The decline of the Knysna elephants: Pattern and hypotheses

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Understanding and identifying drivers of local population declines are important in mitigating future risks and optimising conservation efforts. The Knysna elephants have, after being afforded protection since the early 1900s, declined to near extinction today. We propose three hypotheses as to why the Knysna elephant population declined. The refugee hypothesis suggests that anthropogenic activities forced the elephants to take refuge in the forest and that the low-quality food acted as the primary driver of decline. The illegal killing hypothesis suggests that the elephants adapted to the forest and its immediate fynbos habitat, with the decline being a consequence of illegal kills. The stochastic founder population hypothesis postulates that the population size and structure left it vulnerable to demographic stochasticity. We critically reviewed available evidence for these hypotheses and found that, although the historical elephant range decline most likely resulted through the refugee hypothesis, the weak demographic and life-history information limits elimination of either of the other hypotheses. We touch on the implications for decision-makers and draw attention to information requirements.

Significance:

- We highlight the knowledge and management challenges which exist for small, threatened populations of which long-term demographic data are sparse.
- We provide the first unbiased evaluation of multiple drivers that may have caused the decline of the Knysna elephants.

Introduction

African elephants, *Loxodonta africana*, are declining across the continent, largely because they are poached for their ivory.[1] In contrast to continental trends, elephant populations in South Africa have increased in recent years.[2] The Knysna elephants, however, are an anomaly. They are the most southern group of elephants in Africa, the only remaining free-ranging elephants in South Africa and represent one of four relict populations in the country.[3] This small population failed to flourish after official protection was afforded in 1908, and its chances for persistence are of concern. Here we review the history of this population and develop and explore hypotheses that may explain why this small population failed to recover after protection.

Based on an estimated 3000 elephants that roamed the Cape Floristic Region in pre-colonial times[4], it is likely that about 1000 elephants occupied the Outeniqua–Tsitsikamma area[5]. Between 1856 and 1886, Knysna experienced a marked influx of people and a boom in development which increased human–elephant conflict, often at a cost to the elephants.[6] During the late 1800s, an estimated 400 to 500 elephants lived in the area[7], but by 1900, only 30–50 individuals were left[3].

During the early 1900s, attitudes shifted from regarding the elephants as a nuisance towards favouring them as local assets.[6] Since then, the question of how many elephants are left in the Knysna forest has prevailed among conservationists, scientists and the public. Numerous survey attempts followed, often accompanied by suggestions on how to recover the population.[7-12]

Management of this population is challenging if the cause of the decline is not clear.[13] A key question is thus, why has the population declined even after official protection since 1908?[9,11,14-17] We propose three hypotheses for the decline. The refugee species hypothesis suggests that human disturbance and encroachment displaced the local elephants from other more optimal habitats into poor-quality habitats of the forests and its surrounding fynbos.[18] The decline then resulted from a limitation of good-quality food.[17] The illegal killing hypothesis suggests that the decline resulted from illegal killing.[11,19] The stochastic founder population hypothesis suggests that the founder population's small size and its structure lead to demographic stochasticity[13] that significantly constrained recovery.

Here we review evidence for and perceptions around these three hypotheses. In addition, we discuss information gaps and the management implications of our findings for decision-making on the future of the Knysna elephants.

The refugee hypothesis

Refugee populations are separated from optimal habitats and are confined to suboptimal habitats. This in turn leads to decreased fitness and smaller populations.[18] The Knysna elephants are candidates for refugee status based on their decline in range, fitness and density.[18]

Researchers have suggested that human settlement and agricultural development taking place in the more open areas confined the southern Cape elephant population's historical range to the southern Cape forests.[17,20,21] As early as 1755, travellers in the southern Cape noted the ongoing shooting of the elephants, which subsequently resulted in the elephants seeking refuge in the forests in the Tsitsikamma area.[22] This record implies that these elephants chose the forests as they provided safety from human disturbances, rather than for nutritional and other life-history needs.

The effects of human disturbances on elephant ranging, movement and distribution patterns and behaviour elsewhere illustrate how elephants avoid such disturbances[23-26], which lead to declines in elephant ranges. Such populations remain fragmented within their original distribution range, often in suboptimal habitat that may lead to decreases in fitness.[18]

Here we review available evidence relevant to the refugee concept for the Knysna elephant population. We focus on the historical range decline followed by habitat and resource quality as limits of persistence for a refugee elephant population. We also use a once-off reintroduction of elephants as a case study to evaluate the refugee hypothesis.

Safety – historical range decline

The refugee concept suggests that the range of the Knysna elephant population declined from them living in historically open areas to being confined to the forest and its immediate surrounding fynbos habitat. Genetic evidence illustrates that the Knysna elephants once belonged to a single South African population[27], which ranged widely across South Africa from the Cape Peninsula to Limpopo[3,20]. This large historical population occurred in eight different biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket and Forest.[28] Today, the Knysna elephants have access to only two habitat types – the afro-temperate forest and immediate surrounding fynbos. Their modern-day range, about 185 km^2 in size, spans the fragmented afro-temperate forest which occurs mostly on the footslopes of the Outeniqua mountain range, interspersed with fynbos and commercial pine plantations.

Historically, elephants occupied open areas of varied habitat types outside of the southern Cape afro-temperate forests. Elephants were observed between Mossel Bay and George in 1497 by Vasco da Gama, in 1601 by Paulus van Caerden[29] and between 1773 and 1776 by other travellers[30]. Local farmers and residents regularly reported elephant sightings east of George in the late 1800s[6] with records at Wittedrift (north of Plettenberg Bay) dated 1782 and 1816[29]. Further away, in the Little Karoo, local newspapers[31] reported a 'troop' of elephants barring the road to the Uitenhage Ostrich Farming Company in 1883. Further east, in the Langkloof, Sparrman recorded elephants close to Humansdorp in 1775, as did Rev C.I. la Trobe in 1816.[29]

Increases in human settlement and population growth, the growing ivory trade, and crop protection exterminated most of South Africa's elephant population between 1652 and 1870.[3] Demand for ivory as well as habitat transformation were the main driving forces for the southern Cape elephants' demise in the 19th century.[32] The expulsion of elephants from open areas outside the southern Cape forests[6,15,17,33] started taking place in the late 1700s[29]. The pressures and dangers that existed for the elephants on the perimeters and in neighbouring areas to the Outeniqua (Knysna) and Tsitsikamma forests were ongoing during the 18th century. Anders Sparrman wrote in 1775 of the continuous shooting of elephants in the George and Knysna areas[29] while Le Vaillant recorded elephant pitfalls at Kaaimansgat, east of George, in 1782[30]. This small population survived most likely because hunters had difficulty in finding them in the forest terrain.[29] These historical accounts suggest that elephants primarily moved into the forest areas to avoid human disturbances.

Food quality

A second element of the refugee hypothesis is that confinement of Knysna elephants to suboptimal habitats affected their fitness and that ultimately led to their decline. The range of modern-day Knysna elephants covers afro-temperate forest, fynbos and commercial pine plantations growing on nutrient-poor soils derived from sandstone.[34] Several studies have attempted to evaluate the link between low nutrients of forest plants and the Knysna elephant decline[15,17,21,35], but with no conclusive support or rejection of the suboptimal habitat concept.

Key studies focused on Knysna elephant faecal and browse mineral contents[15,21,35] and faecal N/C ratios[17]. These studies hypothesised nutrient and mineral deficiencies as the primary drivers of the decline in elephant numbers. However, these assessments were lacking knowledge of what constitutes diet deficiencies that affect fitness for wildlife as most of this information is available mainly for domestic and laboratory animals.[36] Koen and colleagues[15,21,35] used nutrient limits set for domestic livestock for the Knysna elephant diet assessment, but acknowledged that livestock nutrient limits are unreliable standards for assessing elephant diet deficiencies.

Because of their simple digestive systems, which have relatively low digestive efficiency as a result of fast passage, and their low metabolic rate per unit of body mass, elephants can tolerate lower quality forage than smaller herbivores can, but require a higher abundance of plants.[37] Olff[38] illustrated that, on a global scale, the occurrence of elephant and Cape buffalo was independent of plant-available nutrients and dependent on plant-available moisture. In east and southern Africa, megaherbivore abundance increased with rainfall, but was independent of soil nutrient status and it was suggested that megaherbivores are therefore limited by food quantity and not quality.[39]

A second approach to quantify potential Knysna elephant diet deficiencies and consequences for fitness focused on comparing browse and faecal nutrient and mineral contents with those of fit elephant populations such as those of the Addo Elephant National Park (AENP) and Kruger National Park[15,17,21], both of which have a higher soil nutrient status. Alternatively, more insightful comparisons would be between the Knysna population and healthy, growing populations occurring in other areas of low habitat quality or soil nutrient status e.g. in the Kalahari-sand region of Hwange National Park in Zimbabwe[40] or Tembe Elephant Park in KwaZulu-Natal, South Africa[41]. Sodium concentrations are extremely low throughout elephant ranges[40,42] which suggests that elephants may require much lower concentrations of sodium to maintain condition and survival than commonly perceived[43].

Finally, a key mechanism associated with the low N/C ratio in the Knysna elephant faeces, results from the lack of C4 grasses in the Knysna elephants' forest range.[17] In areas where African elephant populations have access to woodlands, forests and grassland habitats, they prefer grass species during the rainy season and browse species during the dry season.[44,45] Isotope records in historical and prehistoric elephant bones originating from areas in the Western Cape, however, illustrate that these elephants utilised much less C4 grass than elephants in the Kruger National Park, suggesting that C4 grasses cannot be considered a limiting factor in elephant distribution.[46] This finding implies that the lack of C4 grasses in the Knysna elephant range may not be an indicator of suboptimal habitat.

The failure of an introduction of some elephants sourced from Kruger National Park to the Knysna forest was linked to the low quality of the local food[17], which would support the suboptimal habitat concept and refugee hypothesis. This link was based on a prediction that the introduced elephants would bond and remain with the native elephants in the forest. The Kruger elephants, however, rejected the forest habitat and spent most of their time on neighbouring farmland.[16,17] It was suggested that they did so in search of more nutritious food.[17] However, more recent knowledge on elephant behaviour and translocations suggests otherwise (Box 1).

Calf mortality may reflect the outcomes of nutritional stress. If the habitat quality in the Knysna forest and fynbos is inadequate as suggested[15,17,21,35], it may have contributed to the high calf mortality observed. Female elephants under nutritional stress have been shown to have calves which have lower survivorship.[51] A high calf mortality was reported for the Knysna population in the 1900s.[7-10,52,53] Phillips[7] noted for the Knysna population that several calves died between 1922 and 1925 and dead calves were found in 1937, 1942[9] and in 1968[16]. Calf mortality of the Knysna population was estimated to be between 60% and 80%, compared with 7.5% for the AENP population.[53]

Historical records support the refugee hypothesis by illustrating how people forced the southern Cape's elephants out of open areas and into the forest and its surrounding fynbos. A link between the Knysna elephant decline and habitat quality could, however, not be made with the information available.

Box 1: Failed elephant introduction to the Knysna forests

Three cull-orphaned elephant cows aged 7 to 9 years from the Kruger National Park were introduced to the Knysna forest in 1994 to supplement the Knysna elephant population.[16,17] They were released after spending 2 months in an enclosure, and within 1 month the youngest cow had died of stress-related pneumonia.[16,17] The two remaining cows moved to more open fynbos areas within days after their release. Although they made contact with a native elephant cow, after about 7 weeks of following her, they separated and moved back to more open areas, adjacent to the forest area in which the native cow remained. Over the course of 5 years they increasingly moved into open and adjacent farmland areas[17]. In 1999, they were relocated to a private reserve because the responsible authorities were unable to keep them off farmlands.

Whilst still in Knysna, the introduced elephants' faecal N/C ratios were compared to those of the native elephants.[17] The native elephants had low dietary N/C ratios compared to the introduced elephants and it was concluded that this could be the reason for the Knysna elephants' poor reproductive performance as well as the Kruger Park orphans' rejection of the forest habitat. This conclusion was based on available knowledge of elephant social behaviour in natural populations that would predict that the introduced cows would bond and remain with the native cow. It was therefore speculated that the introduced cows separated from the older native cow in search for more nutritious habitats outside of the native elephant forest range that matched their source habitat, in support of the suboptimal habitat concept and refugee hypothesis.

Recent findings, however, illustrate how animals move away from release sites and choose to settle in habitats familiar to their natal habitat[47], in some cases even when the new chosen habitat is of lower quality than the release site[48]. This behaviour is referred to as natal habitat preference induction (NHPI) in which an individual's experience with a natal habitat shapes its future habitat preference.[47,48] NHPI implies that reintroduction and translocation operations may be more likely to succeed if animals are released in habitats comparable to those in which they were raised.[47,48] Elephants have displayed similar behaviours by rejecting their release sites and moving away to settle in a habitat further away, and in some cases even travel back to the source habitat.[49,50] Pinter-Wollman[49] reported female elephants leaving their social group behind at the release site and walking back home, with only their youngest calves in tow.

Rejection of release sights may be perpetuated at locations in which animals have had aversive experiences, as they may associate local cues with negative experiences from their time in captivity, and therefore are more likely to reject habitats containing those cues after release.[47] The cows who were introduced to Knysna experienced a traumatic second immobilisation and collaring operation while in their forest enclosure[16] and the death of one of their group's members whilst in the forest, straight after release. Their rejection of the Knysna forest release site, and subsequent separation from the unrelated native cow, may therefore not have been as unpredicted as suggested[17], and may have been driven by factors other than food quality.

The illegal killing hypothesis

The illegal killing hypothesis suggests that elephants were adapted to the forest and fynbos habitats, and their decline resulted from illegal killing.[11,19] Predictions of forest adaptation focused on attempts to describe the Knysna elephants as a different sub-species.[11,54] Lydekker[54] assigned the Knysna elephant as *Elephas africanus toxotis*, based on comparisons of ear-shapes of specimens from Knysna and AENP, but later discovered that the museum specimen labelled as a Knysna elephant, was in fact a specimen from the Addo area[14]. Carter[11] speculated that although these elephants are *L. africana* and not a sub-species, their 'habits appeared to have become modified for existence in the forest'. This perception of forest adaptation remains, and media, blogging sites and local tourism and property agencies' brochures refer to Knysna's forest elephants. There is, however, no published evidence of genetic, behavioural or morphological adaptations of the Knysna elephants to forest habitats.

Official protection was realised when the Knysna elephants were declared Royal Game in 1908.[17] In 1920, authorities issued Major P.J. Pretorius with a permit to shoot one elephant for scientific purposes – a hunt which ultimately caused the death of five elephants.[16] In 1971, an old bull known as Aftand was shot by forestry officials because of his crop-raiding behaviour on smallholdings.[16] Apart from this shooting, there were no elephant shootings officially reported after 1908.[17]

Although the elephants roamed mostly on forestry land, forestry officials had no authority to protect the elephants when they moved off forestry land, even after they were declared Royal Game.[53] Speculations claimed that the Forestry Department harboured a negative attitude towards the elephants and that 'the total destruction of the elephants was advocated in some quarters' during the 1920s because of the considerable damage they caused to State Blackwood plantings.[8] Later, Carter[11,55] reported the killing of four elephants between 1940 and 1970 and found the remains of a young elephant that had apparently been shot.

Several advocates of the illegal killing hypothesis argued that protection required more effort than mere declaration of protection, such as physical protection on the ground or fencing the elephants.[10,11,14,52,53] The Knysna elephants' crop-raiding excursions[10,11,52,53] often made headlines[56-59]. A major concern was that landowners shot at the elephants to chase them off their land and that these injured animals died only later of their injuries.[9,11] In 1976, a local newspaper[60] reported several requests to the Knysna Department of Forestry to destroy a damage-causing elephant. In addition, indirect and long-lasting effects of traumatic events, such as poaching or attempted poaching, have been reported elsewhere[61] and include social fragmentation, potentially higher calf mortalities and lowered reproductive success.

Similarly, it was suggested that mere declaration of protection of the AENP elephants, with the proclamation of the park in 1931, did not lead to a recovery of the population as wandering elephants were shot on neighbouring farms.[62] Reduction in elephant mortality and population recovery was only realised by erecting a boundary elephant-proof fence 23 years after park proclamation.[53,62] Whitehouse and Hall-Martin[63] identified the loss of the founder population's sexually mature bulls, between 1932 and 1940 as another factor that caused the initial slow growth rate of AENP's elephant population. The remaining young bulls reached sexual maturity by 1946, after which the population started its recovery.[62,63]

The available evidence highlighted here does not allow for a robust evaluation of the illegal killing hypothesis. However, it is likely that some illegal killing contributed to the slow demise of the Knysna elephants.

The stochastic founder hypothesis

Demographic stochasticity is a fluctuation in a population's growth rate caused by chance independent events of individual mortality and reproduction.[13,64] With regard to extinction risk, small populations are particularly vulnerable to demographic stochasticity.[13,64] The stochastic founder hypothesis suggests that after protection, the small population size and structure of the Knysna elephants exposed them to demographic stochasticity.

Between 1920 and 1970, it was estimated that four cows of breeding age were present in the Knysna elephant population.[17] Forestry scientists argued that more than the observed two calves should therefore have been present if breeding was normal and suboptimal habitat did not reduce fertility.[17] However, available information on the Knysna elephant population size, structure and individual life histories is vague or lacking. Between 1920 and 1970, a number of surveys recorded only one or two adult cows[8,9,52], while Carter's[11] survey concluded the presence of three adult cows (Table 1). The assumption of four sexually mature cows present during this time[17] may therefore be an overestimate. In addition, even if there were four adult cows between 1920 and 1970, not all of them may have been fertile.

The differences between the Knysna and AENP elephants' founder populations lend credibility to the stochastic founder population hypothesis by illustrating how the Knysna population's small size and structure likely enhanced chance events that determined its fate. The Knysna elephant founder population consisted of 1–4 adult cows of unknown reproductive status, whereas the AENP founder population consisted of six sexually mature adult cows.[63] By 1935/1936, eight sexually mature cows were present and eight calves were born during this time.[63]

Another difference between the populations is that the AENP cows seemed to have existed as one social group[63] whereas the Knysna elephants were mostly sighted in small groups, containing only one adult cow and her offspring[8,11,19,52]. Such minimal group sizes may have contributed to the high calf mortality reported for the Knysna population.[7-10,52,53] Elephants live in matriarchal societies consisting of family units of related adult females and their calves[66,67] in which

Table 1: Knysna elephant population size estimates from the late 1800s to 2007

Year	Elephant number	Elephant group structure	Nature of estimate/survey methods	Source
1876	400–500			Phillips, 1925[7]
1902	30–50		Forestry Department records	Dommisse, 1951[8]
1904	20		Forestry Department records	Dommisse, 1951[8]
1908	20		Forestry Department records	Dommisse, 1951[8]
1910	17	15 'large' and 2 'small' elephants of unknown sex	Forestry Department records	Dommisse, 1951[8]
1914	13		Forestry Department records	Dommisse, 1951[8]
1916	10–12		Forestry Department records	Koen, 1984[35]
1918	15/16		Forestry Department records	Koen, 1984[35]
1920	7–13		Forestry Department record less 5 killed by Major Pretorius	Dommisse, 1951[8]
1921	12		Forestry Department records	Koen, 1984[35]
1925	12	6 bulls, 4 'large' cows and 2 calves of unknown sex		Phillips, 1925[7]
1931	13		Forestry Department records	Koen, 1984[35]
1951	4	2 adult bulls, 1 cow and 1 young bull	Bernard Carp Expedition	Woods, 1952[9]
1957	7	4 adult bulls, 1 old bull, 1 adult cow and 1 calf	Cape Department of Nature Conservation Expedition (Fraser Expedition)	Woods, 1958[65]
1958	3	2 adults of unknown sex and 1 female calf	Wildlife Society Expedition	Greig, 1982[14]
1968	7		Wildlife Society Expedition	Greig, 1982[14]
1970	11	3 old bulls, 2 young bulls, 3 cows, 1 adult of unknown sex, 2 calves	Wildlife Society Survey	Carter, 1970[11]
1970	13	3 old bulls, 2 adult bulls, 1 young bull, 1 old cow, 4 adult cows, 2 calves	Forestry Department records	Koen, 1984[35]
1974	6		Forestry Department records	Koen, 1984[35]
1976	4		Forestry Department records	Koen, 1984[35]
1977	6		Stroebel family records	Koen, 1984[35]
1979	4		Forestry Department records	Koen, 1984[35]
1981	3		Forestry Department records	Koen, 1984[35]
1989	4		Forestry Department records plus 1 (birth of calf)	Mackay, 1996[16]
2007	5	5 cows	Faecal DNA genotyping survey	Eggert et al., 2007[12]
2018	1	1 cow	Camera trap survey	Moolman et al., 2019[75]

allomothering enhances survivorship[68]. One can therefore speculate that if there were sexually mature bulls and cows present between 1920 and the late 1900s, and the cows were mostly split into small groups consisting of an adult cow and her calf, the lack of allomothering may have played a significant role in reduced calf survival. Additionally, small group sizes may cause higher stress levels in African elephant cows which subsequently could lead to lowered reproductive outputs.[61]

It is highly likely that demographic stochasticity played a role in the inability of the small founder Knysna elephant population to recover after protection had been afforded.

Synthesis

Historical accounts illustrate how the southern Cape elephants were decimated by humans in the more open areas outside the afro-temperate forests, with the survivors taking up refuge in the forests during the late 1700s and 1800s. The elephant range thus decreased from a diverse array of habitats to only two habitat types: the afro-temperate forest and the surrounding fynbos. Ever-increasing human development eventually confined these elephants to the forests and isolated them from previously available habitat types. Range restriction – being one of the predictions of the refugee hypothesis – was thus realised.

Why the small surviving group of elephants in the Knysna forest never recovered, even after being afforded protection through their declaration of Royal Game in 1908, is less clear. Most of the scientific undertakings attempted to answer this question by linking habitat quality and population fitness by using density estimations obtained during the 1900s. Apart from the unreliability of the Knysna elephant density figures[52], density can be a misleading indicator of habitat quality without demographic data to validate it[18,69]. The importance of demographic data in understanding processes that influence elephant populations has been clearly illustrated.[70] In addition, habitat quality has been assessed in terms of food quality only, and other habitat aspects, for example, the availability of areas for socialising, that may be important to elephant, have been ignored. In light of this, we argue that the published works to date are too weak to link habitat quality to fitness, and the refugee hypothesis can thus not be eliminated.

Records of conflict between humans and the small surviving group of elephants on land neighbouring the Knysna forests suggest that landowners occasionally shot at elephants. In addition, some locals were of the opinion that the Forestry Department, in charge of the elephants' protection, harboured a negative attitude towards the elephants at the time. Besides the recorded Major Pretorius hunt, which saw five elephants killed in 1920, and the killing of a bull in 1971 by the Forestry Department, no records of killings are available. In addition, once again, demographic data are lacking. The illegal killing hypothesis can therefore not be eliminated.

The comparative records of the AENP and Knysna elephant founder populations' group structures reflect on potential stochastic effects. The small size and fragmented structure of the founder population may have played a significant role in the population decline, exacerbated by human disturbances such as illegal killings. We can thus not eliminate the stochastic effect hypothesis.

The results suggest that the failure of Knysna elephants to recover result from synergistic mechanisms.[71] After the decimation of the southern Cape population in the 1700 and 1800s, the surviving population experienced a range restriction and took up refuge in the forests. Recovery of this refugee population was challenged because the habitat was sub-optimal. Conflict with humans, including illegal killings, most likely imposed an additional stressor on recovery. It is likely that small population stochastic effects accentuated the consequences of illegal killing and suboptimal habitats.

The Knysna elephant population exhibits similarities to other wildlife populations identified as refugee populations.[18,72] Individuals of these refugee populations elsewhere had no access to historically optimal habitats and were subsequently managed and confined to suboptimal habitats. In these cases, population fitness was reduced with consequent declines in numbers. A major conservation risk is when authorities actively manage such populations under the false perception that the focal population occupies suitable habitats. Such perceptions restrict the development of appropriate mitigating management strategies.[18]

Determining the Knysna elephants' refugee status would therefore be a crucial and responsible consideration for their future short- and long-term management planning. The challenge, however, is the limited demographical data available as illustrated throughout this review. To overcome this challenge, we propose that an alternative approach be to investigate how the southern Cape elephants used the landscape before human barriers denied them the choice and access to more suitable habitat. The estuarine lake system, which has a higher soil nutrient status compared to the forest and fynbos habitats[73] and which occurs along the southern Cape coast only 15–30 km south of the elephants' current range, could potentially be a more suitable habitat. These lake systems became cut-off from the current elephant range by farmlands, a national highway and towns. A scientific investigation into the historical southern Cape elephant population's seasonal habitat use patterns and potential diet shifts could be undertaken by analysing the stable isotopes of elements such as carbon, nitrogen and oxygen along ivory growth trajectories[74] and the Knysna elephant population refugee status can thereby be robustly tested.

Management implications

The synergistic mechanisms of decline that we highlight have three implications for management. If elephant presence is desirable in the Knysna forest, the recovery of elephants requires innovative elephant reintroductions from elsewhere, as the forests have been isolated from potential elephant source populations for a long time and constructed barriers will prevent natural colonisation. A primary challenge is how to reintroduce elephants given the failure of the previous reintroduction.[16,17] However, reintroductions will overcome the predictions of the stochastic small population hypothesis. Furthermore, the persistence of elephants will require regular supplementary introductions to overcome the predictions of the suboptimal habitat element of the refugee hypothesis. Additionally, the availability of optimal habitat types, close to the Knysna elephant range, and the possibilities of range expansion, should be investigated. In addition, authorities will need to implement effective anti-poaching and law enforcement programmes to overcome the predictions of the illegal killing hypothesis.

Authors' contributions

L.M.: Conceptualisation, data collection, writing the initial draft, writing revisions, preparing the submitted draft. S.M.F.: Conceptualisation, writing revisions. A.G. and D.Z.: Writing revisions. G.I.H.K.: Conceptualisation, writing the initial draft, writing revisions, project leadership.

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