Movement tortuosity and speed reveal the trade-offs of crop raiding for African elephants

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ARTICLE INFO

Animals living in heterogeneous landscapes are often faced with making a trade-off between maximizing foraging success and avoiding risk. Using high-resolution GPS-tracking data, this study explored the fine-scale movement patterns and risk sensitivity of crop-raiding African elephants, Loxodonta africana, in the anthropogenic landscape of Tsavo, Kenya. We analysed patterns in the speed and tortuosity of elephant movements over the 24 h surrounding crop-raiding events and compared them with those of nonraiding elephants during corresponding periods. Crop-raiding elephants moved faster and straighter (less tortuously) with closer temporal proximity to farmland, which we argue reflects their increased intensity of risk avoidance behaviours in response to approaching humans. Once inside farmland, elephants appeared to reduce movements associated with risk avoidance to forage intensively on crops, decreasing their speed and reducing the likelihood of moving in straight lines while crop raiding. These results highlight trade-offs in the fine-scale movement patterns of elephants living in anthropogenic landscapes with differing levels of habitat quality and exposure to humans, providing new insight into how they perceive the risks associated with crop raiding.
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Predator-sensitive foraging describes the trade-off animals often make when living in heterogeneous landscapes, where they must find a balance between foraging on high-quality resources and avoiding predation risk (reviewed by Verdolin, 2006). An animal's 'landscape of fear' is a measure of how it perceives the surrounding environment as a result of the cost−benefit analysis of foraging in such landscapes, and can assist in explaining patterns in its space use (Bleicher, 2017; Laundré, Hernández, & Ripple, 2010).

While foraging, animals will often alternate between two distinct movement strategies that can be described in terms of their speed and tortuosity, or the extent to which they twist and turn along a path. 'Intensive' searches are expected in areas of high resource availability, and can be characterized by low speed and high tortuosity, thereby maximizing the time spent in areas of rich resources (De Knegt, Hengeveld, Van Langevelde, De Boer, & Kirkman, 2007; Hoskins, Costa, & Arnould, 2015). On the other hand, when resource density is low it may be more efficient to perform extensive searches, moving straighter and faster to cover an area in less detail (Barraquand & Benhamou, 2008; Hein, Gombert, Hovestadt, & Poethke, 2003). Patterns in the speed and tortuosity of movement can also be used to describe how animals avoid predation. Animals will often increase their speed (Cooper Jr., 2003; Graham, Douglas-Hamilton, Adams, & Lee, 2009) and decrease their path tortuosity (Hodges, Cunningham, & Mills, 2015; Ihwagi et al., 2019) to minimize the time spent in unsafe areas or escape predators. Foraging in resource-rich but unsafe areas therefore presents the animal with a trade-off between moving slowly and in a more tortuous manner to increase foraging efficiency and moving faster with less tortuosity to avoid risk.

Human−elephant conflict, specifically crop raiding by African elephants, Loxodonta africana, is widespread across Africa (Chase et al., 2016; Hoare, 2000). When crop raiding, elephants are likely to perform intensive foraging behaviour (as they raid farmland), but are equally likely to avoid risk as they come into contact with humans, who are likely to retaliate. It is well documented that at

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certain times of the year the nutritional value of crops outweighs that of natural forage (Branco et al., 2019; Rode, Chiyo, Chapman, & McDowell, 2006; Sukumar, 1990; Sukumar & Gadgil, 1988), and as a result crop-raiding elephants have been found to maintain high nutritional levels (Pokharel, Singh, Seshagiri, & Sukumar, 2019). However, crop raiding also poses a significant risk to the survival of elephants through injury from farmers (Mijele et al., 2013; Obanda et al., 2008). It therefore presents elephants with the trade-off between moving more slowly and tortuously to maximize foraging efficiency during relatively short bouts in resource-rich farmland and moving faster and straighter to avoid the risk of retaliatory attack by farmers.

Elephants have been shown to exhibit strong risk avoidance behaviour around humans, moving faster through areas presenting a risk of mortality (Blake et al., 2008; Douglas-Hamilton, Krink, & Vollrath, 2005; Graham et al., 2009), and spending more time at night than during the day in these risky areas (Graham et al., 2009; Ihwagi et al., 2018). They also move with lower tortuosity in core areas with high poaching levels than in those with lower poaching levels (Ihwagi et al., 2019), and similarly with lower tortuosity and faster speed when moving through corridors than in their core range when stressed (Jachowski, Slotow, & Millspaugh, 2013). In comparison, while foraging elephants will increase their tortuosity in favourable areas (Duffy, Dai, Shannon, Slotow, & Page, 2011; Vanak, Thaker, & Slotow, 2010), they increase their speed in areas of low forage resources (Gara et al., 2017).

We investigated patterns in the fine-scale movement of African elephants over 24 h periods in the anthropogenic landscape of Tsavo, Kenya. A number of studies have analysed patterns in the daily movement speed of elephants (Ihwagi, 2018; Ngene, 2010; Wilkie & Douglas-Hamilton, 2018), yet only Wilkie and Douglas-Hamilton (2018) have additionally included an index of linearity, and focused on movement specifically around farmland. Their study provides a descriptive analysis of three distinct patterns of crop raiding, using GPS-tracking data from one habitual crop-raiding bull elephant in the community lands adjacent to Kenya's Amboseli National Park. Our study builds on their work, presenting a statistical analysis of the movement of multiple male and female crop-raiding and nonraiding elephants over multiple years and seasons. We discuss our results in the context of predator-sensitive foraging and antipredator behaviours, providing one of the first insights into how elephants (as opposed to humans) may perceive crop raiding. Specifically, our study sought to understand changes in the movement speed and tortuosity of crop-raiding elephants throughout the day, defined by the hours before, during and after crop raiding. We then compared these movements with those of nonraiding elephants representing average or 'normal' behaviour, during corresponding periods.

Crop-raiding elephants are likely to experience a landscape of fear that varies depending on whether they are on their way to entering farmland, actively engaging in crop raiding or have recently left farmland. By comparison, elephants that do not raid crops may be expected to experience fear more constantly throughout the day. As such, we predicted the period would have a significant effect on the movement of crop-raiding elephants. We hypothesized (H1) that with increasing time before or after crop raiding, elephants would exhibit reduced intensities of antipredator behaviours, such that their movement speed and tortuosity would more closely resemble that of nonraiding elephant movement. In addition, we hypothesized (H2) the risk associated with crop raiding to be outweighed by the benefits of foraging intensively on crops, such that elephants would decrease their speed and increase their tortuosity while in farmland.

METHODS

Study Area

The Tsavo Conservation Area (TCA) covers approximately 42 000 km^2 in southeastern Kenya (-2°57′59.99″S, 38°27′59.99E). Tsavo East and Tsavo West National Parks occupy an area of 21 000 km^2 (Smith & Kasiki, 2000), and together with the Chyulu Hills National Park form the largest Protected Area in Kenya. The Taita Taveta County separates the Tsavo National Parks, and acts as a vital corridor and dispersal area for wildlife travelling between the two areas (Smith & Kasiki, 2000; Williams, Bartholomew, Amakobe, & Githiru, 2018). Taita Taveta largely comprises agricultural areas, as well as human settlements, private ranches and conservancies. In 2015 the County's human population stood at 329 000, with the most common livelihood being small-scale farming (MoALF, 2016). Tsavo is also home to an estimated 12 866 elephants (Ngene et al., 2017), the largest population of elephants in Kenya and one of the largest in Africa.

The climate in Tsavo is semiarid, with bimodal rainfall. The short, heavy wet season occurs from November to December, followed by the long, weaker rains from March to May (Omondi, Bitok, Mukeka, Mayienda, & Litoroh, 2008). Spatial and temporal patterns of rainfall are unpredictable, ranging from 250 to 700 mm with an average of 550 mm annually (Ngene et al., 2014; van Wijngaarden, 1985). There are two permanent water sources (the Galana and Tsavo Rivers), in addition to several seasonal rivers (including the Tiva and Voi Rivers; van Wijngaarden, 1985).

Position Data and Path Speed and Tortuosity Calculation

The movements of nine (five female and four male) African elephants fitted with AWT Satellite collars in March 2016 and 19 (nine female and 10 male) elephants fitted with Savannah Tracking GL200 GPS collars in January 2018 were analysed from the time of their collaring until April 2019, leading to a total of 28 GPS-collared elephants used in the study. All collars were deployed in a collaboration between Save the Elephants, the Kenya Wildlife Service and the Tsavo Trust. Each collar was programmed to record a GPS location every hour, as a trade-off between maximizing battery life and acquiring high-frequency data. However, we acknowledge that this may have resulted in some more fine-scale risk avoidance behaviours having not been captured. Hourly GPS locations were transmitted in real time to a centralized database where the data could be accessed remotely and were projected on the Universal Transverse Mercator (UTM) WGS-84 reference system.

Movement speed (km/h) was calculated by Save the Elephants' Real-time Monitoring (RTM) system, using the locational (coordinate) data. The spherical law of cosines was used to calculate the distance travelled between two consecutive fixes, which was then divided by the time interval between those two fixes (Wilkie & Douglas-Hamilton, 2018). The locational data were also applied to calculate tortuosity as a measure of straightness, using the trajr package (McLean & Skowron Volponi, 2018) in R version 3.5.1 (R Core Team, 2019). The straightness index (Batschelet, 1981) is calculated as the ratio D/L (where D is the distance travelled and L is the path length), and ranges between 0 and 1 (where 1 is perfectly straight). A summary of our R code is provided in the Supplementary Material.

Identification and Isolation of Crop-Raiding Events

Identification and isolation of elephant crop-raiding events was completed in ArcMap 10.6.1 (ESRI, 2019), and a summary of steps can be seen in Fig. 1. We created a polygon data set of cropland in

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│ Shape files of IUCN Gazetteer data for Kenya and Protected Areas  │
│          of Kenya clipped according to study site                 │
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│ 8 km buffer created around Populated Areas exported from          │
│                      Gazetteer data                               │
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│ NoData set outside raster data set of 8 km buffer around          │
│ Populated Areas, and inside Tsavo National Parks from IUCN        │
│             Protected Areas raster data set                       │
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│ Raster data sets of 8 km buffer and IUCN Protected Areas          │
│ multiplied together to identify land cover within 8 km of         │
│        Populated Areas outside Protected Areas                    │
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│ ESA land cover and cropland data extracted for areas within 8 km  │
│ of Populated Areas and outside Protected Areas, converted to a    │
│                      shape file                                    │
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│ Select by Location function used to identify GPS tracks that      │
│            intersected cropland shape file                        │
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│ Manual verification of GPS tracks intersecting farmland against   │
│          a base map of high-resolution imagery                    │
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│ 24 h periods of GPS tracks surrounding a crop-raiding event       │
│     isolated, with tracks inside farmland located in the centre   │
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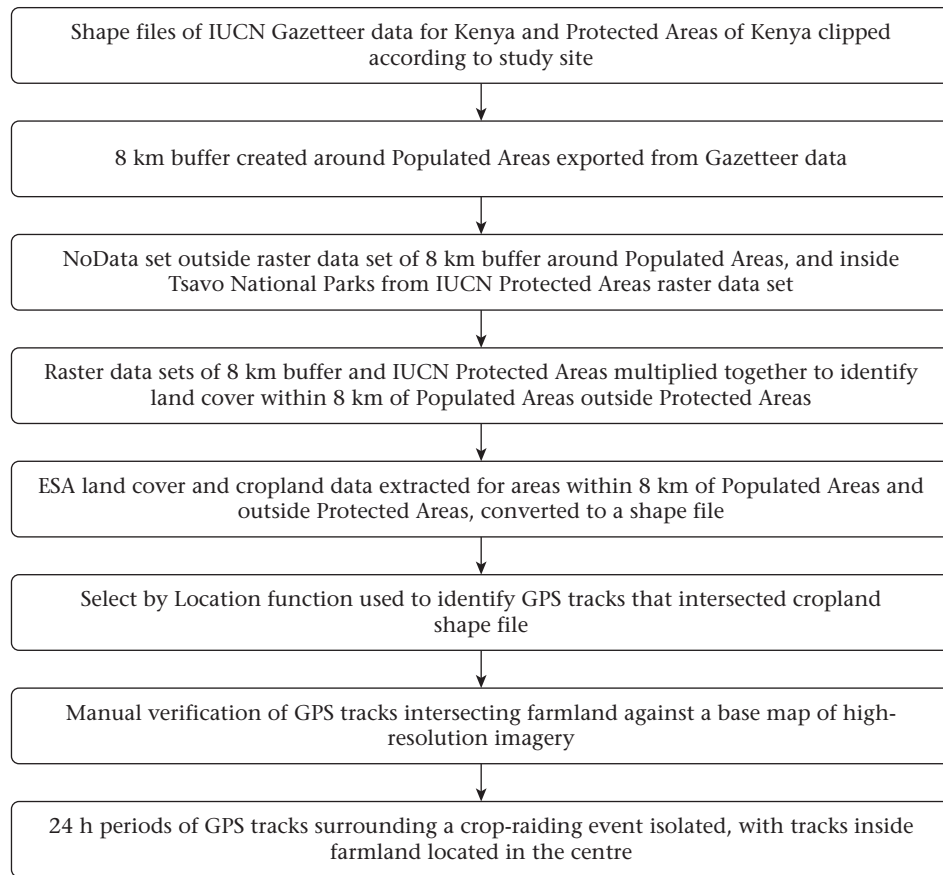
Figure 1. Flow diagram summarizing steps taken to identify and isolate crop-raiding events in ArcMap 10.6.1.

the study area using ESA Africa land cover data (ESA, 2019), then applied the Select by Location function in ArcMap to identify any locations where the tracking data of each elephant intersected this polygon. Briefly, shape files of IUCN Protected Areas for Kenya and Gazetteer (geographical index) data for Kenya were clipped according to the study site, and then an 8 km buffer was created around populated areas exported from the Gazetteer data. Raster data sets of the 8 km buffer with NoData (absence of data) set outside the buffer, and the IUCN Protected Areas with NoData set inside the Tsavo National Parks, were then multiplied together to identify land cover within 8 km of populated areas outside Protected Areas. ESA land cover data and cropland data were finally extracted for areas within 8 km of populated areas and outside Protected Areas and converted to a shape file for use with the Select by Location function and elephant tracking data. Incursion into farmland was considered indicative of crop raiding, as it is unlikely that elephants enter and exit farmland without foraging on crops. To ensure that no clear crop-raiding events were missed, each section of all elephant tracks was additionally manually verified against a base map of high-resolution imagery in ArcMap.

Once a crop-raiding event was identified, 24 h periods of the tracks were isolated, with tracks occurring in farmland positioned in the centre of the period. An equal number of tracks before and after the central crop-raiding event that brought the entirety of the isolated period to 24 h were then added. In this way, for each 24 h period surrounding a crop-raiding event, the number of tracks before (BC), during (DC) and after crop raiding (AC) were variable. The movement behaviour of crop-raiding elephants before and after crop raiding was predicted to vary with increasing distance from farmland. Therefore, we further separated the BC and AC crop-raiding periods of the GPS data into the tracks less than 3 h directly before and after crop raiding, and the tracks more than 3 h before and after crop raiding (the remaining hours of movement making up the BC and AC periods). Movement behaviour was hence assessed based on temporal, and not spatial, proximity to farmland. A common pattern has been reported whereby elephants leave national parks during night hours, raid farms and then return to the national parks by the morning. This suggests that in the hours immediately after crop raiding, elephants are increasing their distance from farmland; therefore, we did not consider it necessary to additionally analyse spatial proximity. We used 3 h as a time interval because three location points are the minimum number required to calculate a value of tortuosity (two points is a straight line), and using more than 3 h would not have allowed a sufficient number of time points within the 24 h period to define each of the five periods (more than 3 h BC, less than 3 h BC, DC, less than 3 h AC, more than 3 h AC) if a crop raid lasted >12 h.

From the sample of 28 collared elephants, we identified 12 crop-raiding elephants (nine male and three female), totalling 243 crop-raiding events between them. We removed from the analysis any 24 h periods that were missing one or more hourly fixes of GPS location data, or that could not be clearly separated into BC, DC and AC periods,. This resulted in 212 clear 24 h periods surrounding (including) crop-raiding events (5088 locations). A map of the study area including the ESA cropland layer and all crop-raiding and nonraiding elephant movement tracks analysed in the study can be seen in Fig. 2.

Nonraiding Elephant Movements

For comparison, nonraiding elephant movement data representing 'normal' or average behaviour were analysed against the speed and tortuosity of elephant movement in association with crop-raiding events. In R (R Core Team, 2019), we filtered all 24 h periods of movement data that directly corresponded (i.e. same date and time, from the same sex) with each 24 h period surrounding a crop-raiding event, from all of the remaining (by default, nonraiding) 16 (11 female and five male) collared elephants where movement data were recorded (24 399 locations). This included identifying movement data within the 24 h periods that specifically corresponded to the five periods separated for crop-

raiding elephant movement data. Our analysis of the speed and tortuosity of crop-raiding elephants included a single combined category for nonraiding elephants that grouped data over the five periods, labelled 'NC'.

Factors Influencing Speed and Tortuosity

During the 3-year study period, Tsavo experienced marked extremes in weather (most notably a devastating drought in the second half of 2016, which extended until the end of 2017). Elephants have been shown to display distinct 'break-points' in speed at the end of the dry and wet seasons (Birkett, Vanak, Muggeo, Ferreira, & Slotow, 2012), and move faster during the
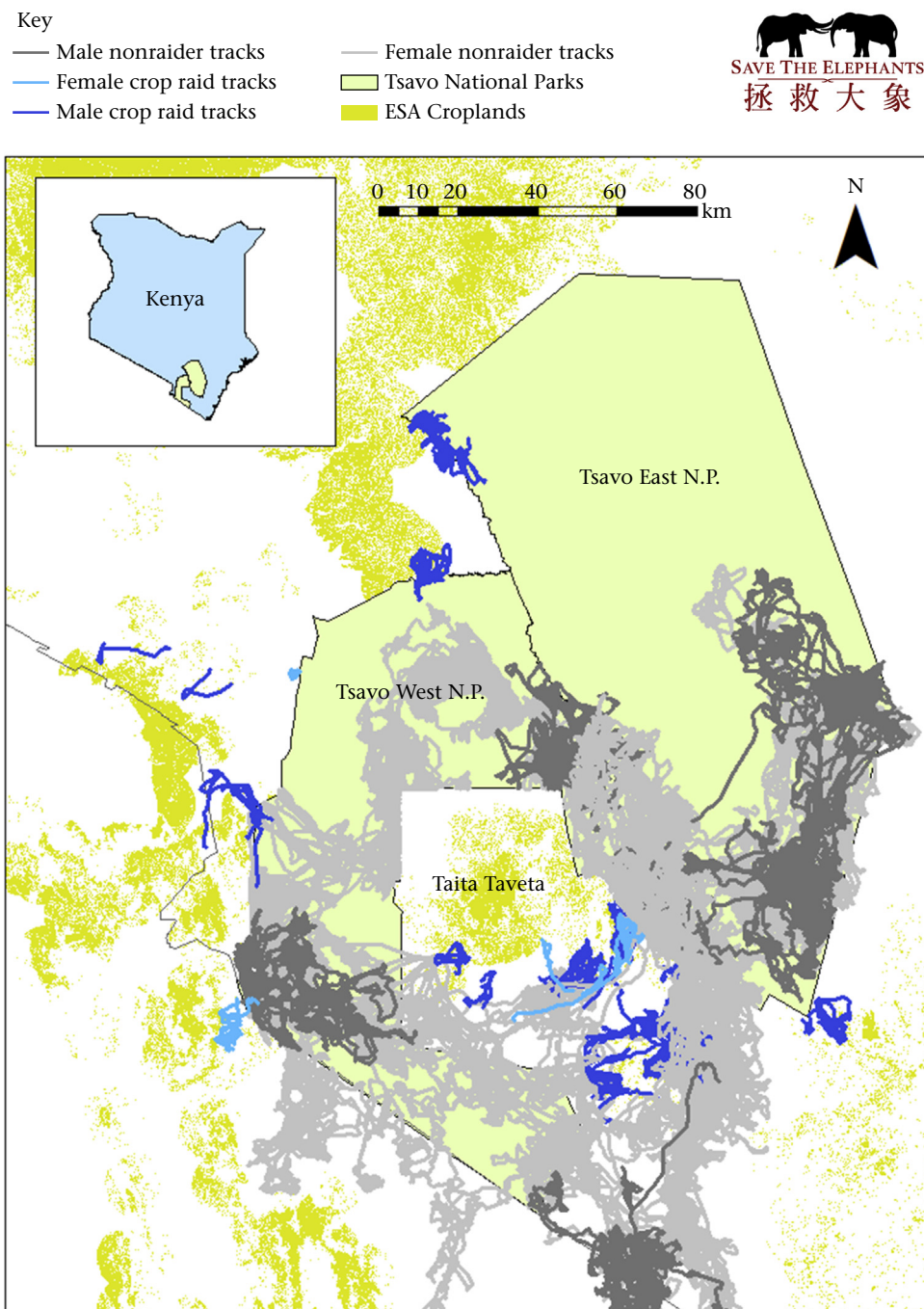
Figure 2. Map of the study area. Female and male crop raid tracks (24 h periods) are presented with nonraiding female and male elephant movement tracks during the study period (March 2016–April 2019). Data source: Save The Elephants/Kenya Wildlife Service.

intermediate and wet seasons (Mills et al., 2018; Ngene et al., 2010); therefore, we considered the potential effect of season on the speed and tortuosity of elephant movement. As rainfall is highly variable and unpredictable in Tsavo, we defined seasons based on daily rainfall records. Those collected by the Tsavo East Research Center staff (captured from a rain gauge located at the Research Center, inside the Tsavo East N.P. Voi Entrance) were averaged with those collected by Save the Elephants' Elephants and Bees Project (captured from a rain gauge at the Projects Research Center, located in the small-scale farming community of Sagalla, adjacent to Tsavo East N.P). Wet, early dry and late dry (drought) seasons were then defined following the methods of Rasmussen, Wittemyer, and Douglas-Hamilton (2006), based on the amount of precipitation required to bring about a vegetative response.

Elephants have been shown to increase their speed when crossing unprotected roads (Blake et al., 2008), as well as towards the beginning and end of a trip to water (Chamaillé-Jammes, Mtare, Makuwe, & Fritz, 2013). They also decrease their tortuosity when needing to get to water sources quickly (Duffy et al., 2011). Therefore, the Nairobi-Mombasa highway running between Tsavo East N.P. and the adjacent farming villages in Taita Taveta County was considered a potential factor influencing the speed of elephants moving to and from the two areas. In addition, the presence of waterholes and permanent rivers/lakes (specifically the Galana and Athi Rivers, as well as Lake Jipe) throughout the study area were considered to potentially impact both the speed and tortuosity of

elephant movement. To include these three effects (the Nairobi-Mombasa Highway and various water sources) in our analysis, we used high-resolution, remotely sensed imagery provided as a base map in ArcMap 10.6.1. to determine when elephants crossed a highway or approached a frequently visited waterhole or permanent river/lake within our 24 h periods surrounding crop-raiding events (Fig. 3).

Ethical Note

Tracking data used for this study were retrieved remotely from 28 GPS-collared African elephants. Save the Elephants obtained the relevant permissions to carry out both collaring operations (2016: NACOSTI/P/15/3934/5447, 2018: NACOSTI/P/17/3934/19124). The data from 14 male and 14 female elephants were analysed; all elephants were aged between 20 and 45 years old. Save the Elephants are expert at collaring elephants and have successfully collared over 600 elephants across Kenya, Mali, Gabon/Congo and South Africa. Every effort is made to minimize distress for the elephants. The drugs used to anaesthetize the elephants have no long-lasting effect and a trained Kenya Wildlife Service government-certified vet is present at every operation in case there are any complications during the collaring. There is no evidence that wearing a collar affects the elephants' natural behaviour, feeding patterns or drinking capabilities.
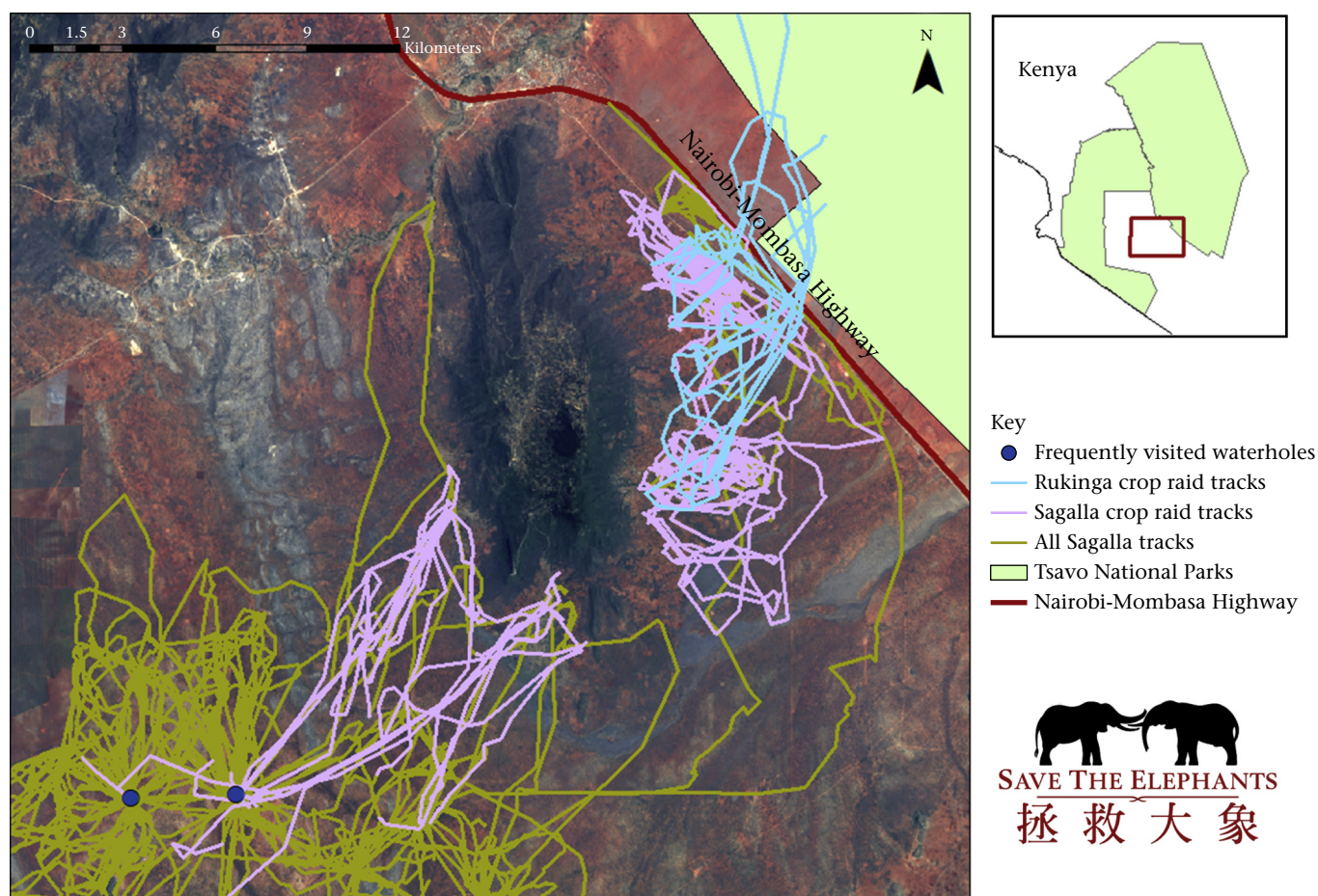

Figure 3. Frequently visited waterholes were determined by pin-pointing locations in the tracking data of each crop-raiding elephant where tracks were concentrated. Crop-raiding elephants often crossed the Nairobi-Mombasa Highway between Tsavo National Park and community areas to raid crops. Data source: Save The Elephants/Kenya Wildlife Service.

Statistical Analysis

We performed all statistical analysis in Genstat (12th edn; Payne, Murray, Harding, Baird, & Soutar, 2009). A restricted maximum likelihood (REML) model was used to analyse movement speeds of crop-raiding and nonraiding elephants over the 24 h periods. Speed was used as a dependent variable, and the data were $\log_e$ transformed to normalize the residuals. As fixed effects we used period (more than 3 h BC, less than 3 h BC, DC, less than 3 h AC, more than 3 h AC, NC), season (wet, early dry, late dry/drought) and sex. As random effects to control for repeated measures, we included individual elephant ID for 28 elephants, as well as crop raid ID and the interaction between these two variables.

We used a generalized linear mixed model (GLMM) with a binomial distribution and logit link function to analyse the likelihood that the movement of crop-raiding and nonraiding elephants over the 24 h periods was straight or tortuous. Straightness was used as the dependent variable, and we included the same fixed and random effects as in our speed model. Straightness data were skewed towards higher values and difficult to normalize the residuals; therefore, we transformed the data into a binary variable by relabelling all values above the mean 'straight', and all values below the mean 'not straight' (tortuous).

To assess whether the presence of the Nairobi-Mombasa highway, frequently visited waterholes and perennial rivers had an effect on crop-raiding elephant movement speed and tortuosity throughout the day surrounding a raiding event, we performed further REML and GLMM models on data restricted to crop raids only. If an elephant approached/crossed one of the three points of interest during a particular period (BC, DC or AC) they were labelled as a 'yes'; otherwise, they were labelled as a 'no'. The same random and fixed effects were used as above.

RESULTS

Crop raiding by our 12 elephants largely took place at night, with the vast majority of raids occurring after 1800 (65%) and before 0600 hours (100%). Crop-raiding events lasted between 1 h (the finest time interval able to be detected given the 1 h sampling frequency of our tracking data) and 13 h, with the average crop raid spanning 5 h. To quantify the potential nutritional benefit crop raiding may provide elephants, an overview of an assessment of differences in the nutritional quality of crops and wild forage in Tsavo is provided in the Appendix. Crops collected from the small-scale farming villages of Sagalla and Mackinnon in Taita Taveta were found to contain higher nitrogen (N, an indicator of forage quality) concentration than wild forage (browse and grass) from Tsavo East N.P. during wet and dry seasons, although the differences were not significant (see Table A1).

Speed of Crop-Raiding and Nonraiding Elephants

An initial analysis including the speed of all elephants in our data set showed an interaction between crop-raiding status (crop-raiders or nonraiders) and the five periods (more than 3 h BC, less than 3 h BC, DC, less than 3 h AC, more than 3 h AC). Nonraiders

were consistently slower than crop-raiding elephants in each corresponding period ($\chi^2_4 = 208.3$, $P < 0.001$), and showed less variation between periods (Table 1). We subsequently grouped the five periods for nonraiding elephant movements into one category for use in our more detailed investigation of crop-raiding elephant movements.

There was a significant three-way interaction between sex, season and period on elephant movement speed ($\chi^2_{10} = 25.99$, $P = 0.004$). Predicted means of $\log_e$ speed ($\pm$SE) are given in Table 2. Back-transformed values for periods according to seasonal changes are presented separately for females and males in Fig. 4.

Nonraiding female elephants were slightly faster than female crop-raiding elephants on average (0.51 and 0.42 km/h, respectively), but speeds of crop-raiding elephants depended on the period of the crop raid and season. A general pattern can be seen across seasons where mean movement was fastest during the 3 h AC (range 0.65−0.92 km/h; Fig. 4a). Female elephants moved slowest during crop raiding (0.39 km/h) in the wet season, but during the dry seasons they moved slowest in the period 3 h BC (range 0.23−0.31 km/h). Across all seasons, speeds during crop raiding, as well as in the periods more than 3 h BC and AC, were always (on average) slower than in the periods less than 3 h BC and AC (Fig. 4a).

Nonraiding male elephants generally travelled at slower speeds than crop-raiders (0.46 km/h and 0.60 km/h, respectively). A similar pattern can be seen in male elephants compared to females across all seasons, where movement was fastest in the 3 h AC (range 1.07−1.35 km/h; Fig. 4b). Movement was slowest in the period more than 3 h BC during the late dry season and wet seasons (range 0.45−0.55 km/h); however, during the early dry season nonraiding elephants moved slowest overall (0.45 km/h). Across all seasons, speeds during the periods DC and more than 3 h BC and AC were always (on average) slower than within 3 h BC and AC (Fig. 4b).

Tortuosity of Crop-Raiding and Nonraiding Elephants

An initial analysis of the tortuosity of all elephants in our data set showed an interaction between crop raid status (crop-raiders or nonraiders) and the five periods (more than 3 h BC, less than 3 h BC, DC, less than 3 h AC, more than 3 h AC). Nonraiders' movements were straighter than those of crop-raiding elephants across the five periods ($\chi^2_4 = 25.05$, $P < 0.001$; Table 3). We subsequently grouped the five periods for nonraiding elephant movements into one category for comparison in our more detailed investigation of crop-raiding elephant movements.

There were significant effects of season ($\chi^2_2 = 13.5$, $P = 0.001$) and period ($\chi^2_5 = 249.2$, $P < 0.001$) but not sex ($\chi^2_1 = 3.03$, $P = 0.10$) on movement straightness. There were no significant interactions between any of these variables ($\chi^2_{10} = 13.3$, $P > 0.211$). Logit link-predicted means and SEs of the proportion of straight movements were 0.280 ± 0.24 ($N = 1004$) for nonraiding elephants, 0.622 ± 0.24 ($N = 212$) for crop-raiding elephants more than 3 h BC, 1.572 ± 0.24 ($N = 212$) less than 3 h BC, -1.805 ± 0.24 ($N = 212$) DC, 2.327 ± 0.24 ($N = 212$) less than 3 h AC and 0.094 ± 0.24 ($N = 212$) more than 3 h AC. Logit link-predicted

Table 1
Summary of predicted means and SEs of $\log_e$ speed for crop-raiding and corresponding nonraiding periods

Crop raid status	More than 3 h BC	Less than 3 h BC	DC	Less than 3 h AC	More than 3 h AC
Crop-raider	-0.657 ± 0.10	-0.392 ± 0.10	-0.654 ± 0.11	-0.570 ± 0.10	-0.474 ± 0.10
Nonraider	-1.127 ± 0.08	-0.862 ± 0.08	-1.123 ± 0.10	-1.039 ± 0.08	-0.944 ± 0.08

BC: before crop raiding; DC: during crop raiding; AC: after crop raiding.

Table 2
Summary of predicted means and SEs of $\log_e$ speed

Sex	Season	NC	More than 3 h BC	Less than 3 h BC	DC	Less than 3 h AC	More than 3 h AC
F	Early dry	−0.693 ±0.10	−1.530 ±0.27	−0.476 ±0.27	−1.481 ±0.27	−0.591 ±0.27	−0.844 ±0.27
F	Late dry	−0.880 ±0.10	−1.295 ±0.32	−0.124 ±0.32	−0.527 ±0.32	−0.269 ±0.32	−0.871 ±0.32
F	Wet	−0.688 ±0.13	−0.809 ±0.32	−0.513 ±0.32	−1.094 ±0.32	−0.680 ±0.32	−1.045 ±0.32
M	Early dry	−0.949 ±0.13	−0.956 ±0.11	−0.072 ±0.11	−0.500 ±0.11	0.170 ±0.11	−0.767 ±0.11
M	Late dry	−0.945 ±0.14	−1.078 ±0.14	−0.252 ±0.14	−0.633 ±0.14	−0.300 ±0.14	−0.829 ±0.14
M	Wet	−0.759 ±0.13	−1.152 ±0.13	−0.102 ±0.13	−0.774 ±0.13	−0.033 ±0.13	−1.012 ±0.13

F: female; M: male; NC: nonraiding elephants; BC: before crop raiding; DC: during crop raiding; AC: after crop raiding. The movement data for 212 crop-raiding events from nine male and three female crop-raiding elephants were used in our analysis. In addition, 1004 movement paths (corresponding to the periods of crop-raiding events) from five male and 11 female nonraiding elephants were analysed for comparison.
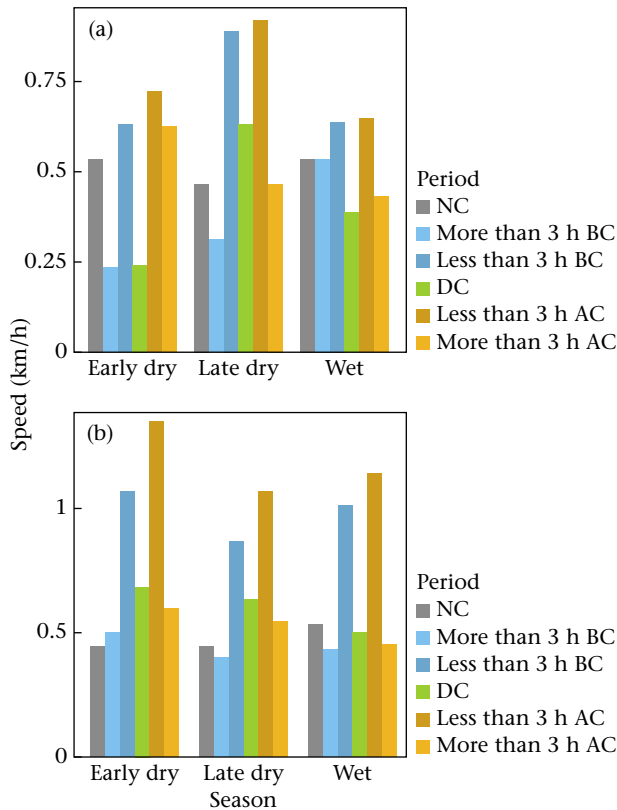
Figure 4. Back-transformed means of (a) female and (b) male elephant movement speed (km/h) for each season, during each period over 24 h surrounding a crop raid event. Nonraiding elephant speed comparisons (for males and females) are represented as one period, averaged over the corresponding 24 h. NC: nonraiding elephants; BC: before crop raiding; DC: during crop raiding; AC: after crop raiding.

means and SEs of the proportion of straight movements for crop-raiding and nonraiding elephant movements combined were 0.727 ± 0.14 (N = 1216) during the early dry season, 0.616 ± 0.14 (N = 1216) during the late dry season and 0.203 ± 0.14 (N = 1216) during the wet season. Back-transformed mean percentages per period and season are shown in Figs. 5 and 6, respectively.

The likelihood of straight (not tortuous) movements for nonraiding elephants was similar to that for crop-raiding elephants in the periods more than 3 h BC and AC (for nonraiding elephants the mean percentage of straight movements = 57%). Elephants were more likely to have straight movements during the period 3 h AC (mean percentage of straight movements = 91%), and tortuous movements DC (mean percentage of straight movements = 14%). Fig. 7 highlights an example of differences in tortuosity between crop-raiding and nonraiding elephants. Elephants were more likely to have tortuous movements in the periods more than 3 h BC and

AC than in the periods 3 h BC and AC (Fig. 5). In general, crop-raiding and nonraiding elephant movement was more likely to be tortuous during the wet season (mean percentage of straight movements = 55%) compared to the two dry seasons (mean percentage of straight movements = 65–67%; Fig. 6).

Other Impacts on Crop-Raiding Elephant Speed and Tortuosity

There were significant effects of the presence of frequently visited waterholes ($\chi^2_1 = 35.6$, $P < 0.001$) and the Nairobi-Mombasa highway ($\chi^2_1 = 8.38$, $P = 0.004$), but not perennial rivers ($\chi^2_1 = 0.00$, $P = 0.96$), on the movement speed of crop-raiding elephants. There were no significant two- or three- way interactions between these variables ($P > 0.76$). Predicted means for $\log_e$ speed ±SE were -0.406 ± 0.14 ($N = 178$) in the absence and 0.187 ± 0.14 ($N = 34$) in the presence of frequently visited waterholes and -0.303 ± 0.14 ($N = 196$) in the absence and 0.084 ± 0.14 ($N = 16$) in the presence of the Nairobi–Mombasa highway. Back-transformed predicted means of crop-raiding elephant speed (km/h) were 0.67 in the absence and 1.2 in the presence of waterholes and 0.74 in the absence and 1.09 in the presence of the Nairobi–Mombasa highway.

There were no significant effects of the Nairobi-Mombasa highway ($\chi^2_1 = 0.31$, $P = 0.58$), perennial rivers ($\chi^2_1 = 0.2$, $P = 0.65$) or frequently visited waterholes ($\chi^2_1 = 2.26$, $P = 0.133$) on crop-raiding elephant movement straightness. In addition, there were no significant two- or three- way interactions between the Nairobi-Mombasa highway, perennial rivers, frequently visited waterholes and period on crop-raiding elephant movement straightness ($P > 0.58$).

DISCUSSION

This study explored the fine-scale movement patterns and risk sensitivity of GPS-collared crop-raiding African elephants over the 24 h surrounding crop-raiding events, providing important insights into how they adjust their behaviour according to the risks associated with crop raiding. We found the speed and tortuosity of crop-raiding elephant movements varied throughout the day depending on whether they were actively engaging in crop raiding, preparing to raid crops or following a crop raid. In support of our first hypothesis (H1), elephants moved more slowly and were more likely to move tortuously in the periods more than 3 h BC and AC, where their movements began to more closely resemble those of nonraiding elephants. In line with our second hypothesis (H2), elephants were more likely to move tortuously during crop raiding than in any other period and compared to nonraiding elephants. However, while their speed generally decreased during crop raiding, it varied in comparison to the other periods with sex and season. In addition, crop-raiding elephants always moved fastest and were most likely to move in straight lines in the periods less

Table 3
Back-transformed mean values of the proportion of straight movements for crop-raiding and corresponding nonraiding periods

Crop raid status	More than 3 h BC	Less than 3 h BC	DC	Less than 3 h AC	More than 3 h AC
Crop-raider	0.690	0.844	0.189	0.927	0.549
Nonraider	0.578	0.747	0.617	0.733	0.576

BC: before crop raiding; DC: during crop raiding; AC: after crop raiding.
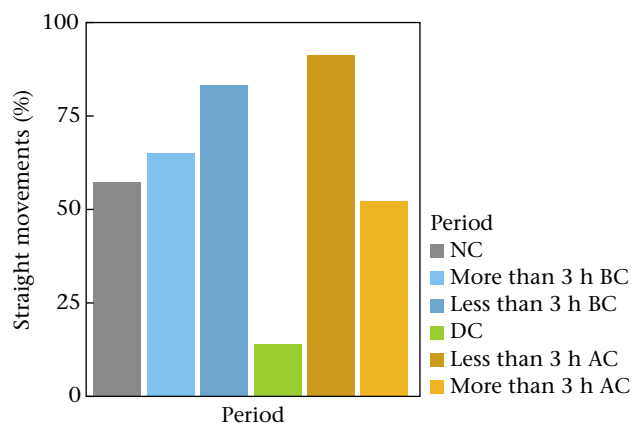
Figure 5. Back-transformed predicted means of the percentage of straight movements during each period over 24 h (including a comparison with nonraiding elephant movement, represented as one period averaged over the corresponding 24 h). NC: nonraiding elephants; BC: before crop raiding; DC: during crop raiding; AC: after crop raiding.
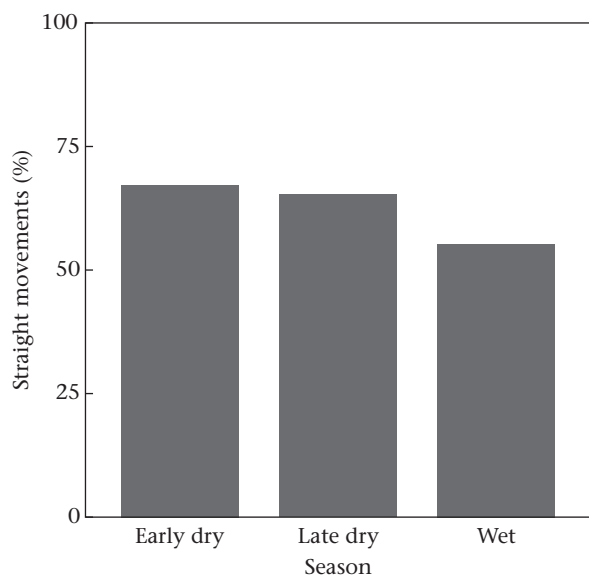
Figure 6. Back-transformed predicted means of the percentage of straight movements during each season, for crop-raiding and nonraiding elephant movements combined.

than 3 h BC and AC. Here we discuss how these results may reflect changes in the landscapes of fear, as well as trade-offs in the predator-sensitive foraging behaviour, of elephants living in anthropogenic landscapes.

Variation in space use by animals can be described as a function of resource distribution and landscapes of fear that are shaped by the animals' behavioural responses to perceived predation risk (Willems & Hill, 2009). While exploring the nutritional motivation for crop raiding by elephants, Branco et al. (2019) proposed that the behaviour might be modified by altering the perception of the

associated risks. In line with this, we found that elephants moved fastest and were more likely to move in straight lines close in time to the crop raid, and by comparison slower with less likelihood of moving in straight lines at other times. The antipredator responses of other animals have also been shown to vary with distance to the perceived predator (Thomson, Forsman, Sardà-Palomera, & Mönkkönen, 2006), as well as with distance to escape terrain (Hochman & Kotler, 2007). Eurasian lynx, *Lynx lynx*, increase their travelling speed and remain more under cover when close to areas of high prey density and human disturbance (Gehr et al., 2017). Similarly, chimpanzees, *Pan troglodytes*, exhibit higher frequencies of antipredator behaviours with decreasing distance to areas of high anthropogenic disturbance and fruit abundance (Lindshield, Danielson, Rothman, & Pruetz, 2017).

Moving faster and straighter have been shown to be risk avoidance strategies employed by elephants (Douglas-Hamilton et al., 2005; Graham et al., 2009; Ihwagi et al., 2019); hence, our results suggest that the perceived risk of crop raiding by elephants is influenced by their proximity to farmland (and corresponding human presence), and that they alter their intensity of risk avoidance behaviours as a result of changes in their landscape of fear. More specifically, our results indicate that with closer temporal proximity to farmland, elephants exhibit an increased intensity of risk avoidance behaviours, which they relax with increasing time from cultivated areas.

Once in farmland, elephants are presented with a trade-off between moving slowly in a more tortuous manner to forage intensively on crops and moving faster with less tortuosity to avoid the risk of retaliatory attack by farmers. Our study shows that during crop raiding, elephants will generally decrease their speed and are less likely to move in straight lines, indicative of intensive foraging on crops and not risk avoidance. Although elephants are more active during the day than at night when undisturbed (Galanti, Preatoni, Martinoli, Wauters, & Tosi, 2006), crop raiding almost exclusively occurs during night hours when human activity is at its lowest (Jackson, Mosojane, Ferreira, & Van Aarde, 2008; Sitati & Walpole, 2005; Wilkie & Douglas-Hamilton, 2018). This suggests that elephants perceive crop raiding to be risky, and hence may be expected to experience a heightened landscape of fear. However, it is likely that elephants do not consider the risk of crop raiding great enough under the cover of darkness to exhibit fine-scale movement behaviours indicative of risk avoidance, especially considering the high nutritional quality of crops (Branco et al., 2019; Rode et al., 2006; Sukumar, 1990; Sukumar & Gadgil, 1988). In Tsavo, the nutritional quality of crops is generally higher (although not significantly) than wild forage from the National Park (see Appendix). Further, optimal foraging theory predicts that animals will maximize their net rate of energy per unit time (Stephens & Krebs, 1986), and farmland provides a forage patch with relatively low search time. In comparison to wild forage density in semiarid Tsavo N.P., crops are grown in highly concentrated patches to maximize economic gain. Therefore, supplementing their diets with crops would allow elephants in Tsavo to meet their daily nutrient requirements more efficiently than if consuming browse and grass alone (see Chiyo & Cochrane, 2005). This is of value during dry periods, when the quality of natural forage is at its
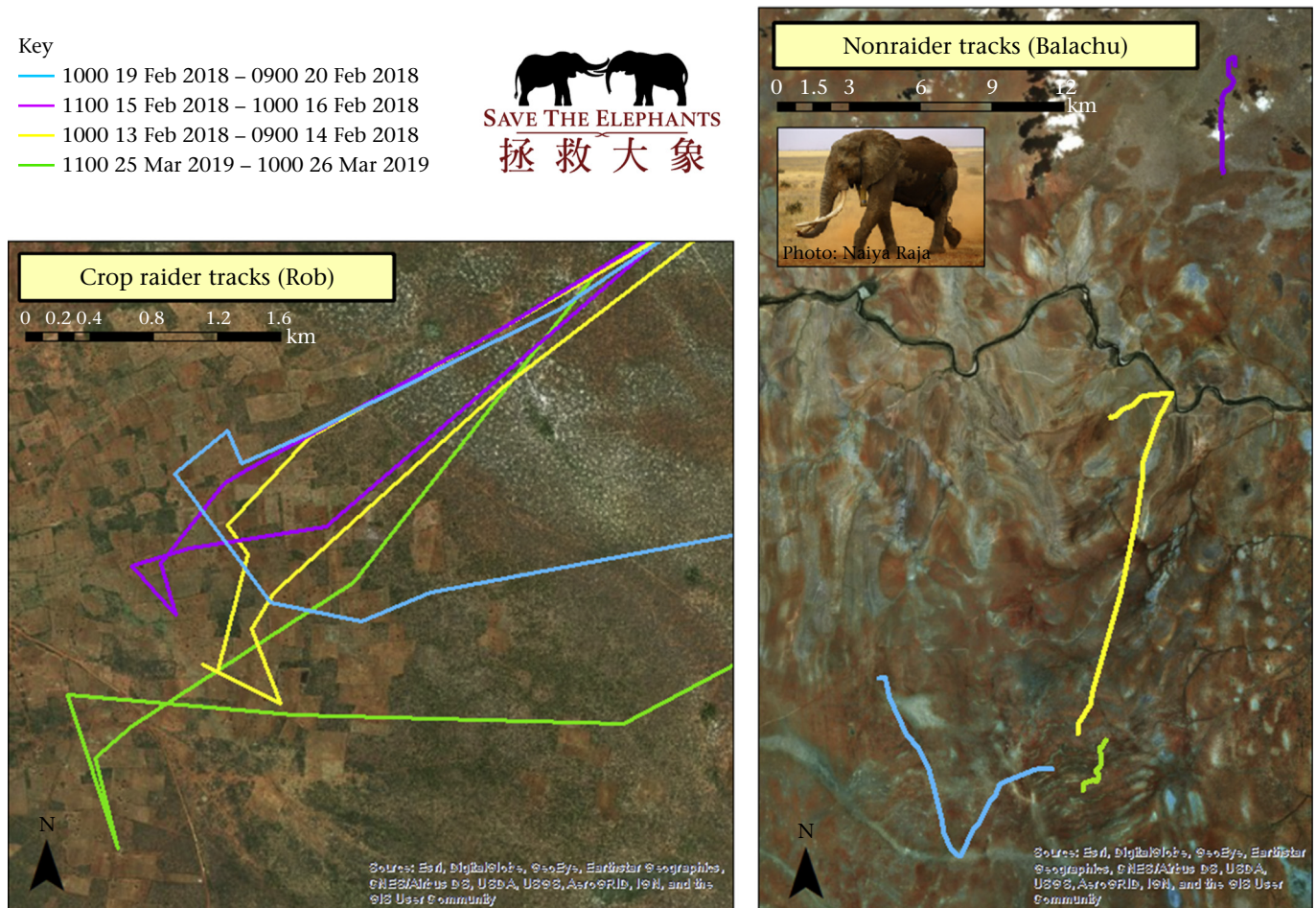
Figure 7. Matched 24 h periods of movement tracks compared between one male crop-raiding elephant ('Rob') and one male nonraiding elephant ('Balachu'), highlighting distinct differences in movement tortuosity. Data source: Save The Elephants/Kenya Wildlife Service.

lowest and meeting nutrient demands from browse and grass becomes more challenging.

Our results suggest that elephants instead alter their timing of foraging in risky areas. Temporal adjustment of activity patterns to avoid contact with potential predators while foraging is a common antipredator behaviour, and has been observed in a wide range of animal species (Bool, Witcomb, Kydd, & Brown, 2011; Tambling et al., 2015; van der Veen, 2008). This strategy alone may be adequate in minimizing the risk of coming into contact with farmers, while also allowing elephants to benefit from the enhanced nutrition (Pokharel et al., 2019) and foraging efficiency (Chiyo & Cochrane, 2005) associated with foraging in farmland. In further support of this theory, the fear of predation has been shown to induce a stress response in animals (Narayan, Cockrem, & Hero, 2013); however, there is mixed evidence to suggest that crop-raiding elephants exhibit increased levels of stress (Ahlering et al., 2013; Ahlering, Millspaugh, Woods, Western, & Eggert, 2011; Pokharel et al., 2019).

The severity of deterrents used by farmers may also help to explain these movement patterns. If a threatening deterrent (such as throwing a spear) is employed, this is likely to result in elephants developing a stronger perception of risk associated with crop raiding than if more passive deterrents are utilized (such as shouting), as the risk to their survival is far greater. The Tsavo ecosystem is vast and extensively populated with small-scale farming communities, although common deterrents are probably utilized widely and are representative of most areas. Farmers in Lower Sagalla most commonly make a noise (either through shouting or banging iron sheets), flash torchlights, call the Kenya Wildlife Service for assistance or light small fires (Weinmann, 2018). Lower Sagalla is also the primary site for deployment of Beehive Fences around farms as a natural elephant deterrent (King, Lala, Nzumu, Mwambingu, & Douglas-Hamilton, 2017); however, these fences are not distributed uniformly throughout the ecosystem. Elephants have been found with spear wounds throughout Tsavo, particularly in areas close to human settlements (McKnight, 2004; Tiller et al., 2018), indicating that the severity of deterrents used by humans in Taita Taveta varies widely. Although farm deterrents are prevalent, our results suggest that in general they may not elicit a fear response in elephants that is great enough to outweigh their perception of the benefits of foraging in farmland.

Our finding that crop-raiding elephants moved faster when near waterholes aligns with the work of Chamaillé-Jammes et al. (2013), who reported that elephants increase their speed towards the beginning and end of trips to water (or in close proximity to water). Elephants also increase their speed when crossing unprotected roads (Blake et al., 2008), which is supported by our finding that crop-raiding elephants moved faster in the presence of the Nairobi-Mombasa highway separating Tsavo East N.P. and the community areas. Ngene et al. (2010) found elephant movement speed to be largely affected by water points and major roads; however, movements were significantly slower close to water and major roads. We

did not observe any other effect on the tortuosity of elephant movement, which contradicts the results of Duffy et al. (2011) who found elephant movement paths to be less tortuous the further they were from water. This may be due to our coarse analysis of straightness (movement either straight or tortuous), resulting in oversimplification of our straightness data and hence an inability to detect such an effect.

The general pattern of movement speed we observed in crop-raiding elephants over 24 h periods closely resembled the 'purposeful' and 'incidental' crop-raiding patterns described by Wilkie and Douglas-Hamilton (2018), based on one habitual crop-raiding bull elephant. During these two patterns of raiding behaviour, movement speed (km/h) was slowest during crop raiding, peaked in the several hours immediately before and after crop raiding and then gradually slowed as the time away from farmland increased before and after the raid. This contradicts the observations of Graham et al. (2009) who found that elephants moved fastest in smallholder areas; however, this is probably due to differences in defining incursion into farmland. Crop-raiding elephants can be described as either habitual or occasional raiders, with the small proportion of habitual crop-raiders being responsible for the majority of raiding events (Chiyo, Moss, Archie, Hollister-Smith, & Alberts, 2011). It is possible that habitual and occasional crop-raiders vary in their risk avoidance behaviours (as expressed through movement speed and tortuosity) around farmland as a result of differences in their frequency of exposure to the risks associated with crop raiding. We chose to analyse the movement data of our 12 crop-raiding elephants separated by sex and season, but future studies may benefit from separating their data into those from 'habitual' and 'occasional' crop-raiders.

We suggest that to best understand (and therefore mitigate) human−elephant conflict, we need to do so inclusive of the elephants' perspective. In their overview of the conservation behaviour field, Blumstein and Fernández-Juricic (2010) provided insight into how an awareness of habitat selection, foraging and antipredator behaviours can be applied to conservation and management. Currently, our knowledge of crop-raiding behaviour is largely limited to the perspective of humans, particularly in regard to the social and economic loss that often results (Jackson et al., 2008; Mackenzie & Ahabyona, 2012), as well as (in extreme cases) injury or death (Kioko, Kiringe, & Omondi, 2006). Our finding that elephants appear to increase the intensity of their risk avoidance behaviours when close to cultivated areas, but forgo these behaviours once inside farmland, could prove insightful for management plans. Specifically, they suggest it may be effective to apply selected deterrents in a buffer zone outside the periphery of farmland, such has been shown in the case of electric fences, elephant-proof trenches and the planting of nonpalatable crops (Kioko, Muruthi, Omondi, & Chiyo, 2009; Parker & Osborn, 2006; Sukumar, 2003). We recommend testing the success of employing deterrents already utilized by farmers inside cultivated areas more widely to include areas outside the periphery of farmland or human settlements. To avoid the financial costs associated with purchasing supplementary deterrents, farmers could allocate some of the deterrents they already employ around their farms for use in these buffer zones. Supplementary deterrents may take time to maintain but this should be outweighed by their potential benefit. Deterrents would target approaching elephants in their most anxious state and could therefore be effective in diverting them away from farmland.

Conclusion

As measured by their movement speed and tortuosity, our results support our hypotheses that, with increasing time before or after crop raiding, elephants reduce their intensity of risk avoidance behaviours, and that the risk associated with crop raiding is outweighed by the benefits of foraging intensively on crops. Crop-raiding elephants alter the speed and tortuosity of their movements throughout the day as a result of the trade-off between risk avoidance and foraging success in farmland. With decreasing distance to cultivated areas, crop-raiding elephants exhibit heightened intensities of risk avoidance behaviours (increasing their speed and moving straight more frequently). During crop raiding, elephants generally decrease their speed and are more likely to move tortuously, forgoing movements indicative of risk avoidance to intensively forage on nutritious crops that are grown in high concentration instead. These results highlight how elephants living in anthropogenic landscapes may adjust their fine-scale movement behaviours when simultaneously foraging and avoiding risk. Further, our study provides insight into how elephants perceive the risks associated with crop raiding, which may prove useful for management efforts.

Declaration of Interest

Acknowledgments

Supplementary Material

Supplementary material associated with this article can be found online at https://doi.org/10.1016/j.anbehav.2020.08.009.

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Appendix

We analysed the nitrogen (N) content of wild forage (browse and grass) and crop samples as part of a larger nutritional study of elephant forage and diet quality in Tsavo carried out between December 2016 and September 2016 (Troup, 2020). Nitrogen provides an estimate of protein, and is widely used as an indicator of forage quality (Ecarnot, Compan, & Roumet, 2013; Petisco et al., 2005). Briefly, we collected samples of the most common grass and browse species observed to be consumed by free-ranging elephants in Tsavo East N.P. In addition, we collected crop samples from regularly crop-raided farms in the small-scale farming communities of Sagalla and Mackinnon, adjacent to Tsavo East N.P. We chemically analysed the available N concentration of a subset of our samples, and employed near infrared spectroscopy (NIRS; Foley, McIlwee, & Lawler, 1998) to predict the N concentration of all our samples. Statistical analysis was completed in R version 3.5.1. (R Core Team, 2019), using the spaMM package (Rousset & Ferdy, 2014) considering spatial autocorrelation. GLMMs with variables to account for spatial dependence were used to analyse differences in the available N concentration of wild forage (grass and browse combined) collected in Tsavo East N.P. and various crop species collected in adjacent farmland, during wet and dry seasons.

Results showed that during the wet season, the nutritional quality (as indicated by available N) of crops was higher than that of wild forage (crops: 2.93% N, SE = 0.27; wild forage: 2.37% N, SE = 0.17). Similarly, during the dry season the nutritional quality of crops was higher than wild forage (crops: 2.02% N, SE = 0.25; wild forage: 1.4% N, SE = 0.05). However, these differences were not statistically significant (Table A1).

Table A1
Effect of location on available nitrogen (N) of plants (browse/grass, crops) in Tsavo, separated by wet and dry seasons (based on spatial GLMMs)

	Response	Predictor	Estimate	SE	t	χ^2 LRT	P
Plants (wet season)	Square root (available N)	Intercept: farmland (crops)	1.69	0.15	11.12	0.68	0.41
		Location: TENP (grass and browse)	−0.16	0.18	−0.87		
Plants (dry season)	Square root (available N)	Intercept: farmland (crops)	1.47	0.17	8.59	1.18	0.28
		Location: TENP (grass and browse)	−0.26	0.23	−1.12		

TENP: Tsavo East National Park. LRT: likelihood ratio test.

mental factors affecting the distribution of African elephants in the Kasigau