Fig. 5). On commercial ranches, when considering the distance to the nearest boma, lion speed was best explained by the model 'distance to boma  $\times$  direction of movement + moonlight index  $\times$  human activity period + mean daily rainfall' (Appendix Table A5). Here, the interaction between human activity period and moonlight index was the same as that for land use (Fig. 5). Lion speed also decreased with increasing rainfall (estimate  $\pm$  SE =  $-0.024 \pm 0.007$ ). A second interaction between distance to boma and lion direction of approach was such that when lions were moving towards a boma, their speed decreased significantly with distance to the nearest boma, whereas when the direction of movement was away from a boma speed increased significantly with distance to a boma (Fig. 6a, b). Three zones of boma influence on lion movements could be differentiated (Fig. 6b, d), particularly for the movement parameter 'speed'. At distances within approximately 1.5 km of a boma, the relationship between lion movement and distance to the nearest boma appears strongest. At distances between 1.5 and 4.5 km, this relationship was still clear, whereas there started to be much more variation in the data for all movement parameters at distances above 4.5 km away from bomas.

#### Turn angle

The models best describing turn angle using data sets including the variables 'land use type' or 'distance to boma' are shown in Appendix Tables A6 and A7, respectively. When considering land use type, the best fit model was 'land use + moonlight index  $\times$  human activity period + mean daily rainfall'. Turn angle was significantly lower on pastoral land than it was on commercial

ranch land (estimate  $\pm$  SE =  $-5.604 \pm 1.106$ ) and this remained constant for all hours for which data were collected (Fig. 4b). The interaction between moonlight and human activity period was such that lion turn angle increased with increasing moonlight during medium human activity periods but moonlight had less effect on turn angle during periods of low human activity (Fig. 7). Turn angle also increased as rainfall increased (estimate  $\pm$  SE =  $1.137 \pm 0.238$ ). On commercial ranches, when considering the distance to the nearest boma, the best fit model was 'distance to boma + human activity period  $\times$  moonlight index + mean daily rainfall'. Turn angle increased with distance to a boma (estimate  $\pm$  SE =  $0.0017 \pm 0.0003$ ; Fig. 6c, d). The interaction between human activity and moonlight levels was the same as for land use (Fig. 7). Turn angle again increased with rainfall (estimate  $\pm$  SE =  $1.164 \pm 0.259$ ).

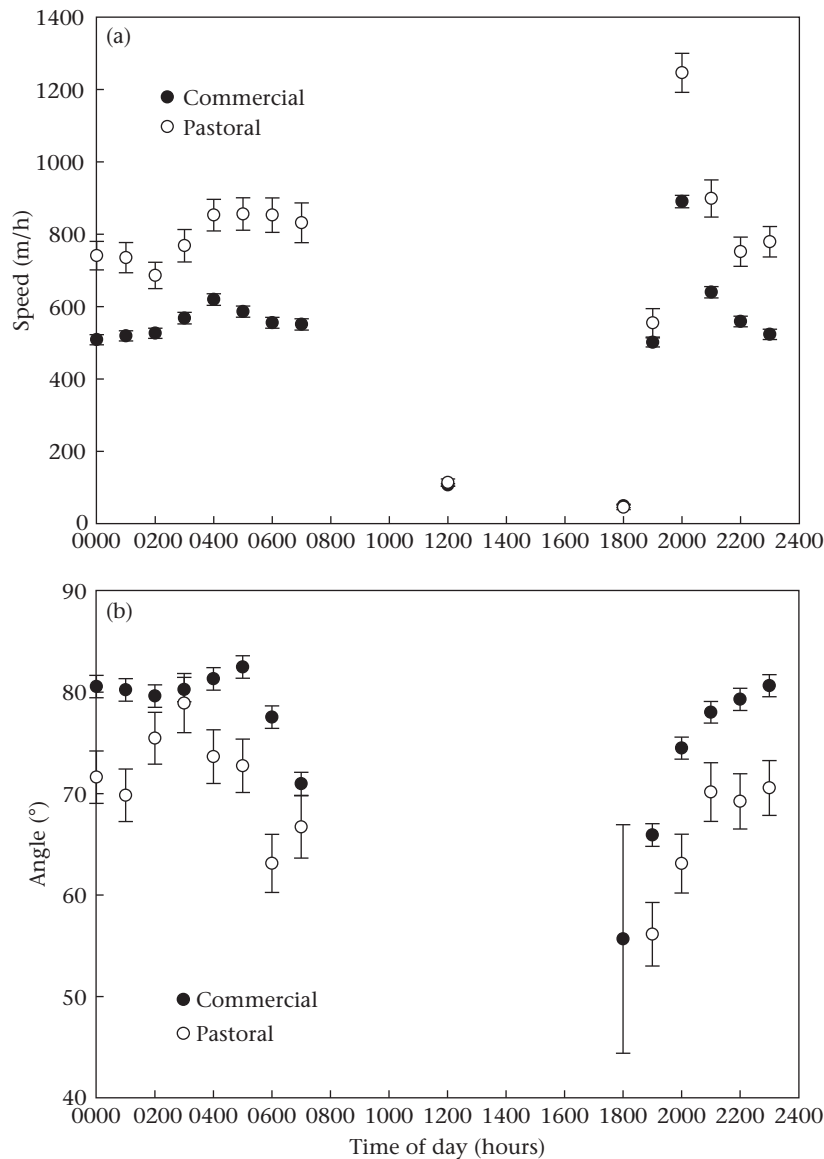
#### Stop duration

None of the models describing the variable 'stop duration' performed better than the null model, using either the data set including 'land use type' or 'distance to boma' (Appendix Tables A8 and A9, respectively). This indicates that stop duration was not significantly affected by any of the variables we measured in this study.

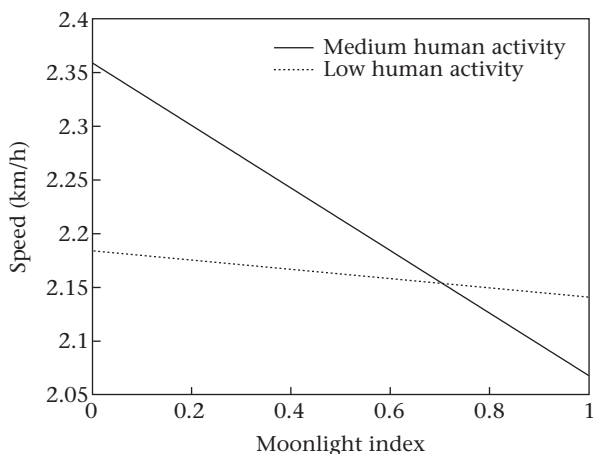
## DISCUSSION

### Spatial Avoidance: Scale Matters

The spatial and temporal scales at which avoidance of human activities becomes significant for large carnivores will affect the cost of this behavioural effect of human-caused mortality risk. Pre-emptive avoidance at larger spatial scales could limit the ability of large carnivores to utilize Landscapes of Coexistence, particularly where the density and distribution of people and livestock are such that complete avoidance is difficult. Study lions showed a preference for commercial ranch land over pastoral land, thus showing some spatial avoidance of humans at the land

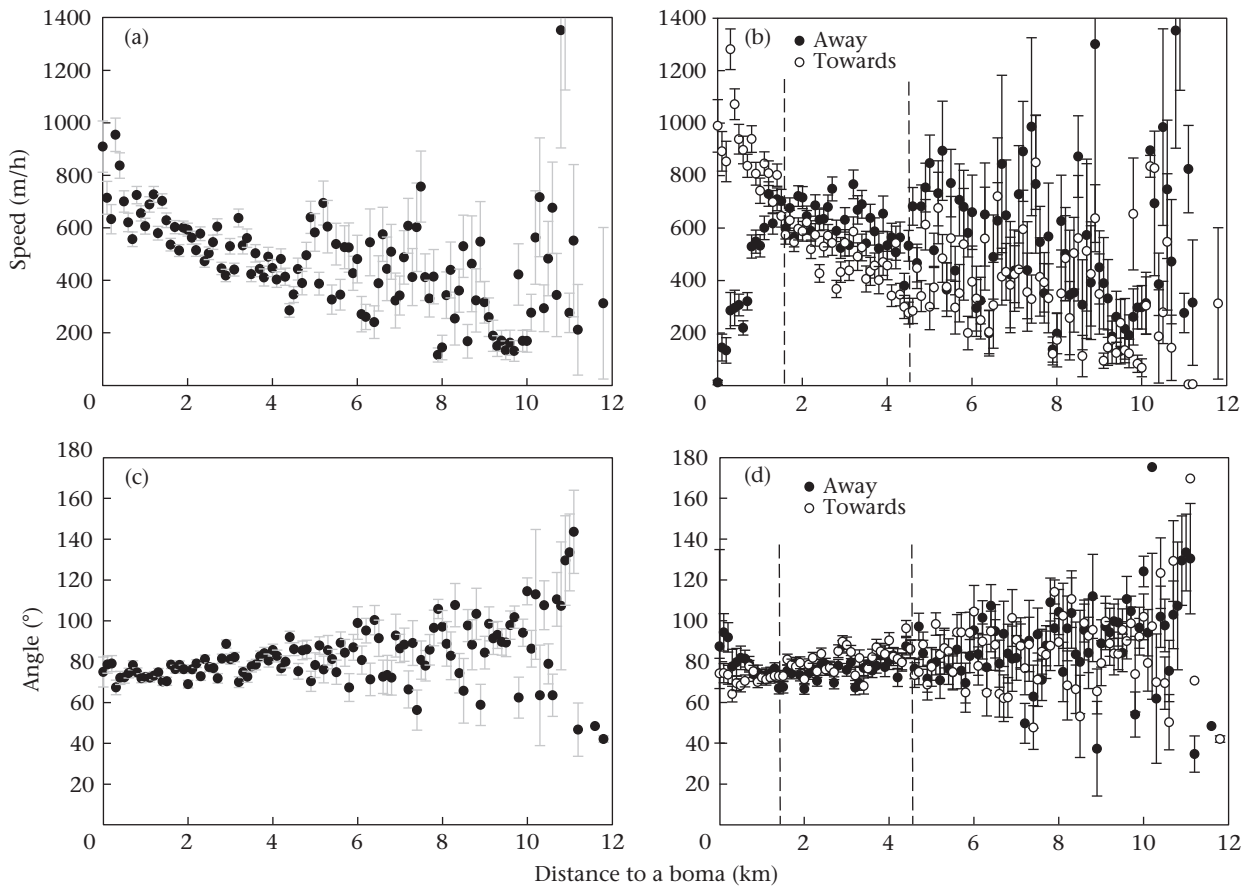


**Figure 4.** Distribution of mean  $\pm$  SE (a) speed and (b) turn angle for all collared lions over the 24 h period. Only hours in which fixes were recorded by the GPS collars are represented. Corresponding human activity periods are as follows: high activity = 0800–1800 hours, medium activity = 1800–2200 hours and 0600–0700 hours, low activity = 2300–0500 hours.



**Figure 5.** The interaction between moonlight index (0 = new moon; 1 = full moon) and human activity period in the best fit model explaining 'speed' for study lions.

use scale. Several studies have demonstrated carnivore avoidance of areas characterized by intense human activity (Boydston et al., 2003; Mattson, 1990; Olson & Gilbert, 1994; Schuette, Creel, et al., 2013; Schuette, Wagner, et al., 2013; Van Dyke et al., 1986). Here, we have shown that a lion's response to people is not as simple as total spatial avoidance. In this study, lions preferred to use commercial ranch land but they still spent 13% of their time in pastoral land showing that avoidance is not total. Our results showed that lions made other behavioural adjustments when using high-risk areas depending on the scale, adopting different strategies in the vicinity of a boma than on pastoral land. At the broader landscape scale, lions showed significant (but not total, see above) avoidance of pastoral land under all the conditions measured. When lions used pastoral land, they did so more during the dark hours than they did during the daylight hours, and during higher moonlight levels. Use of high-risk areas was positively influenced at the local scale by a lower likelihood of human activity, higher rainfall and lower levels of moonlight



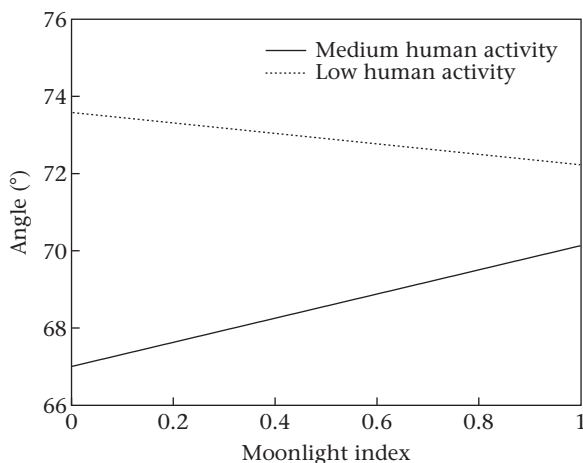
**Figure 6.** Mean  $\pm$  SE value of movement parameter against distance to the nearest boma for (a) speed (all data combined), (b) speed (data separated for direction of travel), (c) turn angle (all data combined), (d) turn angle (data separated for direction of travel).

when humans are still active at bomas. Avoidance on smaller spatiotemporal scales has been shown to optimize the behavioural costs of avoiding predation in other guilds (Frid & Dill, 2002), and is a strategy used by carnivores at risk of predation by larger carnivores (Broekhuis et al., 2013; Durant, 2000). It is probably the most efficient way in which large carnivores can optimize the trade-off between maximizing use of resources in a

Landscape of Coexistence and minimizing the risk of human-caused mortality. Behavioural adjustments to people may be better revealed at the local scale, i.e. by a carnivore's response to actual locations of people and livestock.

#### *Utilizing High-risk Areas Undetected by People*

Lions are generally crepuscular and nocturnal (Cozzi et al., 2012; Hayward & Slotow, 2009; Prins & Iason, 1989; Schaller, 1972). Livestock in the study area is kept in bomas between 1800 and 0700 hours. However, although also confined to boma sites during the dark hours, people remained active in situ during the predawn and postsunset periods (personal communication with herders and ranchers in the study area), which have been shown to be important active periods for lions (Cozzi et al., 2012). Limiting all activities to periods when people were least active, therefore, would constrain lions to be more nocturnal than they would be in safer areas and could potentially result in significant foraging costs. Mean hourly speeds (Fig. 4a) indicate that there was some overlap in active periods between lions and people predawn and postsunset. Lion speed in combination with location, however, demonstrate that heterogeneity in the distribution of people and livestock across the study area allowed lions to use a combination of temporal and spatial partitioning to utilize high-risk areas when risk of detection by people was reduced: lions utilized areas close to bomas most when people were least active (i.e. between 2300 and 0500 hours), and used pastoral land during the dark hours (when people and livestock were confined to boma



**Figure 7.** The interaction between moonlight index (0 = new moon; 1 = full moon) and human activity period in the best fit model explaining 'turn angle' for study lions.



locations) more than they did during the daylight hours (when people were active on the landscape), but remained more active further from people and livestock during times when people were also active. Additionally, lions were found to be closer to bomas in which people were still active during hours when moonlight levels were lower. Packer et al. (2011) showed that dark periods overlapping with times when people are still active represent the highest probability of lion attacks on people in southern Tanzania, possibly because during these periods humans are both available and less likely to detect lions, increasing their vulnerability. In Tanzania, where humans represent potential prey, lions may be attracted to human-occupied areas by wild prey (bush-pig) and kill humans opportunistically. In this study area, by contrast, humans represent a threat, and lions may use areas near bomas while people are still active during periods of lower levels of moonlight, in order to access livestock while minimizing detection by people. Moonlight levels were not found to affect lion distance to bomas as much during periods when people were confined to bomas and unlikely to be active, and thus unlikely to detect lions at any visibility levels.

The importance of scale when measuring avoidance was again highlighted, as lions did not use pastoral land more than expected in any human activity period, and yet did utilize areas closer to bomas more than expected during periods when people were least likely to be active (2300–0500 hours). These results at the smaller scale accord with Carter et al.'s (2012) and Rasmussen and Macdonald's (2012) observations that temporal avoidance may facilitate the use of Landscapes of Coexistence by tigers in Nepal and African wild dogs in Zimbabwe, respectively. Broad-scale spatial avoidance of pastoral land in this study, during which human and livestock densities were higher on pastoral land but wild prey densities and habitat conditions were similar on both land use types, indicates that lion–human coexistence may be limited by the risk of human-caused mortality even when resources are not limited. As lions are less tolerated on pastoral land in the study area (Romañach et al., 2007) the threshold human density for coexistence may also vary with the level of human-caused mortality risk that the human population represents, such that lions avoid people to a greater extent where they are less tolerated.

#### *Minimizing use of High-risk Areas*

GPS collar data revealed that human factors (distance to bomas and land use type) were as important in determining lion movement parameters as environmental factors such as rainfall and moonlight. Lions moved significantly faster and straighter when on pastoral land and in close proximity to bomas. Since prey densities were similar on the different land use types, such movement patterns were unlikely to be a response to low resource availability (see Fauchald, 1999; Valeix et al., 2010). A faster straighter path might instead indicate a tendency to pass quickly through an area or a habitat that represents a greater risk to an animal (Douglas-Hamilton et al., 2005; Graham et al., 2009; Wall et al., 2013). While this may be the case on a landscape scale, i.e. when travelling through one land use type versus another, lion movements on a local scale, i.e. in response to actual locations of people (represented by bomas in this study) may be more complex than simply hurrying past higher risk areas. Lions do kill livestock at bomas in the study area (Frank, 2011; Ogada et al., 2003; Woodroffe & Frank, 2005); thus bomas represent a secondary source of prey as well as a focus for human threat (see also Valeix et al., 2012). While risk of detection by people may be reduced by temporal partitioning of activities, lion movement patterns once in the vicinity of bomas

may be indicative of a foraging pattern at a known source of potential prey that does not respond to expected patch disturbance rules, i.e. livestock confined to a boma cannot move away in response to the proximity of a predator (Valeix et al., 2011). Lions sped up and straightened their path as they approached within 1.5 km of a boma, indicating a need to access resources at a known boma location quickly. They left a boma more slowly, however, possibly because livestock constrained within a robust boma are difficult to access but continue to represent a foraging opportunity until lions make a kill, give up or are chased away. Lion movements away from bomas after they have killed compared to when they have not been successful, or when they are chased away by people versus simply giving up, may further reveal the determinants of observed movement patterns. Relationships between speed or path tortuosity and distance to the nearest boma were found to decline at distances greater than 4.5 km suggesting that the presence of people and livestock does not influence lion movements beyond that distance.

Both speed and path tortuosity were generally influenced by moonlight much more during periods when humans were still active at bomas than during periods when humans were inactive. This is likely to be a factor of lion biology rather than human influence, as periods during which humans are active at bomas (dusk and dawn) have also been shown to be periods when lions are most active (Cozzi et al., 2012). Slower more tortuous paths during periods of brighter moonlight may reflect a greater need for lions to take care hunting during times when they are more visible to their prey.

#### *Foraging Opportunities versus Risk of Mortality*

Lions were more likely to utilize areas closer to bomas during periods of wetter weather, which are potential periods of reduced hunting success of wild prey (Funston et al., 2001; Patterson et al., 2004; Schaller, 1972; Van Orsdol, 1984; Woodroffe & Frank, 2005). Increased rainfall was also associated with resting closer to bomas by day. This may be a response to reduced risk of detection owing to increased vegetation thickness and/or increased availability of grass and water reducing the distance livestock and their herders move from bomas. Habitat structure and daytime grazing practices are candidate factors in determining lions' ability to partition their activities with livestock and people in a Landscape of Coexistence.

Our results did not rule out the possibility that the lions were responding to changes in other variables at different rainfall levels. An alternative hypothesis that lions are attracted closer to bomas by an increase in wild prey abundance and/or vulnerability during periods of higher rainfall should be investigated.

#### *Conclusion*

The ecology of fear theory, originally developed to explain the behavioural ecology, distribution and density of prey (Laundré et al., 2001; Sih, 1980), has here been applied to lions under risk of predation by humans. Our results and any conclusions based on data from this study must, of course, take the small sample size into account. Only multiparous females were used in this study and pride size, the presence of cubs, adult males or a combination of the three may be candidate factors in determining the strategies lions use to maximize fitness-enhancing activities while minimizing human-caused mortality in a Landscape of Coexistence, which were not taken into account here. However, behavioural changes in response to human-caused mortality risk, similar to those shown by prey (and smaller

carnivores) in response to predation risk, were revealed for the study lions. A combination of strategies observed in lions may allow them to avoid people on a fine spatiotemporal scale in order to utilize resources in human-occupied areas. The observed fine-scale shifts in these strategies in response to environmental variables are perhaps indicative of the opportunistic nature of the species and an inherent flexibility important to their survival in Landscapes of Coexistence. However, lions did show significant avoidance of pastoral land under all conditions. As pastoral land in the study area had similar wild-prey densities and habitat to commercial ranch land, any spatial avoidance of that land use type represented a cost. Human densities were higher on pastoral land and other studies suggest a threshold value of human density for successful human–lion coexistence; Woodroffe (2000) and Riggio et al. (2012) suggested approximately 25 people/km<sup>2</sup>. While Riggio et al. (2012) suggested that above this threshold value of human density an area ceases to be suitable for lions due to land transformation, there was no land transformation or reduction in resources (prey and cover) on pastoral land in this study area. Our results suggest that, in areas where people regularly kill lions to protect livestock, the presence of people alone may limit lions' use of the landscape.

Foraging costs associated with spatiotemporal avoidance of human-utilized areas could be even greater than indicated by overall prey densities; prey may be attracted to human locations during vulnerable periods, as the presence of people may shield them from carnivores (see Berger, 2007). In this way, prey distribution on a finer scale (not measured in this study) may be tied to human locations, and despite similar overall prey densities, higher densities of people and bomas may make prey less available. The distributions of people and livestock, not just overall densities, may also be important. This study revealed that human locations most strongly influence study lion movements within a 1.5 km radius, but had some influence within a 4.5 km radius. Zoning to cluster human habitation and night-time livestock enclosures could allow large carnivores more space to utilize resources, and avoid people and livestock, while at the same time allowing people to communally and more effectively protect their livestock. Our results suggest that zonation could be done on a relatively small scale, i.e. at a property level rather than on an ecosystem level, and still be effective.

Overall this study indicates that minimizing the risk of human-caused mortality could reduce overall foraging intake for lions. Such trade-offs may have population-level consequences (see Preisser, Bolnick, & Benard, 2005; Werner & Peacor, 2003 for other guilds) that need to be better measured and considered when assessing the full impact of conflict with humans on the density and distribution of large carnivores.

## Acknowledgments

We thank the government of Kenya for permission to carry out this work, and Kenya Wildlife Services for their support. We also thank the land owners and managers of Laikipia for their collaboration, without which this research would not have been possible. Special thanks go to Samson Ituru and Marc Napao for their valuable help in collecting field data. Research for this manuscript was carried out on funds generously provided by Panthera, the Wildlife Conservation Society, Bosack and Kruger Foundation, Arthur M. Blank Family Foundation, Flora Family Foundation, Cheryl Grunbock and Martin King Foundation, Philadelphia Zoo, San Francisco Zoo, Wildlife Conservation Network, National Geographic Society, US National Cancer Institute, Mpala Research Centre, Denver Zoo, Banovich Wildscapes Foundation, Josep Oriol, Mike Calvin and Debby Wettlaufer, Lloyds Family Charitable Foundation, Jonathan

Vannini, Steven Gold, Lisette Gelber, Eric Stumberg, John and Wendy Cotterill, Douglas King, Christoph and Victoria Evard, Philippa Bengough, Jamie Roberts, James and Laria Warwick, John Paul Dekker, Neil Bernie and Claire Newton. Technical guidance was provided by Lyman McDonald, Mary Smulders, Jake Wall and Festus Ihwagi (Save The Elephants), Zeke Davidson (Marwell Zoo), Siva Sundaresan (Denver Zoo), Leela Hazzah and Stephanie Dolrenry (Lion Guardians) and this manuscript was greatly improved by feedback from Gabriele Cozzi.

## References

- Bates, D., Maechler, M., Bolker, B., Walker, S., Cristensen, R. H. B., Singmann, H., et al. (2012). *Package 'lme4'*. <http://cran.r-project.org/web/packages/lme4/index.html>.
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, 3, 620–623.
- Beyer, H. L. (2004). *Hawth's analysis tools for ArcGIS*. [www.spatialecology.com/htools](http://www.spatialecology.com/htools).
- Boydston, E., Kapheim, E. K. M., Watts, H. E., Szykman, M., & Holekamp, K. E. (2003). Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation*, 6, 207–219.
- Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology*, 82, 1098–1105.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer-Verlag.
- Caro, T. M. (1987). Cheetah mothers' vigilance: looking out for prey or for predators? *Behavioral Ecology and Sociobiology*, 20, 351–361.
- Carter, N. H., Shrestha, B. K., Karki, J. B. B., Pradhan, N. M., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 15360–15365.
- Childress, M. J., & Lung, M. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, 66, 389–398.
- Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W., & Schmid, B. (2012). Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, 93, 2590–2599.
- Dickson, B. G., Jennes, J. S., & Beier, P. (2005). Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management*, 69, 264–275.
- Douglas-Hamilton, I., Krink, T., & Volrath, F. (2005). Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften*, 92, 158–163.
- Durant, S. M. (1998). Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology*, 67, 370–386.
- Durant, S. M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, 11, 624–632.
- Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014). The devil is in the dispersers: predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51(5), 1169–1178. <http://dx.doi.org/10.1111/1365-2664.12282>.
- Fauchald, P. (1999). Foraging in a hierarchical patch system. *American Naturalist*, 153, 603–613.
- Frank, L. G. (2011). *Living with lions: lessons from Laikipia. Conserving wildlife in African landscapes: Kenya's Ewaso ecosystem*. Washington D.C.: Smithsonian Institution Scholarly Press.
- Frank, L. G., Simpson, D., & Woodroffe, R. (2003). Foot snares: an effective method for capturing African lions. *Wildlife Society Bulletin*, 31, 309–314.
- Frank, L. G., & Woodroffe, R. (2001). Behaviour of carnivores in exploited and controlled populations. In J. L. Gittleman, S. Funk, D. W. Macdonald, & R. K. Wayne (Eds.), *Carnivore conservation* (pp. 419–442). Cambridge, U.K.: Cambridge University Press.
- Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6(1), 11.
- Funston, P. J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, 253, 419–431.
- Georgiadis, N. J., Olwero, J. G. N., Ojwang', G., & Romañach, S. S. (2007). Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biological Conservation*, 137, 461–472.
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12, 445–455.
- Harrington, L. A., Harrington, A. L., Moorhouse, T., Gelling, M., Bonesi, L., & Macdonald, D. W. (2009). American mink control on inland rivers in southern England: an experimental test of a model strategy. *Biological Conservation*, 142, 839–849.
- Hayward, M. W., & Slotow, R. (2009). Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research*, 39, 109–125.

- Holekamp, K. E., & Dloniak, S. M. (2010). Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Advances in the Study of Behavior*, 42, 189–229.
- Johnson, C. J., Nielson, S. E., Merrill, E. H., McDonald, T. L., & Boyce, M. S. (2006). Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management*, 70, 347–357.
- Knopff, K. H., Knopff, A. A., Warren, M. B., & Boyce, M. S. (2009). Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management*, 73, 586–597.
- Kolowski, J. M., & Holekamp, K. E. (2009). Ecological and anthropogenic influences on space use by spotted hyenas. *Journal of Zoology*, 277, 23–36.
- Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution and Systematics*, 34, 153–158.
- Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79, 1401–1409.
- Liley, S., & Creel, S. (2007). What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology*, 19, 245–254.
- Linnell, J. D. C., & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, 6, 169–176.
- Macdonald, D. W., Ball, F. G., & Hough, N. G. (1980). The evaluation of home range size and configuration using radio tracking data. In C. J. Amlaner, & D. W. Macdonald (Eds.), *A handbook on biotelemetry and radio tracking* (pp. 405–425). Oxford, U.K.: Pergamon Press.
- Macdonald, D. W., Loveridge, A. J., & Rabinowitz, A. (2010). Felid futures: crossing, disciplines borders and generations. In D. W. Macdonald, & A. J. Loveridge (Eds.), *Biology and conservation of wild felids* (pp. 599–649). Oxford, U.K.: Oxford University.
- Macdonald, D. W., & Willis, K. J. (2013). Elephants in the room: tough choices for a maturing discipline. In D. W. Macdonald, & K. J. Willis (Eds.), *Key topics in conservation biology 2* (pp. 469–495). Chichester, U.K.: Wiley-Blackwell.
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: Statistical analysis and design for field studies* (2nd ed.). Boston, MA: Kluwer.
- Mattson, D. J. (1990). Human impacts on bear habitat use. *International Conference for Bear Research and Management*, 8, 33–56.
- McNay, R. S., Morgan, J. A., & Brunnell, F. L. (1994). Characterizing independence of observations in movements of Columbian black-tailed deer. *Journal of Wildlife Management*, 58, 422–429.
- Ogada, M. O., Woodroffe, R., Ouge, N., & Frank, L. G. (2003). Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology*, 17, 1521–1530.
- Olson, T. L., & Gilbert, B. K. (1994). Variable impacts of people on brown bear use of an Alaskan river. *International Conference for Bear Research and Management*, 9, 97–106.
- Packer, C., Swanson, A., Ikanda, D., & Kushnir, H. (2011). Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLoS One*, 6(7), e22285.
- Pangle, W. M., & Holekamp, K. E. (2010a). Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve. *Journal of Mammalogy*, 91, 154–164.
- Pangle, W. M., & Holekamp, K. E. (2010b). Functions of vigilance behaviour in a social carnivore, the spotted hyena, *Crocuta crocuta*. *Animal Behaviour*, 80, 257–267.
- Patterson, B., Kasiki, S. M., Selempo, E., & Kays, R. W. (2004). Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation*, 119, 507–516.
- Preisser, E. L., Bolnick, D. I., & Benard, M. E. (2005). Scared to death? the effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501–509.
- Prins, H. H. T., & Iason, G. R. (1989). Dangerous lions and nonchalant buffalo. *Behaviour*, 108, 262–296.
- Rasmussen, G. S. A., & Macdonald, D. W. (2012). Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. *Journal of Zoology*, 286, 232–242.
- Riggio, J., Jacobsen, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., et al. (2012). The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity Conservation*, 22, 17–35.
- Romañach, S. S., Lindsey, P. A., & Woodroffe, R. (2007). Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. *Oryx*, 41, 185–195.
- Schaller, G. B. (1972). *The Serengeti lion: a study of predator-prey relations*. Chicago, IL: University of Chicago Press.
- Schuetz, P., Creel, S., & Christianson, D. (2013). Coexistence of African lions, livestock, and people in a landscape with variable human land use and seasonal movements. *Biological Conservation*, 157, 148–154.
- Schuetz, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, 158, 301–312.
- Sih, A. (1980). Optimal behavior: can foragers balance two conflicting demands? *Science*, 210, 1041–1043.
- Swihart, R. K., & Slade, N. A. (1985a). Testing for independence of observations in animal movements. *Ecology*, 66, 1176–1184.
- Swihart, R. K., & Slade, N. A. (1985b). Influence of sampling interval on estimates of home range size. *The Journal of Wildlife Management*, 49, 1019–1025.
- Theuerkauf, J. (2009). What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology*, 115, 649–657.
- Valeix, M., Chamaillé-Jammes, S., Loveridge, A. J., Davidson, Z., Hunt, J. E., Madzikanda, H., et al. (2011). Understanding patch departure rules for large carnivores: lion movements support a patch-disturbance hypothesis. *American Naturalist*, 178, 1–7.
- Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F., et al. (2009). Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, 63, 1483–1494.
- Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., & Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, 49, 73–81.
- Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25, 337–351.
- Van Dyke, F. G., Brocke, R. H., Shaw, H. G., Ackerman, B. B., Hemker, T. P., & Lindzey, F. G. (1986). Reactions of mountain lions to logging and human activity. *Journal of Wildlife Management*, 50, 95–102.
- Van Orsdol, K. G. (1984). Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, 22, 79–99.
- Venables, B., & Ripley, B. (2002). *Package 'MASS'*. <http://cran.r-project.org/web/packages/MASS/index.html>.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., & Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biological Conservation*, 157, 60–68.
- Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.
- Whitman, K. (2006). *Modelling, monitoring and the sustainable use of lion populations in Tanzania* (Doctoral dissertation). Minneapolis, MN, U.S.A.: University of Minnesota.
- Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, 3, 165–173.
- Woodroffe, R. (2001). Strategies for carnivore conservation: lessons from contemporary extinctions. In J. L. Gittleman, S. Funk, D. W. Macdonald, & R. K. Wayne (Eds.), *Carnivore conservation* (pp. 61–92). Cambridge, U.K.: Cambridge University Press.
- Woodroffe, R., & Frank, L. G. (2005). Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Animal Conservation*, 8, 91–98.
- Woodroffe, R., Frank, L. G., Lindsey, P. A., ole Ranah, S. M. K., & Romañach, S. (2006). Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity and Conservation*, 16, 1245–1260.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: SpringerLink.

## Appendix

**Table A1**

Summary statistics for mixed-effects logistic regression models comparing actual lion locations (coded '1') and randomly generated locations (coded '0'), with 'land use' as the only explanatory variable, for study lions

Data set	Model	AIC	ΔAIC	Akaike weights
All data	Null	22800	2253	0.00
	<b>Land use</b>	<b>20547</b>	<b>0</b>	<b>1.00</b>
Moonlight index ≥0.75	Null	3497	267	0.00
	<b>Land use</b>	<b>3230</b>	<b>0</b>	<b>1.00</b>
Moonlight index ≤0.25	Null	9054	857	0.00
	<b>Land use</b>	<b>8197</b>	<b>0</b>	<b>1.00</b>
Rainfall >2.5 mm	Null	7454	730	0.00
	<b>Land use</b>	<b>6724</b>	<b>0</b>	<b>1.00</b>
Rainfall < 0.65 mm	Null	8449	771	0.00
	<b>Land use</b>	<b>7678</b>	<b>0</b>	<b>1.00</b>
Low human activity	Null	7218	565	0.00
	<b>Land use</b>	<b>6653</b>	<b>0</b>	<b>1.00</b>
Medium human activity	Null	8311	854	0.00
	<b>Land use</b>	<b>7457</b>	<b>0</b>	<b>1.00</b>
High human activity	Null	7279	815	0.00
	<b>Land use</b>	<b>6464</b>	<b>0</b>	<b>1.00</b>

'Lion identity' was included in every model as a random effect. Data were analysed as a whole, and after being split into different subsections according to levels of moonlight index (0 = new moon; 1 = full moon), rainfall and human activity. The best fit model for each data subsection is in bold italics.

**Table A2**

Summary statistics for mixed-effects logistic regression models comparing actual lion locations (coded '1') and randomly generated locations (coded '0'), with 'distance to boma' as the only explanatory variable, for study lions

Data set	Model	AIC	ΔAIC	Akaike weights
All data	<b>Null</b>	<b>18051</b>	<b>0</b>	<b>0.73</b>
	Distance to boma	18053	2	0.27
Moonlight index $\geq 0.75$	<b>Null</b>	<b>2958</b>	<b>0</b>	<b>0.50</b>
	Distance to boma	2958	0	0.50
Moonlight index $\leq 0.25$	<b>Null</b>	<b>7555</b>	<b>0</b>	<b>0.82</b>
	Distance to boma	7558	3	0.18
Rainfall >2.5 mm	<b>Null</b>	<b>5455</b>	<b>0</b>	<b>0.88</b>
	Distance to boma	5459	4	0.12
Rainfall <0.65 mm	<b>Null</b>	<b>7139</b>	<b>0</b>	<b>0.82</b>
	Distance to boma	7142	3	0.18
Low human activity	Null	5949	8	0.02
	<b>Distance to boma</b>	<b>5941</b>	<b>0</b>	<b>0.98</b>
Medium human activity	<b>Null</b>	<b>6470</b>	<b>0</b>	<b>0.88</b>
	Distance to boma	6474	4	0.12
High human activity	<b>Null</b>	<b>5358</b>	<b>0</b>	<b>0.88</b>
	Distance to boma	5642	4	0.12

'Lion identity' was included as a random effect in every model. Data were analysed as a whole, and after being split into different subsections according to levels of moonlight index (0 = new moon; 1 = full moon), rainfall and human activity. The best fit model for each data subsection is in bold italics.

**Table A3**

Summary statistics for models explaining mean distance to the nearest boma for study lions

Model	AIC	ΔAIC	Akaike weights
Null	540705.30	290.00	0.00
Human activity	540459.40	44.10	0.00
Rainfall	540681.80	266.50	0.00
Moonlight	540690.60	275.30	0.00
Human activity+Rainfall	540436.10	20.80	0.00
Human activity+Moonlight	540453.30	38.00	0.00
Rainfall+Moonlight	540667.20	251.90	0.00
Human activity×Moonlight	540438.60	23.30	0.00
Human activity+Rainfall+Moonlight	540430.00	14.70	0.00
<b>Human activity×Moonlight+Rainfall</b>	<b>540415.30</b>	<b>0.00</b>	<b>1.00</b>

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.

**Table A4**

Summary statistics for models explaining the movement parameter 'speed', using data sets that include the variable 'land use type', for study lions

Model	AIC	ΔAIC	Akaike weights
Null	100996.50	183.90	0.00
Land use	100947.20	134.60	0.00
Rainfall	100976.50	163.90	0.00
Moonlight	100978.20	165.60	0.00
Human activity	100950.50	137.90	0.00
Land use+Rainfall	100924.50	111.90	0.00
Land use+Moonlight	100928.20	115.60	0.00
Land use+Human activity	100896.20	83.60	0.00
Rainfall+Moonlight	100959.00	146.40	0.00
Rainfall+Human activity	100930.50	117.90	0.00
Moonlight+Human activity	100940.60	128.00	0.00
Moonlight×Human activity	100890.00	77.40	0.00
Moonlight×Human activity+Land use	100834.90	22.30	0.00
<b>Moonlight×Human activity+Land use+Rainfall</b>	<b>100812.60</b>	<b>0.00</b>	<b>1.00</b>

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.

**Table A5**

Summary statistics for models explaining the movement parameter 'speed', using data sets that include the variable 'distance to boma', for study lions

Model	AIC	ΔAIC	Akaike weights
Null	80510.26	515.40	0.00
Distance to boma	80455.36	460.50	0.00
Rain	80511.81	516.95	0.00
Moonlight	80430.94	436.08	0.00
Human activity	80405.91	411.05	0.00
Direction of movement	80457.35	462.49	0.00
Distance to boma+Rain	80452.78	457.92	0.00
Distance to boma+Moonlight	80372.95	378.09	0.00
Distance to boma+Human activity	80340.10	345.24	0.00
Distance to boma+Direction of movement	80373.89	379.03	0.00
Rainfall+Moonlight	80433.98	439.12	0.00
Rainfall+Human activity	80407.58	412.72	0.00
Rainfall+Direction of movement	80458.90	464.04	0.00
Moonlight+Human activity	80359.11	364.25	0.00
Moonlight+Direction of movement	80376.47	381.61	0.00
Human activity+Direction of movement	80353.39	358.53	0.00
Moonlight×Human activity	80288.25	293.39	0.00
Distance to boma×Direction of movement	80231.12	236.26	0.00
Distance to boma×Direction of movement+Moonlight×Human activity	79996.97	2.11	0.26
<b>Distance to boma×Direction of movement+Moonlight×Human activity+Rainfall</b>	<b>79994.86</b>	<b>0.00</b>	<b>0.74</b>

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.

**Table A6**

Summary statistics for models explaining the movement parameter 'turn angle', using data sets that include the variable 'land use type', for study lions

Model	AIC	ΔAIC	Akaike weights
Null	375907.30	155.00	0.00
Land use	375887.80	135.50	0.00
Rainfall	375889.70	137.40	0.00
Moonlight	375904.30	152.00	0.00
Human activity	375812.20	59.90	0.00
Land use+Rainfall	375868.50	116.20	0.00
Land use+Moonlight	375884.70	132.40	0.00
Land use+Human activity	375788.90	36.60	0.00
Rainfall+Moonlight	375886.90	134.60	0.00
Rainfall+Human activity	375794.60	42.30	0.00
Moonlight+Human activity	375812.50	60.20	0.00
Moonlight×Human activity	375795.20	42.90	0.00
Land use+Moonlight×Human activity	375772.00	19.70	0.00
<b>Land use+Moonlight×Human activity+Rainfall</b>	<b>375752.30</b>	<b>0.00</b>	<b>1.00</b>

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.

**Table A7**

Summary statistics for models explaining the movement parameter 'turn angle', using data sets that include the variable 'distance to boma', for study lions

Model	AIC	ΔAIC	Akaike weights
Null	285674.70	102.30	0.00
Distance to boma	285660.70	88.30	0.00
Rain	285662.00	89.60	0.00
Moonlight	285672.20	99.80	0.00
Human activity	285615.60	43.20	0.00
Direction of movement	285674.90	102.50	0.00
Distance to boma+Rain	285643.90	71.50	0.00
Distance to boma+Moonlight	285657.70	85.30	0.00
Distance to Boma+Human activity	285598.00	25.60	0.00
Distance to Boma+Direction of movement	285659.40	87.00	0.00
Rainfall+Moonlight	285660.00	87.60	0.00
Rainfall+Human activity	285603.00	30.60	0.00
Rainfall+Direction of movement	285662.30	89.90	0.00



**Table A7** (continued)

Model	AIC	$\Delta$ AIC	Akaike weights
Moonlight+Human activity	285618.40	46.00	0.00
Moonlight+Direction of movement	285672.50	100.10	0.00
Human activity+Direction of movement	285615.80	43.40	0.00
Moonlight $\times$ Human activity	285608.90	36.50	0.00
<b><i>Distance to boma+Human activity<math>\times</math> Moonlight +Rainfall</i></b>	<b>285574.20</b>	<b>1.80</b>	<b>0.29</b>
<b><i>Distance to boma+Human activity<math>\times</math> Moonlight+Rainfall+Direction</i></b>	<b>285572.40</b>	<b>0.00</b>	<b>0.71</b>

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.

**Table A8**

Summary statistics for models explaining the movement parameter 'Stop duration', using data sets that include the variable 'land use type', for study lions

Model	AIC	$\Delta$ AIC	Akaike weights
Null	1927.54	0.58	0.34
Land use	1928.88	1.93	0.17
<b><i>Rainfall</i></b>	<b>1926.95</b>	<b>0.00</b>	<b>0.46</b>
Moonlight	1932.48	5.53	0.03

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.

**Table A9**

Summary statistics for models explaining the movement parameter 'Stop duration', using data sets that include the variable 'distance to boma', for study lions

Model	AIC	$\Delta$ AIC	Akaike weights
<b><i>Null</i></b>	<b>1546.87</b>	<b>0.00</b>	<b>0.83</b>
Distance to boma	1565.88	19.01	0.00
Rain	1551.12	4.25	0.10
Moonlight	1551.89	5.03	0.07

'Night identity' nested in 'lion identity' was included in every model as a random effect. The model in bold italics is the model providing the best fit.