

1 **Using camera traps to study the age-sex structure and behaviour of crop-**
2 **using elephants in Udzungwa Mountains National Park, Tanzania**

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26 **ABSTRACT**

27 Crop losses from elephants are one of the primary obstacles to the coexistence of
28 elephants and people and one of the contributing causes to elephant population
29 decline. Understanding if some individuals in an elephant population are more likely
30 to forage on crops, and the temporal patterns of elephant visits to farms, is key to
31 mitigating the negative impacts of elephants on farmers. We used camera traps as a
32 novel technique to study elephant crop foraging behaviour in farmland adjacent to
33 the Udzungwa Mountains National Park in southern Tanzania from October 2010 to
34 August 2014. Camera traps placed on elephant trails into farmland captured
35 elephants on 336 occasions over the four-year study period. We successfully
36 identified individual elephants from camera trap images for 126 of these occasions.
37 All individuals detected on the camera traps were independent males, and we
38 identified 48 unique bulls aged between 10 and 29 years. Two-thirds of the bulls
39 identified were detected only once by camera traps over the study period, a pattern
40 that also held during the last year of study when camera trapping effort was
41 continuous. Our findings are consistent with previous studies that found that adult
42 males are more likely to adopt high-risk feeding behaviours such as crop foraging,
43 though young males dispersing from maternal family units also consume crops in
44 Udzungwa. Our study found a large number of occasional crop-users (32 of the 48
45 bulls identified) and a smaller number of repeat crop-users (16 out of 48), suggesting
46 that lethal elimination of crop-using elephants is unlikely to be an effective long-term
47 strategy for reducing crop losses from elephants.

48

49 **KEYWORDS** human-elephant coexistence, HEC, crop foraging, Problem Animal
50 Control, PAC, Udzungwa Mountains, Tanzania

51 INTRODUCTION

52 The dramatic population decline of African elephants (*Loxodonta africana*) is one of
53 the most pressing conservation issues currently facing sub-Saharan Africa (Maisels
54 et al., 2014; Wittemyer et al., 2015; Chase et al., 2016). Another great challenge for
55 elephant conservation in the long-term is coexistence with people, in particular
56 where elephants consume or damage human crops (Hoare, 2012). As a taxon with
57 large range requirements and long-distance movements (Graham et al., 2009),
58 elephants spend considerable time outside of protected areas (Blanc et al. 2007; van
59 Aarde & Jackson, 2007; Kikoti, 2009), where they are more likely to share and
60 compete for space and resources with people. The impacts of elephants outside
61 protected areas include loss of crops and reduced yields, damage to human
62 property, death of livestock, human injury and in some cases, death (Thouless,
63 1994; Ngure, 1995; Kangwana, 1996; Lahm, 1996). These impacts of elephants on
64 people's livelihoods can lead to retaliatory and legal killing of elephants under
65 Problem Animal Control policies (Hoare, 2000; Hoare, 2012). In this context,
66 understanding which elephants in a population are more likely to forage on crops,
67 and investigating temporal patterns in crop foraging behaviour, are integral to
68 developing effective strategies for reducing crop losses from elephants (Naughton-
69 Treves, 1998).

70 Previous studies have highlighted a male bias in elephant crop foraging
71 behaviour (Osborn, 1998; Hoare, 1999; Sitati et al., 2003; Graham et al., 2010;
72 Chiyo et al., 2011; 2012; Ekanayaka et al., 2011). Crop foraging has been observed
73 as a 'high-risk, high-gain' foraging strategy for male elephants to maximise nutrient
74 intake while minimizing time spent and distance travelled while foraging (Sukumar &
75 Gadgil, 1988; Chiyo & Cochrane, 2005), a behaviour that has also been documented

76 in males from other polygamous species, including at least nine species of African
77 primates (Trivers, 1985; Davenport et al., 2006; Wallace & Hill, 2012). In contrast,
78 females might not show this behaviour as often as males owing to the potential risk
79 incurred in agricultural landscapes by dependent offspring (Sukumar & Gadgil,
80 1988). This may not always be the case, as studies in south-eastern Tanzania and
81 around Tsavo National Park, Kenya, found that mixed groups consisting of bulls,
82 females, and calves were responsible for the majority of crop loss incidents (Smith &
83 Kasiki, 2000; Malima et al., 2005). However, age and sex data from enumerator-
84 based studies may be unreliable because they commonly rely on interviews with
85 farmers who are usually not formally trained in sexing and ageing elephants (Smith &
86 Kasiki, 2000).

87 Moreover, 'repeat' or 'habitual' crop use has previously been documented in
88 African elephants (Hoare, 2001; Chiyo & Cochrane, 2005; Chiyo et al., 2011; 2012).
89 A study in Amboseli, Kenya revealed considerable individual variation in crop use
90 (Chiyo et al., 2011), with a small number of bulls feeding on crops relatively
91 frequently and others sporadically. Bulls may also acquire crop foraging behaviour
92 through social learning, and therefore the structure of male association networks
93 may influence the tendency for crop foraging in bulls and drive differences in crop
94 foraging behaviour between individuals (Chiyo et al., 2012).

95 Elephant crop foraging behaviour is difficult to study because incidents usually
96 occur at night (Gunn et al., 2014), and thus direct observation in the field is often
97 risky and hampered by poor visibility. Previous studies have employed indirect
98 methods to assess the sex and age structure of crop-users, such as estimating
99 elephant age from dung size and footprint diameter (Chiyo & Cochrane, 2005;
100 Morrison et al., 2005). Others have studied elephant crop use at the individual level

101 using genetic data collected from elephant dung (Chiyo et al., 2011). Camera traps
102 have been widely implemented to identify individuals (Karanth & Nichols, 1998;
103 Silver et al., 2004) and study animal behaviour that may be challenging to document
104 using direct observations (Griffiths & van Schaik, 1993); however, until now, they
105 have not been used to study crop foraging behaviour in elephants.

106 In this study, we used camera traps to investigate patterns of crop use and to
107 establish the number and sex and age structure of crop-using elephants along the
108 boundary between Udzungwa Mountains National Park and adjacent farmland in
109 south-central Tanzania. We first assess whether elephants photographed on camera
110 traps are likely to be foraging on crops. We then estimate the minimum number and
111 the age and sex structure of crop-using elephants between October 2010 and
112 August 2014. Finally, we discuss the implications of our results in the context of
113 current policies for managing crop losses from elephants at our study site, in
114 Tanzania, and more generally across Africa where elephants and people co-occur.

115

116

117 **STUDY AREA**

118 The study site is located in Njokomoni, a small area of farmland (approximately 2.5
119 km²) directly adjacent to the Udzungwa Mountains National Park (UMNP) in south-
120 central Tanzania. The Udzungwa Mountains encompass the largest and biologically
121 richest forest blocks of the Eastern Arc Mountains (Burgess et al., 2007), and are
122 home to a relatively young, recovering population of forest-using African savannah
123 elephants (Nowak et al., 2009). After heavy poaching between the 1960s and 80s
124 led to the near extinction of elephants in the Udzungwa Mountains, this elephant
125 population – presumed to have taken refuge at high elevations (Jones & Nowak,

126 2015) – began to recover following the gazetting of the National Park in 1992
127 (Joram, 2011).

128 The Njokomoni area is farmed by villagers from two villages known as
129 Man'gula A and Mang'ula B, both of which are located along the east-facing
130 escarpment of the Udzungwa Mountains (Fig. 1). The vegetation along the eastern
131 side of the National Park comprises lowland rainforest and miombo woodland, which
132 extend to the Park boundary. Crop losses from elephants in the area emerged as a
133 regular occurrence in 2008 (Joram, 2011) and appeared to be related to the
134 blockage of elephant movements associated with the loss of wildlife corridors
135 between the Udzungwa Mountains and the Selous Game Reserve (Jones et al.
136 2012).

137 The Njokomoni farmland holds over 120 farms, with individual farm size
138 ranging from 0.25 to 2 ha. Over 30 different crops are cultivated in a mixed
139 intercropping system (Joram, 2011). The wet season spans November to May, and
140 the dry season June to October (Lovett et al., 2006). Farming activity occurs year-
141 round, with rain-fed farming during the wet season and irrigation farming during the
142 dry season enabled by perennial streams. Crop losses to elephants occur
143 throughout the year, but are generally more frequent in the dry season, peaking in
144 September when the irrigated maize crop matures. A 2010-2011 survey of six
145 adjacent villages along the eastern boundary of the National Park identified
146 Njokomoni as a hotspot of elephant crop use, as over 75% of verified reports of crop
147 losses came from farmers in the Njokomoni farmland (Joram, 2011). The major
148 reason for high levels of elephant activity in this area is the lack of a buffer zone
149 between the National Park and adjacent farms (Joram, 2011).

150

151 **METHODS**

152 **Camera trapping**

153 Between October 2010 and August 2014, a total of 23 camera trap sites were
154 monitored along an approximately 1 km stretch of the eastern boundary of
155 Udzungwa Mountains National Park. Effort and coverage were variable over this
156 period, with one to ten camera traps active each night from October 2010 to April
157 2012, one to three from August 2012 to January 2013, and ten from July 2013 to
158 August 2014 (see Supplementary Material, Table S1). Heat and motion camera traps
159 (Cuddeback Capture) were placed along current known elephant pathways going in
160 and out of farms and were shifted according to elephant activity. More specifically,
161 camera traps were removed from trails that became less frequently used by
162 elephants and shifted to new trails with more observed elephant activity (as indicated
163 by the presence of elephant dung and tracks). Due to a limited number of cameras,
164 only one camera trap was placed per trail. In order to obtain suitable portrait
165 photographs for individual identification, camera traps were mounted on a tree at a
166 height of 3 meters and oriented downward to best capture the head, pinnae, and
167 tusks of passing elephants. Camera traps were programmed to take colour
168 photographs with an incandescent flash, and the trigger interval was set to 30
169 seconds (the minimum possible for the model). Batteries were replaced and SD
170 cards downloaded every two weeks.

171 A database of all camera trap images of elephants was created, which
172 included the site, date and time of capture, and the direction of elephant movement
173 (into or out of the farmland area, i.e. back into the National Park). In addition, each
174 image was classified according to whether or not it was suitable for individual
175 identification. For those images that were deemed suitable, the elephant's sex, and

176 when possible, age, were determined and individual identifications made based on
177 unique characteristics of individuals' pinnae and tusks (Moss, 1996). The sexing and
178 ageing of elephants was carried out by one main researcher (J. Smit) following
179 training at the Amboseli Elephant Research Project, Kenya on known-age elephants.
180

181 **Monitoring crop losses from elephants**

182 Monitoring of crop losses from elephants in this focal area has been carried out since
183 2010 following a modified protocol developed by the African Elephant Specialist
184 Group of the International Union for Conservation of Nature (IUCN) (Parker et al.,
185 2007). Two local enumerators employed by the Southern Tanzania Elephant
186 Program (STEP) responded to calls from farmers reporting crop-loss incidents and
187 surveyed farms within the study area six days a week for additional unreported
188 incidents. They recorded the date and location of the crop-loss incident, the type(s)
189 of crops and trees eaten or trampled, and the size of the area affected (Joram,
190 2011).

191

192 **Data analysis**

193 To account for inconsistent camera trapping effort, we considered two time periods
194 over which different analyses were carried out: the entire study period (hereafter,
195 "study period") and the last year of monitoring between July 2013 and August 2014
196 (hereafter, "last year"). We first ran a temporal analysis comparing the timing of
197 camera trap captures of elephants observed to travel into or out of the farmland
198 area. More specifically, we used a non-parametric Kolmogorov-Smirnov test to
199 determine whether the distributions of timings of captures into and out of farmland
200 were significantly different. To do this, we used data collected over the entire study

201 period since temporal activity at the scale of a single night is unlikely to be affected
202 by inconsistent camera trap effort. Image time stamps were classified into hourly
203 bins (0-23), resulting in a frequency distribution spread over 24 hours.

204 We also tested for a significant association between the occurrence of an
205 elephant detection on any of the camera traps in operation (absence = 0, presence =
206 1) and that of a crop-loss incident in the Njokomoni farmland recorded on the
207 following day by enumerators (absence = 0, presence = 1) using data collected
208 between July 2013 and August 2014. We arranged corresponding frequencies into a
209 2 by 2 contingency table and performed a Pearson's chi-square test of
210 independence to investigate whether observed frequencies were more or less than
211 expected by chance. We used data from the last year of monitoring to do this, as
212 camera trap effort during this period was constant (10 cameras operating every
213 night). In addition, to assess whether monthly patterns of camera trapping events
214 served as a good indicator of crop-loss incidences, we correlated the proportion of
215 days in the month for which at least one elephant picture was obtained and the
216 proportion of days for which a crop-loss incident had been recorded by the
217 enumerators.

218 In addition, we estimated the minimum number of elephants known to use the
219 forest/farm boundary area over both the study period and the last year based on
220 individuals identified from camera trap images. Identification photographs of two
221 bulls detected multiple times by our camera traps are available as supplementary
222 material (Fig. S2). We also assessed the number of nights that individual bulls had
223 been detected by camera traps, and used this as an indicator of a bull's relative
224 likelihood to visit the Njokomoni farmland area. We repeated this assessment using
225 a subset of our data for which camera detections of elephants were positively

226 associated with crop-loss incidents (see Supplementary Material). Lastly, we
227 investigated the sex and age structure of individuals identified over the four-year
228 study period. We classified elephants identified in camera trap photos into four age
229 classes (Moss, 1996): 10-14, 15-19, 20-24 and 25-29 years old (we did not observe
230 any individuals over 30 years old). As our cameras detected only male elephants, we
231 relied primarily on head size and shape for ageing because these features change
232 noticeably with age and are easily seen on camera trap photos. With age, the male
233 head increases in size and takes on a pronounced hourglass shape around the age
234 of 25 (Moss, 1996). We also used height and body size for ageing when we had full
235 body photos of bulls. Images of bulls representative of the four age classes used in
236 our study are provided as supplementary material (Fig. S1).

237 R v3.0.1 was used for all statistical analysis in this study (R Core Team
238 2014).

239

240 **RESULTS**

241 We obtained 443 elephant photographs over 5,314 trap-nights between October
242 2010 and August 2014, representing 336 independent events. We defined an event
243 as the capture of a unique elephant at a unique date and time, as this best
244 represented one visit by a single elephant. In cases where an event could not be
245 defined by distinguishing between individual elephants, an arbitrary time threshold of
246 5 minutes between separate events was assumed. Elephants were photographed
247 traveling into the farmland predominantly between 18:00 and 00:00 (median = 19:00)
248 and back into the National Park between 00:00 and 07:00 (median = 04:00)
249 (Kolmogorov-Smirnov test: $D = 0.541$, $p < 0.001$) (Fig. 2). We found a similar pattern
250 in elephant movements into and out of farmland when we used a subset of the data

251 for which camera detections of elephants were associated with crop-loss incidents
252 (Fig. S3). During the last year of study, we found that camera trap data and crop-loss
253 incidents as recorded by enumerators co-occurred more than expected by chance (n
254 = 39, $\chi^2 = 13.6$, $df = 1$, $p < 0.001$). Despite this, instances when crop losses were
255 reported and no elephants were photographed remained high ($n = 98$), as were
256 instances when cameras detected elephants but no crop losses were recorded ($n =$
257 118). We also found a positive, albeit non-significant, correlation between the
258 proportion of days in the month for which we obtained camera trap images of
259 elephants and that for which crop losses were reported ($r^2 = 0.407$, $df = 10$, $p = 0.19$;
260 Fig. 3).

261 Of the 336 camera trap events, 37% ($n = 126$) were suitable for individual
262 elephant identification. All of the elephants identified were males, representing a total
263 of 48 individuals (Fig. 4). No females were observed in any of the camera trap
264 images for which the sex of the individual could be assessed. Most of the bulls
265 identified were detected only once by camera traps across the study period (66.7%,
266 Fig. 5), a pattern that was also found during the last year of study when camera
267 trapping effort was constant (70.6%, Fig. 5). A skew towards single detections was
268 also found when we used only those camera detections of bulls associated with
269 crop-loss incidents (Fig. S4).

270 Sixteen individuals were photographed multiple times over the entire study
271 period (Fig. 5), with one individual detected over 30 times. Five of the 17 bulls
272 identified in the last year of the study were captured multiple times on camera (Fig.
273 5). The 48 bulls identified from camera trap images over the study period were
274 primarily between 25 and 29 years old. (Fig. 6). Bulls who were detected multiple
275 times on the camera traps were also primarily 25-29 year olds, followed by younger

276 bulls aged 10-14 and 15-19 years. The time between successive detections of
277 individual bulls was highly variable (range 0-681 days, median 13.5 days), probably
278 mostly because of the inconsistency of camera trap effort (although we cannot
279 exclude the possibility that some of the bulls had breaks in visits to the study area).
280 However, a conservative estimate is that 24% of re-captures occurred on two
281 consecutive days, and 43% of re-captures occurred within 7 days.

282

283 **DISCUSSION**

284 We tested camera trapping as a tool to investigate the behaviour, number, and age
285 and sex structure of crop-using elephants along the boundary between Udzungwa
286 Mountains National Park and a small area (2.5 km²) of adjacent farmland in south-
287 central Tanzania. Camera trap images of elephants showed a distinct pattern of
288 elephant activity, with elephants heading into farmland at night and returning to the
289 National Park early in the morning along regular trails. This is consistent with
290 previous studies that highlight elephant avoidance of farmers and a propensity for
291 nocturnal crop foraging behaviour (Graham et al., 2010; Chiyo et al., 2012; Gunn et
292 al., 2014; Smith & Kasiki, 2000). The evidence for elephants using these trails for the
293 purpose of entering farms and consuming crops is strengthened by the significant
294 pattern of co-occurrence between elephant visits captured on cameras and crop-loss
295 incidents recorded by local enumerators.

296 However, we did not find a significant temporal correlation between recorded
297 crop losses and camera detections of elephants. This could be because not every
298 crop foraging attempt by a bull was successful, such that bulls photographed while
299 heading to farmland did not always consume crops because of risk factors
300 encountered there (such as the presence of farmers, fire, or dogs). This suggests

301 that the frequency of elephant visits to farmland as detected by camera traps, and
302 the extent of crop damage recorded by enumerators, may be independent measures
303 of elephant crop foraging behaviour. Additionally, it may be that bulls occasionally
304 used routes to farmland that were not sampled by our camera traps. Camera
305 trapping may therefore not be suitable for studying temporal patterns in crop losses
306 from elephants. Nevertheless, we view camera trapping and enumeration of crop
307 losses as highly complementary indices with the potential to improve the reliability of
308 data on elephant crop use if used jointly, especially in areas where elephants use
309 well-established trails into farmland.

310 Using standard ways of identifying individual elephants on the basis of tusks
311 and ears from camera trap photographs, we identified a minimum of 48 bulls in our
312 study area over the period of four years. However, only about one-third of images
313 from the study period were suitable for reliable individual identification. Future
314 studies could increase the success rate of identification by increasing the number of
315 camera traps active per night, and by using two opposite-facing camera traps per
316 trail as is done in studies of large cats (Kelly et al., 2008; Harihar et al., 2010).

317 Most of the bulls identified in this study were aged 20-29 years (55%),
318 followed by younger bulls aged 10-14 (34%) and 15-19 (11%) years; raising the
319 possibility that older bulls are leading younger bulls into farms, or that they comprise
320 a larger portion of the boundary-visiting population. The age structure of crop-using
321 bulls in Udzungwa is consistent with previous studies carried out in Kibale, Uganda
322 (Chiyo & Cochrane, 2005) and Amboseli, Kenya (Chiyo et al., 2012) (Table 1). Our
323 results indicate that crop use in Udzungwa could be an example of a high-risk, high-
324 gain foraging strategy linked to male life history milestones, including dispersal from

325 the maternal family unit and the initiation of reproduction, with associated increases
326 in energetic demands (Chiyo et al., 2012).

327 In Udzungwa, as in Kibale, the youngest bulls involved in crop foraging were
328 10-14 year olds, suggesting that crop use may be initiated during male dispersal
329 (Chiyo & Cochrane, 2005). This is a time when males leave their natal groups and
330 search for new feeding areas, and show greater exploratory and risk-taking
331 behaviour thus increasing their chances of coming into contact with crops (Chiyo &
332 Cochrane, 2005). In Amboseli, over 40% of crop-using bulls were aged over 30
333 years (Chiyo et al., 2012), while the present study in Udzungwa identified no bulls
334 over the age of 30. This likely reflects the history of poaching experienced by the
335 Udzungwa population, which typically leaves populations with few older bulls
336 (Mondol et al., 2014) and a population structure biased towards younger age classes
337 (Poole, 1989; Nowak et al., 2009).

338 Our study suggests considerable variation in crop foraging behaviour between
339 individual bulls, with camera traps detecting some bulls more frequently than others.
340 Over two-thirds of the 48 bulls identified were detected only once on the camera
341 traps over the study period, a pattern that also held for the 17 bulls identified in the
342 last year of study. This suggests that a large number of bulls are 'occasional' crop-
343 users. Sixteen bulls were detected multiple times (2-32) on camera over the study
344 period suggesting these individuals may be 'repeat' crop-users. There was
345 considerable variation in detection rates of the repeat crop-users, with one bull
346 detected four times more frequently than any other repeat crop-user. Importantly,
347 these are likely to be conservative numbers, and we acknowledge that a great
348 number of elephants could have gone undetected owing to the small number of
349 cameras available throughout our study, the large proportion of photos that were not

350 conducive to individual identification, and the likelihood of cameras missing elephant
351 visits.

352 Nevertheless, we highlight a large pool of occasional crop-users and a few
353 repeat crop-users, a pattern also detected using genetic data in Amboseli, Kenya
354 (Chiyo et al., 2011). Repeat crop use by certain individuals was also observed in a
355 study of radio-tracked bull elephants in Muzarabani District in Zimbabwe (Hoare,
356 2001), and via the presence of crop remains in elephant dung on farms bordering
357 Kibale National Park (Chiyo & Cochrane, 2005). Repeat crop use seems to be more
358 common among older males in Udzungwa, as nearly half of the repeat crop-users
359 were bulls aged 25-29 years. Studies in Kibale and Amboseli similarly found a
360 positive correlation between age of the bull and the likelihood of repeat crop use
361 (Chiyo & Cochrane, 2005; Chiyo et al., 2011).

362 The time between successive camera captures of bulls with multiple
363 detections was highly variable (range 0-681 days, median 13.5 days). Though
364 inconsistent camera trapping effort complicates the picture, it is possible that some
365 of these potentially repeat crop-users had breaks in visits to our study area. For
366 three of the bulls identified in this study, a year or longer passed between successive
367 detections on the camera traps. These results bear some similarity to forest elephant
368 visitation patterns to the Dzanga Bai in Dzanga-Ndoki National Park, Central African
369 Republic (Turkalo et al., 2013). Long-term monitoring of the Dzanga Bai showed that
370 individual visitation patterns were highly variable especially among males, some of
371 whom were absent for years at a time (Turkalo et al., 2013).

372 Our study has important implications for strategies to mitigate crop losses
373 from elephants, particularly the legal killing of animals considered to be 'pests' under
374 Problem Animal Control policies. Such an approach has been applied across

375 elephant range in Africa and Asia to in an attempt to reduce crop losses from
376 elephants (Hoare, 2001). However, the persistence of crop foraging behaviour in
377 areas where Problem Animal Control has been implemented in the long-term, such
378 as in the Selous Game Reserve in Tanzania and Muzarabani District in Zimbabwe,
379 has led to concerns regarding its effectiveness and motivation (Malima et al., 2005;
380 Hoare, 2012). Although we found evidence for repeat crop use by elephants, the
381 presence of a much larger pool of occasional crop-users argues against the killing of
382 elephants as an effective crop loss reduction method in Udzungwa. Furthermore, the
383 finding that a large number of bulls use a small area of farmland that is a hotspot of
384 elephant crop use (Joram, 2011), suggests that high levels of crop losses at such
385 hotspots do not result from the activity of a handful of habitual crop-users. Lethal
386 elimination of crop-users carries the risk of misidentifying elephants, and can also be
387 used as justification of elephant poaching or ivory accumulation under the pretext of
388 Problem Animal Control (Masunzu, 1998; Malima et al., 2005). Removal of habitual
389 crop-users may also create a gap or opportunity for new habitual crop-users to
390 emerge (Hoare, 2012). Therefore, our study is in agreement with previous work
391 questioning the effectiveness of killing elephants under Problem Animal Control
392 policies for crop-loss mitigation.

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394

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407

408 **AUTHOR CONTRIBUTIONS**

409 The study was conceptualized by T.J., K.N, and J.S. Data collection and processing
410 were carried out by J.S., T.J. and K.N. Data were analysed by R.P, J.C, and J.S. All
411 authors contributed to writing of the manuscript.

412

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558

559 **BIOGRAPHICAL SKETCHES**

560 **Josephine Smit** is a co-founder of STEP and manages its elephant monitoring
561 programs in southern Tanzania. She is interested in incorporating elephant
562 behavioural ecology into conservation strategies.

563 **Rocío A. Pozo** is a conservation biologist interested in human-wildlife conflict with a
564 particular focus on elephants, wildlife management and its implications for local
565 communities.

566 **Jeremy J. Cusack** is a conservation ecologist with an interest in the optimisation of
567 ecological monitoring methods.

568 **Katarzyna Nowak** has studied primate and elephant behaviour and conservation in
569 Tanzania and South Africa. She is a co-founder of STEP and advises the project in a

570 scientific capacity. She's currently a 2016-2017 AAAS Science & Technology Policy
571 fellow.

572 **Trevor Jones** has worked in wildlife research and conservation in Tanzania since
573 2002 and co-founded STEP in 2014.

574

575 TABLES

576

577 **Table 1.** Age structure of crop-using bull elephants at three different East African
578 sites: Udzungwa Mountains National Park, Tanzania (this study), Kibale National
579 Park, Uganda (Chiyo & Cochrane, 2005) and Amboseli National Park, Kenya (Chiyo
580 et al. 2012).

Age class (years)	Udzungwa (% population)	Kibale (% dung piles)	Amboseli (% population)
5-9	0	6	0
10-14	34	22	0
15-19	11	32	7
20-24	15	27	-
25-29	40	13 (>25 years)	50 (20-30 years)
>30	0	-	43

581

582

583 FIGURES

584

585 **Figure 1.** Map of Njokomoni study area. a) inset map of the location of Udzungwa
586 Mountains National Park (black rectangle) in south-eastern Tanzania. b) Njokomoni
587 study area along the east-facing escarpment of the Udzungwa Mountains (grey) and
588 village farmland (white). c) Njokomoni study site between the National Park (grey) and
589 farmland (white) showing GPS location of camera traps (black dots). Due to the steep
590 gradients of the Udzungwa Mountains, elephants use distinct trails into farms along

591 preferred slopes. Camera traps were placed on elephant trails and sampled an
592 approximately 1km stretch of the National Park boundary.

593

594 **Figure 2.** Temporal patterns of elephant detections at camera traps placed along the
595 eastern border of Udzungwa Mountains National Park. Black and grey bars represent
596 frequencies of elephants going into and out of adjacent farmland, respectively.

597

598 **Figure 3.** Proportion of days in the month when crop-loss incidents (light grey bars)
599 and camera trap images of elephants (dark grey bars) were reported and detected,
600 respectively.

601

602 **Figure 4.** Camera trap detection rates for 48 identified bulls over the study period. The
603 colour of each square represents the number of detections per month for a particular
604 bull. The histogram at the top of the figure depicts sampling effort as measured by the
605 number of trap-nights (the number of camera trap deployment days multiplied by the
606 number of cameras) per month.

607

608 **Figure 5.** Frequency distributions of the number of nights identified bulls were
609 detected on camera traps a) for the entire study period, and b) for the last year only.

610

611 **Figure 6.** Age structure of a) 40 of the 48 bulls identified over the entire study period,
612 and b) for 14 of the 16 bulls who were detected multiple times over the study period
613 for whom ageing was possible.

614

615

616 **SUPPLEMENTARY MATERIALS**

617

618 **Table S1.** Camera trapping effort over the study.

619

620 **Figure S1.** Photographs of bulls representative of the four age classes used in the
621 study.

622

623 **Figure S2.** Camera trap photographs of two bulls (B03 and B01) detected multiple
624 times over the study period.

625

626 **Figure S3:** Temporal patterns of elephant detections at camera traps placed along the
627 eastern border of Udzungwa Mountains National Park, when a reduced dataset
628 including the 35% (n=67) of camera trap detections associated with recorded crop-
629 loss incidents is used. Black and grey bars represent frequencies of elephants going
630 into and out of adjacent farmland, respectively. A Kolmogorov-Smirnov test on timings
631 of detections of elephants moving into and out of farmland was not significant.

632

633 **Figure S4:** Frequency distributions of the number of nights identified bulls (n=21) were
634 detected on camera traps a) for the entire study period, and b) for the last year only
635 when a reduced dataset including only camera trap detections (n=67) associated with
636 recorded crop-loss incidents is used. The stronger skew towards low detections in this
637 figure likely results from a reduction in sample size, as only 28 (42%) of detections
638 had photographs suitable for elephant identification.