Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns

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ABSTRACT

The ability of animals to adapt to their changing environment will depend in part on shifts in their ranging patterns, but when and why individuals choose to move requires detailed understanding of their decision-making processes. We develop a simple decision-making model accounting for resource availability in habitually used ranges. We suggest that disparities between model predictions and animal tracking data indicate additional factors influencing movement decisions, which may be identified given detailed system-specific knowledge. The model was evaluated using movement data from satellite-tracked elephants (*Loxodonta africana*) inhabiting the Amboseli Ecosystem in Kenya, moving from savannah areas with low quality but constant resource availability, to areas with temporally-constrained higher nutrient availability. Overall, the model fit the data well: there was a good correlation between predicted and observed locations for the combined data from all elephants, but variation between individuals in how well the model fits. For those elephants where model

predictions were less successful, additional factors likely to affect movement decisions, reproduction, anthropogenic threats, memory and perception, are suggested. This protocol for building and testing decision-making models should contribute to success in attempts to preserve sufficient space for large herbivores in their increasingly human-dominated ecosystems.

KEYWORDS

Decision-making; Large herbivores; Movement ecology; NDVI; Optimal foraging; Remote sensing

INTRODUCTION

In the face of a changing climate and the rapid conversion of natural habitats to human-dominated landscapes, the future of many species will depend on their ability to adapt to new circumstances. Adaptation may involve behavioural changes or innovations (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005), but geographical shifts in a species range (Laidre et al., 2018) or in how a species moves through its existing range (Olden, Schooley, Monroe, & Poff, 2004; Tucker et al., 2018) may allow it to cope with novel environmental conditions or constraints. Range shifts require animals to make the decision to relocate from one site to another and have often been predicted through the use of simple decision models (Bastille-Rousseau, Douglas-Hamilton, Blake, Northrup, & Wittemyer, 2018). Whilst these shifts are largely guided by suitable climatic conditions and the provision of sufficient food and water, movement decisions are also likely mediated by other factors. The predicted shifts can be incorporated into conservation and management strategies for species of concern, but are unlikely to be accurate unless the full range of factors influencing movement can be taken into account.

Here we present a means of identifying factors other than simple resource-requirements which mediate movement decisions for large herbivores negotiating heterogeneous landscapes. Our method uses disparities between a simple model of resource-driven decision making and animal tracking data to indicate the need to incorporate other factors that affect movement decisions. Given a detailed understanding of the study system, these factors can be identified using local knowledge (see also Bastille-Rousseau et al., 2018). Models were developed and evaluated using elephants (*Loxodonta africana*) inhabiting the Amboseli Basin in Kenya as a case study. Ensuring a future for elephants in this increasingly human-dominated landscape hinges on understanding how and why elephants use the landscape through space and over time.

Long-term monitoring of elephant populations and remote tracking studies have greatly improved our understanding of general patterns in elephant ranging behaviour (e.g. Wall et al. 2013). Elephants show large-scale, purposeful space use (Polansky, Kilian, & Wittemyer, 2015) and so require large areas over which to roam to access heterogeneously distributed resources (e.g. Leuthold 1977; Lindeque & Lindeque 1991; Thouless 1996; Blake et al. 2003; Birkett et al. 2012). It is also clear that elephants do not use the space available to them at random. Instead, elephants generally shift ranges seasonally (Leggett, 2006; Loarie, Van Aarde, & Pimm, 2009; Western & Lindsay, 1984), searching for water (Chamaillé-Jammes & Valeix, 2007; de Beer & van Aarde, 2008; Redfern, Grant, Biggs, & Getz, 2015) and the highest quality vegetation (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Loarie et al., 2009). This results in dynamic habitat and food type preferences (Cerling et al., 2006; Loarie et al., 2009; Shannon, Page, Slotow, & Duffy, 2006).

We developed a simple decision-making model which tracked the food available within habitually-used ranges to satellite-tracked individuals from five family groups (representing the movements of over 220 elephants in the Amboseli population), whilst taking into account the daily need of individuals for water. The individuals had complete perceptual knowledge of resource availability in their home range and the model assumed that, when water availability allowed, individuals moved to maximise their nutrient intake rate and subsequent fitness (Okello, Njumbi, Kiringe, & Isiiche, 2015), as in optimal foraging theory (Bastille-Rousseau et al., 2017; Roever, van Aarde, & Chase, 2013; Stephens & Krebs, 1986; Vasconcelos, Fortes, & Kacelnik, 2017). We assumed that individuals make daily choices whether to relocate to an alternative location or to stay in the current location (Petit & Bon, 2010). Where model predictions did not match those of tracking data, we used detailed knowledge of the elephants and ecosystem to identify additional factors, such as physiological or social needs, which depend inter alia on an individual's sex, age, reproductive status and body condition (Lindsay, 2011).

MATERIALS AND METHODS

Case study site information

The study was carried out in the Amboseli basin (bounding coordinates: -2.02N, -3.28S, 38.03E, 36.67W), an area of approximately 8000km^2 straddling the border of southern Kenya and northern Tanzania, comprising the central Amboseli National Park (392km^2; ANP hereafter) and surrounding landscape (Croze & Lindsay, 2011; see Supplementary Information). The habitat consists of semi-arid savannah that responds seasonally to highly variable rainfall. Rain predominantly occurs in two seasons; a short wet season (November and December) and the long rains (March through May; Altmann, Alberts, Altmann, & Roy, 2002). During dry seasons, a series of swamps in the central basin provide the primary source of water, fed by groundwater flow from the slopes of Kilimanjaro in the south (Croze & Lindsay, 2011), though other perennial sources occur in the Selenkay Conservancy and in Kitenden, in the form of a borehole and two natural springs. Wildlife concentrates in the central basin during dry seasons and disperses following rain (Western, 1975). Amboseli has been described as a 'non-equilibrium' ecosystem (Croze & Lindsay, 2011) and over the past half century has experienced a decline in habitat diversity with contraction of woodlands, loss of woody vegetation and thinning of dense bushland (Western, 2007) – similar to changes in the long term past (Croze & Lindsay, 2011). Changes have been attributed to a combination of climate, salinization and increasing elephant density (Western & Maitumo, 2004; Western & Van Praet, 1973). The Amboseli basin is home to around 1670 individually known and monitored elephants (Lee, Bussiere, Webber, Poole, & Moss, 2013). Unlike most other African populations, the Amboseli elephants have been relatively undisturbed by human activities. However, recent human population growth in Kenya and a lifestyle shift from nomadic pastoralism to sedentary farming (Western, Groom, & Worden, 2009) presents growing challenges for the persistence of Amboseli's wildlife.

Animal tracking data

GPS-GSM collars (@ Savannah Tracking) were fitted in July 2011 to five adult female elephants (Ida, Lobelia, Maureen, Vicky and Willow) from different family groups, representing locations of over 220 individuals (because families forage as units). Habitat heterogeneity around the central protected area affects ranging strategies and reproductive success, so not all dispersal directions are equal for Amboseli elephants. Target females were selected based on more than 40 years of observations to

represent the known diversity in dispersal areas and foraging opportunities in Amboseli (which are largely inherited through generations unless disrupted by human disturbance; Croze & Moss, 2011; Moss, 1988) and to minimise risks to target elephants, family members and staff. Individual females were selected according to ethical and safety criteria, minimising the disturbance of each intervention. Target females were 1) not matriarchs, 2) without a calf aged <2 years and 3) closely related to matriarchs so shared movement patterns. Matriarchs were not collared due to the drastic potential impact of matriarch loss on families given the small but present risks of immobilisation, and the greater ease of managing non-target family members during immobilisations when they had a safe rallying point around their matriarch. Collars were fitted under the authority of the Kenya Wildlife Service, the Kenyan body regulating interactions with elephants, and with research clearance to Amboseli Trust for Elephants from the National Commission for Science, Technology and Innovation (NACOSTI/P/15/9605/5732).

GPS fixes were recorded at hourly intervals for roughly 12 months, giving in sum 43,728 location fixes. Collar data was summarised into daily presence or absence from ANP. Given the reliance of elephant families on water, an elephant was considered present in ANP on any day in which distance from the swamp was zero at any time during that day. Conversely if the distance from the swamp was never zero, the elephant was considered that day to have dispersed from ANP. The dispersal area of each female was identified as the 95% kernel density estimates (ArcMap; ESRI 2017) of her locations outside the park boundary.

Resource-driven movement model

We developed a profitability index to indicate the resource availability of each dispersal area and of ANP, while taking into account the daily need of female elephants for water (Fig. 1). Water was considered essential and elephants were only able to move to areas where water was available. The swamp edge habitat alone was used to indicate profitability for ANP, as elephants consistently return to the park to feed on the reliable and abundant swamp edge vegetation, as well as drink. Swamp edge was therefore used as representative of the resources drawing elephants back to ANP from their dispersal areas.

$$\underset{\textit{of specified area}}{\text{Profitability}} = \underset{\textit{Median NDVI}}{\text{Quantity of vegetation}} \times \underset{\textit{Protein content (\%)}}{\text{Quality of vegetation}} \times \underset{\textit{Binary}}{\text{Water availability}}$$

Figure 1. Profitability of each dispersal area and ANP, calculated daily. See Methods for definitions of vegetation quantity and quality. Water availability is a binary variable taking values of 1 or 0 depending on whether or not water is available in the specified area.

Vegetation quantity

Data on vegetation quantity were acquired using the Normalised Difference Vegetation Index (NDVI), which exploits the marked difference in reflectance in red and near infra-red wavelengths characteristic of healthy green vegetation (Huete et al., 2002). We used 16-day composite values of NDVI retrieved from Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) to infer time-specific values of vegetation quantity. Specifically we used the MOD13Q1 product accessed via the

Oak Ridge National Laboratory Web Service (Vannan, Cook, Pan, & Wilson, 2011). Median NDVI values were calculated for each individual's dispersal area (i.e. 95% kernel density estimates outside ANP) and swamp edge for each 16-day interval. Data were filtered using the MOD13Q1 QA flags such that only 'good' quality NDVI observations were used in our calculations. For extended remote sensing methodology, see Supplementary Information.

Vegetation quality

Food selection in elephants is not only a function of quantity but also quality, itself a function of metabolisable energy, digestible protein and mineral content (Lindsay, 2011; van der Merwe, Lee-Thorpe, & Bell, 1988). The importance of minerals has been demonstrated through selection of sodium (Bowell, Warren, & Redmond, 1996) and varying levels of potassium, calcium, magnesium and sulphur (Fishlock, 2010; Seydack, Vermeulen, & Huisamen, 2000), and avoidance of copper (Koen, 1988). However, quantification of the distribution of food quality is limited in Amboseli to crude protein. Crude protein is an important limiting factor for herbivores inhabiting savannah ecosystems (Sinclair, 1975) and we therefore assessed vegetation quality by its protein content (%). The diet of Amboseli elephants is dominated by grasses, so we used grass protein content as our measure of vegetation quality. Protein content varies seasonally, peaking during the green-up of vegetation following the onset of rains (Georgiadis & McNaughton, 1990; Lindsay, 1994). Here we estimate protein content depending on whether or not it rained in the previous month. Lindsay (1994) measured the protein content of Amboseli swamp edge vegetation and rainfall throughout the course of a year. From these data, we assigned protein content of swamp edge vegetation as 11.8% or 8.4% depending on whether or not it rained in the preceding month. Georgiadis & McNaughton (1990) collected similar measurements in the broader Amboseli basin outside the Amboseli swamps and found protein contents of 23.0% during the green-up following rains and 10.0% in the subsequent drying phases. We used the figure of 23.0% if the change in NDVI was positive, indicating green-up in the month after rains, at all other times 10.0%.

Water availability

Permanent water sources were available in ANP and in the dispersal areas of Vicky (Selenkay), and Ida and Lobelia (Kitenden). We deemed water available year-round in these areas. We used daily measures of rainfall from the rainfall gauge in the Amboseli Elephant Research Camp (-2.679S, 37.267E) to indicate rainfall across the entire Amboseli basin since NDVI fluctuations across the ecosystem are generally synchronous. Rainfall contributed to surface water availability in all areas and so water was considered available across the entire basin for seven days following rains.

Movement-decision model fit

We assumed that if individual movement behaviour was governed by resource availability, individuals should move to maximise profitability throughout the year. Therefore, when ANP profitability was greater than that of the dispersal area, the individual should be present in ANP on that day, and vice versa. If profitability for the two locations was very close (difference < 0.3) no prediction was made as to which provided the optimal foraging location.

The daily absence or presence of the elephants as predicted by profitability was compared to actual absence or presence indicated by the collar data. The correlation between predicted and observed presences and absences was calculated as a ϕ statistic (Conover, 1971). ϕ is the equivalent of

Pearson's correlation that is applicable to binary data. ϕ values were tested for significance using chi-square with 1 degree of freedom.

RESULTS

Ranging behaviour

The ranging behaviour of the five collared elephants over a 12-month period is illustrated in Fig. 2. Ida and Lobelia spent most of their time (c. 85%) in ANP, primarily in the southeast around the southern tip of the eastern swamp (Longinye; see Supplementary Information for detailed park map). From there both elephants regularly moved southwest into the Kitenden region and occasionally east to the Kimana Sanctuary. Maureen, Vicky and Willow spent about half their time in the park. Maureen used the eastern swamp and the area around and including the western swamp (Longolong). From there, she dispersed south through the Kitirua Conservancy and then southwest across the foothills of Kilimanjaro into Tanzania. Vicky and Willow also used the eastern swamp, but additionally used the northern tip of the central swamp (Enkongo Narok). Within the park Vicky frequented the north and dispersed north to spend much time in the Selenkay Conservancy. Willow by contrast used the west of the park from which she dispersed northwest to the Meshanani region.

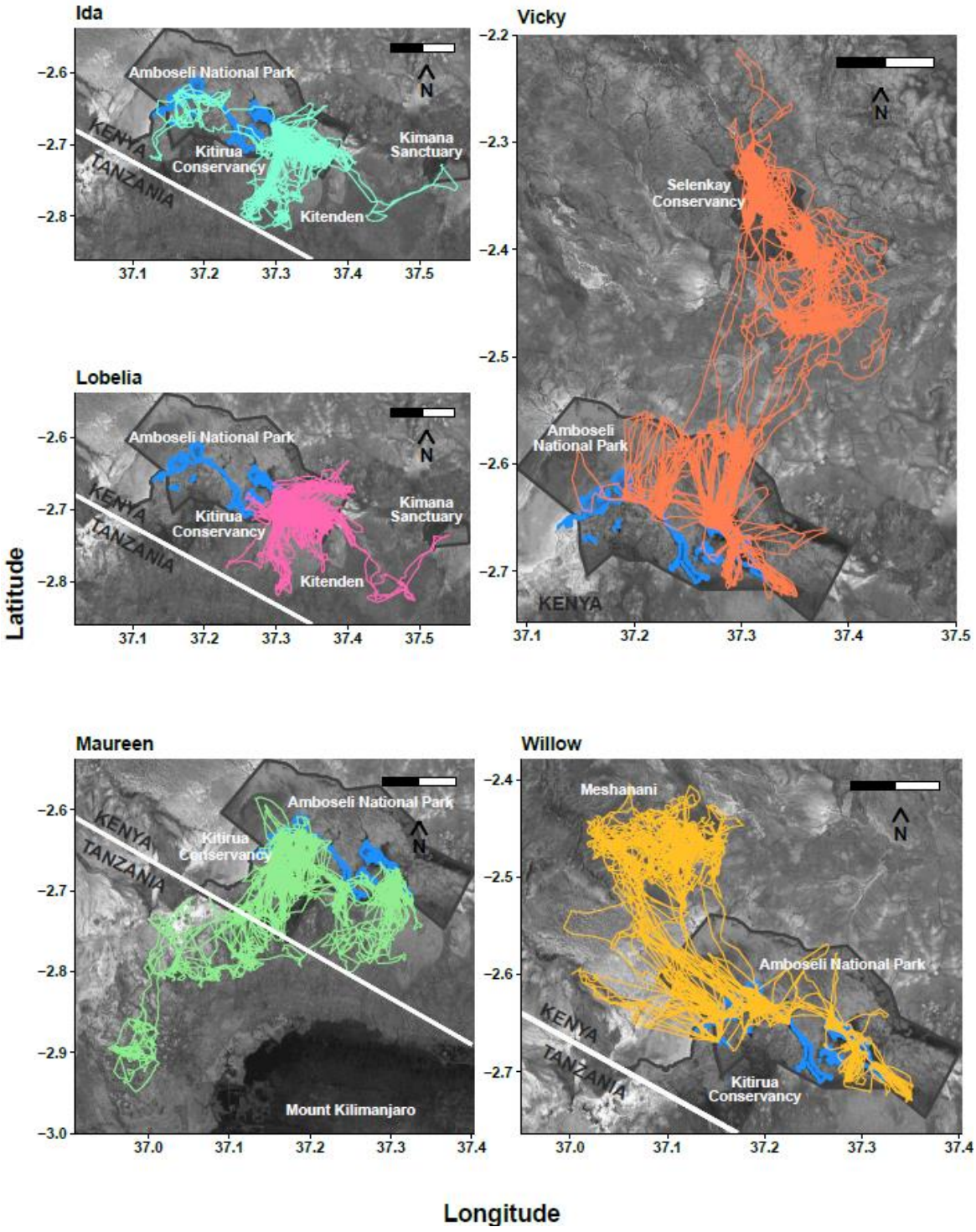

Figure 2. Tracks of five collared elephants displaying use of Amboseli National Park and dispersal areas (coloured lines: different colour for each female). Protected areas are indicated by grey boundaries, the international border between Kenya and Tanzania by the white line, and the central Amboseli swamps in blue. Scale bar represents 10km (divisions of 5km). Two females used the same dispersal area (Kitenden, southeast); other females ranged to the north, northwest and southwest when leaving ANP.

Profitability

Profitabilities calculated for the swamp edge and dispersal areas (Kitenden, Kitirua-Tanzania, Selenkay and Meshanani) captured spatial and temporal variation (Fig. 3). Temporally, profitability generally increased following the onset of the rains and declined as the rains subsided. Spatially, areas differed in the precise timing and extent of increases and decreases in profitability. ANP profitability varied less than the profitability of the dispersal areas because in the dry seasons the swamps retained abundant green vegetation but did not experience the dramatic increase in protein content seen in dispersal area vegetation following rain. As a result, there was temporal variation in whether profitability was higher in ANP or in the dispersal area, predicting switches in the optimal foraging location between ANP and the dispersal areas. Generally, profitability indices predicted that elephants should be present in the national park during August, September and October 2011, January and February 2012 and from May 2012 onwards. At other times they were predicted to move out to their family dispersal areas.

Movement-decision model fit

Overall the model fitted the data well: there was good correlation between predicted and observed presences and absences for the combined data from all five elephants (ϕ = 0. 37, p<0.001), but there was variation between elephants in how well the model fitted (Breslow-Day test, χ_4 = 67.4, p<0.001, Fig. 4). The locations of Vicky were well predicted by the model (ϕ = 0.60, p < 0.001, Fig. 4) though the model was unable to predict Vicky's brief excursions between August and October 2011, nor her absence from the park in May to June 2012. The model was moderately successful in predicting the

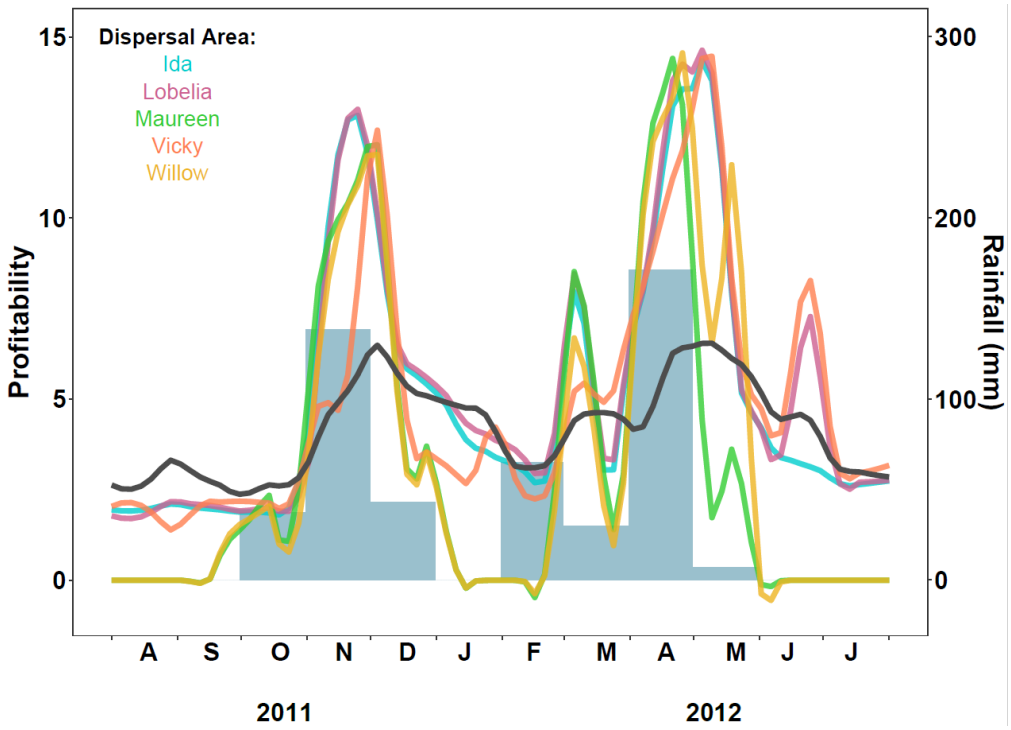

Figure 3. Response of profitability (lines: black = swamp edge, coloured = dispersal areas), the product of the quantity and quality of vegetation, and water availability, to monthly rainfall (bar: blue).

locations of Ida, Lobelia, Maureen and Willow (ϕ = 0.42, 0.27, 0.39 and 0.46 respectively, $p < 0.001$ for each), but failed to predict the regular presence of Ida and Lobelia in ANP throughout both wet seasons. Maureen was regularly absent between August and October 2011 and in June and July 2012 when the model assumed presence throughout. The timings of Maureen's major excursions from the park were also slightly ahead of those predicted by the model. Willow's movements were well predicted with the exception of brief excursions during August and September 2011 and of her continued absence from the park during June and July 2012.

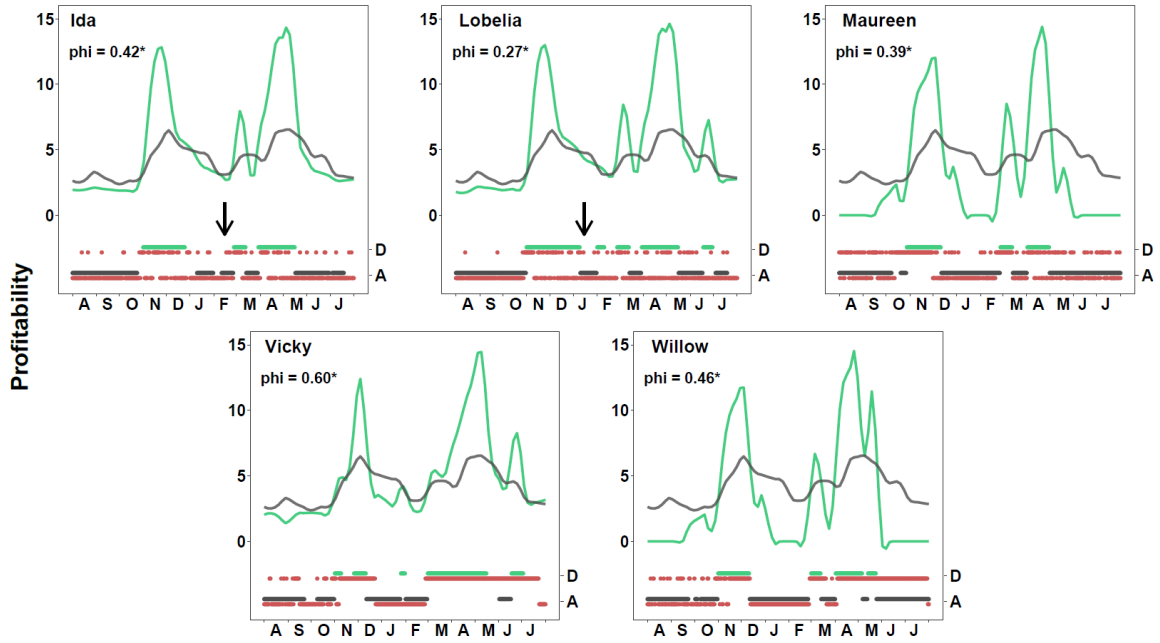

Figure 4. Profitabilities of swamp edge (black curve) and dispersal area (green curve) for each collared individual. Horizontal lines at bottom of each panel indicate model predictions (black, A = Amboseli National Park; green, D = dispersal area) and collar data (red). No predictions were made if profitabilities were within 0.3 of each other. Arrows indicate parturition events for Ida and Lobelia. Phi coefficients indicate correlation between model predictions and collar data; * indicates significance of this relationship (Chi-squared: $p < 0.001$).

DISCUSSION

By modelling the profitability of the traditional foraging areas of each of the five elephant families while taking account of their daily need for water, we predicted the timings of their shifts in optimal locations. The shift timings were similar despite the different dispersal areas used by the collared elephants (Fig. 3). In general, ANP offered the highest rate of nutrient intake during the dry seasons until the onset of rains, at which point the dispersal areas provided better foraging locations provided that water was available. While the model fitted the data well overall, there was variation among elephants in the ability of the model to correctly predict park absence and presence. Predictions and observations were significantly correlated for all five individuals, but while the correlation was good for Vicky, it is likely that other factors also influenced the movement decisions of Ida, Lobelia, Maureen and Willow. Given an in-depth knowledge of the study system (AERP long term data), we

now attempt to identify these factors and suggest how they can be incorporated into future movement models for elephants.

The sustained residency of Ida and Lobelia in ANP is likely due to the fact that both females gave birth during the 2012 short wet season (January-February). Elephants usually seek safe areas as parturition approaches and for some time after as new-born calves are vulnerable to disturbance and predation (Ruggiero, 1991). For family units experiencing recent parturition events, the motivation to remain in ANP increases because it is perceived as a relatively safe area. During the period of sampling, Ida and Lobelia's dispersal areas of Kitenden and Kimana were relatively high risk because a number of elephants were killed or injured as a result of human interactions (Big Life Foundation/AERP long term data). In elephants, risks in the form of anthropogenic threats are known to deter long-term elephant habitat use (Roever et al., 2013) and alter the daily locations of resting sites (Wittemyer, Keating, Vollrath, & Douglas-Hamilton, 2017). Risks affect animal decision making more widely when animals sacrifice optimum nutrient intake to minimise the risks of predation (Barnier et al., 2014; Bastille-Rousseau et al., 2017). Including the risks associated with human-elephant interactions should improve the model fit. Relative risk could be measured in terms of the number of negative human-elephant interactions (injuries or mortalities) over a specified period, land use type (pastoralist vs. agricultural vs. wildlife zones) or human density in an area (which is also a function of land use type). Over the longer-term, periods of drought could also be used as an indirect predictor of human-associated risk, because competition for water sources and high-quality food patches increases contact between humans and elephants (Chiyo, Cochrane, Naughton, & Basuta, 2005) and the economic threats of livestock loss erode tolerance for wildlife (Western, Nightingale, Sipitiek, Mose, & Kamiti, pers. comm.).

Behavioural differences between conspecifics can be viewed as evidence of personality; consistent differences in the behavioural responses of individuals across various spatial and temporal contexts (Beekman & Jordan, 2017). Here therefore, we may alternatively consider the residency of Ida and Lobelia could be to be due to their 'wary' personalities, whilst Vicky is more 'bold' (Jolles, Boogert, Sridhar, Couzin, & Manica, 2017). Personality has been reliably demonstrated for elephants (Lee & Moss, 2012; Seltmann, Helle, Adams, Mar, & Lahdenperä, 2018) but we have yet to systematically sample the subject families and can only speculate at this point. However, our long-term observations suggest that personality is shaped by family members (particularly the matriarch) and by experiences, especially early in life. We can propose that, as seen in many other bird, fish and mammal species (Weiss, 2018), personality may both shape and be shaped by exposure to risk.

Maureen displayed much lower use of ANP than predicted by the model, suggesting she was less reliant on the swamps for dry season water as she had access to an alternative water source in the Kitirua Conservancy. Elephants share this water point with livestock and people, often at high concentrations, but this area also showed high tolerance for wildlife during the study period. The model was also unable to predict the timing of Maureen's location shift, consistently predicting a later dispersal than seen in the collar data. The dispersal area used by Maureen in Tanzania is characterised by mature Acacia woodlands rather than the open bushed savannah associated with the majority of the ecosystem. Acacia flower ahead of the onset of rains and Maureen's early excursions may coincide with this phenological event, rather than the NDVI observed green-up. Flowering in bushlands might be associated with higher sugar and other nutrient transport in Acacia stems, which are desirable elephant foods (Lindsay, 1994). Incorporating nutrient fluxes that are independent of

vegetation green-up will require both phenological monitoring of the timing of flowering and quantifying the associated nutrient benefits. The remotely sensed measures of greenness used here are insensitive to the spectral changes associated with flowering, thus suitable alternative remote sensing techniques are needed for a more comprehensive accounting for foraging movements.

While we can suggest other factors that operate in combination with nutrient intake to affect movement decisions, the behavioural mechanisms underlying movement patterns remain poorly understood (Bolger, Newmark, Morrison, & Doak, 2008); indeed whether movement decisions are guided by animals' perceptions of current environmental conditions or predictions based on memory is uncertain. The capacity of elephants to remember the spatial locations of out-of-sight individuals (Bates et al., 2008) and the purposeful movement to water resources beyond the senses of sight or smell (Polansky et al., 2015) shows that elephants have a keen spatial memory. Despite this, our data show that decision points (Polansky et al., 2015) coincide with the onset of the rains, suggesting that the onset of rains may be used as a key environmental cue to instigate range shifts (Holdo, Holt, & Fryxell, 2009; Prins, 1996). Also relevant to this question are several brief excursions by Vicky and Willow to their respective dispersal areas prior to their longer-term range shifts. This 'scouting' behaviour (Bracis & Mueller, 2017) suggests sampling of the conditions at their destination before committing to the final range shift. Both of these factors suggest perception-guided movement. However, rainfall across the Amboseli basin is perhaps more temporally and spatially variable than accounted for here, meaning elephants cannot rely on the same rules each year. Memory alone is likely to be less effective in such a patchy environment, and so individuals will use both immediate perception and memory when making movement decisions. Although memory is important in defining the destination of movements based on previous experiences of improved nutrient intake rate, perception is crucial in remaining flexible to local environmental changes in climatic conditions and risk.

We have introduced a simple decision-making model of the resource-driven factors affecting key decisions of where individuals go and when. Where individuals fit the model well, a key benefit of movement over an ecosystem is indicated, which is to maximise nutrient intake rates. That individuals do not perfectly fit the model suggests that other factors need to be included in combination with nutrient intake rates. High residency of elephants that disperse to the eastern part of the ecosystem suggests that individuals and families make movement decisions based on trade-offs between the resource-related benefits of dispersal and the associated risks (see also Chiyo et al., 2014). For Ida and Lobelia, it is hard to determine whether perceived risks resulted from human-elephant interactions, the dangers involved with moving new-born calves over long distances, or the limited travel speed of those vulnerable calves. More data characterising risks and associated movements are important (Nielsen, Stenhouse, & Boyce, 2006; Roever et al., 2013) and necessary before these factors can be reliably included in an enhanced model of movement decision making. Male elephants were not considered here due to differences in resource requirements. Males are less reliant on water than females and forage less selectively, prioritising quantity over quality (Shannon, Page, Duffy, & Slotow, 2006). When in musth, male elephant movement is largely focused on the pursuit of oestrous females, with little consideration for food (Poole, 1987). Previous work in Amboseli has demonstrated the importance of both food (NDVI) and social needs (Chiyo et al. 2014) on male ranging, so we expect that our model could be extended to non-musth males but would need further modification to take into account the energy demands of musth, which is a topic for future study. Further

development of our model will ultimately provide a basis for robust prediction of elephant movements under a variety of environmental and physiological conditions.

We argue that simple resource-driven movement models based on easily accessible resource availability data in combination with animal tracking studies will be useful in identifying additional features influencing movements in well-studied systems, where anecdotal evidence can add to understanding movement decisions. This will allow conservationists and wildlife managers to better understand how large herbivore movements will respond to management scenarios (e.g. fences, new roads) and future environmental changes (e.g. shifting rainfall patterns), and in this way can help manage conflicts of interest between humans and wildlife and ensure sufficient space for wildlife.

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REFERENCES

Altmann, J., Alberts, S. C., Altmann, S. A., & Roy, S. B. (2002). Dramatic change in local climate patterns in the Amboseli basin, Kenya. *African Journal of Ecology*, *40*(3), 248–251. https://doi.org/10.1046/j.1365-2028.2002.00366.x

Barnier, F., Valeix, M., Duncan, P., Chamaillé-Jammes, S., Barre, P., Loveridge, A. J., … Fritz, H. (2014). Diet quality in a wild grazer declines under the threat of an ambush predator. *Proc Biol Sci*, *281*. https://doi.org/10.1098/rspb.2014.0446

Bastille-Rousseau, G., Douglas-Hamilton, I., Blake, S., Northrup, J. M., & Wittemyer, G. (2018). Applying network theory to animal movements to identify properties of landscape space use. *Ecological Applications*. https://doi.org/10.1002/eap.1697

Bastille-Rousseau, G., Murray, D. L., Schaefer, J. A., Lewis, M. A., Mahoney, S. P., & Potts, J. R. (2017). Spatial scales of habitat selection decisions: Implications for telemetry-based movement modelling. *Ecography*, (315). https://doi.org/10.1111/ecog.02655

Bates, L. A., Sayialel, K. N., Njiraini, N. W., Poole, J. H., Moss, C. J., & Byrne, R. W. (2008). African elephants have expectations about the locations of out-of-sight family members. *Biol. Lett*, *4*, 34–36. https://doi.org/10.1098/rsbl.2007.0529

Beekman, M., & Jordan, L. A. (2017). Does the field of animal personality provide any new insights for behavioral ecology? *Behavioral Ecology*, *28*(3), 617–623. https://doi.org/10.1093/beheco/arx022

Birkett, P. J., Vanak, A. T., Muggeo, V. M. R., Ferreira, S. M., & Slotow, R. (2012). Animal perception of seasonal thresholds: Changes in elephant movement in relation to rainfall patterns. *PLoS ONE*,

7(6), 1–8. https://doi.org/10.1371/journal.pone.0038363

Blake, S., Bouché, P., Rasmussen, H., Orlando, A., & Douglas-Hamilton, I. (2003). *The Last Sahelian Elephants Ranging Behavior, Population Status and Recent History of the Desert Elephants of Mali*. https://doi.org/11858/00-001M-0000-002D-0B5D-1

Bohrer, G., Beck, P. S., Ngene, S. M., Skidmore, A. K., & Douglas-Hamilton, I. (2014). Elephant movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape. *Movement Ecology*, *2*(2), 1–12. https://doi.org/10.1186/2051-3933-2-2

Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, *11*, 63–77. https://doi.org/10.1111/j.1461-0248.2007.01109.x

Bowell, R. J., Warren, A., & Redmond, I. (1996). Formation of cave salts and utilization by elephants in the Mount Elgon region, Kenya. *Geological Society, London, Special Publications*, *113*(1), 63–79. https://doi.org/10.1144/GSL.SP.1996.113.01.06

Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B*, *284*. https://doi.org/10.1098/rspb.2017.0449

Cerling, T. E., Wittemyer, G., Rasmussen, H. B., Vollrath, F., Cerling, C. E., Robinson, T. J., & Douglas-Hamilton, I. (2006). Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences*, *103*(2), 371–373. https://doi.org/10.1073/pnas.0509606102

Chamaillé-Jammes, S., & Valeix, M. (2007). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, *44*, 625–633. https://doi.org/10.1111/j.1365-2664.2007.01300.x

Chiyo, P. I., Cochrane, E. P., Naughton, L., & Basuta, G. I. (2005). Temporal patterns of crop raiding by elephants: A response to changes in forage quality or crop availability? *African Journal of Ecology*, *43*, 48–55. https://doi.org/10.1111/j.1365-2028.2004.00544.x

Chiyo, P. I., Wilson, J. W., Archie, E. A., Lee, P. C., Moss, C. J., & Alberts, S. C. (2014). The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants. *Behavioural Ecology*, 1–11. https://doi.org/10.1093/beheco/aru152

Conover, W. J. (1971). *Practical Nonparametric Statistics*. New York: John Wiley & Sons Inc.

Croze, H., & Lindsay, W. K. (2011). Amboseli Ecosystem Context: Past and Present. In C. J. Moss, H. Croze, & P. C. Lee (Eds.), *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal* (pp. 11–28). Chicago: University of Chicago Press.

Croze, H., & Moss, C. J. (2011). Patterns of Occupancy in Space and Time. In C. J. Moss, H. Croze, & P. C. Lee (Eds.), *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal* (pp. 89–105). Chicago: University of Chicago Press.

de Beer, Y., & van Aarde, R. J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid*

Environments, *72*(11), 2017–2025. https://doi.org/10.1016/j.jaridenv.2008.07.002

Fishlock, V. L. (2010). *Bai Use in Forest Elephants (Loxodonta africana cyclotis) : Ecology, Sociality and Risk*. *PhD Thesis*. University of Stirling.

Georgiadis, N. J., & McNaughton, S. J. (1990). Elemental and fibre contents of savanna grasses: variation with grazing, soil type, season and species. *Journal of Applied Ecology*, *27*(2), 623–634. https://doi.org/10.2307/2404307

Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti. *The American Naturalist*, *173*(4), 431–445. https://doi.org/10.1086/597229

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, *83*(1), 195–213. https://doi.org/10.1016/S0034-4257(02)00096-2

Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D., & Manica, A. (2017). Consistent individual differences drive collective behaviour and group functioning of schooling fish. *BioRxiv*, *131094*, 1–18. https://doi.org/10.1101/131094

Koen, J. H. (1988). Trace elements and some other nutrients in the diet of the Knysna elephans. *South African Journal of Wildlife Research*, *18*(3), 109–110. https://doi.org/10.3109/03630268009042386

Laidre, K. L., Born, E. W., Atkinson, S. N., Wiig, Ø., Andersen, L. W., Lunn, N. J., … Heagerty, P. (2018). Range contraction and increasing isolation of a polar bear subpopulation in an era of sea-ice loss. *Ecology and Evolution*, 2062–2075. https://doi.org/10.1002/ece3.3809

Lee, P. C., Bussiere, L. F., Webber, C. E., Poole, J. H., & Moss, C. J. (2013). Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (Loxodonta africana). *Biology Letters*, *9*(2). https://doi.org/10.1098/rsbl.2013.0011

Lee, P. C., & Moss, C. J. (2012). Wild female African elephants (Loxodonta africana) exhibit personality traits of leadership and social integration. *Journal of Comparative Psychology*, *126*(3), 224–232. https://doi.org/10.1037/a0026566

Leggett, K. E. A. (2006). Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology*, *41*(1), 17–36. https://doi.org/10.1080/15627020.2006.11407332

Leuthold, W. (1977). Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Zeitschrift Fur Saugetierkunde*, *42*, 358–379.

Lindeque, M., & Lindeque, P. M. (1991). Satellite tracking of elephants in northwestern Namibia. *Journal of African Ecology*, *29*(3), 196–206. https://doi.org/10.1111/j.1365-2028.1991.tb01002.x

Lindsay, W. K. (1994). *Feeding ecology and population demography of African elephants in Amboseli, Kenya (PhD)*. University of Cambridge.

Lindsay, W. K. (2011). Habitat Use, Diet Choice, and Nutritional Status in Female and Male Amboseli Elephants. In C. J. Moss, H. Croze, & P. C. Lee (Eds.), *The Amboseli Elephants: A Long-Term*

Perspective on a Long-Lived Mammal (pp. 51–73). The University of Chicago Press.

Loarie, S. R., Van Aarde, R. J., & Pimm, S. L. (2009). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, *142*(12), 3099–3107. https://doi.org/10.1016/j.biocon.2009.08.021

Moss, C. J. (1988). *Elephant Memories: Thirteen Years in the Life of an Elephant Family*. Chicago: University of Chicago Press.

Nielsen, S. E., Stenhouse, G. B., & Boyce, M. S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, *130*(2), 217–229. https://doi.org/10.1016/j.biocon.2005.12.016

Okello, M. M., Njumbi, S. J., Kiringe, J. W., & Isiiche, J. (2015). Habitat use and preference by the African elephant outside of the protected area, and management implications in the Amboseli Landscape, Kenya. *International Journal of Biodiversity and Conservation*, *7*(3), 211–236. https://doi.org/10.5897/IJBC2014.0795

Olden, J. D., Schooley, R. L., Monroe, J. B., & Poff, N. L. (2004). Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology*. https://doi.org/10.1111/j.0021-8790.2004.00889.x

Petit, O., & Bon, R. (2010). Decision-making processes: The case of collective movements. *Behavioural Processes*, *84*, 635–647. https://doi.org/10.1016/j.beproc.2010.04.009

Polansky, L., Kilian, W., & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proceedings of the Royal Society B: Biological Sciences*, *282*. https://doi.org/10.1098/rspb.2014.3042

Poole, J. H. (1987). Rutting behaviour in African elephants: the phenomenon of musth. *Behaviour*, *102*(34), 283–316. https://doi.org/10.1163/156853986X00171

Prins, H. H. T. (1996). *Ecology and Behaviour of the African Buffalo*. Chapman & Hall. https://doi.org/10.1007/978-94-009-1527-5

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2015). Surface-Water Constraints on Herbivore Foraging in the Kruger National Park , South Africa. *Ecology*, *84*(8), 2092–2107. https://doi.org/10.1890/01-0625

Roever, C. L., van Aarde, R. J., & Chase, M. J. (2013). Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants. *Biological Conservation*, *164*, 98–106. https://doi.org/10.1016/j.biocon.2013.04.006

Ruggiero, R. G. (1991). Opportunistic predation on elephant calves. *African Journal of Ecology*, *29*(1), 86–89. https://doi.org/10.1111/j.1365-2028.1991.tb00823.x

Seltmann, M. W., Helle, S., Adams, M. J., Mar, K. U., & Lahdenperä, M. (2018). Evaluating the personality structure of semi-captive Asian elephants living in their natural habitat. *Royal Society Open Science*, *5*. https://doi.org/http://dx.doi.org/10.1098/rsos.172026

Seydack, A., Vermeulen, C., & Huisamen, H. (2000). Habitat quality and the decline of an African elephant population: implications for conservation. *South African Journal of Wildlife Research*,

30(1), 34–42.

Shannon, G., Page, B. R., Duffy, K. J., & Slotow, R. (2006). The Role of Foraging Behaviour in the Sexual Segregation of the African Elephant. *Oecologia*, *150*(2), 344–354.

Shannon, G., Page, B., Slotow, R., & Duffy, K. (2006). African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, *41*(1), 37–44. https://doi.org/10.1080/15627020.2006.11407333

Sinclair, A. R. E. (1975). The Resource Limitation of Trophic Levels in Tropical Grassland Ecosystems. *Source Journal of Animal Ecology*, *44*(2), 497–520. https://doi.org/10.2307/3608

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences*, *102*(15), 5460–5465. https://doi.org/10.1073/pnas.0408145102

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. New Jersey: Princetown University Press.

Thouless, C. R. (1996). Home ranges and social organization of female elephants in northern Kenya. *African Journal of Ecology*, *34*(3), 284–297. https://doi.org/10.1111/j.1365-2028.1996.tb00623.x

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*, 466–469.

van der Merwe, N. J., Lee-Thorpe, J. A., & Bell, R. H. V. (1988). Carbon isotopes as indicators of elephant diets and African environments. *African Journal of Ecology*, *26*, 163–172.

Vannan, S. K. S., Cook, R. B., Pan, J. Y., & Wilson, B. E. (2011). A SOAP Web Service for accessing MODIS land product subsets. *Earth Science Informatics*, *4*(2), 97–106. https://doi.org/10.1007/s12145-011-0079-2

Vasconcelos, M., Fortes, I., & Kacelnik, A. (2017). On the structure and role of optimality models in the study of behavior. In J. Call (Ed.), *APA Handbook of Comparative Psychology* (pp. 287–307). Washington DC: American Psychological Association.

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. https://doi.org/10.1016/j.biocon.2012.07.019

Weiss, A. (2018). Personality Traits: A View From the Animal Kingdom. *Journal of Personality*, *86*(1), 12–22. https://doi.org/10.1111/jopy.12310

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal*, *13*, 265–286. https://doi.org/10.1111/j.1365-2028.1975.tb00139.x

Western, D. (2007). A half a century of habitat change in Amboseli National Park, Kenya. *African Journal of Ecology*, *45*, 302–310. https://doi.org/10.1111/j.1365-2028.2006.00710.x

Western, D., Groom, R., & Worden, J. (2009). The impact of subdivision and sedentarization of

pastoral lands on wildlife in an African savanna ecosystem. *Biological Conservation*, *142*(11), 2538–2546. https://doi.org/10.1016/j.biocon.2009.05.025

Western, D., & Lindsay, W. K. (1984). Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology*, *22*(4), 229–244. https://doi.org/10.1111/j.1365-2028.1984.tb00699.x

Western, D., & Maitumo, D. (2004). Woodland loss and restoration in a savanna park: a 20-year experiment. *African Journal of Ecology*, *42*(2), 111–121. https://doi.org/10.1111/j.1365-2028.2004.00506.x

Western, D., & Van Praet, C. (1973). Cyclical changes in the habitat and climate of an East African ecosystem. *Nature*, *241*, 104–106.

Wittemyer, G., Keating, L. M., Vollrath, F., & Douglas-Hamilton, I. (2017). Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. *Ecography*, *40*, 598–605. https://doi.org/10.1111/ecog.02379