



HAL
open science

Factors driving the discovery and utilization of a newly available area by African elephants

Anne Pandraud, Adrian M. Shrader, Craig Sholto-Douglas, Simon Chamaille-Jammes

► To cite this version:

Anne Pandraud, Adrian M. Shrader, Craig Sholto-Douglas, Simon Chamaille-Jammes. Factors driving the discovery and utilization of a newly available area by African elephants. *Journal of Tropical Ecology*, 2020. hal-03015498

HAL Id: hal-03015498

<https://hal.science/hal-03015498>

Submitted on 19 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Factors driving the discovery and utilisation of a newly available area by African elephants

Anne Pandraud¹, Adrian M. Shrader¹, Craig Sholto-Douglas², Simon Chamaillé-Jammes^{1,3}

1. Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, South Africa

2. &Beyond, Phinda Private Game Reserve and Mun-Ya-Wana Conservancy, South Africa

3. CEFÉ, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France

Corresponding author

Anne Pandraud; Phinda Private Game Reserve, 1 Old Sodwana Bay Road 3960 Hluhluwe, South Africa;
pandraudanne@gmail.com. 16-digit ORCID: 0000-0002-2831-7283.

Acknowledgments

We are thankful to Phinda Private Game Reserve for providing logistical support and for sharing their historical data. S. Chamaillé-Jammes was partially supported by grant ANR-16-CE02-0001-01 from the French 'Agence Nationale de la Recherche'. An anonymous reviewer provided useful suggestions.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Abstract

For large mammals, area expansion is a key conservation measure to prevent species' decline and extinction. Yet, its success depends on whether animals discover and later use these areas. Here, using GPS data, we investigated how herds of elephants detected and used an area made available to them after the removal of a fence. We studied the elephants' behaviour before and after the fence removal, accounting for seasonal changes in movement patterns. In contrast to previous studies, herds visited the newly available area within a month of the fence removal, and the maximum distance they moved into the new area was reached between five and nine months after the fence removal. Yet, elephants did not preferentially visit the new area at night. By the second year, all herds had shifted their seasonal home ranges and incorporated the new area, in contrast to a previous range expansion event. Our analyses show that the regular proximity of elephants to the original fence, and the fact that the new area was generally composed of preferred habitats of the elephants, likely explained the rapid discovery and use of the area. Our study improves our understanding of animal exploration and the role of habitat quality, and thus may improve range expansion and corridor programmes.

Key-words

Discovery, landscape exploration, habitat selection, *Loxodonta africana*, protected area expansion

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

Introduction

Space is critical to the conservation of most species, and this is particularly true for large mammals that tend to roam over large areas (e.g. Fryxell & Sinclair, 1988, Mueller et al. 2011). However, in human-modified landscapes, space has become a limiting factor for many species (Tucker et al. 2018). To overcome species' decline and extinction (Cardillo et al. 2004, Harris et al. 2009) some conservation efforts have focussed on preventing the destruction of existing natural areas through the creation of new protected areas (Naughton-Treves et al. 2005). For example, over the last four years 30,000 sites were added to the World Database on Protected Areas (UNEP-WCMC 2018). In addition, range expansion via corridors (e.g. Douglas-Hamilton et al. 2005, Osborn & Parker 2003), protected area expansion (e.g. Druce et al. 2007), and the amalgamation of protected areas (e.g. fence removal between Kruger National Park (South Africa) and Limpopo National Park (Mozambique) in 2002) are key conservation measures.

However, despite the growing use of the strategy of protected area expansion, we know very little about how animals detect and later use these new areas. Thus, we are unsure just how successful these conservation measures may be. Discovery of newly available areas likely depends on factors such as the proximity of the animals to these areas and their exploratory behaviour (Druce et al. 2007). Yet, this latter aspect remains poorly understood (e.g. Mettke-Hofmann et al. 2002, Switzer 1993).

Exploration might be limited in favourable environments (e.g. Mettke-Hofmann et al. 2002, Switzer 1993) or, conversely, when overall conditions in an animal's range are bad (e.g. Larkin et al. 2004, van Moorter et al. 2013). Generally, animals show relatively strong site fidelity that limits exploration and may even delay the discovery of new places (e.g. de Knegt et al. 2010, Switzer 1993). For instance, black rhinoceros (*Diceros bicornis*) have been found shown to be slow to colonize a harvested neighbour's range (Linklater et al. 2010). In central Idaho, introduced grey wolves (*Canis lupus*) limited their movements to within a small core area the first year after their reintroduction, only after that took a long time before exploring beyond this core (Bangs & Fritts 1996). Similarly, newly introduced black bear (*Ursus americanus*) limited their movements and even tried to move back to their previous range (Eastridge & Clark 2001).

African elephant (*Loxodonta africana*) populations provide an interesting case study in the context of range expansion. Space is critical for these large, wide-ranging species (Owen-Smith 1988). As such, many populations have been exposed to area expansion, often either to: (1) allow for population expansion (e.g. fence

1 removal, Druce et al. 2007), or (2) reduce the impact of dense elephant populations on the landscape (Biggs et al.
2 2008). Elephants have shown contrasting responses when faced with one of these different expansion measures.
3 For instance, elephants moved rapidly into new areas after the fence was removed between Kruger and Sabi
4 Sand Wildtuin and migration paths were re-established (Grant et al. 2008). In contrast, when the fence between
5 Marakele National Park and Marakele Pty Ltd was removed in 2001, it took elephants two years before they
6 visited the newly available area (Bezuidenhout 2004). Similarly, when the boundary fence between Phinda
7 Private Game Reserve and one neighbouring reserve was removed in 2004, it took resident family groups
8 between six and nine months to venture into the new area (Druce et al. 2007). Moreover, only one herd expanded
9 its core range to incorporate this newly available area despite its relatively small size (3,850 ha; Druce et al.
10 2007). However, despite these studies, we still have a poor understanding of the factors associated to elephants'
11 discovery of a newly opened area and which factors influence their response to area expansion. In fact little
12 attention has been given to the factors (e.g. spatial distribution, diet and habitat preferences) that underlie
13 elephants' response to range expansion measures.

14 Here we studied the response of African elephant breeding herds to the removal of a fence between
15 Phinda Private Game Reserve and a neighbouring reserve, in South Africa. We did so by using data from GPS
16 collars fitted on each matriarch. We describe the discovery and use of the newly available area, but unlike
17 previous studies (Druce et al. 2007) we also analyse elephant behaviour (habitat selection, distribution in relation
18 to the fence) before the fence removal to understand the factors that could have facilitated the discovery and use
19 of the new section, accounting for seasonal changes in movement patterns.

20 We hypothesised that the proximity to the new section might determine how long it takes herds to find
21 and use the section. Thus, we expected herds regularly close to the previous fence to discover and explore this
22 section quicker than herds which were usually located farther away. For instance, it has been shown that
23 elephants use their sense of smell to make foraging decisions (Schmitt et al. 2018) and being close to the new
24 area might increase the chances of smelling a new foraging place. Because animals have habitat preferences (e.g.
25 de Knegt et al. 2010, Switzer 1993), we expected that elephants would move more rapidly into areas containing
26 the preferred habitats compared to those with the less preferred habitats.

27

28 Methods

29 *Study area*

1 Phinda Private Game Reserve (referred to as Phinda from here on) (16,826 ha) is located within the Mun-Ya-
2 Wana Conservancy (MYW), Kwa-Zulu-Natal Province, South Africa (27°51'30''S, 32°19'00''E) (Fig. 1)
3 Phinda comprises nine different vegetation types across a mosaic of savanna woodlands and sand forests (Supp.
4 Appendix 1.) (Druce et al. 2007, Slotow & Page 2002). The climate is subtropical with annual temperatures
5 ranging from 10 °C to 35 °C and a mean annual rainfall of 700 mm and a standard deviation of \pm 230 mm (1995-
6 2018). Rain falls in every month of the year but the summer wet season (all months with >50 mm of
7 precipitation. Knoch & Schulze 1957) runs from October to March (mean rainfall of 89 mm), while the winter
8 dry season runs from April to September (mean rainfall of 27 mm).

9 Between 1993 and 2011 more properties were added to MYW which currently comprises three private
10 game reserves that were initially separated by fences (Fig. 1). Elephants were introduced into Phinda between
11 1992 and 1994 (Druce et al. 2007, Slotow & Page 2002) from the Kruger National Park (Slotow & Page 2002).
12 Currently the population is estimated to be around 110 elephants, divided in six breeding herds of ~10
13 individuals each, and various sized bachelor herds (ranging from two to five individuals each) incorporating the
14 reserve's 25 males. Elephants are free ranging within MYW.

15 On 4 October 2017, which correspond to the beginning of the wet season, the boundary fence between
16 Phinda and the neighbouring Lulubush Game Reserve (LGR) (1,612 hectares) was removed. As a result, MYW
17 now contains 243 natural and artificial waterpoints, with 21 in LGR. Most of the LGR waterpoints are man-made
18 but none of them are supplied by a pump. In the dry season, water is available in MYW in three non-perennial
19 rivers and six artificial water sources that are maintained during the dry season.

20

21 *Data*

22 We collected elephant positional data every four hours using GPS/GSM manufactured by African Wildlife
23 Tracking fitted to the matriarch of each of the six breeding herds. Collars were put on two years prior to the start
24 of our study by a trained veterinarian after the elephant had been tranquilised from an helicopter. The movement
25 of these females was assumed to represent the movement of the whole breeding herd to which they belonged
26 (Druce et al. 2007). For each of the herds, we collected location data one year before and one year after the fence
27 removal. However, for one herd (FH1), positional data were only available from after the removal of the fence.
28 As a result, we could only use the data from this herd in the analysis focusing on elephant behaviour post fence
29 removal.

30

1 *Identifying independent herds*

2 Field observations indicated that some of the herds spent a significant amount of time together. As these herds
3 would not provide independent information, we considered two herds to be “together” when the distance
4 between the herds, obtained from locations acquired less than 30 min apart, was less than 250 m. Results (Supp.
5 Appendix 2) showed that two herds (FH5 and FH2) were together more than 68% of the time. As these herds
6 would provide pseudo-replicated information, we randomly selected the data from herd FH5 in the analyses.
7 Nevertheless, we explored whether using the data from herd FH2 would change the results and they did not.
8 Thus, we only used the data from herd FH5. We did not include the data from both herd when they were apart
9 because the sample size of FH2 alone was too small to be representative of the herd's behaviour and to bring a
10 significant information to the other data.

11

12 *Habitat selection*

13 We first determined the habitat composition of the newly available LGR section using a vegetation map (Supp.
14 Appendix 1). From this, we defined seven different vegetation types: (1) palm veld, (2) mixed acacia and
15 lebombo woodlands, (3) floodplain grasslands, (4) bush clump thickets, (5) mixed zululand lowveld savanna, (6)
16 riparian, and (7) sand forest and sandveld woodlands. As the elephants are fenced out of a large part of the sand
17 forest we grouped sand forest and sandveld woodlands into one habitat type. This avoided creating instability in
18 estimates due to the small number of locations in the sand forest. Then, to understand whether the available
19 habitats in the LGR were those preferred by elephants, we analysed the habitat selection of the elephants before
20 the fence removal, for the wet and dry season separately. We calculated, for each herd and each season, the
21 selection ratio (SR; $SR = Prop_{used} / Prop_{available}$) and the associated confidence intervals (confidence limits: 2.5%
22 and 97.5%) (Chamaillé-Jammes 2019, Manly 2002) for each habitat. We estimated $Prop_{used}$ using the actual GPS
23 locations of elephants, and $Prop_{available}$ by plotting 2,500 random points within each herd seasonal home range.

24

25 *Individual herd exploratory behaviour*

26 We studied the temporal dynamics of exploration and use of the newly opened section during the wet season
27 following the removal of the fence. In particular, we studied how long it took the elephant herds to enter the
28 section. For each herd, we measured the time to first visit as the time between the fence removal and the first
29 location of the herd at least 50 m (to account for potential GPS error) within the new section. We investigated
30 whether the time to first visit was related to: (1) the distance at which elephants were to the fence the day the

1 fence was removed, (2) the proportion of time elephants spent within 100 m of the fence during both the wet and
2 the dry seasons a year before the fence removal, and (3) the average return time to within 100 m of the fence in
3 both seasons a year before the fence was removed.

4 We calculated how far herds ventured into the newly opened section during their first visit and
5 measured the maximum distance travelled within this section from the date of the first visit (Druce et al. 2007).
6 Finally, we determined whether the elephant herds used the new section more at night (18h30 to 05h30) as found
7 in another study (Druce et al. 2007) or during the day (05h30 to 18h29) by comparing the mean number of
8 locations within the section during these periods.

9

10 *Home-range shifts*

11 We studied whether the opening of the LGR affected the size and location of the seasonal home ranges of each
12 elephant herd. As the fence removal occurred at the beginning of the wet season, we computed wet and dry
13 season home ranges before the fence removal, and the wet and the dry season home ranges after the removal.
14 The overall study site is fenced, which creates limitation to elephant movement that should be accounted for
15 when estimating home ranges. We therefore used local convex hull (LoCoH) nonparametric kernel method to
16 estimate home ranges as they naturally allow for hard boundaries in home ranges (Getz et al. 2007). We defined
17 a home range as the area within the 90% isopleth, estimated following the 'fixed number of points' approach (k-
18 LoCoH, Getz et al. 2007), with k chosen following the "rules of thumb" proposed by Getz et al. (2007). Selected
19 values of k ranged between 33.0 and 46.5 (the values are reported in the caption of Table 4).

20 To determine whether elephants had relocated or extended their home ranges after the fence removal, we
21 first determined whether there were seasonal changes in home ranges irrespective of the range expansion event.
22 We did this by computing the overlap between wet and dry season home ranges, in the year before the fence
23 removal, to measure what proportion of the wet season home range was in the dry season home range. Once we
24 had done this, we then computed the proportion of the pre-removal wet and dry season home ranges which
25 remained in the wet and dry season home ranges after the fence was removed.

26 Finally, we assessed whether any post fence removal changes to the seasonal home ranges altered the
27 seasonal habitat composition of the home ranges. We did this by estimating, for each herd, the percentage of
28 each vegetation type included in their dry and wet season home range separately, a year before and a year after
29 the fence removal (results are reported in Supp. Appendix 3).

30

1 Results

2 *Habitat selection*

3 Although elephant habitat selection prior to the fence being removed was variable (Fig. 5), the herds preferred
4 the 1) palm veld, and 2) sandveld woodlands and sand forest habitat types (Fig. 5), with FH3, FH4 and FH5's
5 seasonal home ranges dominated by these habitat types prior to the fence being removed. Moreover, these
6 habitats respectively accounted for on average 21% and 46% of their dry season home range and on average
7 19% and 35% of their wet season home range (Supp. Appendix 3). Palm veld, sandveld woodlands and sand
8 forest were also the most available habitats in FH3, FH4 and FH5's seasonal home ranges before the fence
9 removal (Supp. Appendix 4). Only FH6's seasonal home ranges were dominated by mixed acacia woodlands,
10 with 65% included in the dry season home range and 76% in the wet season home range (Supp. Appendix 3).

11 The LGR comprised five different vegetation types: 62% sandveld woodlands and sand forest, 27% palm
12 veld, 10% mixed acacia woodlands, and 1% riparian forest. As these habitats were key in the herds' home ranges
13 prior to the fencing being removed, it suggested that the herds would find suitable habitats in the LGR after the
14 fence separating the properties was taken down.

15

16 *Exploratory behaviour*

17 All of the elephant herds visited the newly opened section soon after the fence was removed (Fig. 2). Herd FH4
18 visited five days after the removal, while three other herds (FH1, FH3 and FH5) went into the section between
19 nine and 13 days after the fence was removed. Finally, FH6 visited the section 34 days after the fence was
20 removed.

21 Although the herds had spent only between 0.1 and 2.0% of their time within 100 m of the LGR (Table 1),
22 they were regularly within 100 m during the dry season preceding the removal of the fence. For example, FH4
23 was within 100 m of the fence on average every 6.8 days, FH5 every 10.1 days, and FH3 every 19.1 days. This
24 was far more frequent than in the preceding wet season, when the herds were <100m of the fence somewhere
25 between 11 and 170 days (Table 1). The day of the fence removal, all the herds were approximately 11 km from
26 the fence, and a negative relationship appeared between the time taken to go into LGR after the fence removal
27 and the percentage of time spent within 100 m of the previous fence (Fig. 3).

28 From the day the fence was removed to their first entry, the elephants were on average 6.3 km (\pm 3.7 km)
29 from the edge of the LGR (Fig. 2). Before their first entry, FH3 and FH5 were the only family herds that went

1 relatively close to the boundary (309 m and 312 m respectively). During this period, the others remained
 2 between 1.3 km and 2.1 km from the boundary, until they moved directly into the LGR (Fig. 2).

3 During their first visit into the LGR, all of the herds stayed less than eight hours, and three herds less than
 4 five hours, in the LGR. Upon entering, the herds only travelled between 278 m and 672 m into the LGR (Table
 5 2). Only, herd FH6, which was the last one to enter LGR, travelled a distance greater than 1 km into the LGR
 6 during its first entry (Table 2). Ultimately, it took nine months for all the herds to travel 3.5 km into the LGR
 7 (Table 2).

8 During the wet season following the removal of the fence (i.e. the first six months after the removal), the
 9 elephants went into the LGR regularly. The average period between visits for the herds FH1, FH3, FH4 and FH5
 10 was between 0.48 and 0.60 days. For FH6, it was every two days (Fig. 2). However, FH6 was regularly in the
 11 new area between the 7th of November and the 13th of December with on average, 0.51 days between visits (Fig.
 12 2). After this period, FH6 left LGR and only came back six months later. All of the herds visited LGR during
 13 both day and night with: 61% (FH1), 67% (FH3), 52% (FH4), 57% (FH5) and 49% (FH6) of locations during
 14 the day. Overall, none of the herds showed a preference with regards to the time of the day in which they visited
 15 the LGR (Wilcoxon signed-rank test: $N = 5$, $V = 14$, p -value = 0.125).

16

17 *Home range shift*

18 Before the fence was taken down, the home ranges of FH3, FH4 and FH5 were located primarily in the northern
 19 part of the reserve (Fig. 4). However, during the wet season, all three of these home ranges expanded into the
 20 South of the reserve. During both seasons, all of the herds' home ranges surrounded the LGR (Fig. 4). Despite
 21 the seasonal changes in the home ranges, these home ranges overlapped between 65% and 79% (Table 4.). One
 22 year after the fence removal, all of the herds had incorporated LGR into their home ranges (Fig. 4). However,
 23 there was no significant change in the overall size of either the dry or wet season home ranges after the fence
 24 was taken down (Wilcoxon signed-rank test: dry home ranges, $V = 5$, $N = 4$, p -value = 1; wet home ranges, $V =$
 25 4 , $N = 4$, p -value = 0.87). On average 81% ($\pm 13\%$) of the previous wet season home ranges were still included
 26 into the new wet season home ranges, and the mean overlapping between the previous and the new dry season
 27 home ranges was 76% ($\pm 16\%$) (Table 4).

28 A year after the fence removal, despite few modifications in the percentages of vegetation types (e.g. the
 29 cover of sandveld woodlands and sand forest increased. Supp. Appendix 3), the habitat composition of the wet

1 and dry season home ranges had not significantly changed (Wilcoxon signed-rank test: dry-season habitat
2 composition, $V = 13$, $N = 7$, p -value = 0.94 ; wet home ranges, $V = 14$, $N = 7$, p -value = 1).

3

4 Discussion

5 After the expansion of MYW, we observed a rapid expansion of the resident elephant breeding herds into the
6 newly available LGR. The month following the opening, all of herds had visited LGR at least once, despite being
7 more than 10 km from the fence when it was taken down. They explored the new section quickly and regularly
8 during the wet season following the fence removal. After a year, all of the herds had incorporated the LGR into
9 their home ranges and thus modified the habitat composition of their seasonal home ranges.

10 Our results contrast to those of Druce et al. (2007) who found that the exploration of new areas by the same
11 elephant herds took between four and eight months after the fence was removed. In our study, prior to the
12 removal of the fence, the herds regularly visited the area in the vicinity of the fence, with a minimum of one visit
13 every seven days. We also observed that when the average of the return time to the vicinity of LGR was short,
14 the time taken to enter the new section was also short. This suggests that the frequent visits to the area next to the
15 fence could have facilitated the rapid discovery of the newly opened area once the fence was taken down.

16 After the first entry, all herds continued to use LGR, and incorporated parts of it into their seasonal home
17 ranges. The herds visited this section regularly, during both the day and night, at least every two days. In contrast,
18 Druce et al. (2007) found that the same herds acted cautiously during their exploration of a new area. This was
19 indicated by the significant preference for exploring at night, and the fact that the longest exploration distance
20 within the new area occurred only six to 12 months after the first entry.

21 Druce et al. (2007) tentatively explained this slow exploration by suggesting that the resources and space
22 for the elephants in the previously available area were probably sufficient. In that study, however, the new area
23 composed mostly mixed acacia woodlands (92%), a habitat avoided by elephants in our study, and only 6%
24 riparian, and 2% palm veld, two habitat types preferred by elephants. In our study, the LGR was mostly covered
25 by sandveld woodlands and sand forest (62%) and palm veld (26%), which were strongly selected for by the
26 elephants and the most available vegetation types in their previous seasonal home ranges (Supp. Appendix 4).
27 Thus, it is possible that the difference observed between Druce et al. (2007) and our study is the result of the
28 preferred habitat composition of the newly available LGR attracting the elephants in our study.

29 In contrast, in the study by Druce et al. (2007), where none of the herds incorporated the new area into their
30 home range, all of the herds in our study incorporated the LGR into their seasonal home ranges after a year. The

1 sizes of the home ranges, however, did not increase. Thus, the home ranges of the elephants shifted such that
2 they no longer used portions of their previous home ranges. Moreover, the habitat compositions of the seasonal
3 home ranges were also not modified after the fence removal.

4 Contrast between our results and those of Druce et al. (2007) indicate that the expansion of a protected area
5 can lead to variable animal exploration and utilisation of the newly available area. Previous studies have
6 demonstrated that a low exploration may be due to a high site fidelity of animals (e.g. de Knecht et al. 2010,
7 Linklater et al. 2010) driven by their condition (e.g. age. Switzer 1993) and exogenous environmental variables
8 (e.g. tree cover, nutritional quality, water proximity, etc. de Knecht et al. 2010). In addition, our findings suggest
9 that animals' habitat preferences likely define the attractiveness of new areas and thus might influence the
10 response they have towards area expansion. This is also likely true for the utilisation of newly established
11 corridors. Overall, there is a clear need to better understand the factors underlying site fidelity and exploration
12 behaviour.

13 Here we suggest that the quality of the habitat (as indexed by habitat selection) made available to the
14 elephants in the new section and the fact that the herds regularly used the area close to the fence, have facilitated
15 the rapid discovery and use of the LGR by all the herds. It may, however, simply be that the elephants
16 incorporated the area as it is small (1,612 hectares) in relation to the elephant herds' seasonal home ranges (mean
17 wet and dry season home range sizes: 126.7 km² and 107.4 km²). Yet, in the study by Druce et al. (2007), they
18 found that in the same reserve, the elephants did not incorporate a small section (3,850 hectares) that was opened
19 adjacent to the elephants' home ranges. The elephants visited this area a few months after the fence was removed
20 (Druce et al. 2007) but now 15 years down the line, they still have not incorporated it (see Fig. 4). This suggests
21 that the elephants likely use habitat quality as a key driver when utilising and incorporating newly available areas
22 and do not simply move into areas because they are available.

23 We, however, acknowledge that this remains a tentative explanation due to the very low sample size of the
24 study. This limitation was mostly imposed by the small size of the population, as virtually the whole female
25 segment of the population was monitored. Yet, we believe that studies on rare and endangered species, for which
26 area expansion might be critical, will often be constrained by population size and financial or logistical
27 constraints. If so, the depth and robustness of our global knowledge will likely arise from the multiplicity of
28 studies with small sample size like ours. We therefore call for publication of these studies, to avoid knowledge
29 loss due to file-drawer effects or publication in grey literature. Also, when possible, systematic reviews or

1 comparison between very similar situations (like the comparison between our study and the one from Druce et al.
2 2007) may improve, or at least challenge, our understanding.

3 In human-modified landscape, space is a limiting factor for many animals, particularly for large wide-
4 ranging species such as elephants. The addition of space within protected areas is currently a common practice to
5 try to overcome this, and thus to try to maintain a sustainable population and ecosystem. However, we do not
6 know how successful these measures may be as we do not know how long it takes animals to find new areas. By
7 suggesting what factors could have influenced the discovery and the use of a new area by elephants, our study
8 join others to fill this research gap and thus to help protected area managers to reach their conservation aims.

9

10

11 References

12 **Bangs EE and Fritts SH** (1996) Reintroducing the gray wolf to central Idaho and Yellowstone National Park.

13 *Wildlife Society Bulletin* **24**, 402–413. Retrieved from www.wolfology.com. Accessed April 2019.

14 **Biggs HC, Slotow R, Scholes B, Carruthers J, van Aarde R, Graham K, Twine W, Grobler D,**

15 **Berthshinger H, Grant R, Lötter H, Blignaut J and Hopkinson, L** (2008) Towards integrated decision-
16 making for elephant management. In Scholes RJ and Mennell KG (ed.), *Assessment of South African*
17 *Elephant Management*. Witwatersr: Johannesburg, pp. 530–578.

18 **Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J and Mace GM** (2004) Human Population Density
19 **and Extinction Risk in the World ' s Carnivores. *PloS Biol* 2, 909–914.**

20 **Chamaillé-Jammes S** (2019) A reformulation of the selection ratio shed light on resource selection functions
21 and leads to a unified framework for habitat selection studies. bioRxiv 565838.

22 **de Knegt HJ, Pretorius Y, van Langevelde F, de Boer WF, Gort G, Skidmore AK, Slotow R, Henley S,**

23 **Delsink A, Grant CC and Prins HHT** (2010) Visited sites revisited - site fidelity in African elephants. In
24 HJ de Knegt (ed.), *Beyond the here and now: herbivore ecology in a spatial-temporal context*.
25 Wageningen: Wageningen University, p. vii + pp. 140.

26 **Douglas-Hamilton I, Krink T and Vollrath F** (2005) Movements and corridors of African elephants in relation
27 to protected areas. *Naturwissenschaften* **92**, 158–163.

28 **Druce HC, Pretorius K and Slotow R** (2007) The response of an elephant population to conservation area
29 expansion: Phinda Private Game Reserve, South Africa. *Biol. Conserv.* **141**, 3127–3138.

30 **Eastridge R and Clark JD** (2001) Linked references are available on JSTOR for this article : Evaluation of 2

- 1 soft-release techniques to reintroduce black bears. *Wildl. Soc. Bull.* (1973-2006) **29**, 1163–1174. Retrieved
 2 from www.wolfology.com
- 3 **Fryxell JM and Sinclair RE** (1988) Seasonal migration by white-eared kob in relation to resources. *Afr. J. Ecol.*
 4 **26**, 17–31.
- 5 **Getz WM, Fortmann-roe S, Cross PC, Lyons AJ, Ryan SJ and Wilmers CC** (2007) LoCoH :
 6 Nonparameteric Kernel Methods for Constructing Home Ranges and Utilization Distributions. *PLoS ONE*
 7 **e207(2)**, 1–8.
- 8 **Grant RC, Bengis RG, Balfour D, Peel MJS, Africa S and Mostert W** (2008) Controlling the distribution of
 9 elephants. In Scholes RJ and Mennell KG (ed.), *Elephant Management: A Scientific Assessment for South*
 10 *Africa*. Wits University Press: Johannesburg, pp. 329–369.
- 11 **Harris G, Thirgood S, Hopcraft JGC, Crooms J and Berger J** (2009) Global decline in aggregated
 12 migrations of large terrestrial mammals. *Endangered Species Research* **7**, 55–76.
- 13 **Larkin JL, Cox JJ, Wichrowski MW, Dzialak MR, Maehr DS** (2004) Influences on Release-Site Fidelity of
 14 Translocated Elk. *Restoration Ecol.* **12**, 97-105.
- 15 **Linklater WL, Macdonald EA, Flamand JRB and Czekala NM** (2010) Declining and low fecal corticoids are
 16 associated with distress, not acclimation to stress, during the translocation of African rhinoceros. *Anim.*
 17 *Conserv.* **13**, 104–111.
- 18 **Manly BFJ** (2002) Estimating a Resource Selection Function With Line Transect Sampling. *Journal of Appli.*
 19 *Math. Decis. Sci.* **6**, 213–228.
- 20 **Mettke-Hofmann C, Winkler H and Leisler B** (2002) The significance of ecological factors for exploration
 21 and neophobia in parrots. *Ethol.* **108**, 249–272.
- 22 **Mueller T, Olson KA, Dressler G, Leimgruber P, Fuller TK, Nicolson C, Novaro AJ, Bolgeri MJ, Wattles**
 23 **D, DeStefano S, Calabrese JM and Fagan WF** (2011) How landscape dynamics link individual to
 24 population-level movement patterns : a multispecies comparison of ungulate relocation data. *Glob. Ecol.*
 25 *Biog.* **20**, 683–694.
- 26 **Naughton-treves L, Holland MB and Brandon K** (2005) The role of protected areas in conserving biodiversity
 27 and sustaining local livelihoods. *Annu. Rev. Env. Resour.* **30**, 219–252.
- 28 **Osborn FV and Parker GE** (2003) Linking two elephant refuges with a corridor in the communal lands of
 29 Zimbabwe. *Afr. J. Ecol.* **41**, 68–74.
- 30 **Owen-Smith RN** (1988) Megaherbivores. The influence of very large body size on ecology. (Cambridge).

1 Cambridge. Retrieved from <http://dx.doi.org/10.1017/CBO9780511565441>

2 **Schmitt MH, Shuttleworth A, Ward D and Shrader AM** (2018) African elephants use plant odours to make
3 foraging decisions across multiple spatial scales. *Anim. Behav.* **141**, 17–27.

4 **Slotow R and Page B** (2002) Preliminary Report on Elephant Vegetation Utilization at Phinda Resource
5 Reserve.

6 **Switzer PV** (1993) Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**, 533–555.

7 **Tucker MA, Böhning-gaese K, Fagan WF, Fryxell JM, van Moorter B, Alberts SC, ... Rimmler M** (2018)
8 Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **359**, 466–
9 469.

10 **van Moorter B, Bunnefeld N, Panzacchi M, Rolandsen CM, Solberg EJ and Saether BE** (2013)
11 Understanding scales of movement: animals ride waves and ripples of environmental change. *J. Anim.*
12 *Ecol.* **82**, 770–780.

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27

Figure captions

Fig. 1 Map of the Mun-Ya-Wana Conservancy. Each colour represents one of the three private game reserves (i.e. Phinda Private Game Reserve, Zuka Private Game Reserve, Bumbeni) included into the Mun-Ya-Wana Conservancy. The striped black polygon represents the Lulubush section added the 4th of October 2017. During the dry season, water can only be found in six dry season water points (black circles) and two non-perennial rivers (black thick lines). The shaded area in the insert map is the KwaZulu-Natal province.

Fig. 2 Distance to the former fence estimated between two weeks before the fence removal and the end of the wet season after the fence removal. Positive values represent locations within the newly available Lulubush section, negative values represent locations within the area already accessible before the fence removal. The grey polygon covers the two-week period before the fence removal.

Fig. 3 The relationship between the percentage of time spent within 100 m of the fence during the year before the fence removal and the time taken for the elephant herds to move within the newly available Lulubush section. The time taken to move is defined as the time from the fence removal to the first entry into Lulubush.

Fig. 4 Estimation of the breeding family herds' home ranges before the fence removal in the wet and dry seasons, and after the fence removal in the wet and dry seasons. Home ranges were obtained by using the k-LoCoH method (90% isopleth).

1 **Fig. 5** Selection ratios for the seven vegetation types (1-7) by the different elephant herds before the fence
2 removal in the wet (a) and dry (b) seasons. Each dot indicates the mean selection ratio of the corresponding
3 elephant herd for the seven vegetation types, with the associated confidence intervals (confidence limits: 2.5%
4 and 97.5%). When both limits of the confidence interval were different to 1, we estimated a significant positive
5 selection (above) and a significant avoidance (below).

6
7

Elephants' response to an area expansion

1 Table 1. Time taken for the elephant herds to move into the newly available area, reported as information about
 2 their use of the area within 100 m of the fence during the year before the fence removal.

3

Family Herds	Time from fence removal to first entry into new area (days)	Proportion of time spent within 100 m of the fence (%)	Return time (days) within 100 m of the fence, dry season (mean \pm s.d.)	Return time (days) within 100 m of the fence, wet season (mean \pm s.d.)
FH1	9	-	-	-
FH3	13	0.6	19.1 \pm 22.4	170
FH4	5	2.0	6.8 \pm 9.1	11 \pm 17.9
FH5	9	1.3	10.1 \pm 13.3	20.6 \pm 35.8
FH6	34	0.1	-	-

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

Elephants' response to an area expansion

1 Table 2. Maximum distance travelled into the newly available area during the initial exploration by each of the
2 elephant herd. In addition, we report the maximum distance travelled into the new area during the year following
3 the fence removal, and the number of days after fence removal when this occurred.

4

Family Herds	Maximum distance travelled during initial entry (m)	Duration of time before the greatest distance moved (month)	Maximum distance travelled into the new area (m)
FH1	508	8.5	3,477
FH3	672	8.7	3,439
FH4	313	7.3	3,487
FH5	278	5.5	3,388
FH6	1,428	9.0	3,321

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

Elephants' response to an area expansion

1 Table 3. Size of the seasonal home ranges of each elephant herd estimated before and after the fence removal. In
 2 addition, we report the estimation of the overlap between seasonal home ranges for each elephant herd. WHR
 3 and DHR refer to wet and dry season home ranges respectively.

4

Family Herds	Size WHR	Size DHR	Size WHR	Size DHR	WHR/DHR	Pre WHR/ Post WHR	Pre DHR/ Post WHR	Pre WHR/ Post DHR	Pre DHR/ Post DHR
	Pre-opening (km ²)	Pre-opening (km ²)	Post-Opening (km ²)	Post-Opening (km ²)	Overlap Pre-opening (%)	Overlap (%)	Overlap (%)	Overlap (%)	Overlap (%)
FH3	139.3	117.1	127.9	100.3	68.8	72.9	82.0	54.1	76.5
FH4	141.1	101.3	99.4	97.4	65.3	71.5	82.9	53.1	96.7
FH5	153.9	115.2	155.3	100.8	73.4	80.2	88.5	54.0	69.7
FH6	72.5	96.1	124.4	126.5	79.4	100	95.2	98.7	59.9

Selected values for k for home ranges computation (see text for details):

- for WHR pre-opening: FH3 39.5 / FH4 43.5 / FH5 45.5 / FH6 40.0
- for DHR pre-opening: FH3 35.0 / FH4 40.5 / FH5 36.5 / FH6 36.5
- for WHR post-opening: FH3 45.0 / FH4 46.5 / FH5 42.5 / FH6 37
- for DHR post-opening: FH3 42.0 / FH4 38.0 / FH5 42.5 / FH6 33.0

5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

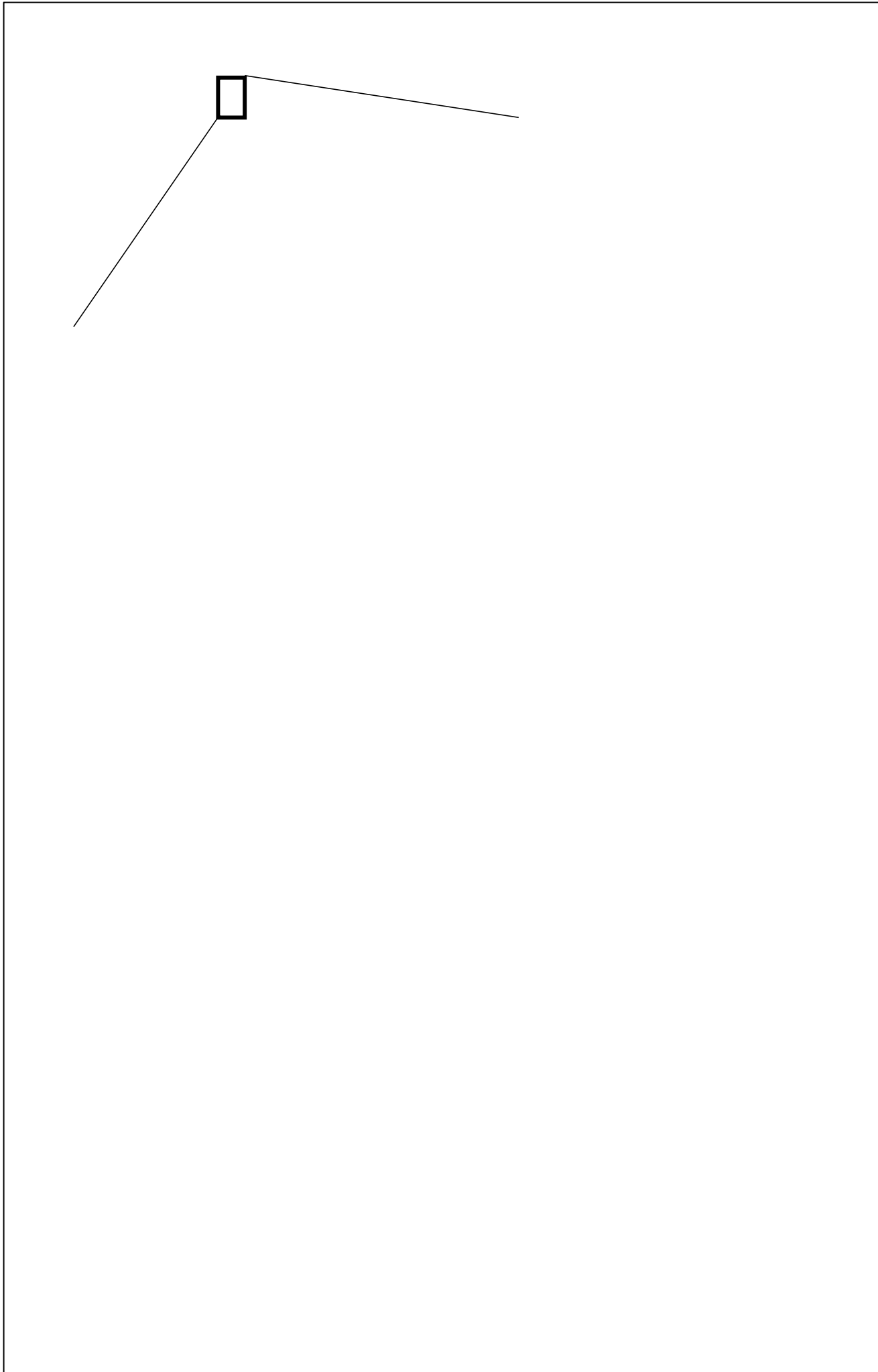


Fig. 1

1
2
3

4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36

Fig. 2

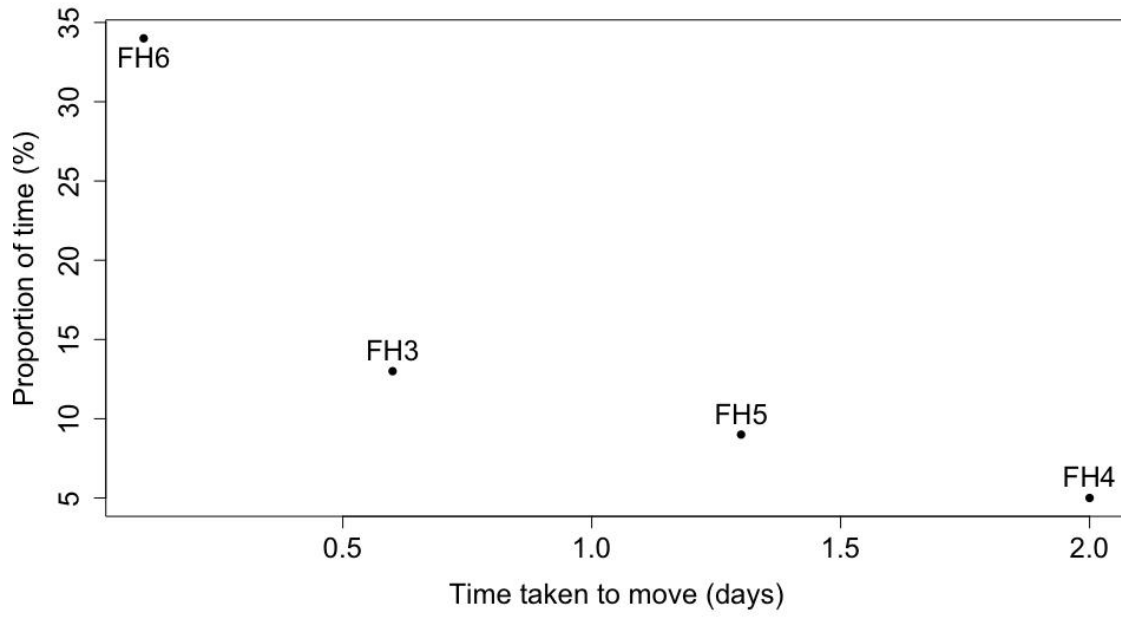


Fig. 3

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Fig. 4

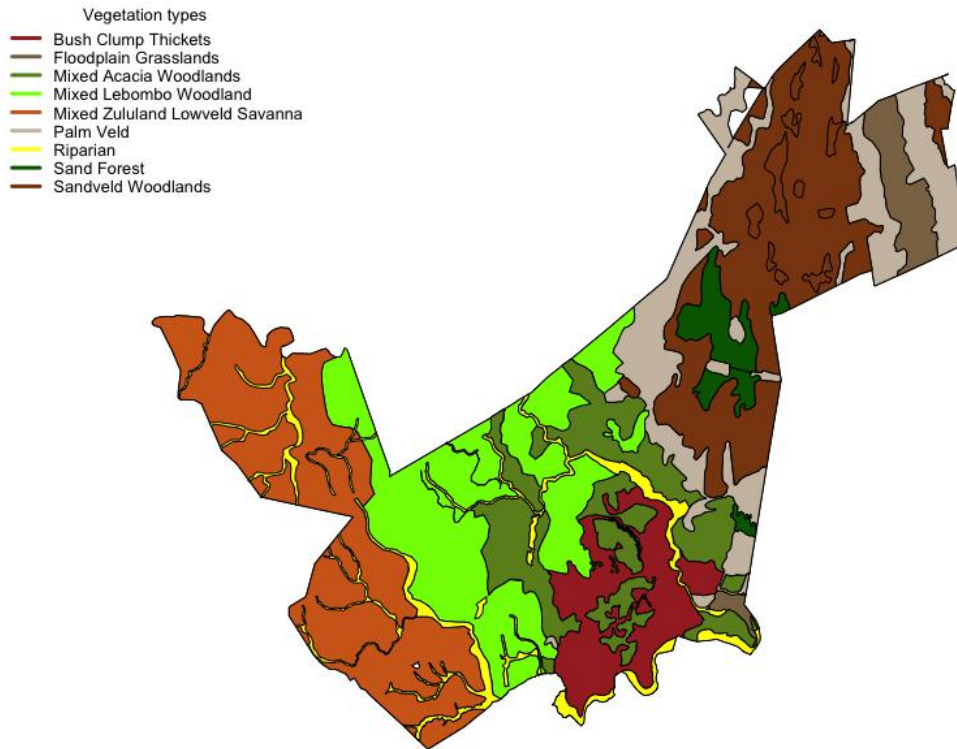
1

2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

SUPPLEMENTARY MATERIAL

1
2
3
4
5
6

Supplementary material 1. Vegetation map of the Mun-Ya-Wana conservancy.



7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

Elephants' response to an area expansion

1
2
3
4
5
6
7

Supplementary material 2. Percentage of locations acquired at most 30 min apart and that are at least 250 meters apart, for each possible pair of elephant herds. The first line presents calculations made from data collected during the year before the fence. The second and third lines present calculations made from data collected during the dry and the wet seasons respectively, following the fence removal.

	FH2 / FH3	FH2 / FH4	FH2 / FH5	FH2 / FH6	FH3 / FH4	FH3 / FH5	FH3 / FH6	FH4 / FH5	FH4 / FH6	FH5 / FH6
The whole year	1.3	15.5	68.9	0	2.2	2.0	1.1	14.1	0	0
Wet season	11.0	14.3	81.7	0.2	0	13.0	1.0	12.6	0.6	0
Dry season	19.0	10.2	78.9	0.9	12.9	17.4	0	14.0	4.7	1.9

8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52

Supplementary material 3. Percentages of each vegetation type with the elephant herds' seasonal home ranges (wet and dry), before and after the fence removal.

Elephants' response to an area expansion

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

Pre-opening								
	Family herds	Palm Veld	Mixed Acacia Lebombo Woodlands	Floodplain Grassland	Buch Clump Thicket	Mixed Zululand Lowveld Savanna	Riperian	Sand Forest and Sandveld Woodlands
Wet Season	FH3	19.3	23.9	6.4	2.3	10.9	3.9	33.1
	FH4	19.2	18.8	7.1	2.7	11.9	3.9	36.3
	FH5	18.8	14.8	5.8	9.6	9.4	5.2	36.3
	FH6	0.6	75.9	0	1.4	14.8	7.1	0
Dry Season	FH3	23.6	19.3	7.0	2.2	0	2.6	45.2
	FH4	20.7	11.4	6.4	9.1	0	2.6	49.7
	FH5	19.4	15.3	3.4	15.1	0	2.3	44.5
	FH6	7.1	65.1	0	19.8	0.2	5.2	2.6
Post-opening								
Wet Season	FH3	17.4	18.3	6.2	3.5	5.7	4.1	44.6
	FH4	22.7	12.0	6.6	9.9	0	2.1	46.5
	FH5	25.5	8.2	8.1	1.2	0	1.3	55.6
	FH6	10.6	52.1	0	2.8	12.9	5.9	15.8
Dry Season	FH3	24.0	8.4	8.3	5.9	0	2.0	51.4
	FH4	24.6	9.0	7.5	4.1	0	1.6	53.1
	FH5	25.2	8.1	7.1	1.8	0	1.4	56.4
	FH6	7.9	43.5	0	5.3	24.3	6.1	12.9

Elephants' response to an area expansion

1 Supplementary material 4. Proportions of availability of each vegetation type within the elephant herds' seasonal
 2 home ranges, before the fence removal.
 3
 4

	Family herds	Palm Veld	Mixed Acacia Lebombo Woodlands	Floodplain Grassland	Buch Clump Thicket	Mixed Zululand Lowveld Savanna	Riperian	Sand Forest and Sandveld Woodlands
Wet Season	FH3	18.2	25.3	6.4	2.2	11.0	4.2	32.5
	FH4	19.4	19.3	7.3	2.9	11.9	3.8	35.4
	FH5	18.9	15.7	5.8	9.9	9.3	4.8	35.4
Dry Season	FH6	0.66	75.6	1.5	0	15.1	7.2	0
	FH3	23.9	20.3	7.4	2.2	0	2.7	43.4
	FH4	20.7	11.2	6.7	9.6	0	2.6	49.1
	FH5	19.4	15.7	3.8	15.6	0	2.2	43.3
	FH6	7.7	63.5	0	20.8	0.3	4.8	2.9

5
 6
 7