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The movement of African elephants in a human-dominated land-use mosaic

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Abstract

Land outside of gazetted protected areas is increasingly seen as important to the future of elephant persistence in Africa. However, other than inferential studies on crop raiding, very little is understood about how elephants *Loxodonta africana* use and are affected by human-occupied landscapes. This is largely a result of restrictions in technology, which made detailed assessments of elephant movement outside of protected areas challenging. Recent advances in radio telemetry have changed this, enabling researchers to establish over a 24-h period where tagged animals spend their time. We assessed the movement of 13 elephants outside of gazetted protected areas across a range of land-use types on the Laikipia plateau in north-central Kenya. The elephants monitored spent more time at night than during the day in areas under land use that presented a risk of mortality associated with human occupants. The opposite pattern was found on large-scale ranches where elephants were tolerated. Furthermore, speed of movement was found to be higher where elephants were at risk. These results demonstrate that elephants facultatively alter their behaviour to avoid risk in human-dominated landscapes. This helps them to maintain connectivity between habitat refugia in fragmented land-use mosaics, possibly alleviating some of the potential negative impacts of fragmentation. At the same time, however, it allows elephants to penetrate smallholder farmland to raid crops. The greater the amount of smallholder land within an elephant's range, the more it was utilized, with consequent implications for conflict. These findings underscore the importance of (1) land-use planning to maintain refugia; (2) incentives to prevent further habitat fragmentation; (3) the testing and application of conflict mitigation measures where fragmentation has already taken place.

Introduction

Understanding of the way elephants *Loxodonta africana* persist in human-dominated landscapes is important to conservation in several ways. First, elephants are a species of conservation concern, with numbers reduced dramatically over the last 100 years so that they now form a highly discontinuous population (Blanc *et al*., 2007). These declines have largely been attributed to legal and illegal trade in ivory and more recently, to competition and conflict with people. Existing protected areas are too small and isolated to provide sufficient habitat for the long-term conservation of elephants. The management of elephants in these isolated protected areas is challenging and controversial (Dickson & Adams, 2009). Second, elephants are adapted to long-distance movement. Such movement is thought to be critical for accessing resources that are scarce in time and space demonstrated by the inverse relationship between annual rainfall and home-range size recorded among African elephants (Thouless, 1996). An extreme example of this is in the arid environments of Mali and Namibia where elephants travel enormous distances to meet their nutritional requirements, with recorded home ranges of 24 000 and 12 800 km^2, respectively (Blake *et al*., 2003; Leggett, 2006). Across longer time scales, such mobility in large mammals enables populations to respond to stochastic events, cope with the impact of climate change and maintain the ecological integrity of the landscapes these mammals inhabit. Third, wildlife movement is important for genetic exchange and the maintenance of a genetically viable population (Noss *et al*., 1996). These are some of the reasons behind the emerging calls for mega-reserves and the creation of trans-boundary protected areas (Van Aarde, 2005).

Fourth, elephants are keystone species with significant roles in ecological dynamics (Lewis, 1987; Owen-Smith, 1988; Baxter & Getz, 2005) and therefore their persistence outside protected areas is important to the conservation of other elements of biodiversity (e.g. Du Toit, Rogers & Biggs, 2003). Fifth, in human-dominated landscapes, human–wildlife conflict, especially crop raiding and related risks to life and livelihood in the case of elephants (Sukumar, 1991; Barnes, 1996; Hoare, 1999), has major implications for public support for conservation (Kangwana, 1995; Naughton-Treves, 1997; Woodroffe, Thirgood & Rabinowitz, 2005). From the perspective of both biodiversity conservation and human welfare it is therefore critical to gain an understanding of how and under what circumstances elephants use different land-use types within human-dominated landscapes. This requires new research into wildlife movement patterns outside protected areas.

Accommodating movement by large mammals, such as elephants, in human-dominated landscapes is an important conservation goal, but is challenging. Human activities such as hunting, the conversion of natural habitat into cropland and settlements and the construction of roads and fences impede wildlife movement. There is evidence that elephants do not occur in landscapes with human populations above a certain level of density (Parker & Graham, 1989; Eltringham, 1990; Barnes *et al*., 1991; Happold, 1995; Hoare & Du Toit, 1999). However, elephants and people do coexist across a range of different land uses and human population densities in Africa (Said *et al*., 1995; Blanc *et al*., 2007). In the absence of poaching for ivory, conflict with people over crops and resources is a significant source of mortality among African elephants (Thouless, 1994; Wittemyer, Douglas-Hamilton & Getz, 2005; Graham, 2007). Conservation policy has placed increasing emphasis on such landscapes (e.g. Norton-Griffiths & Southey, 1995), because of the biogeographic problem of isolated protected areas, and the adoption of various forms of 'community conservation' initiatives (Western, Wright & Strum, 1994; Hulme & Murphree, 2001; Brandon and Wells, 1992).

Use by elephants of human-occupied landscapes is likely to be affected by a range of factors, including land use (e.g. cropping or pastoralism), and the extent to which people tolerate the presence of elephants (itself related to land use, and the likely costs of elephant activity such as crop raiding, as well as personal/attitudinal, cultural and social factors). Land use and human occupancy can be thought of as comprising a mosaic of risk, as people respond to the presence of elephants in different ways and different levels of effectiveness. The ways elephant movement is affected and responds to the resulting mosaic of risk will determine the way elephants use that landscape. That usage can be thought of in terms of timing (whether at particular times of day or night), residence (how long they stay in landscape elements) and speed of movement.

There is evidence to suggest that carnivores move outside areas of natural habitat into areas with a higher risk from people at night (e.g. Weaver, Paquet & Ruggiero, 1996). Inferential studies of crop raiding suggest that African elephants move into and through cultivated fields at night (Bell, 1984; Thouless, 1994; Hoare, 1995; Osborn, 1998; Sitati *et al*., 2003; Barnes *et al*., 2006). This apparent behavioural strategy of risk avoidance through spatial partitioning in time, while obvious, has been difficult to demonstrate directly as nocturnal observation data were difficult to collect until recent advances in radio telemetry. Other than using the cover of darkness as a risk-avoidance strategy, there is some limited evidence to suggest that elephants also increase their speed of movement within human-dominated landscape elements compared with gazetted protected areas (Douglas-Hamilton, Krink & Vollrath, 2005; Galanti *et al*., 2006), suggesting a further risk-avoidance strategy to reduce the time within and therefore the risk associated with human-occupied landscapes.

Assessments of interactions between wildlife and people at the landscape scale from seasonal or annual aerial counts (e.g. Parker & Graham, 1989; Hoare & Du Toit, 1999) provide a 'snap shot' of daytime distribution and relative abundance. Ground-transect data allow identification of broad patterns of distribution in relation to human activities (e.g. Barnes *et al*., 1991; Blom *et al*., 2005). However, neither method allows assessment of finer scale behavioural responses to different land-use types within human-dominated landscapes. Recent technological developments have enabled high-resolution global positioning system (GPS) tracking, allowing researchers to establish over a 24-h period where tagged animals spend their time. While many applications of such technology involve studies of home range and/or habitat selection (Lindeque & Lindeque, 1991; Galanti *et al*., 2006; Legett, 2006) and more recently, social behaviour (Wittemyer *et al*., 2005), the application of this technology has enormous potential to contribute to understanding the interaction of people with wild species, especially in the context of human-dominated landscapes. Here we use radio-tracking data to examine elephant movement in relation to human land-use types in the unprotected landscape of Laikipia District, Kenya and discuss the implications for conservation.

Materials and methods

Study area

Laikipia District (9700 km^2) is located in north-central Kenya at an elevation of 1700–2000 m a.s.l., north-west of Mt. Kenya, north-east of the Aberdare highlands, west of the Rift Valley and south of Samburu District. Rainfall in Laikipia is bimodal, mostly falling in two seasons, the 'long rains', between April and June, and the 'short rains', between October and December, although rain is unpredictable and may fall at any time of year. Annual rainfall is strongly influenced by the presence of Mt. Kenya and the Aberdares, falling along a steep gradient from between 750 mm in the southern part of the district to 300 mm in the lower, northern part of the district (Berger, 1989; Gichuki, Hanspeter & Schwilch, 1998).

The variation in altitude and rainfall across the district are associated with marked changes in land use, from protected upland forest, through a belt of smallholder cultivation to savannah under large-scale commercial ranching, to traditional transhumant pastoralism and wildlife conservation. There is extensive commercial wheat and irrigated flower and vegetable cultivation in eastern

Laikipia, near the growing urban centre of Nanyuki. Unusually for a landscape without government gazetted wildlife areas, Laikipia hosts the second highest densities of wildlife in Kenya, after the Maasai Mara, including the country's second largest population of elephants (Omondi, Bitok & Mayienda, 2002; Georgiadis *et al.*, 2007). Tourism based on this wildlife resource plays an increasing role in the local economy. Today there are wildlife-based tourism enterprises on 18 of the 41 large-scale ranches (2000–93 000 acres) which cover 42% of the district, and five of the nine communally owned group ranches, which collectively cover 11% of the district.

Elephant numbers in Laikipia are high today (Blanc *et al.*, 2007), but historical records suggest that this is a relatively recent phenomenon. Elephants were not observed on the Laikipia plateau by early European explorers (von Höhnel, 1894; Neumann, 1898). From the 1960s, elephants were occasional visitors to the Laikipia plains. By the late 1970s, they were present in significant numbers (Thouless, 1994). Intense poaching in Samburu District in 1970s and into the 1980s is likely to have prompted elephant immigration into Laikipia; an aerial count in 1977 estimated 2093 live elephants to 51 dead elephants in Laikipia, while in neighbouring Samburu District there were an estimated 710 live elephants to 2793 dead (Thouless, 1993).

An aerial survey of Laikipia in 2002 recorded 3036 elephants (Omondi *et al.*, 2002), an increase of *c.* 1000 individuals in 30 years. Elephant numbers have also increased in neighbouring Samburu District (Wittemyer *et al.*, 2005) suggesting *in situ* population growth in Laikipia, rather than immigration. The presence of relatively large numbers of elephants contribute to high levels of human–elephant conflict, particularly crop raiding on smallholder farms in the south of the District (Thouless, 1994; Graham, 2007). Electrified fencing has emerged as the preferred management tool for addressing this problem and a district-wide fencing configuration has been proposed on a number of occasions (Jenkins & Hamilton, 1982; Thouless, 1993; Wafula, 1998; Thouless *et al.*, 2002). In 2007, funds were secured by a local NGO, the Laikipia Wildlife Forum, to construct 163 km of fence across the district. This construction is in progress, and will change the location and severity of human–elephant conflict.

Data collection

GPS tracking data

Fifteen elephants (eight males and seven females) were fitted with GPS collars in 2004 and were monitored until April 2006, when the fieldwork component of this research project ended. GPS data continue to be collected for some of the collars in ongoing research by Save the Elephants. Collaring operations took place in April and September when the collars became available. The collars were manufactured by African Wildlife Tracking in South Africa (http://www.awt.co.za/) and were provided by Save the Elephants. A 2002 elephant distribution map (Omondi *et al.*, 2002) and an updated land-use map were used for purposively identifying locations for collaring operations with the aim of capturing elephant movement across different land-use types (Fig. 1). Elephants were immobilized using gun-propelled syringes containing between 12 and 21 mg of etorphine (Novartis International AG, Basel, Switzerland), depending on the size of the target animal and were revived using deprenorphine.

GPS telemetry units used for tracking elephants have been described in detail by Douglas-Hamilton (1998). In contrast to previous designs, the units deployed in this study used a global system for mobile communication (GSM) modem for two-way data communication through mobile phone network ground stations installed by Safaricom Ltd (Nairobi, Kenya), the largest GSM service provider in Kenya. Data could be downloaded remotely via the internet and the settings of the GPS receivers could be programmed remotely.

Because adult female elephants live with kin and their immature offspring in cohesive family units within a complex, multi-tiered social structure (Douglas-Hamilton, 1971; Moss & Poole, 1983; Wittemyer *et al.*, 2005), GPS collars deployed on adult female elephants capture the movements of an entire family group. The size of the family groups associated with each female elephant collared in this study was unknown. However, median family size for the adjacent Samburu subpopulation was nine with a range of 3–36 individuals (Wittemyer, 2001). In contrast to female elephants, male elephants become independent of their natal families after 14 years (Lee & Moss 1999), and have complex association patterns, being found alone, with other males, or family groups. Male associations are temporally and seasonally variable, depending on age and sexual state (Poole & Moss, 1989). GPS tracking results for male elephants were, therefore, held to be representative of a single individual.

Human land use

Outline data on human land use in Laikipia from digital mapping (Kohler, 1987) by the Centre for Training and Research in Arid and Semi-Arid Lands Development were updated to identify four different land-use types (smallholder, ranch, pastoral and forest). Ranches were defined as individually owned areas for commercial activity, while pastoralist areas were communally owned and managed areas for livestock grazing. Human population density is low on large-scale ranches and forest reserves (1 km^{-2}), higher on pastoralist areas (10 km^{-2}) and highest on small-scale farming areas (50–300 km^2; Thouless, 1994). A transect survey found a similar distribution of human activity across these land-use types, although human sign was relatively high in forest reserves as these are used for wood extraction and extensively to provide grazing for livestock owned by neighbouring communities (Graham, 2007). Tolerance of the presence of elephants on privately owned large-scale ranches and pastoral areas was assessed on the basis of formal and informal interviews with local landowners, managers and key informants (Graham, 2007). 'Tolerant' was defined as little or no risk to elephants of human-inflicted injury/mortality while 'intolerant' was

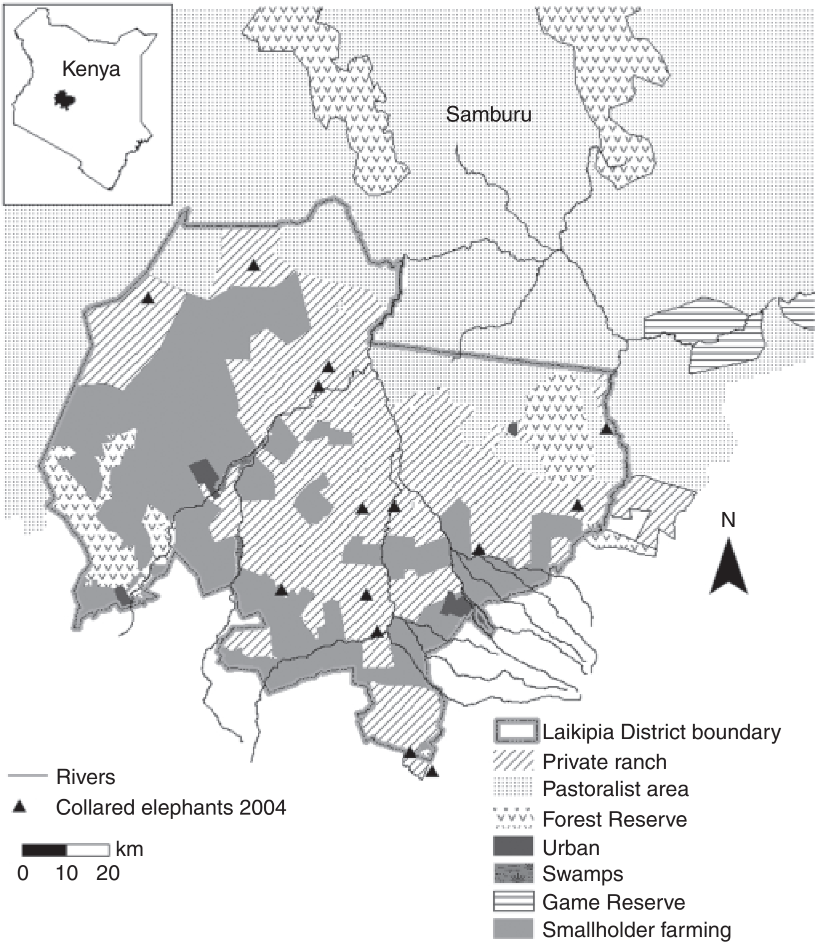

Figure 1 Laikipia District and neighbouring areas, showing land use and the location of individual elephants *Loxodonta africana* fitted with GPS collars in 2004.

defined as a risk to elephants of injury or mortality through contact with human occupants.

Land cover

A 30 m resolution land-cover raster image for Laikipia and the surrounding areas, derived from a supervised classification of two 2002 Landsat ETM scenes, was made available by Mpala Research Centre. This classified image includes 14 categories, five of which are abiotic (urban, smoke, water, ice and bare rock), eight relate to vegetation types, plus one category 'unknown'. These 14 categories were grouped into two broad categories: (1) open (i.e. grassland, cultivation or bare rock); (2) closed (i.e. woodland, forest and/or bushland).

Data analysis

All GPS collars used in this study, with one exception, were programmed to take GPS fixes every hour. As this was the highest resolution of data available, hourly fixes were chosen as the unit of analysis. However, due to technical problems associated with downloads, data storage and transmission to the database, there were occasions when data were lost. Before analysis, all elephant tracking data were filtered for spurious GPS fixes. These were identified by attributing a speed value to each GPS location, based on distance from the preceding location and time. GPS locations with highly improbable speed values ($>13\,\mathrm{km\,h^{-1}}$) were eliminated from the analysis. Occasionally GPS collars recorded more than one fix per hour and these were deleted so as to generate a dataset with hourly GPS fixes only. One collar did not function properly and data generated by this collar were removed before analysis. Another collar only generated 1.6 GPS fixes every 24 h. As approximately half of these data were daytime positions and half were recorded at night, we retained these data in the analysis. After the data were cleaned in the manner described a total of 137 816 GPS locations remained for analyses.

Before analyses, all spatial data were pre-processed in a geographical information system (GIS) using ArcGIS 9 (ESRI, 2004). This allowed us to ascribe land use, tolerance, time of day and speed values to each of the elephant GPS locations used in our analyses. Statistical tests were carried out using SPSS v. 16 (SPSS, 2002). Where data were not normally distributed they were transformed for parametric testing. In most cases, data were highly skewed and transformation did not achieve a normal distribution. However, because log transformations reduced the skew to that acceptable for parametric statistical testing and samples sizes were large, we used non-parametric tests only where distributions were extreme.

To test how the time spent by elephants in different parts of the Laikipia landscape was associated with risk, we assessed elephant use with availability of each of four types: (1) ranch; (2) smallholder; (3) pastoral; (4) forest. Elephant use was calculated as the proportion of an animal's tracking locations that fell within a particular land-use type, while availability was calculated as the proportion of an animal's total home range, as measured by minimum convex polygons (MCPs) that fell within a particular land-use type. MCPs were calculated using the Animal Movement Extension to ArcView (Hooge & Eichenlaub, 1997). While MCP home-range estimates overestimate space use (Harris *et al.*, 1990; Kernohan, Gitzen & Millspaugh, 2001; Douglas-Hamilton *et al.*, 2005), they are used here to indicate the total potential area available to each elephant.

Elephant use in land-use types, by day or night, was normally distributed. The proportion of time that each elephant spent in each different land-use category was correlated with the availability of each land-use category to that elephant. Matched *t*-tests were used to compare the proportion of time spent during the day with proportion of time spent at night within each land-use type.

Speed of elephant movement was calculated as the distance between consecutive locations divided by time ($km\,h^{-1}$). We tested for a variation in speed among the elephants monitored in response to different situations of risk by comparing speed values among different land-use categories, by habitat cover and by time of day. Speed of movement was highly skewed, and was log transformed for parametric analysis. Log transformation removed the majority of the skew (from 4.5 to −0.6) but data still did not conform to a strictly normal distribution. Given the large sample size and therefore general power of the statistical tests, the use of parametric statistics was justified, with the proviso that we were cautious in assessing our effect sizes. We used an analysis of variance with a type I (hierarchical) model to assess the factors influencing speed of elephant movement, with Bonferroni *post hoc* tests for comparisons of three or more groups and *t*-tests for *post hoc* comparisons between two groups.

Results

Elephant movement in relation to human land use

A total of 137 816 locations from 2004 to 2006 from 13 elephants were available for analyses. The average home-range size, as measured by MCPs, recorded among the elephants monitored was 1537 km^2 (±446.6, $n = 13$). Distribution of elephant locations across the four human land-use types varied significantly from that expected based on land use availability ($\chi^2 = 30\,911.3$; d.f. = 3; $P<0.001$). The elephants monitored consistently preferred ranches (mean availability: 58%; mean occupancy: 76%), and to a lesser extent, forest reserves (mean availability: 5%; mean occupancy: 10%) over smallholder land (mean availability: 22%; mean occupancy: 8%) and pastoral land (mean availability: 14%; mean occupancy: 5%). A similar pattern emerged when diurnal and nocturnal locations were analysed separately. The per cent of elephant use correlated with area available within ranches overall, and during the day and night ($r = 0.678$ overall, 0.640 day, 0.678 night, $P<0.05$, $n = 12$). For smallholder areas, however, elephant use was correlated with availability only during the night ($r = 0.633$, $n = 12$, $P = 0.03$; Fig. 2). Elephant use was unrelated to either pastoral land or forest availability during either the day or the night.

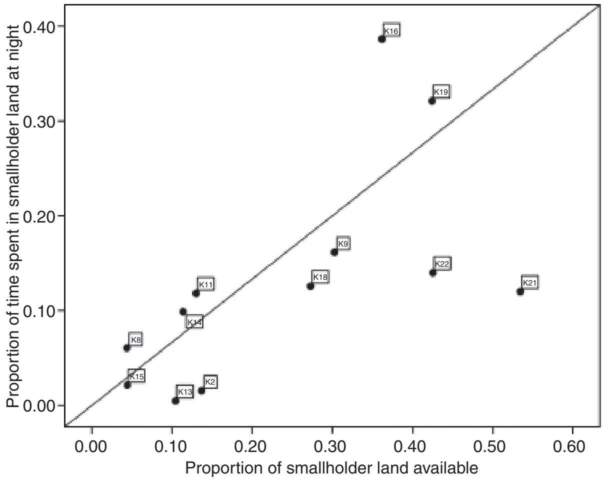

Figure 2 Proportion of nocturnal locations in smallholder areas at night compared with proportion of smallholder land available within 100% minimum convex polygons.

There were also marked differences in intensity of elephant use among each of the four land-use types between day and night (Fig. 3). At night, elephants spent significantly less time in ranches ($t = -4.69$, d.f. = 11, $P = 0.001$), and significantly more time in smallholder areas ($t = 3.83$, d.f. = 11, $P = 0.003$) than during the day. They also tended to spend less time in forest reserves at night than by day ($t = -2.18$, $P = 0.066$, d.f. = 7). These differences between day and night are illustrated by the nocturnal and diurnal locations of K16, a habitual crop-raiding male elephant, in Fig. 4. This spatial use pattern explains why home ranges based on nocturnal location data were consistently and significantly larger than home ranges based on diurnal data across the sample of elephants tracked in this study [median day = 846.3 km, interquartile range (IQR) = 953.7; median night = 981.4, IQR = 1253.1; Mann–Whitney $z = -2.97$, $P = 0.004$, $n = 13$ for 100% MCPs]. While the overall comparisons suggested that elephants generally avoided smallholder areas, the absolute extent of use of smallholder areas varied considerably among individuals (Table 1), with for example K16, an adult male crop-raiding elephant, appearing to demonstrate a preference for smallholder areas at night.

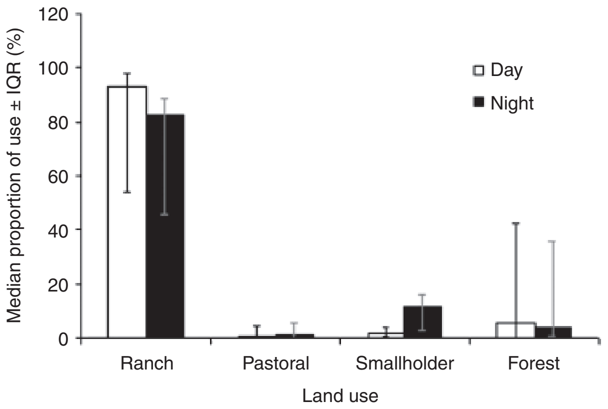

Figure 3 Comparison of median proportion of elephant *Loxodonta africana* use of different land-use types during day and night.

Speed of elephant movement within different land-use types

On average the monitored elephants moved at a speed of $0.36\,\mathrm{km\,h^{-1}}$ ($n = 137\,416$), although this varied significantly among land-use types (ANOVA $F_{3,132\,972} = 741.46$, $P < 0.001$, Bonferroni *post hoc* tests, all $P < 0.001$). Elephants moved fastest in smallholder areas (mean-$0.52\,\mathrm{km\,h^{-1}}$; $n = 11\,819$) followed by pastoralist areas (mean = $0.42\,\mathrm{km\,h^{-1}}$; $n = 7027$), private ranches (mean-$0.35\,\mathrm{km\,h^{-1}}$; $n = 105\,858$) and slowest in forest reserves (mean = $0.23\,\mathrm{km\,h^{-1}}$; $n = 12{,}697$).

Speed varied significantly between day and night ($F_{1,13\,972} = 2241.4$, $P < 0.001$) as well as varying by land-use types between day and night (ANOVA, interaction $F_{3,13\,972} = 434.4$, $P < 0.001$). Within ranches, elephants moved more quickly during the day than at night, while the opposite pattern was evident within smallholder areas, pastoral areas and forest reserves (Fig. 5).

Speed of movement was significantly different between elephant-intolerant private ranches (mean = $0.43\,\mathrm{km\,h^{-1}}$, $n = 5597$) and on tolerant ranches (mean = 0.35; $n = 100\,261$; $F = 176.5$, $P < 0.001$). This effect was

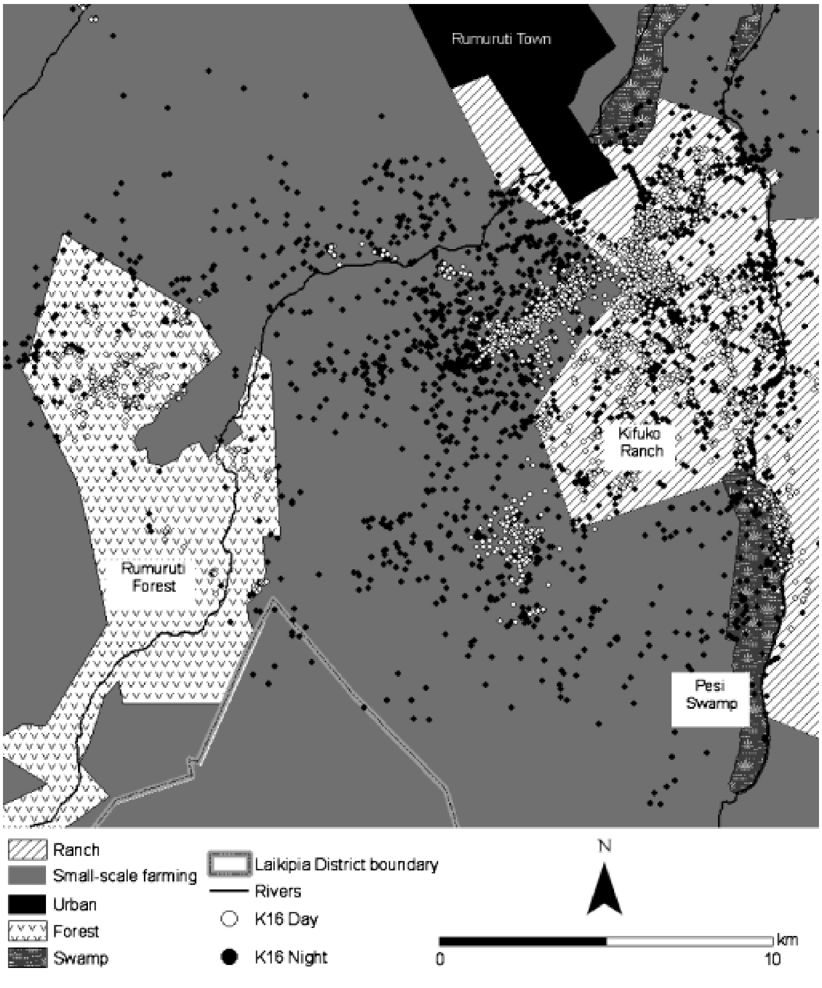

Figure 4 Diurnal and nocturnal locations for K16 in south-west Laikipia. Diurnal minimum convex polygon = $2775.5\,\mathrm{km^2}$, nocturnal minimum convex polygon = $3126.70\,\mathrm{km^2}$. These location data illustrate differences in diurnal and nocturnal use of space in a land-use mosaic.

Table 1 100% minimum convex polygons (MCP) and proportion of time spent in different land-use types among elephants in Laikipia

		n			Ranch			Pastoral			Smallholder			Forest		
ID	Sex	day (night)	Period tracked	MCP (km^2)	A	Ud	Un	A	Ud	Un	A	Ud	Un	A	Ud	Un
K09	♂	11 853 (11 442)	23/04/04–20/04/06	2177	0.70	0.91	0.84	0.00	0.00	0.00	0.30	0.09	0.16	0.00	0.00	0.00
K02	♂	8363 (8357)	21/04/04–18/04/06	1439	0.70	0.99	0.96	0.11	0.01	0.01	0.14	0.00	0.02	0.04	0.00	0.01
K11	♂	6440 (6173)	24/04/04–18/04/06	665	0.59	0.95	0.84	0.15	0.01	0.02	0.13	0.02	0.12	0.13	0.02	0.02
K21	♂	6381 (6162)	12/10/04–18/05/06	1021	0.45	0.99	0.88	0.00	0.00	0.00	0.53	0.01	0.12	0.02	0.00	0.00
K15	♂	5613 (5495)	04/05/04–18/03/06	6235	0.28	0.41	0.32	0.59	0.50	0.59	0.04	0.00	0.02	0.08	0.08	0.07
K16	♂	5186 (5137)	04/05/04–18/04/06	3127	0.61	0.71	0.59	0.02	0.00	0.01	0.36	0.25	0.39	0.01	0.04	0.02
K19	♂	2497 (2583)	28/08/04–19/05/05	967	0.34	0.56	0.39	0.00	0.00	0.00	0.42	0.03	0.32	0.23	0.41	0.29
K18	♂	343 (326)	18/08/04–25/11/05	1048	0.32	0.98	0.87	0.40	0.01	0.01	0.27	0.02	0.12	0.00	0.00	0.00
K14	♀	8227 (8203)	22/04/04–20/04/06	1190	0.83	0.95	0.90	0.05	0.00	0.00	0.11	0.05	0.10	0.00	0.00	0.00
K22	♀	7172 (7080)	13/10/04–18/04/06	530	0.49	0.54	0.47	0.00	0.00	0.00	0.42	0.01	0.14	0.09	0.44	0.39
K08	♀	3991 (3777)	20/12/03–10/01/05	748	0.35	0.43	0.46	0.53	0.06	0.07	0.04	0.04	0.06	0.07	0.47	0.41
K20	♀	2197 (2142)	18/08/04–08/08/05	64	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
K13	♀	1226 (1215)	04/05/04–01/08/05	774	0.89	0.99	0.99	0.00	0.00	0.00	0.10	0.00	0.01	0.00	0.00	0.00

A, proportion of land use type available within the home range of the elephant; Ud, proportion of diurnal locations that fall within the land-use type; Un, proportion of nocturnal locations that fall within the land-use type.

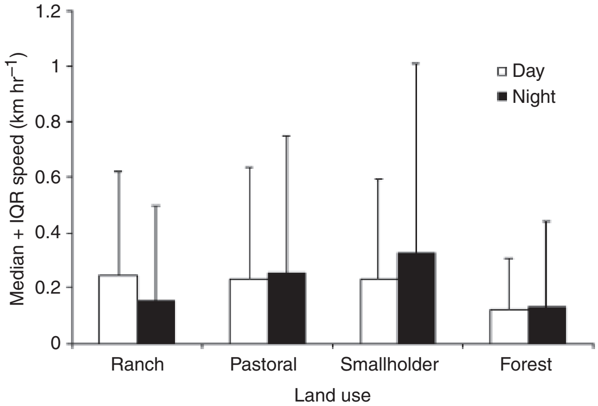

Figure 5 Speed of elephant *Loxodonta africana* movement within four different land-use types at night and at day. Median values and interquartile range (IQR).

particularly marked between day and night (ANOVA interaction: $F = 510.1$, $P < 0.001$). Elephants moved faster at night on intolerant ranches ($t = -22.3$, d.f. = 5597, $P < 0.001$), while the opposite was the case for elephant-tolerant ranches ($t = 8.9$, d.f. = 100 638, $P < 0.001$). On ranches, there was a further interaction between tolerance and cover ($F = 7.7$, $P = 0.005$), such that while speed was greater in the intolerant ranches, it was also significantly faster in open than closed habitats.

Discussion

The elephants monitored in this study preferred areas with low levels of human activity, especially large-scale ranches. This is broadly consistent with previous studies of large mammal distribution in relation to anthropogenic factors (Parker & Graham, 1989; Eltringham, 1990; Barnes *et al.*, 1991; Hoare & Du Toit, 1999; Blom *et al.*, 2005). However, more detailed GPS tracking data analyses show that some of the elephants monitored did typically use areas, in particular smallholder land, pastoral areas and forest reserves where human use and associated risk were far higher. Hoare (1999) proposed that movement by an elephant into settled areas exposed it to disturbance or predation by humans. This is certainly the case on smallholder land in Laikipia where elephants have been killed in defence of crops both legally, by the wildlife authorities, and illegally by local farmers (Thouless, 1994; Graham, 2007). On pastoral land in Laikipia and adjacent Samburu District, ivory poaching has been significant in the past but is today reduced to low levels. However, conflict with livestock over water or grazing continues to be a major cause of elephant mortality (Thouless, 1994; Wittemyer *et al.*, 2005; Graham, 2007). Therefore, use of smallholder, pastoralist areas and forests among the elephants monitored exposed them to predation risk associated with human occupants. By using high-resolution GPS tracking data, we demonstrate that elephants alter their behaviour in response to this risk.

While it is well known that African elephants use the cover of darkness to move onto smallholder land where they raid crops through evidence provided by inferential studies (Bell, 1984; Hillman Smith *et al.*, 1995; Hoare, 1995; Tchamba, 1996; Sitati *et al.*, 2003), we were able to demonstrate this fact directly using high-resolution GPS tracking data. The use of the cover of darkness as a risk-avoidance strategy appears to be consistent with the limited research carried out into temporal patterns of elephant movement in relation to protected and unprotected areas (Lewis, 1986; Galanti *et al.*, 2006; Wittemyer *et al.*, 2007). For example, elephants in Zambia were observed to be more active at night once outside of park boundaries (Lewis, 1986). Radio-collared elephants in the Tangire–Manyara ecosystem in Tanzania were more active at night outside of protected areas compared with inside protected areas (Galanti *et al.*, 2006). In and around Samburu Game Reserve in north

Kenya radio-tagged elephants spent more time near permanent rivers during the day inside protected areas compared with outside of protected areas where elephants spent more time near permanent rivers at night (Wittemyer *et al*., 2007). In this latter case the pattern of spatial partitioning in time was most likely due to the presence of livestock and herders near rivers during the day outside of protected areas. Limited evidence suggests that other species also use the cover of darkness to exploit resources within human-occupied areas such as cougars *Puma concolor* (Van Dyke *et al*., 1986; Beier, 1995); bears *Ursus arctos horribilis* (Aune & Kasworm, 1989) and golden jackals *Canis aureus* (Admasu *et al*., 2004). However, this is the first time to our knowledge that this particular form of risk-avoidance behaviour among elephants has been demonstrated across a range of different land-use types outside of gazetted protected areas.

The variation in the speed of movement among the elephants monitored in relation to human land use and the associated tolerance of land owners, managers and occupants, further confirms that elephants are actively managing risk via their behaviour. Once again this finding is consistent with the limited research into speed of elephant movement in relation to protected areas. For example, Douglas-Hamilton *et al*. (2005) and Galanti *et al*. (2006) demonstrated that speed of elephant movement was higher outside of protected areas compared with inside protected areas.

The behavioural response to risk in human-dominated landscapes demonstrated in this paper has implications for conservation in several ways. Firstly, these results suggest that elephants can help to maintain connectivity between refugia (Fahrig, 1988) by moving at night and at speed across the intervening human-dominated matrix. There was some evidence that the elephants monitored did exactly this. For example, two of the elephants monitored (K19 and K22) regularly used the cover of darkness to move relatively quickly across a main road and 7 km of small-scale farming land separating a large-scale private ranch and a forest reserve. Other recent studies of elephant movement have described similar behaviour among elephants moving across the human-dominated matrix between protected areas (Douglas-Hamilton *et al*., 2005; Galanti *et al*., 2006). Maintaining connectivity between refugia could improve the prospect of elephant persistence in the wider Laikipia landscape at three levels (Weaver *et al*., 1996). At an individual level, such connectivity allows elephants to meet their nutritional requirements through access to food resources that are otherwise scarce in space and time. At a population level, the maintenance of connectivity between refugia allows elephants to respond to stochastic events, such as drought or a sudden surge in poaching, through the process of dispersal or migration. Lastly, such connectivity also allows elephants to survive as a meta-population, reducing the size necessary for each sub-population to be viable through regular genetic exchange (Meffe & Carroll, 1997).

While acceptance of corridors as tools for conservation far outpaces scientific understanding of their efficacy (Bennet, 2003), given that the elephants monitored demonstrate risk-avoidance behaviour that facilitates connectivity, securing corridors between existing refugia, even if of limited habitat quality, could enhance the persistence of elephants in the Laikipia landscape into the future. Human population density and associated disturbance to wildlife remains relatively low across much of the Laikipia landscape, particularly among privately owned commercial ranches. However, the increasing number of armed pastoralists and their stock in the north and the expansion and intensification of agriculture in the south, is leading to fragmentation and associated isolation effects. Therefore the identification of existing or appropriate elephant corridors between refugia should be a priority for local conservation actors.

Secondly, the ability of elephants to adapt their behaviour to penetrate into and exploit habitat elements within human-dominated landscapes underlies the high correlation found in this study between the area under smallholder land within elephant home ranges and the proportion of time spent by elephants in smallholder land at night. The human–elephant conflict that results undermines local livelihoods and creates hostility to wider conservation programmes (Hoare, 2000; Lee & Graham, 2006). Therefore the increasing fragmentation of elephant ranges outside protected areas in Kenya and other areas, particularly West Africa (Roth & Douglas-Hamilton, 1991; Blanc *et al*., 2007) presents a major challenge for elephant conservationists and managers. This confirms the importance of preventing fragmentation in the first place through appropriate land-use planning and the creation of incentives for the continued protection of large and contiguous refugia. However, where fragmentation has already occurred a combination of conservation planning to allow for a network of refugia connected by corridors, and the application of human–elephant conflict mitigation tools such as farm-based deterrents (Graham & Ochieng, 2008) and electrified fencing (Thouless & Sakwa, 1995), may enable some elephant populations to persist into the future.

While our results demonstrate significant differences in the timing, residence and speed of elephants in response to human land use, our delineation of land-use categories was coarse. More compelling results might be achieved with a finer delineation of land use and cover, with a view to better defining spatial distribution of refugia and risk within human-dominated landscapes. This would provide the basis for studying movement between refugia and sub-populations and could aid our understanding of metapopulation dynamics and the use of corridors among elephants and how natural and human processes influence elephant persistence at the landscape level. There would also be merit in distinguishing between different types of movement such as, for example, temporary incursions into settlement, seasonal migrations and dispersal to better understand the determinants underlying variations in speed of movement across an elephants range. In fragmented human-dominated landscapes, or in other conditions of high risk, behaviour such as that described here may represent facultative responses to local risk conditions and differ from the norm observed in protected areas. Further research into elephant movement behaviour in such contexts, such as assessments of associations between sexes or the maintenance of large aggregations (e.g. Abe, 1994) is vital for understanding the capacity of elephants to survive in the modern African environment, and for crafting conservation strategies that are effective in reducing crop raiding and building tolerance of large mammals among rural communities. The methods used here to track movements day and night may have application in the conservation of other species involved in human–animal conflict, such as other crop raiders or predators.

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