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TITLE

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

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patterns

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RUNNING TITLE

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Modelling large herbivore movement decisions

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31   ABSTRACT

32   The ability of animals to adapt to their changing environment will depend in part on shifts in their

33   ranging patterns, but when and why individuals choose to move requires detailed understanding of

34   their decision-making processes. We develop a simple decision-making model accounting for resource

35   availability in habitually used ranges. We suggest that disparities between model predictions and

36   animal tracking data indicate additional factors influencing movement decisions, which may be

37   identified given detailed system-specific knowledge. The model was evaluated using movement data

38   from satellite-tracked elephants (*Loxodonta africana*) inhabiting the Amboseli Ecosystem in Kenya,

39   moving from savannah areas with low quality but constant resource availability, to areas with

40   temporally-constrained higher nutrient availability. Overall, the model fit the data well: there was a

41   good correlation between predicted and observed locations for the combined data from all elephants,

42   but variation between individuals in how well the model fits. For those elephants where model

43   predictions were less successful, additional factors likely to affect movement decisions, reproduction,

44   anthropogenic threats, memory and perception, are suggested. This protocol for building and testing

45   decision-making models should contribute to success in attempts to preserve sufficient space for

46   large herbivores in their increasingly human-dominated ecosystems.

49   INTRODUCTION

50   In the face of a changing climate and the rapid conversion of natural habitats to human-dominated

51   landscapes, the future of many species will depend on their ability to adapt to new circumstances.

52   Adaptation may involve behavioural changes or innovations (Sol, Duncan, Blackburn, Cassey, &

53   Lefebvre, 2005), but geographical shifts in a species range (Laidre et al., 2018) or in how a species

54   moves through its existing range (Olden, Schooley, Monroe, & Poff, 2004; Tucker et al., 2018) may

55   allow it to cope with novel environmental conditions or constraints. Range shifts require animals to

56   make the decision to relocate from one site to another and have often been predicted through the

57   use of simple decision models (Bastille-Rousseau, Douglas-Hamilton, Blake, Northrup, & Wittemyer,

58   2018). Whilst these shifts are largely guided by suitable climatic conditions and the provision of

59   sufficient food and water, movement decisions are also likely mediated by other factors. The

60   predicted shifts can be incorporated into conservation and management strategies for species of

61   concern, but are unlikely to be accurate unless the full range of factors influencing movement can be

62   taken into account.

63   Here we present a means of identifying factors other than simple resource-requirements which

64   mediate movement decisions for large herbivores negotiating heterogeneous landscapes. Our

65   method uses disparities between a simple model of resource-driven decision making and animal

66   tracking data to indicate the need to incorporate other factors that affect movement decisions. Given

67   a detailed understanding of the study system, these factors can be identified using local knowledge

68   (see also Bastille-Rousseau et al., 2018). Models were developed and evaluated using elephants

69   (*Loxodonta africana*) inhabiting the Amboseli Basin in Kenya as a case study. Ensuring a future for

70   elephants in this increasingly human-dominated landscape hinges on understanding how and why

71   elephants use the landscape through space and over time.

72   Long-term monitoring of elephant populations and remote tracking studies have greatly improved our

73   understanding of general patterns in elephant ranging behaviour (e.g. Wall et al. 2013). Elephants

74   show large-scale, purposeful space use (Polansky, Kilian, & Wittemyer, 2015) and so require large

75   areas over which to roam to access heterogeneously distributed resources (e.g. Leuthold 1977;

76   Lindeque & Lindeque 1991; Thouless 1996; Blake et al. 2003; Birkett et al. 2012). It is also clear that

77   elephants do not use the space available to them at random. Instead, elephants generally shift ranges

78   seasonally (Leggett, 2006; Loarie, Van Aarde, & Pimm, 2009; Western & Lindsay, 1984), searching for

79   water (Chamaille-Jammes & Valeix, 2007; de Beer & van Aarde, 2008; Redfern, Grant, Biggs, & Getz,

80   2015) and the highest quality vegetation (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014;

81   Loarie et al., 2009). This results in dynamic habitat and food type preferences (Cerling et al., 2006;

82   Loarie et al., 2009; G. Shannon, Page, Slotow, & Duffy, 2006).

83   We developed a simple decision-making model which tracked the food available within habitually-

84   used ranges to satellite-tracked individuals from five family groups (representing the movements of

85   over 220 elephants in the Amboseli population), whilst taking into account the daily need of

86   individuals for water. The individuals had complete perceptual knowledge of resource availability in

87   their home range and the model assumed that, when water availability allowed, individuals moved to

88   maximise their nutrient intake rate and subsequent fitness (Okello, Njumbi, Kiringe, & Isiiche, 2015),

89   as in optimal foraging theory (Bastille-Rousseau et al., 2017; Roever, van Aarde, & Chase, 2013;

90   Stephens & Krebs, 1986; Vasconcelos, Fortes, & Kacelnik, 2017). We assumed that individuals make

91   daily choices whether to relocate to an alternative location or to stay in the current location (Petit &

92   Bon, 2010). Where model predictions did not match those of tracking data, we used detailed

93   knowledge of the elephants and ecosystem to identify additional factors, such as physiological or

94   social needs, which depend inter alia on an individual's sex, age, reproductive status and body

95   condition (Lindsay, 2011).

96   **MATERIALS AND METHODS**

97   **Case study site information**

98   The study was carried out in the Amboseli basin (bounding coordinates: -2.02N, -3.28S, 38.03E,

99   36.67W), an area of approximately 8000km^2 straddling the border of southern Kenya and northern

100   Tanzania, comprising the central Amboseli National Park (392km^2; ANP hereafter) and surrounding

101   landscape (Croze & Lindsay, 2011; see Supplementary Information). The habitat consists of semi-arid

102   savannah that responds seasonally to highly variable rainfall. Rain predominantly occurs in two

103   seasons; a short wet season (November and December) and the long rains (March through May;

104   Altmann, Alberts, Altmann, & Roy, 2002). During dry seasons, a series of swamps in the central basin

105   provide the primary source of water, fed by groundwater flow from the slopes of Kilimanjaro in the

106   south (Croze & Lindsay, 2011), though other perennial sources occur in the Selenkay Conservancy and

107   in Kitenden, in the form of a borehole and two natural springs. Wildlife concentrates in the central

108   basin during dry seasons and disperses following rain (Western, 1975). The Amboseli basin is home to

109   around 1670 individually known and monitored elephants (Lee, Bussiere, Webber, Poole, & Moss,

110   2013). Unlike most other African populations, the Amboseli elephants have been relatively

111   undisturbed by human activities. However, recent human population growth in Kenya and a lifestyle

112   shift from nomadic pastoralism to sedentary farming (Western, Groom, & Worden, 2009) presents

113   growing challenges for the persistence of Amboseli's wildlife.

114   **Animal tracking data**

115   GPS-GSM collars (@ Savannah Tracking) were fitted in July 2011 to five adult female elephants (Ida,

116   Lobelia, Maureen, Vicky and Willow) from different family groups, representing locations of over 220

117   individuals (because families forage as units). Habitat heterogeneity around the central protected

118   area affects ranging strategies and reproductive success, so not all dispersal directions are equal for

119   Amboseli elephants. Target females were selected based on more than 40 years of observations to

120   represent the known diversity in dispersal areas and foraging opportunities in Amboseli (which are

121   largely inherited through generations unless disrupted by human disturbance; Croze & Moss, 2011;

122   Moss, 1988) and to minimise risks to target elephants, family members and staff. Individual females

123   were selected according to ethical and safety criteria, minimising the disturbance of each

124   intervention. Target females were 1) not matriarchs, 2) without a calf aged <2 years and 3) closely

125   related to matriarchs so shared movement patterns. Matriarchs were not collared due to the drastic

126   potential impact of matriarch loss on families given the small but present risks of immobilisation, and

127   the greater ease of managing non-target family members during immobilisations when they had a

128   safe rallying point around their matriarch. Collars were fitted under the authority of the Kenya

129   Wildlife Service, the Kenyan body regulating interactions with elephants, and with research clearance

130   to Amboseli Trust for Elephants from the National Commission for Science, Technology and

131   Innovation (NACOSTI/P/15/9605/5732).

132   GPS fixes were recorded at hourly intervals for roughly 12 months, giving in sum 43,728 location fixes.

133   Collar data was summarised into daily presence or absence from ANP. Given the reliance of elephant

134   families on water, an elephant was considered present in ANP on any day in which distance from the

135   swamp was zero at any time during that day. Conversely if the distance from the swamp was never

136   zero, the elephant was considered that day to have dispersed from ANP. The dispersal area of each

137   female was identified as the 95% kernel density estimates (ArcMap; ESRI 2017) of her locations

138   outside the park boundary.

139   **Resource-driven movement model**

140   We developed a profitability index to indicate the resource availability of each dispersal area and of

141   ANP, while taking into account the daily need of female elephants for water (Fig. 1). Water was

142   considered essential and elephants were only able to move to areas where water was available. The

143   swamp edge habitat alone was used to indicate profitability for ANP, as elephants consistently return

144   to the park to feed on the reliable and abundant swamp edge vegetation, as well as drink. Swamp

145   edge was therefore used as representative of the resources drawing elephants back to ANP from their

146   dispersal areas.

147   *Vegetation quantity*

148   Data on vegetation quantity were acquired using the Normalised Difference Vegetation Index (NDVI),

149   which exploits the marked difference in reflectance in red and near infra-red wavelengths

150   characteristic of healthy green vegetation (Huete et al., 2002). We used 16-day composite values of

151   NDVI retrieved from Terra-MODIS (Moderate Resolution Imaging Spectroradiometer) to infer time-

152   specific values of vegetation quantity. Specifically we used the MOD13Q1 product accessed via the

153   Oak Ridge National Laboratory Web Service (Vannan, Cook, Pan, & Wilson, 2011). Median NDVI values

154 were calculated for each individual's dispersal area (i.e. 95% kernel density estimates outside ANP)

155 and swamp edge for each 16-day interval. Data were filtered using the MOD13Q1 QA flags such that

156 only 'good' quality NDVI observations were used in our calculations. For extended remote sensing

157 methodology, see Supplementary Information.

158 *Vegetation quality*

159 Crude protein is an important limiting factor for herbivores inhabiting savannah ecosystems (Sinclair,

160 1975) and we therefore assessed vegetation quality by its protein content (%). The diet of Amboseli

161 elephants is dominated by grasses, so we used grass protein content as our measure of vegetation

162 quality. Protein content varies seasonally, peaking during the green-up of vegetation following the

163 onset of rains (Georgiadis & McNaughton, 1990; Lindsay, 1994). Here we estimate protein content

164 depending on whether or not it rained in the previous month. Lindsay (1994) measured the protein

165 content of Amboseli swamp edge vegetation and rainfall throughout the course of a year. From these

166 data, we assigned protein content of swamp edge vegetation as 11.8% or 8.4% depending on whether

167 or not it rained in the preceding month. Georgiadis & McNaughton (1990) collected similar

168 measurements in the broader Amboseli basin outside the Amboseli swamps and found protein

169 contents of 23.0% during the green-up following rains and 10.0% in the subsequent drying phases.

170 We used the figure of 23.0% if the change in NDVI was positive, indicating green-up in the month

171 after rains, at all other times 10.0%.

172 *Water availability*

173 Permanent water sources were available in ANP and in the dispersal areas of Vicky (Selenkay), and Ida

174 and Lobelia (Kitenden). We deemed water available year-round in these areas. We used daily

175 measures of rainfall from the rainfall gauge in the Amboseli Elephant Research Camp (-2.679S,

176 37.267E) to indicate rainfall across the entire Amboseli basin since NDVI fluctuations across the

177 ecosystem are generally synchronous. Rainfall contributed to surface water availability in all areas and

178 so water was considered available across the entire basin for seven days following rains.

179 *Movement-decision model fit*

180 We assumed that if individual movement behaviour was governed by resource availability, individuals

181 should move to maximise profitability throughout the year. Therefore, when ANP profitability was

182 greater than that of the dispersal area, the individual should be present in ANP on that day, and vice

183 versa. If profitability for the two locations was very close (difference < 0.3) no prediction was made as

184 to which provided the optimal foraging location.

185 The daily absence or presence of the elephants as predicted by profitability was compared to actual

186 absence or presence indicated by the collar data. The correlation between predicted and observed

187 presences and absences was calculated as a ϕ statistic (Conover, 1971). ϕ is the equivalent of

188 Pearson's correlation that is applicable to binary data. ϕ values were tested for significance using chi-

189 square with 1 degree of freedom.

190 **RESULTS**

191 **Ranging behaviour**

192 The ranging behaviour of the five collared elephants over a 12-month period is illustrated in Fig. 2. Ida

193 and Lobelia spent most of their time (c. 85%) in ANP, primarily in the southeast around the southern

194 tip of the eastern swamp (Longinye; see Supplementary Information for detailed park map). From

195 there both elephants regularly moved southwest into the Kitenden region and occasionally east to the

196 Kimana Sanctuary. Maureen, Vicky and Willow spent about half their time in the park. Maureen used

197 the eastern swamp and the area around and including the western swamp (Longolong). From there,

198 she dispersed south through the Kitirua Conservancy and then southwest across the foothills of

199 Kilimanjaro into Tanzania. Vicky and Willow also used the eastern swamp, but additionally used the

200 northern tip of the central swamp (Enkongo Narok). Within the park Vicky frequented the north and

201 dispersed north to spend much time in the Selenkay Conservancy. Willow by contrast used the west

202 of the park from which she dispersed northwest to the Meshanani region.

203 **Profitability**

204 Profitabilities calculated for the swamp edge and dispersal areas (Kitenden, Kitirua-Tanzania, Selenkay

205 and Meshanani) captured spatial and temporal variation (Fig. 3). Temporally, profitability generally

206 increased following the onset of the rains and declined as the rains subsided. Spatially, areas differed

207 in the precise timing and extent of increases and decreases in profitability. ANP profitability varied

208 less than the profitability of the dispersal areas because in the dry seasons the swamps retained

209 abundant green vegetation but did not experience the dramatic increase in protein content seen in

210 dispersal area vegetation following rain. As a result, there was temporal variation in whether

211 profitability was higher in ANP or in the dispersal area, predicting switches in the optimal foraging

212 location between ANP and the dispersal areas. Generally, profitability indices predicted that elephants

213 should be present in the national park during August, September and October 2011, January and

214 February 2012 and from May 2012 onwards. At other times they were predicted to move out to their

215 family dispersal areas.

216 **Movement-decision model fit**

217 Overall the model fitted the data well: there was good correlation between predicted and observed

218 presences and absences for the combined data from all five elephants (ϕ = 0. 37, p<0.001), but there

219 was variation between elephants in how well the model fitted (Breslow-Day test, χ_4 = 67.4, p<0.001,

220 Fig. 4). The locations of Vicky were well predicted by the model (ϕ = 0.60, p < 0.001, Fig. 4) though the

221 model was unable to predict Vicky's brief excursions between August and October 2011, nor her

222 absence from the park in May to June 2012. The model was moderately successful in predicting the

223 locations of Ida, Lobelia, Maureen and Willow (ϕ = 0.42, 0.27, 0.39 and 0.46 respectively, p < 0.001 for

224 each), but failed to predict the regular presence of Ida and Lobelia in ANP throughout both wet

225 seasons. Maureen was regularly absent between August and October 2011 and in June and July 2012

226 when the model assumed presence throughout. The timings of Maureen's major excursions from the

227 park were also slightly ahead of those predicted by the model. Willow's movements were well

228   predicted with the exception of brief excursions during August and September 2011 and of her

229   continued absence from the park during June and July 2012.

230   DISCUSSION

231   By modelling the profitability of the traditional foraging areas of each of the five elephant families

232   while taking account of their daily need for water, we predicted the timings of their shifts in optimal

233   locations. The shift timings were similar despite the different dispersal areas used by the collared

234   elephants (Fig. 3). In general, ANP offered the highest rate of nutrient intake during the dry seasons

235   until the onset of rains, at which point the dispersal areas provided better foraging locations provided

236   that water was available. While the model fitted the data well overall, there was variation among

237   elephants in the ability of the model to correctly predict park absence and presence. Predictions and

238   observations were significantly correlated for all five individuals, but while the correlation was good

239   for Vicky, it is likely that other factors also influenced the movement decisions of Ida, Lobelia,

240   Maureen and Willow. Given an in-depth knowledge of the study system (AERP long term data), we

241   now attempt to identify these factors and suggest how they can be incorporated into future

242   movement models for elephants.

243   The sustained residency of Ida and Lobelia in ANP is likely due to the fact that both females gave birth

244   during the 2012 short wet season (January-February). Elephants usually seek safe areas as parturition

245   approaches and for some time after as new-born calves are vulnerable to disturbance and predation

246   (Ruggiero, 1991). For family units experiencing recent parturition events, the motivation to remain in

247   ANP increases because it is perceived as a relatively safe area. During the period of sampling, Ida and

248   Lobelia's dispersal areas of Kitenden and Kimana were relatively high risk because a number of

249   elephants were killed or injured as a result of human interactions (Big Life Foundation/AERP long term

250   data). In elephants, risks in the form of anthropogenic threats are known to deter long-term elephant

251   habitat use (Roever et al., 2013) and alter the daily locations of resting sites (Wittemyer, Keating,

252   Vollrath, & Douglas-Hamilton, 2017). Risks affect animal decision making more widely when animals

253   sacrifice optimum nutrient intake to minimise the risks of predation (Barnier et al., 2014; Bastille-

254   Rousseau et al., 2017). Including the risks associated with human-elephant interactions should

255   improve the model fit. Relative risk could be measured in terms of the number of negative human-

256   elephant interactions (injuries or mortalities) over a specified period, land use type (pastoralist vs.

257   agricultural vs. wildlife zones) or human density in an area (which is also a function of land use type).

258   Over the longer-term, periods of drought could also be used as an indirect predictor of human-

259   associated risk, because competition for water sources and high-quality food patches increases

260   contact between humans and elephants (Chiyo, Cochrane, Naughton, & Basuta, 2005) and the

261   economic threats of livestock loss erode tolerance for wildlife (Western, Nightingale, Sipitiek, Mose, &

262   Kamiti, pers. comm.).

263   Behavioural differences between conspecifics can be viewed as evidence of personality; consistent

264   differences in the behavioural responses of individuals across various spatial and temporal contexts

265   (Beekman & Jordan, 2017). Here therefore, we may alternatively consider the residency of Ida and

266   Lobelia could be to be due to their 'wary' personalities, whilst Vicky is more 'bold' (Jolles, Boogert,

267   Sridhar, Couzin, & Manica, 2017). Personality has been reliably demonstrated for elephants (Lee &

268   Moss, 2012; Seltmann, Helle, Adams, Mar, & Lahdenperä, 2018) but we have yet to systematically

269   sample the subject families and can only speculate at this point. However, our long-term observations

270   suggest that personality is shaped by family members (particularly the matriarch) and by experiences,

271   especially early in life. We can propose that, as seen in many other bird, fish and mammal species

272   (Weiss, 2018), personality may both shape and be shaped by exposure to risk.

273   Maureen displayed much lower use of ANP than predicted by the model, suggesting she was less

274   reliant on the swamps for dry season water as she had access to an alternative water source in the

275   Kitirua Conservancy. Elephants share this water point with livestock and people, often at high

276   concentrations, but this area also showed high tolerance for wildlife during the study period. The

277   model was also unable to predict the timing of Maureen's location shift, consistently predicting a later

278   dispersal than seen in the collar data. The dispersal area used by Maureen in Tanzania is characterised

279   by mature Acacia woodlands rather than the open bushed savannah associated with the majority of

280   the ecosystem. Acacia flower ahead of the onset of rains and Maureen's early excursions may

281   coincide with this phenological event, rather than the NDVI observed green-up. Flowering in

282   bushlands might be associated with higher sugar and other nutrient transport in Acacia stems, which

283   are desirable elephant foods (Lindsay, 1994). Incorporating nutrient fluxes that are independent of

284   vegetation green-up will require both phenological monitoring of the timing of flowering and

285   quantifying the associated nutrient benefits. The remotely sensed measures of greenness used here

286   are insensitive to the spectral changes associated with flowering, thus suitable alternative remote

287   sensing techniques are needed for a more comprehensive accounting for foraging movements.

288   While we can suggest other factors that operate in combination with nutrient intake to affect

289   movement decisions, the behavioural mechanisms underlying movement patterns remain poorly

290   understood (Bolger, Newmark, Morrison, & Doak, 2008); indeed whether movement decisions are

291   guided by animals' perceptions of current environmental conditions or predictions based on memory

292   is uncertain. The capacity of elephants to remember the spatial locations of out-of-sight individuals

293   (Bates et al., 2008) and the purposeful movement to water resources beyond the senses of sight or

294   smell (Polansky et al., 2015) shows that elephants have a keen spatial memory. Despite this, our data

295   show that decision points (Polansky et al., 2015) coincide with the onset of the rains, suggesting that

296   the onset of rains may be used as a key environmental cue to instigate range shifts (Holdo, Holt, &

297   Fryxell, 2009; Prins, 1996). Also relevant to this question are several brief excursions by Vicky and

298   Willow to their respective dispersal areas prior to their longer-term range shifts. This 'scouting'

299   behaviour (Bracis & Mueller, 2017) suggests sampling of the conditions at their destination before

300   committing to the final range shift. Both of these factors suggest perception-guided movement.

301   However, rainfall across the Amboseli basin is perhaps more temporally and spatially variable than

302   accounted for here, meaning elephants cannot rely on the same rules each year. Memory alone is

303   likely to be less effective in such a patchy environment, and so individuals will use both immediate

304 perception and memory when making movement decisions. Although memory is important in

305 defining the destination of movements based on previous experiences of improved nutrient intake

306 rate, perception is crucial in remaining flexible to local environmental changes in climatic conditions

307 and risk.

308 We have introduced a simple decision-making model of the resource-driven factors affecting key

309 decisions of where individuals go and when. Where individuals fit the model well, a key benefit of

310 movement over an ecosystem is indicated, which is to maximise nutrient intake rates. That individuals

311 do not perfectly fit the model suggests that other factors need to be included in combination with

312 nutrient intake rates. High residency of elephants that disperse to the eastern part of the ecosystem

313 suggests that individuals and families make movement decisions based on trade-offs between the

314 resource-related benefits of dispersal and the associated risks (see also Chiyo et al., 2014). For Ida and

315 Lobelia, it is hard to determine whether perceived risks resulted from human-elephant interactions,

316 the dangers involved with moving new-born calves over long distances, or the limited travel speed of

317 those vulnerable calves. More data characterising risks and associated movements are important

318 (Nielsen, Stenhouse, & Boyce, 2006; Roever et al., 2013) and necessary before these factors can be

319 reliably included in an enhanced model of movement decision making. Male elephants were not

320 considered here due to differences in resource requirements. Males are less reliant on water than

321 females and forage less selectively, prioritising quantity over quality (Graeme Shannon, Page, Duffy, &

322 Slotow, 2006). When in musth, male elephant movement is largely focused on the pursuit of oestrous

323 females, with little consideration for food (Poole, 1987). Previous work in Amboseli has demonstrated

324 the importance of both food (NDVI) and social needs (Chiyo et al. 2014) on male ranging, so we

325 expect that our model could be extended to non-musth males but would need further modification to

326 take into account the energy demands of musth, which is a topic for future study. Further

327 development of our model will ultimately provide a basis for robust prediction of elephant

328 movements under a variety of environmental and physiological conditions.

329 We argue that simple resource-driven movement models based on easily accessible resource

330 availability data in combination with animal tracking studies will be useful in identifying additional

331 features influencing movements in well-studied systems, where anecdotal evidence can add to

332 understanding movement decisions. This will allow conservationists and wildlife managers to better

333 understand how large herbivore movements will respond to management scenarios (e.g. fences, new

334 roads) and future environmental changes (e.g. shifting rainfall patterns), and in this way can help

335 manage conflicts of interest between humans and wildlife and ensure sufficient space for wildlife.

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509

510   **FIGURES**

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

511

512   **Figure 1.** Profitability of each dispersal area and ANP, calculated daily. See Methods for definitions of

513   vegetation quantity and quality. Water availability is a binary variable taking values of 1 or 0

514   depending on whether or not water is available in the specified area.
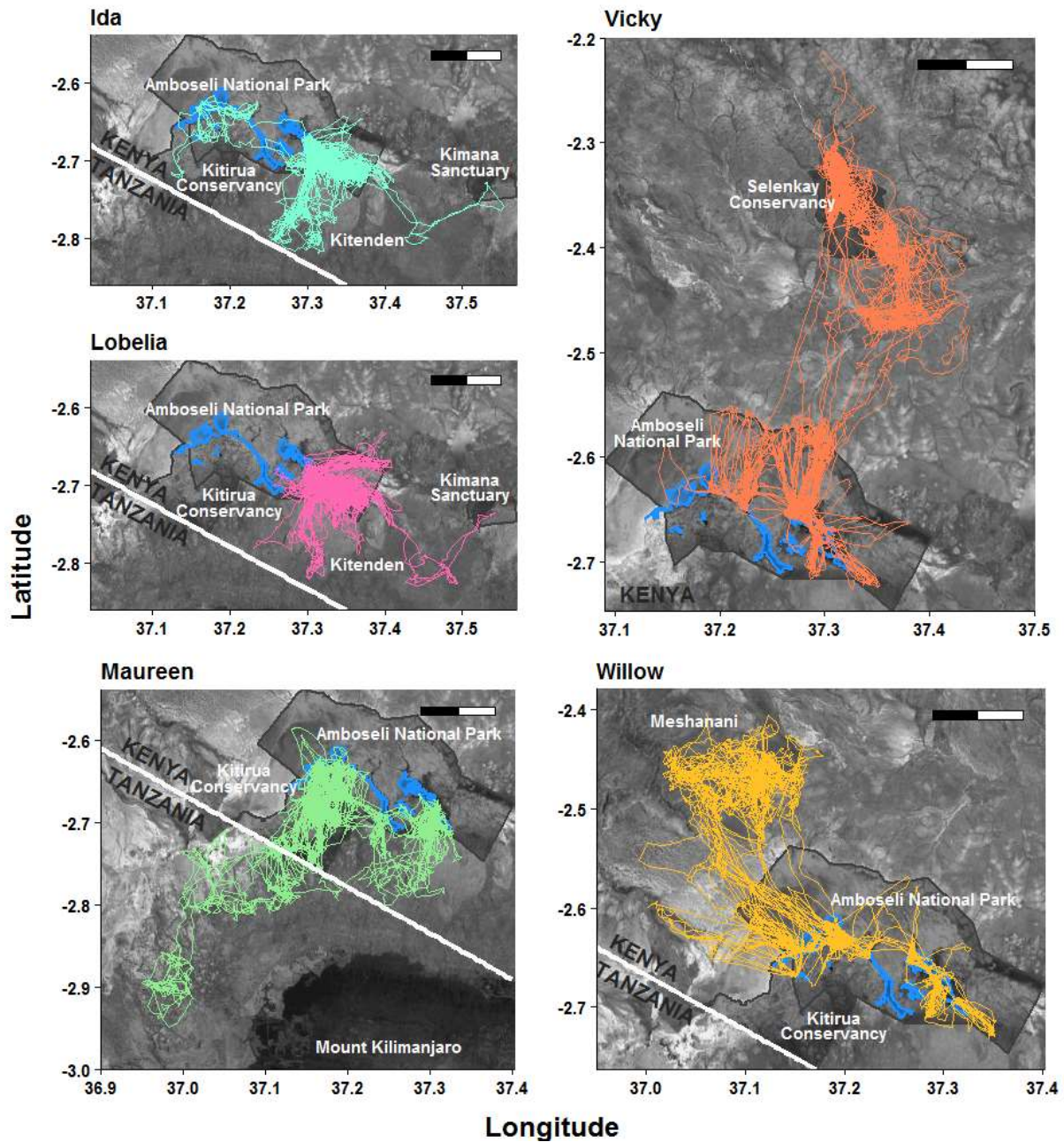
515

516   **Figure 2.** Tracks of five collared elephants displaying use of Amboseli National Park and dispersal areas

517   (coloured lines: different colour for each female). Protected areas are indicated by grey boundaries,

518   the international border between Kenya and Tanzania by the white line, and the central Amboseli

519   swamps in blue. Scale bar represents 10km (divisions of 5km). Two females used the same dispersal

520   area (Kitenden, southeast); other females ranged to the north, northwest and southwest when

521   leaving ANP.

522
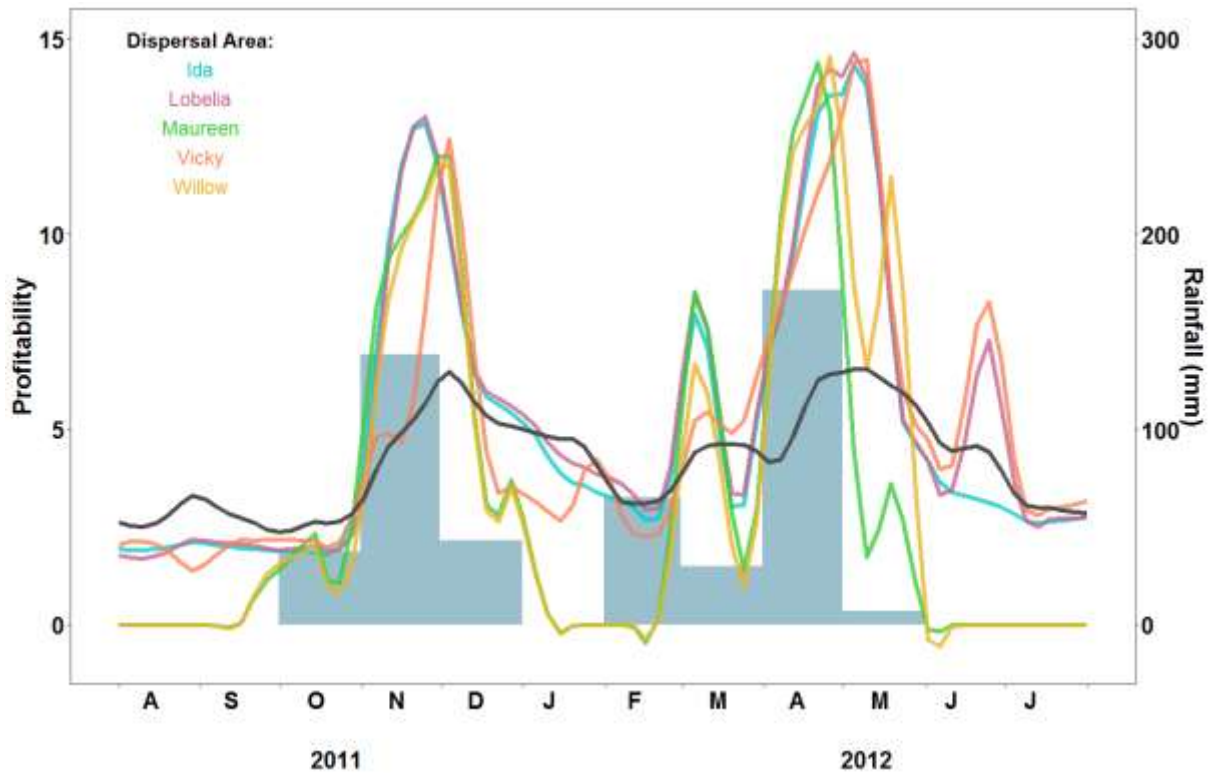
Figure 3. Response of profitability (lines: black = swamp edge, coloured = dispersal areas), the product

of the quantity and quality of vegetation, and water availability, to monthly rainfall (bar: blue).

525
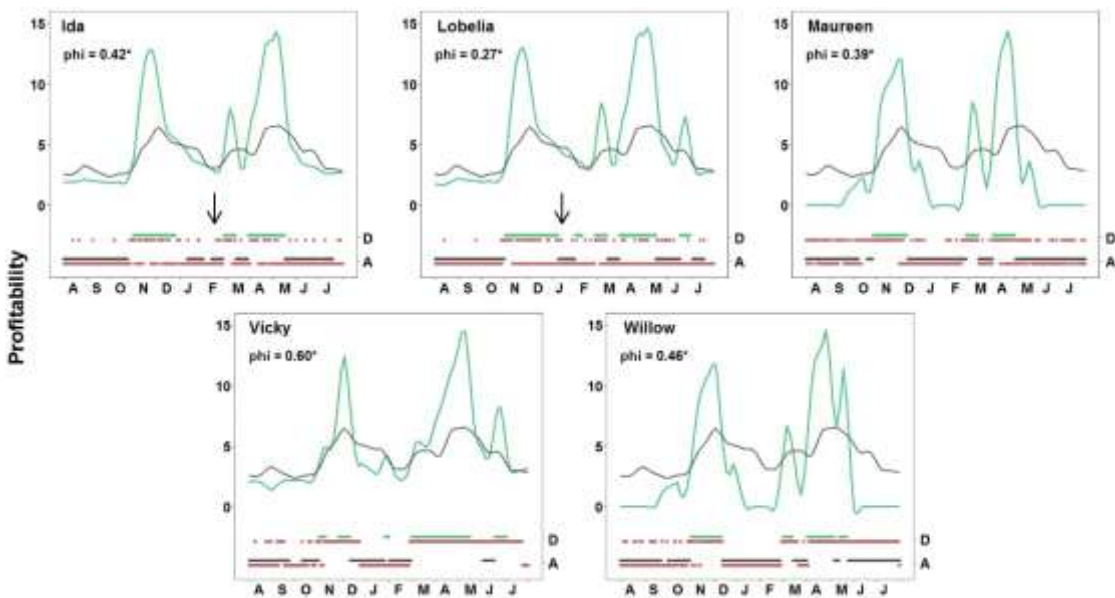
Figure 4. Profitabilities of swamp edge (black curve) and dispersal area (green curve) for each collared

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

529   profitabilities were within 0.3 of each other. Arrows indicate parturition events for Ida and Lobelia. Phi

530   coefficients indicate correlation between model predictions and collar data; * indicates significance of

531   this relationship (Chi-squared: $p < 0.001$).