



## Article

# A Phased Approach to Increase Human Tolerance in Elephant Corridors to Link Protected Areas in Southern Mozambique

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**Abstract:** Pathfinding elephants are moving through human dominated landscapes, often across international boundaries, thereby playing a vital role in connecting protected areas. Their movements are a call to action to not only understand their spatial requirements but to urgently work towards innovative ways to make people's livelihoods compatible with conservation outcomes so that coexistence and connected landscapes can prevail. We discuss the first three phases of a long-term strategy to conserve elephant corridors whilst incorporating the socio-economic needs of the people that share the landscape with them. We present a comprehensive satellite-tracking history of elephants across two transfrontier conservation areas (TFCA), represented by Great Limpopo- and Lubombo TFCAs and involving four countries (South Africa, Zimbabwe, Mozambique and Eswatini) to flag where linking corridors exist. We use innovative cafeteria-style experiments to understand which elephant-unpalatable plants would offer lucrative alternative income streams to farmers living in human–elephant–conflict hotspots. The most suitable unpalatable plants are chosen based not only on whether they are unpalatable to elephants, but also on their life history traits and growth prerequisites. We consider a combination of potential economic values (food, essential oil, medicinal and bee fodder value) to ensure that selected plants would accommodate changing economic markets. Lastly, we highlight the importance of combining food security measures with ensuring people's safety by means of deploying rapid-response units. By implementing these three phases as part of a longer-term strategy, we draw closer to ensuring the protection of bioregions to achieve biodiversity objectives at a landscape scale.

**Keywords:** elephant movements; corridors; elephant unpalatable plants; human safety; coexistence



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## 1. Introduction

On a continental scale, primarily because of the illegal trade in ivory, elephants have recently been listed as Endangered by the IUCN Red List of Threatened Species<sup>TM</sup> [1]. Thirty years ago, the southern African states had a little over 20% of Africa's continental elephant population [2]. Today, these southern states have become the last stronghold of the African elephant as they hold over half of the continental population due to excessive poaching in Central and East Africa. Of the remaining elephants, 76% of elephants are found in populations spread over more than one national border [3], as with the meta-population

of elephants we discuss here who share borders between Mozambique, Zimbabwe, South Africa and Eswatini. Each of these countries have Protected Areas (PAs) with varying densities of elephants. Mozambique and Eswatini have relatively low densities of elephants [4] compared to the neighbouring expanding populations of the Kruger National Park (KNP) in South Africa and Gonarezhou National Park (GNP) in Zimbabwe. As 57.4% of elephants' current range is outside of reserves [5] and elephants are known to move back to areas where they once occurred [6], elephant movement outside of PAs and across human-dominated landscapes is to be expected.

Human–Elephant Conflict (HEC) is rapidly increasing as elephants are being compressed within their natural range alongside burgeoning human populations, resulting in damage, economic losses, injuries and death of people and elephants [7,8]. Crop raiding by elephants represents a common form of HEC and could be driven by a lack of micro-minerals that are not available within the PAs when resources are limited such as during the dry season [9,10], although elephants are known to feed on cultivated crops even when sufficient natural forage is available, due to their high nutritional value, low natural defences and ease of access [11,12]. Irrespective of the drivers of crop-raiding in elephants, HEC represents a problem that poses serious challenges to wildlife managers, local communities, and elephants alike, and as elephants are highly adaptable and intelligent, finding sustainable mitigation solutions can prove difficult [6,13]. Hard barriers such as electric fencing often threaten connected landscapes if not strategically placed around local cluster crops and can prove to be expensive and ineffective if not maintained once elephants learn to breach them [14,15]. Furthermore, labour-intensive methods such as beehive fences or actively repelling elephant incursions using chilli smoke or noise aversion are not practical on a large scale [16]. Novel approaches are thus required to decrease HEC and increase human tolerance towards elephants within defined elephant corridors. One such approach is the growing of alternative crops that are not only unpalatable to elephants, but which can provide a source of alternative income [17]. Previous studies have shown that plants that contain higher amounts of secondary plant products were less attractive to elephants than maize [18].

On an ecological scale and beyond the local scale of crops that require protection within corridor zones, PAs are becoming islands in a sea of human development and over time this will have irreparable biodiversity implications [19,20]. The IUCN's Guidelines for Conserving Connectivity through Ecological Networks and Corridors outlines the importance of connected ecosystems to enable essential ecological functions such as migration, hydrology, nutrient cycling, pollination, seed dispersal, food security, climate resilience and disease resistance [21]. Connecting PAs across political borders, alongside building more sustainable, rural economies with communities that live in and around corridors delineated by elephant movements, is of prime importance [22]. To do so requires an understanding of the linkages between PAs that are being forged by collared, trailblazing elephants. Thereafter, people's financial assets (food crops) require protection, or people need to be equipped with the tools to offset any seasonal crop losses with alternative income streams to increase tolerance [23]. As safety ranks second on Maslov's hierarchy of needs after the psychological need for food as one of the survival prerequisites, human safety against marauding elephants needs to be addressed where people and elephants coexist [24]. Therefore, to contribute towards the ecological processes that propagate the coexistence of elephants, their habitat, and people, we present a phased approach of a long-term strategy developed for southern Mozambique, aimed at promoting coexistence between people and elephants while ensuring that landscape connectivity is maintained. Firstly, we discuss the use of satellite tracking of elephants to identify corridors linking PAs. Secondly, we make use of a cafeteria-type experiment involving semi-habituated free-roaming elephants to determine which literature-based elephant-unpalatable plants and those with commercial, medicinal and/or bee fodder value as potential alternative revenue streams are avoided by elephants. During the experimental setup, we also tested several crops planted by people in potential corridors and known to be palatable to elephants.

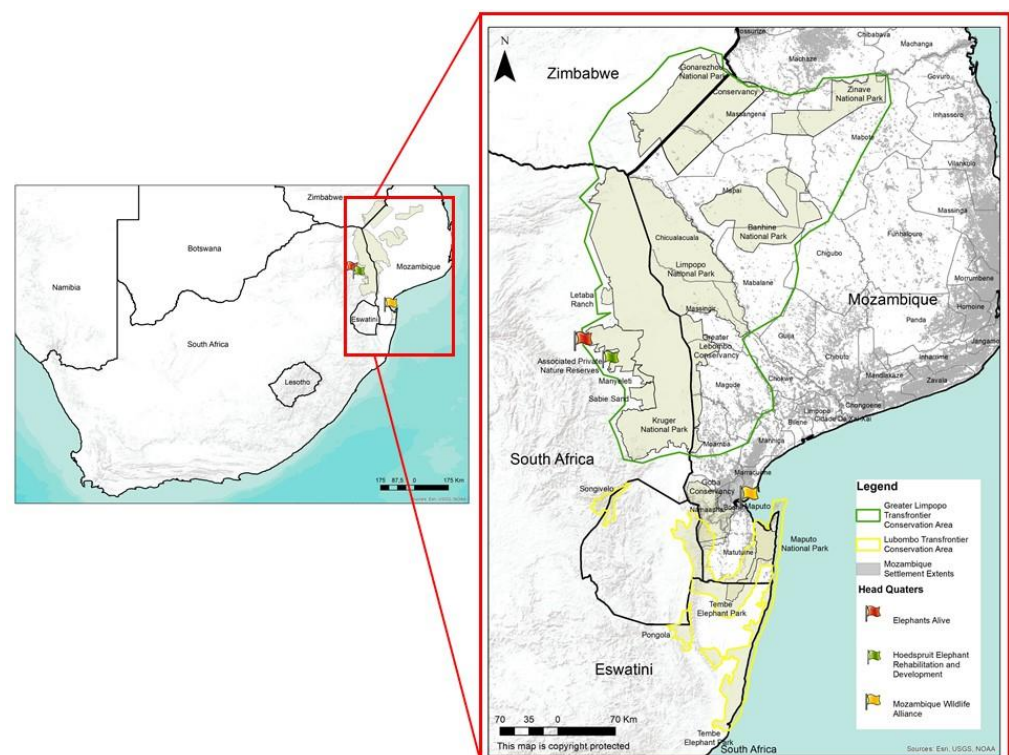
Lastly, we evaluate ways to ensure human safety as a priority once elephant tracking data have revealed potential conflict hotspots.

## 2. Material and Methods

### 2.1. Phase 1—Satellite Tracking Elephants

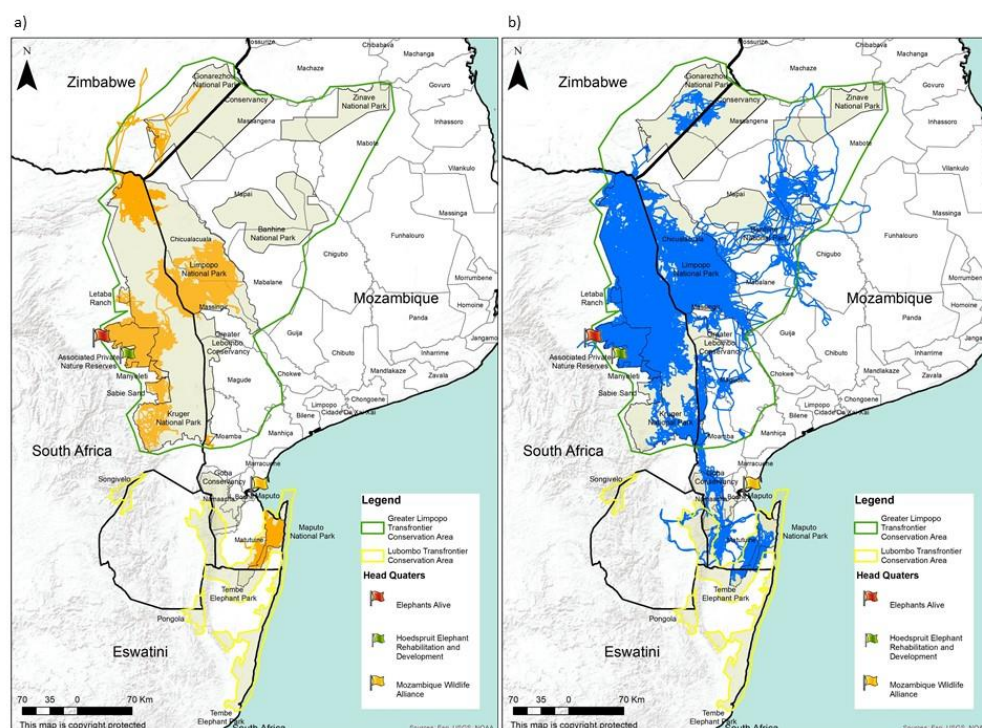
#### Study Site

Our study site is defined by the movements of the global positioning points of satellite-collared elephants. The Great Limpopo Transfrontier Conservation Area (GLTFCA) is located across the international boundaries of South Africa, Mozambique and Zimbabwe. It encompasses an area of around 100,000 km<sup>2</sup>, incorporating the KNP (South Africa), Banine, Limpopo and Zinave National Parks (Mozambique), Gonarezhou National Park (Zimbabwe), as well as other smaller PAs. Midday temperatures range between 20 and 30 °C, with a predominantly summer mean annual rainfall of 500 mm [25]. This Transfrontier Conservation Area is linked to the Lubombo TFCA (LTFCA), which includes Maputo Special Reserve (Mozambique), Hlane Royal National Park (Eswatini), Tembe Elephant Park (South Africa), as well as other smaller PAs (Figure 1). The LTFCA encompasses an area of around 4195 km<sup>2</sup>, with a mean annual rainfall of 500–800 mm and midday temperature ranges of 20–28 °C [26].



**Figure 1.** Maps showing the location of the main headquarters in South Africa and Mozambique. The red square depicts the study site as defined by the elephants' movements. The enlarged map shows a more detailed representation of the protected areas and Mozambican districts within the study site. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)).

Elephants Alive (a South African based NGO) first started collaring elephants in 1998 following the standard operational procedures by the South African National Parks Animal Use and Care Committee [27], using collars sourced from AWT (African Wildlife Tracking, Pretoria, South Africa) and Savannah Tracking (Nairobi, Kenya). All GPS fixes and associated information are kept in a central database managed and curated by Elephants Alive using Ecoscope analytical tools <https://ecoscope.io> (accessed on 1 July 2022) and an Earth Ranger platform <https://www.earthranger.com> (accessed on 1 February 2019). Erroneous GPS fixes were filtered out based on a biologically defined upper movement limit of 7 km/h [28]. All spatial data were projected to the Universal Transverse Mercator (UTM) WGS1984 reference system (Zone 36S). In total 140 elephants have been collared from 1998–2022 (Figure 2).



**Figure 2.** The transboundary movements of elephants between South Africa, Mozambique and Zimbabwe. A total of 38 cows from family units have been collared over time with the first cows (a) collared in 2004 in the Associated Private Nature Reserves (APNR) to the west of the Kruger National Park (KNP). In 2008–2012 elephant cows were collared in the Makuleke Concession in the northern regions of the KNP. In 2016–2021 cows were collared in Limpopo National Park (LNP) and in 2019–2022 in Maputo Special Reserve in Mozambique. The first two cows were collared outside of protected areas (PAs) in 2022. Of the 102 bulls collared over time, the first (b) bulls were collared in 1998 in the APNR, with seven bulls collared on the eastern border of the KNP in 2006. Bulls were also collared from 2008–2012 in northern KNP. The first bulls were collared in LNP in 2016–2021 and in Banhine National Park in 2019. The first bull was collared outside of PAs in Mozambique in 2018. In total 140 elephants have been collared over time, not including any recollaring events. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)).



Within PAs, Elephants Alive first collared elephants in the Associated Private Nature Reserves (APNR) in 1998, on the western boundary of the KNP [29,30] (Figure S1), where to date 18 female and 55 male elephants have been collared of which 37 elephants were recollared to ensure a long-term tracking dataset. We set out to investigate the extent of transboundary movements as amalgamated private conservation areas planned to expand over time. In December 2002 sections of the fence that separated the KNP in South Africa from Limpopo National Park (LNP) in Mozambique were removed [31]. Within the KNP, seven bulls were collared in 2006 on the eastern border with Mozambique to see if they were utilizing LNP to which they had access since sections of the dividing fences were removed (Figure S2). Between 2008 and 2012 we collared 12 and recollared nine elephants in the Makuleke Community of northern KNP to determine whether they were using the Sengwe corridor linking KNP with GNP in Zimbabwe (Figure S3). Collaring elephants within Mozambique's PAs started in 2016 with six female and 13 male elephants collared in LNP from 2016–2021 to further understand cross-border movements (Figure S4). From 2018–2022, we collared a total of 22 elephants outside of PAs of which two were females within a family unit (Figure S5). In 2019 we collared the first bull in Banhine National Park which has a very low density of elephants (Figure S4—individual tracks depicted in black). From 2019–2022 six females were collared in Maputo Special Reserve (Figure S6).

Using elephants as the landscape planners for connectivity over national boundaries, we have identified several corridors in which the knowledge gained from the cafeteria experiments of phase 2 of this study will be applied. Ensuring human safety was phase 3, already commenced in 2021 and applied over the larger landscape with elephant movements enabling us to understand where our efforts can be concentrated across southern Mozambique (Figure S1–6).

## 2.2. Phase 2—Cafeteria Experiments

### 2.2.1. Study Site

Cafeteria experiments took place at the Hoedspruit Elephant Rehabilitation and Development (HERD) orphanage in Kapama Private Game Reserve (Kapama) (24.420343° S; 31.100546° E). The HERD orphanage was built in 2019 and serves as a sanctuary for orphaned African elephants (Figure 1). HERD currently has 16 semi-habituated elephants of which two bulls were made available for the cafeteria experiments, namely Sebakwe (age 37 years) and Somopane (age 35 years) [32]. The HERD orphanage offers elephant interactions in the mornings to tourists, where elephants are fed a combination of peanuts and oranges, after which they are free roaming, feeding on natural vegetation throughout the day.

### 2.2.2. Plant Type Selection and Harvesting Criteria

Eighteen plant or crop types were chosen for the cafeteria experiments, the majority of which have a high essential oil potential (African blue bush (*Ocimum americanum* L.), Cape gold (*Helichrysum splendidum* Thunb.), Cape snowbush (*Ericcephalus africanus* L.), borage (*Borago officinalis* L.), bulbine (*Bulbine frutescens* L.), fever tea (*Lippia javanica* Burm. f.), geranium (*Pelargonium graveolens* L'Heritier), lavender (*Lavandula x intermedia* L.), lemon grass (*Cymbopogon* L.) and worm wood (*Artemisia afra* Jacq.)). The selection of plant types included common food crops cultivated by subsistence farmers in Mozambique (cassava (*Manihot esculenta* Crantz.) and corn (*Zea mays* convar. *Saccharate* var. *rugosa* L.)), unpalatable crops already described in the literature (bird's eye chilli (*Capsicum frutescens* L.), garlic (*Allium sativum* L.), ginger (*Zingiber officinale* Roscoe) and sunflower (*Helianthus annuus* L.)), a potential aromatic herb not yet tested (rosemary (*Rosmarinus officinalis*)) and a commercial crop native to Mozambique and used extensively within the tea industry (hibiscus (*Hibiscus sabdariffa* L.) [33].

Of the plant or crop types selected for their essential oil content and thus a potential alternative crop due to their unpalatability, many also have a multi-purpose value such as medicinal and high bee fodder values (pollen and nectar). Therefore, the cafeteria-style

experiments were used to determine if plants with a known high essential oil, medicinal use or other commercial value were also unpalatable to elephants. As beehive fences have already proven to represent effective barriers to food crops throughout Africa and Asia [34,35], knowing which plants represent good bee fodder would help ensure that subsistence farmers have viable bee swarms not only to protect their crops, but also to pollinate all their agricultural products [36]. Each food type was rated on a 4-point scale according to different categories, with '1' representing a good plant choice within a high HEC area, whilst '4' meant that the plant would not be suitable for several reasons, including requiring considerable protection to prevent HEC (Table 1).

We grew 15 of the plant types at the Elephants Alive HQ (Figure 1) to ensure a fresh supply during experimentation. As the fruit bodies of cassava, corn and garlic were less susceptible to wilting and rapid degradation, they were ordered and transported from elsewhere. All 18 plant types were prepared and packaged in the morning before sunrise and kept in a cooler box until just before experimentation. As we were focussed on comparative selectivity between crop types, and not intake rates, only small portions, of equal weight and irrespective of the structural diversity between plant types, were used. For all the plant types presented, with the exception of corn, cassava, garlic and ginger due to availability, the whole fresh plant was presented to try and represent what crop-raiding elephants might encounter. This also ensured that the elephants could move through the experimental site quickly, assessing the diversity on offer, before becoming bored or satiated after feeding at only a few experimental troughs.

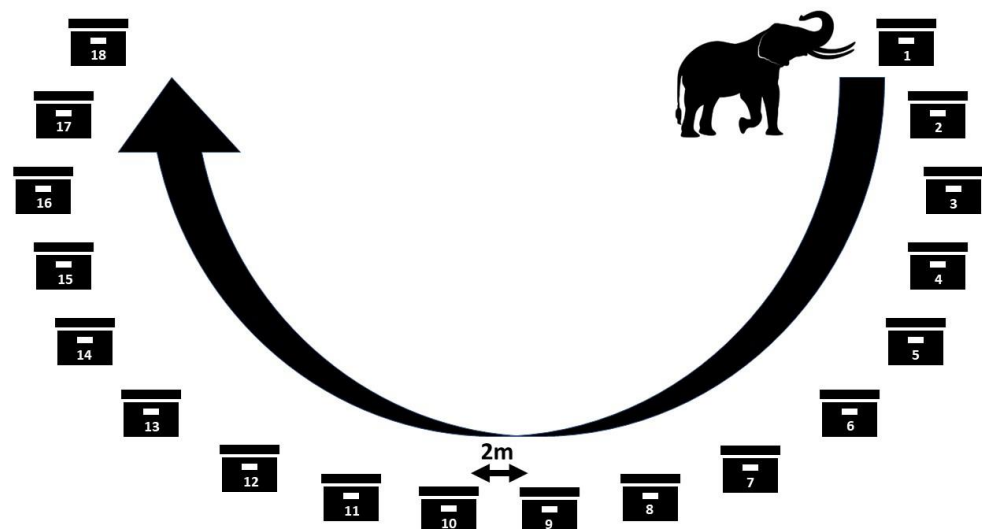
**Table 1.** The 4-point scoring of each of the chosen plant or crop types according to border life cycle characteristics (B), growth requirements (G), their potential economic value based on the literature (E) and their palatability following the cafeteria experiments (P). The reasoning behind the scores is explained under the motivation.

Categories	Score	Motivation
Broader life cycle characteristics	B	
Indigenous & perennial	1	Indigenous plants would be more resistant to pests and if perennial, less labour intensive to farm
Indigenous & annual	2	Indigenous plants would be more resistant to pests and if annual, more labour intensive to farm
Exotic & perennial	3	Non-native species are usually very susceptible to pests and if perennial, less labour intensive to farm
Exotic & annual	4	Non-native species are usually very susceptible to pests and if annual, more labour intensive to farm
Growth requirements	G	
Low rainfall dependent, any soil type & drought tolerant	1	Well adapted to arid regions, doesn't require rich soils and can withstand droughts
Medium rainfall dependent, nutrient rich/any soil type & drought tolerant	2	Adapted to medium rainfall, may or may not depend on particular soil types but still drought resistant
Medium rainfall dependent, nutrient rich/any soil type & drought intolerant	3	Adapted to medium rainfall, may or may not depend on particular soil types but not drought resistant
High rainfall dependent, nutrient rich/any soil type & drought intolerant	4	Requires high rainfall, may or may not depend on a particular soil type and not drought resistant
Economic value	E	
Has food-, essential oil-, medicinal- and bee fodder value	1	A very versatile plant type that has a very wide market value with the processing thereof adaptable to the demand
Has only three of the four potential value types	2	A versatile plant type that can adapt to different market demands
Has only two of the four potential value types	3	A plant type that has economic value, but which is limited in terms of what markets it can serve
Has only one of the four potential value types	4	A plant type that is specialised to only serve one market type
Palatability	P	
Was not eaten/ignored by elephants/spat out after tasting	1	Strongly avoided
Mostly played with the plants and didn't consume them	2	Avoided
Showed some interest and ate parts of the plant but played with other parts	3	Edible
Readily consumed all plant parts each time	4	Favoured

### 2.2.3. Cafeteria Experiments

The cafeteria experiments were run from 24 August–8 September 2022 and were approved by the Animal Ethics Screening Committee of the University of Witwatersrand, Johannesburg (AESC 2022/02/04/B). During this period, five experimental days of both morning and afternoon experimental sessions were carried out. For each experimental session, two cafeteria experiments were completed (one per elephant). Due to logistical constraints regarding the location of the semi-habituated elephant herd throughout the day, two separate experimental sites were used to accommodate the morning and afternoon feeding sessions. Morning sessions began at 9:30 am and afternoon sessions began at 3:15 pm. Wind and temperature measurements were recorded at the start of each feeding session.

The following methodology was carried out per cafeteria experiment (Figure 3): 18 rubber feeding troughs were placed 2 m apart in a semi-circular fashion. Each trough had 50 g of a randomly selected plant or crop type placed inside of it. The random plant type order ensured that no plant type would be favoured by the elephants based on its location throughout the cafeteria-style experimentation. Plant type order, however, remained constant for both elephants within an experimental session as they happened consecutively. Two video cameras were placed on opposite ends of the cafeteria site to record the full experiment. To begin the experiment, the elephant was brought to the same first feeding trough by its handler. Thereafter the handler removed himself from the experiment to avoid further influence. Upon reaching trough one, the elephant would have five minutes to feed throughout the whole cafeteria-style experiment without guidance. As soon as the experimental time was up, recording ceased, the handler guided the elephant away and the experimental session for that particular elephant ended. All remaining food items were removed from the trough and placed in corresponding bags. The same experimental setup was then prepared before the next elephant entered the site. For each trough, we recorded whether the elephant smelt, consumed, played with, or ignored the plant type. For consumed crops, the remaining crop materials were reweighed to calculate the quantity of each food type consumed of the original 50 g.



**Figure 3.** Diagrammatic view of a cafeteria experiment. Elephants were brought to the first feeding trough, after which they were left alone for five minutes to explore the eighteen feeding troughs. Each trough had 50 g of a randomly selected crop or plant type placed inside of it.

### 2.2.4. Data Analyses

All analyses were performed using R version 4.2.1 (R Development Core Team 2012). All tests were two-tailed and were considered significant at  $p < 0.05$ . Parametric tests were



conducted where data fitted the relevant assumptions of normality and homogeneity of variance; otherwise, non-parametric equivalents were used.

We used a classification tree (CT) approach, based on conditional inference [37], to explore the predicting factor effects of crop type, elephant individual, session time (morning/afternoon), temperature and wind speed on crop consumption probability. The conditional inference approach avoids bias towards predicting factors, whilst allowing for data to be partitioned into multiple categories [38]. CTs were constructed using the party package [37].

We calculated Ivlev's electivity index as a measure for utilisation of food, which when consumed in larger proportion were considered preferred [39]:

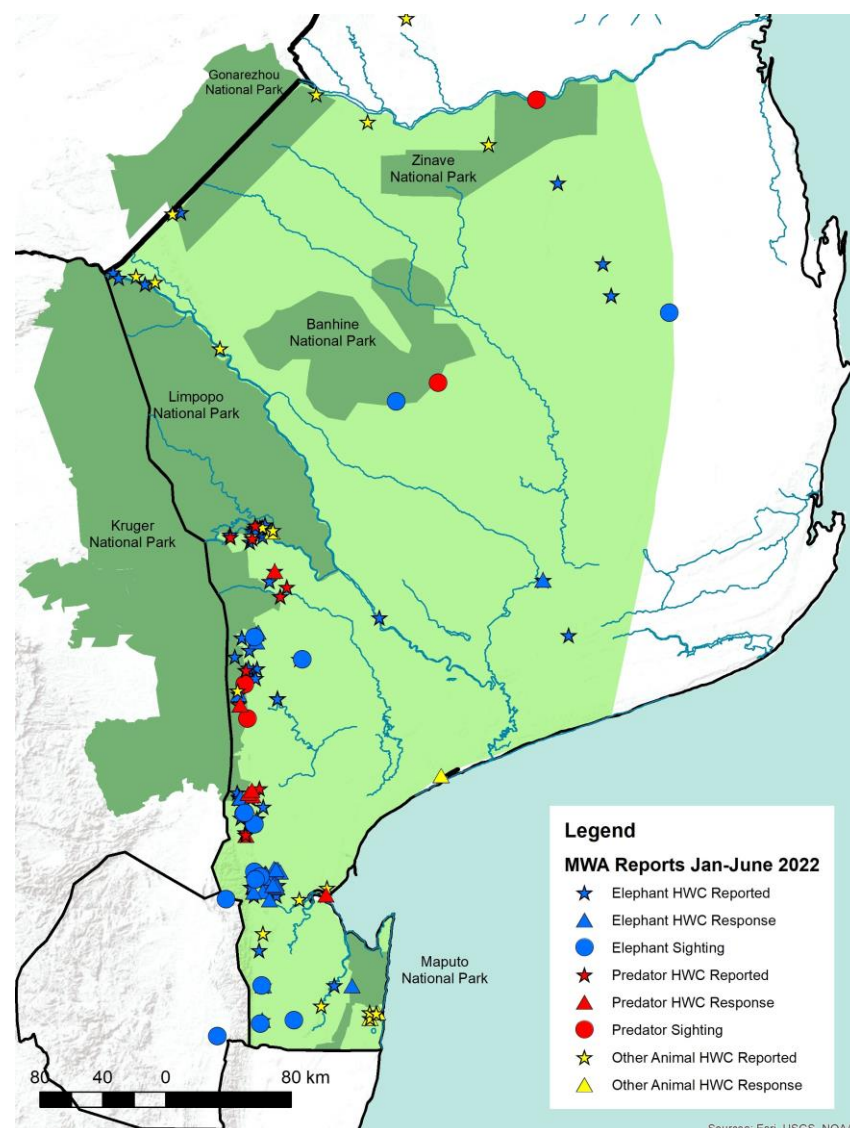
$$E = r_i - p_i/r_i + p_i$$

where  $r$  is the proportion of the plant or crop type utilized and  $p$  the proportion of the plant available per session.

We developed a Generalised Linear Mixed Model following a Gaussian distribution to investigate if elephant selection of plant or crop types was influenced by the time of day, wind and temperature. Electivity was thus used as the response variable in relation to the crop type (categorical), speed of the wind (continuous), temperature (continuous) and time of day the session occurred (categorical), as covariates included as fixed effects. The elephant identity (categorical) was included as a random variable as was the session's number (categorical), accounting for repeated measures for each crop type and individual. Akaike Information Criterion (AIC) ranking was used to select our minimal model [40] (package: MuMIn, [41]). The p-values of the variables' effects were obtained using likelihood ratio tests of the full model with and without the effect in question to provide reliable estimates for regression parameters [42]. Where significance was found, post-hoc Tukey's tests were run using the 'emmeans' package [43] to compare means. Checks revealed no overdispersion (conducted by evaluating if the dispersion parameter (residual deviance/df) was between 0 and 1 [44]).

### 2.3. Phase 3—Ensuring Human Safety

The mobilisation of the first Rapid Response Unit (RRU) in Mozambique in June 2021 consisted of two trained people on a motorbike together with a backup vehicle. Toolkits for mitigating human–wildlife conflict (HWC) consisted of the following: firecrackers, foghorns, vuvuzelas, paintball guns with chilli pellets, double shot launchers (15 mm) and danger tape. The Mozambique Wildlife Alliance (MWA) strategically operated the RRU and ensured their day-to-day running with strategic and financial support from Elephants Alive via our existing donor base. The RRU covered 15,480 km since being in operation (June 2021–June 2022) and responded to both reported HEC incidents as well as pre-empted incidents based on predicting elephant crop raids from elephant tracking histories. The reported incidents were obtained by phoning 21 districts every two weeks and working closely with Servico Distrital de Actividades Economicas (SDAE), which have been mandated by the Administração Nacional das Áreas de Conservação (ANAC) to deal with HWC in Mozambique. The RRU's scope of work is aimed not only at deterring elephants from potential crop-raiding at night, but also at spending considerable time educating the community about how to behave around elephants pre-and post-incursion events. Although most HEC incidents were mitigated within identified elephant corridor regions, HEC in Mozambique with its unfenced PAs is not restricted to corridors flagged by collared elephants but occurs widely throughout southern Mozambique (Figure 4).



**Figure 4.** Human–wildlife conflict (HWC) events for a six-month period indicating that most conflict events are occurring within the corridor regions flagged by the satellite-collared animals moving between PAs.

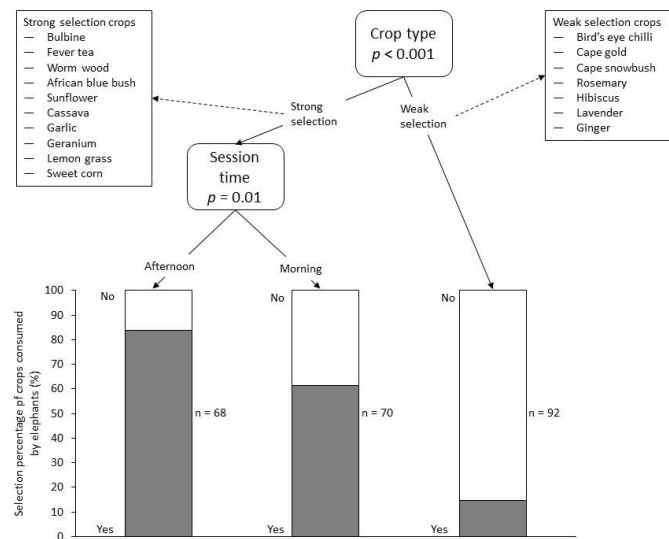
### 3. Results

#### 3.1. Phase 1—Satellite Tracking Elephants

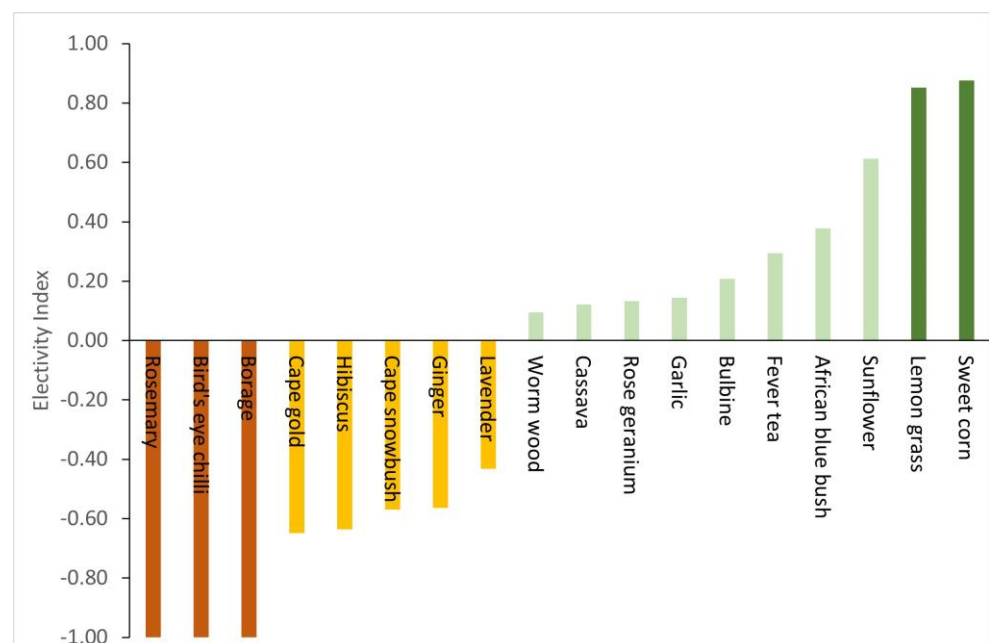
After 24 years of tracking elephant movements in relation to expanding conservation areas using satellite collars, we have amassed over two million data points. Of the two million data points through time, 9.5% are found outside of PAs. These related to 37 elephants having moved outside of PAs over time. Within South Africa (the APNR–KNP complex), seven elephants have moved outside of the PAs to the west and south. Seven elephants have moved out of KNP in South Africa into Mozambique, and two moved from northern KNP into Zimbabwe and back. Furthermore, six elephants have moved from southern KNP across southern Mozambique of which one entered Tembe National Park in South Africa and then proceeded to Eswatini with another bull. The other collared bull returned to the KNP and later Mozambique while the bull in Eswatini has remained trapped within an enclosure of 4.13 km<sup>2</sup> for almost a year (Figure S1–S6). The accurate delineation of the corridors used by elephants as well as the use of elephant tracking data to predict crop-raiding events forms part of larger study by Elephants Alive with publication of the results underway.

### 3.2. Phase 2—Cafeteria Experiments

The analysis of the cafeteria experiments produced a CT of two inner nodes and three terminal nodes, with a 77.4% prediction success value. The results indicated that plant or crop type ( $p < 0.001$ ), followed by session time ( $p < 0.05$ ), were significantly associated with plant consumption probabilities (Figure 5). The CT divided the 18 plant types into 10 palatables and eight unpalatables (Figure 5) with varying degrees of selectivity (Figure 6), whilst further dividing the palatables into increased consumption probability in the afternoon sessions in comparison to the mornings (Figure S6).



**Figure 5.** Results of the classification tree analysis representing the selection percentage of plant or crop types consumed by elephants in the cafeteria experiments.



**Figure 6.** The Electivity Index in ascending order as calculated across all sessions for both elephants combined.

Electivity indices were significantly influenced by crop type (GLMM  $\chi^2_{17} = 135.08$ ,  $p < 0.0001$ , Figure 6, Table S1) and if the session took place in the morning or afternoon (GLMM  $\chi^2_1 = 16.49$ ,  $p < 0.0001$ , Figure S2, Table S1). Tukey’s post-hoc testing with 95% con-

confidence intervals when averaged over time of the session (see Table S1) showed that sweet corn ( $E_{\text{mean}} = 0.82 \pm 0.30$ ) and lemon grass ( $E_{\text{mean}} = 0.88 \pm 0.28$ ) were significantly preferred whereas borage ( $E_{\text{mean}} = -1.00 \pm 0.29$ ), bird's eye chilli ( $E_{\text{mean}} = -1.00 \pm 0.29$ ) and rosemary ( $E_{\text{mean}} = -0.99 \pm 0.287$ ) significantly avoided. Furthermore, significantly higher electivity indices were observed during the afternoon sessions ( $E_{\text{mean}} = 0.14 \pm 0.22$ ) compared to the morning sessions ( $E_{\text{mean}} = -0.38 \pm 0.22$ ). Moreover, there was no significant effect of wind ( $p = 0.25$ ) nor temperature ( $p = 0.12$ ) on the electivity index. Lastly, Elephant ID had a significant effect (GLMM  $\chi^2_{17} = 13.268$ ,  $p = 0.0003$ , Table S1), with Sebakwe selecting more crop types ( $E_{\text{mean}} = 0.09 \pm 0.08$ ) compared to Somopane ( $E_{\text{mean}} = -0.27 \pm 0.09$ ), but this only explained 14% of the variance. The number of the session did not have an effect on the electivity indices (GLMM  $\chi^2_{17} = 1.16$ ,  $p = 0.28$ , Table S1).

The growth traits, economic value and palatability of each plant were categorised according to the four-point scale mentioned earlier (Table 2). We then summed the scores per plant and rated them as (1) highly favourable to propagate in elephant corridors (the lowest overall score, i.e., 6), (2) favourable to propagate as an income-generating soft barrier (scores between 7 and 10), (3) not favourable to propagate as they were edible to the semi-habituated elephants, with the exception of ginger whose growth characteristics would not make it suitable given potential climatic effects (scores ranged from 11–15) and (4) only suitable as a food crop in need of protection from elephants (score above 16). Using these scores, a final list of potential alternative crops was generated to compare with what is available in the literature based on the crop's palatability, essential oil potential, medicinal and bee value (Table 3).

**Table 2.** The 18 plant types that were included in the cafeteria-type experiments. Their broad life cycle characteristics (B) were scored, while their growth requirements (G) and their economic value (E) were based on information available in the literature. Their palatability scoring was derived from the electivity indices of the elephants during the cafeteria experimental setup (P). The score for each category was based on the reasoning explained in Table 1. The colours under the economic value correspond with those of Figure 6 with rust representing the strongly avoided plants, yellow those that were avoided, light green those that were edible and dark green those that were favoured.

Crop	Latin Name	Origin	Native to Southern Africa	Life Cycle	Growing Condition		Drought Tolerant	Economic Value				Palatability to Elephants	Scoring				
					Rainfall	Soils		Food	Oil	Med	Bee		B	G	E	P	O
Borage	<i>Borago officinalis</i>	Middle East	No	Annual	Low	Any	Yes				N *	Strongly avoid	4	1	1	1	7
Bird's eye chilli	<i>Capsicum frutescens</i>	Africa & southeast Asia	Yes	Perennial	Medium	Any	Yes					Strongly avoid	1	2	2	1	6
Rosemary	<i>Rosmarinus officinalis</i>	Mediterranean region	No	Perennial	Low	Any	Yes				N	Strongly avoid	3	1	1	1	6
Cape gold	<i>Helichrysum splendidum</i>	Africa & Ethiopia	Yes	Perennial	Low	Any	Yes				P *	Avoid	1	1	2	2	6
Cape snowbush	<i>Eriocephalus africanus</i>	South Africa	No	Perennial	Low	Any	Yes				N	Avoid	3	1	2	2	8
Ginger	<i>Zingiber officinale</i>	Southeast Asia, India & China	No	Annual	High	Nutrient rich	No					Avoid	4	4	2	2	12
Hibiscus	<i>Hibiscus sabdariffa</i>	Africa	Yes	Perennial	Medium	Any	No				N	Avoid	1	3	1	2	7
Lavender	<i>Lavandula x intermedia</i>	France	No	Perennial	Low	Any	Yes				N	Avoid	3	1	2	2	8
Bulbine	<i>Bulbine frutescens</i>	South Africa	Yes	Perennial	Low	Any	Yes			Gel	P	Edible	1	1	2	3	7
Cassava	<i>Manihot esculenta</i>	South America	No	Perennial	Medium	Any	Yes				N	Edible	3	2	3	3	11
Fever tea	<i>Lippia javanica</i>	South Africa	Yes	Perennial	Low	Any	Yes				N	Edible	1	1	2	3	7
Garlic	<i>Allium sativum</i>	Middle Asia	No	Annual	Medium	Nutrient rich	Yes					Edible	4	2	2	3	11
Geranium	<i>Pelargonium graveolens</i>	South Africa	No	Perennial	Medium	Nutrient rich	No					Edible	3	3	3	3	12
African blue bush	<i>Ocimum americanum</i>	Africa, India & southeast Asia	Yes	Perennial	Medium	Nutrient rich	No				N	Edible	1	3	1	3	8
Worm wood	<i>Artemisia afra</i>	Africa & Ethiopia	Yes	Perennial	Low	Any	Yes				P	Edible	1	1	2	3	7
Sunflower	<i>Helianthus</i>	North America	No	Annual	Low	Any	Yes			Food	P	Favour	4	1	1	3	9
Lemon grass	<i>Cymbopogon</i>	Southeast Asia	No	Perennial	High	Nutrient rich	No					Favour	3	4	2	4	13
Sweet corn	<i>Zea mays convar. saccharata</i> var. <i>rugosa</i>	South America	No	Annual	High	Nutrient rich	No					Favour	4	4	4	4	16

\* A pollen index (P) refers to the availability of pollen on a given beeplant, ranging from 0 (no pollen available) to 3 (major pollen source) [45]. The nectar (N) or 'sugar' value of a beeplant refers to the number of milligrams of sugar available per flower over a 24 h period [46].



**Table 3.** The final recommendation for the 18 crops tested in terms of their palatability. The scores were obtained from several factors and not their palatability to elephants alone. Overall scores refer to crops that will be very suitable to test due to their unpalatability to elephants, their growing requirements as well as their versatile economic value (score below 7). Some crops may be unpalatable or edible, but they would be suitable for propagation and have high market values (score 7–10). Others were all edible to the elephants except for ginger so they would be at risk of crop damage (score above 10).

Type	Overall Score	Literature Description	Reference
Bird's eye chilli	6	Unpalatable	<sup>b</sup> [45], <sup>a</sup> [47]
Cape gold	6	Unknown	<sup>o</sup> [48], <sup>m</sup> [49], <sup>b</sup> [45]
Cape snowbush	6	Unknown	<sup>o</sup> [50], <sup>m</sup> [51], <sup>b</sup> [45]
Rosemary	6	Unknown	<sup>o</sup> [48], <sup>m</sup> [52], <sup>b</sup> [45]
Borage	7	Unknown	<sup>o, m</sup> [53], <sup>b</sup> [45]
Bulbine	7	Unknown	<sup>o, m</sup> [54], <sup>b</sup> [45]
Fever tea	7	Unknown	<sup>o</sup> [48], <sup>m</sup> [50], <sup>b</sup> [45]
Hibiscus	7	Unknown	<sup>m</sup> [55], <sup>b</sup> [45]
Worm wood	7	Unknown	<sup>o</sup> [48], <sup>m</sup> [56], <sup>b</sup> [45]
African blue bush	8	Unknown	<sup>o</sup> [57], <sup>m</sup> [58], <sup>b</sup> [45]
Lavender	8	Unknown	<sup>o</sup> [48], <sup>m</sup> [59], <sup>b</sup> [45]
Sunflower	9	Unpalatable	<sup>o</sup> [60], <sup>b</sup> [45], <sup>a</sup> [61]
Cassava	11	Palatable	<sup>b</sup> [45], <sup>a</sup> [62]
Garlic	11	Unpalatable	<sup>o</sup> [48], <sup>a</sup> [17]
Geranium	12	Unknown	<sup>o</sup> [48], <sup>m</sup> [63]
Ginger	12	Unpalatable	<sup>o</sup> [48], <sup>a</sup> [17]
Lemon grass	13	Unpalatable	<sup>o</sup> [48], <sup>m</sup> [64], <sup>a</sup> [17]
Sweet corn	16	Palatable	<sup>a</sup> [62]

<sup>o</sup>—oil property, <sup>m</sup>—medicinal property, <sup>b</sup>—bee food property, <sup>a</sup>—attractiveness to elephants.

### 3.3. Phase 3—Ensuring Human Safety

The reach of the RRU involves three districts (Namaacha, Moamba and Matutuine), which have all been identified as high-HWC areas (Figure 1). A total of 270 conflict events have been reported in the past year of which 65% of all HWC incidents involved elephants. A seasonal effect is apparent in elephant crop-raiding events with the highest frequency of events occurring in the early dry season. Despite the near doubling of conflict reports in the second half of the study year, there has been a concurrent 34% decline in actual conflict events that the RRU needed to try and deal with over the same period. The efficacy of the RRU has also increased over time as unsuccessful mitigation events led by the RRU have decreased from 64% in the first half of the year to 36% in the second half of the study year. Overall, the RRU has mitigated 76% of all HWC conflict events (Table 4). They have also played a considerable role in pre-emptive mitigation through educational workshops. In 16 training sessions they have trained 178 people in the last year, delivering 37 toolboxes to trained community members. The RRU has empowered community members to deal with conflict themselves by delivering deterrence equipment after training or teaching them to manufacture their own means of mitigation such as chilli bricks. The RRU has recorded 725 units of deterrence equipment used by themselves while in total 4685 units of equipment have been delivered to the communities.

**Table 4.** The metrics of the RRU in operation within southern Mozambique over a 12-month period with the proportional difference in the categories over time and as divided into two six-month periods to evaluate the progress made to date in terms of mitigating HEC.

Description	1st 6 mon.	2nd 6 mon.	1 Year	Prop. diff. between Periods
Number of conflict cases	91	179	270	34% vs. 66%
Conflict cases involving elephants	54	121	175	31% vs. 69%
Conflict cases involving predators and other ungulates	37	58	95	39% vs. 61%
Number of responses by the RRU	82	39	121	68% vs. 32%
Number of successful chases	64	28	92	70% vs. 30%
Number of unsuccessful chases	18	10	28	64% vs. 36%

#### 4. Discussion

Bioregions represent areas of land or water where the geographical distribution of biophysical attributes, ecological systems and human communities define the area [65]. They redefine the scale at which biodiversity can be protected and often involve a network of transfrontier conservation areas that necessitate collaboration between states, the private sector, and communities [66]. Elephants have large spatial requirements driven by a need to access resources over vast areas, causing a substantial proportion of elephants to be distributed across more than one national border [3,28]. Connecting PAs across political borders, whilst building more sustainable, rural economies in collaboration with communities that live in and around corridors delineated by elephant movements, becomes a critical long-term solution to achieving biodiversity outcomes. However, where elephants and people intersect, increased HEC and retaliation killings of corridor-moving elephants could terminate landscape connectivity [67]. Insight into elephant movements outside of PAs thus helps place localized HEC incidents within a larger perspective, assisting with predicting when and for how long HEC incidents in particular areas along the length of mapped corridor zones can be expected. This enables us to formulate both reactive short-term mitigation strategies whilst working towards longer, proactive mitigation strategies to decrease HEC. We discuss the first three phases of a long-term transnational community-based approach to protect African elephants and their habitat through a unique multidimensional and integrated approach of community engagement, knowledge creation and practical conservation action.

Elephants moving beyond PAs with satellite tracking devices become important landscape planners for bioregions. Mapping potential corridors with the elephants as the intelligence agents represents the first step to understanding landscape connectivity. These movements occur under the cover of darkness due to the risky human-dominated landscapes they need to cross [68]. Although our elephant tracking history revealed only 9.5% of data recordings have occurred outside of PAs, this can be explained by a long initial history of recording elephant movements within fortified PAs within South Africa. When considering only the PAs in neighbouring Mozambique, we found that 28% of movements were outside of PAs, which was closer to the findings of [5] where more than half of elephant movements over largely unfenced PAs across Africa were outside of PAs. The tracking data have shown us that Transfrontier Conservation Areas (TFCAs), where the management of PAs considers neighbouring PAs across international boundaries [69], are too small for elephants. We show that both the GLTFCAs and LTFCAs have been linked by trailblazing bulls with this connectivity involving two South African national parks (KNP and Tembe Elephant Park) and five PAs within Eswatini (Big Bend Conservancy, Hlane Royal National Park, Mkhaya Game Reserve, Mlawula Nature Reserve and Panata Ranch) over an international border and across three political borders (South Africa, Eswatini and Mozambique). The next step will be to model the occurrence of elephant locations versus suitable habitat (see [70]). This is being carried out in a follow up study (Bedetti et al. in prep.).

Although HEC is widespread throughout southern Mozambique, most conflict is occurring in the corridor regions linking PAs (Figure 4, Figure S5). The satellite tracking enables mitigation efforts to be concentrated in HEC hotspot regions instead of diluting manpower and resources across the whole region. Training workshops by the RRU can then also be focussed on strategic areas.

The cafeteria-style experiments proved to be effective in evaluating several plants that have never been tested in terms of their palatability to elephants. Experiments such as these can assist in saving time and resources and avoid demoralizing poverty-stricken community members that often must share the landscape with crop-raiding elephants. The experiments, as a precursor to planting alternative crops with a market value in the corridor regions, delivered some interesting results. Herbs such as borage and rosemary with medicinal and aromatic properties, respectively, were strongly avoided together with bird's eye chilli. Elephants' avoidance of antifeedants such as capsaicin found in chillies is well-documented [71]. Their avoidance of medicinal or aromatic plants may be due to it being energetically costly to detoxify the secondary compounds [17,18], despite having well-developed salivary glands with proteins efficient at neutralizing tannins [72]. As most crop raiding occurs at night [73], it would follow that the elephants have a short window in which they need to optimize their foraging to obtain as much protein and micro-minerals as possible to make up for deficits elsewhere [9]. We found that lemon grass and sunflowers, presented as whole fresh plants to the elephants, were highly sought after by the elephants. The results require further investigation as both these plant types have been described as unpalatable to both Asian and African elephants alike [17,18]. As lemon grass needs high rainfall and soil nutrients, as well as being drought intolerant, we rated it as the second-least-suitable plant to propagate in corridor regions linking GLTFCA and LTFCFA. Our results also showed that it would be preferable to plant cassava as a staple compared to any corn variant which was highly favoured by the elephants. According to the overall scoring system, four food types, with only one of them tested before on elephants, proved best suited for the proposed corridor region (bird's eye chilli, Cape gold, Cape snowbush and rosemary). The latter three plant types have been used in producing essential oil and hold great promise. The global market for essential oils continues to reflect a strong upward trend, having increased by an average of 15% from 2018 to 2019. Global production is estimated to be more than 150,000 t, valued at USD6.5bn and projected to rise at a compound annual growth rate of 8.4% to 11.8% (valued at USD15.8bn) by 2024–2025 [74].

The overall scoring system, which combined the lifecycle traits of the plants, together with the growth requisites, their combined economic value (food, essential oil, medicinal and bee fodder value) and their palatability to elephants, proved to be a novel way in which a more holistic approach can be taken towards encouraging community members to try to offset their losses by growing alternative crops with a market value. Following this approach, more plant types can be chosen and tested according to the climatic conditions of the proposed areas in which they may be propagated. Following cafeteria trials, market research is needed [71], as well as yields to sufficiently equip communities with the right produce that will achieve the desired outcome of increasing tolerance in as short a time as possible.

Knowledge gained through trials such as these open the doors to two possible scales at which land-use planning can take place. At a more local scale a combination of hard barriers, such as electric fences, around small cluster farms that do not prohibit the movement of elephants can be used. Within these hard boundaries, highly palatable crops are secured. Outside of these areas, income-generating barriers (unpalatable crops with a market value), pollinated by the bees occupying beehive fences, not only add to the protection of the palatable crops but also diversify the income of the farmers [34]. Softer barriers other than electric fences can also be implemented, such as beehive fences together with intercropping, to lower HEC [34,47]. New research in the field of melissopalynology has revealed how pollen grains stored in the bees' honey, can be used as an indicator for bee foraging behaviour. This technique, when combined with vegetation surveys, can therefore be

used to identify the diversity of plants available to bees within a given area, as well as the distances that bees are willing to travel to forage [75], and could become a valuable tool to assess the general health and biodiversity objectives of the corridor regions. Thus, strategic use of beehive fences at a local scale would not only offer a second barrier next to unpalatable crops, but they would also function as alternative income streams—the bees would pollinate the produce and could be strategically used as biodiversity indicators. At a much larger scale, in crop-raiding hotspots identified through tracking data and reported information via RRUs, farmers can be encouraged to only farm with viable unpalatable crops with high market values and yields. With the sale of these ‘elephant-friendly products’, staple food sources could be bought where the conflict risk is low [76]. Irrespective of the scale at which HEC mitigation is being offered, assistance should be offered to communities to encourage a switch to income-generating softer barriers where needed by either implementing buy-back schemes or helping with transport to obtain elephant-palatable staples that may be grown outside of conflict areas.

The income-generating soft barriers being proposed here represent a longer-term, more proactive strategy to decrease conflict over time. However, this should not distract from the need for a short-term reactive RRU to ensure human safety. After a 12-month assessment of the RRU, the overall HWC and HEC reports had doubled in the second half of the one-year study period, which can be attributed to a greater awareness in reporting due to the presence of the RRU operating on the landscape. Changing weather patterns could also be driving elephants to range over larger areas as elephants are known to expand their range during the wet season [77,78]. As elephants become accustomed to breaking out of formerly fortified areas, such as the south of KNP, more elephants are expected to follow the trailblazing individuals over time [67,79]. Nevertheless, the RRU experienced a decline in actual conflict events and concurrently became more successful and experienced at mitigating over time. As the RRU also educated and empowered the communities they were protecting, the farmers readily took on the responsibility to ensure their own safety after training in the mitigation techniques. We propose that the initial strategy to address HEC at landscape scale along the length of an elephant corridor would involve satellite tracking of elephants over time and having RRUs run concurrently with getting farmers in high-conflict areas to adopt alternative crops with a high market value.

## 5. Conclusions

This work will contribute to the ecological processes that propagate the coexistence of elephants, their habitat, and people. If elephants are to survive, we need scientific knowledge and an intimate understanding of their movements and spatial requirements in combination with understanding the socio-economic needs of the people that share the landscape with elephants. This is particularly necessary where vital corridors have been identified and within which we can strive towards innovative ways to make people’s livelihoods compatible with conservation outcomes.

The three phases presented here form part of a longer-term strategy to increase the tolerance of people that occupy the corridor areas. By understanding elephants’ movements and ensuring food security and human safety, farmers’ tolerance will increase. Social surveys, after earmarking suitable unpalatable crops through cafeteria-style experiments and conducting the necessary research on market values and yields, then need to be conducted before the implementation of alternative crops that have never been propagated before so that changes in farmers’ attitudes can be monitored over time. Once softer income-generating barriers such as elephant-unpalatable crops with a market value, potentially combined with beehive fences, start offering lucrative alternative income, thereby offsetting any potential losses or supplementing existing income, people will realise that living with wildlife can be a bonus and not a burden.

Elephants moving across human-dominated landscapes depend on places where they can hide from people during the day, and these are often characterized by vegetation of a specific height and stem density (unpublished data, Elephants Alive). Thus, creating

vegetation ‘stepping stones’ [80] functioning as a mosaic of woodlots over time should be implemented as additional income both locally and internationally as part of a carbon credit system, because elephants play an important role in combatting global climate change [81,82]. Elephants moving along corridors also represent crucial seed-dispersing agents in the larger landscape [83]. Established corridors thus offer valuable employment opportunities in the long term either to women as a part of spatially explicit tree planting schemes or to both men and women in terms of patrolling corridors to ensure the safety of both wildlife and people [84]. Within an integrated and holistic approach of TFCAs linked by functioning corridors, bioregions and biosphere will be realized.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15010085/s1>, Figure S1: Map showing the accumulated data of 55 male (blue) and 18 female (orange) elephant in the APNR from 1998 to 2022. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)); Figure S2: Map showing the accumulated data of seven male elephants collared in Eastern Kruger from 2006 to 2010. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)); Figure S3: Map showing the accumulated data of six male (blue) and six female (orange) elephant collared in the Northern Kruger (Pafuri) from 2008 to 2015. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)); Figure S4: Map showing the accumulated data of 13 male (blue) and six female (orange) elephants collared in the LNP from 2016 to 2022. The black trajectory is from the one elephant male that was collared in Banhine in 2019. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)); Figure S5: Map showing the accumulated data of 20 male (blue) and two female (orange) elephants outside the protected areas from 2018 to 2022. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)); Figure S6: Map showing the accumulated data of six female (orange) elephants collared within Maputo National Park from 2018 to 2022. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow



flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: <https://wopr.worldpop.org/?MOZ/Population> (accessed on 11 October 2022)); Figure S7: The electivity indices calculated per elephant during the morning sessions (a) and afternoon sessions (b); Table S1: Output from the General Linear Mixed Model investigating the electivity index in relation to the different crops for two semi-habituated elephant bulls. Significant fixed terms shown in bold; variance ( $\pm$ SD) reported for random terms (in italics); Table S2: Post-hoc pairwise contrasts for significant interaction terms from the generalised linear mixed model presented in Table S1. Results are averaged over the levels of morning and afternoon session.

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