Evaluation of the Elephant Immunocontraception Program at Hluhluwe-iMfolozi Park, South Africa

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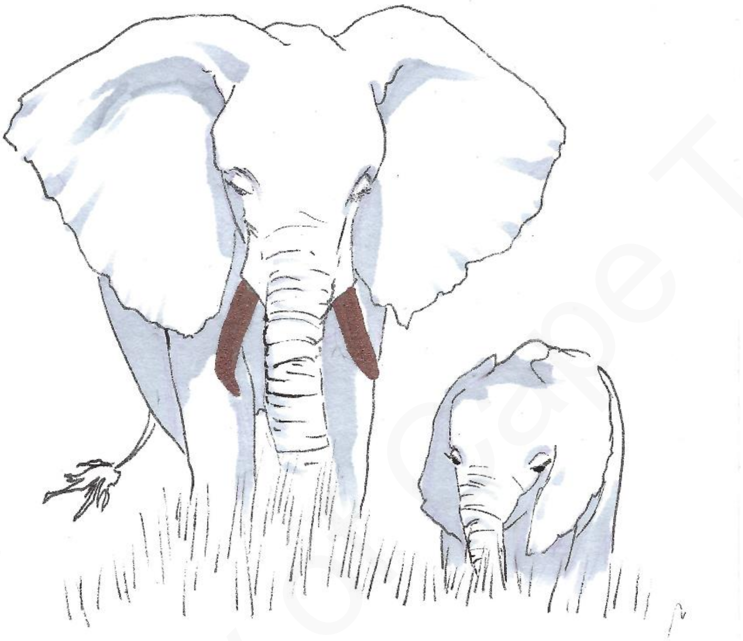

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Abstract

Managing African savannah elephant (*Loxodonta africana*) overpopulation in enclosed reserves is currently a major issue in southern Africa due to the potential negative impact of high elephant density on biodiversity. Immunocontraception of elephants has been proven to be an effective method of population control on small reserves with populations of less than 250 individuals, but there is uncertainty regarding its application in larger populations. South Africa's Hluhluwe-iMfolozi Park (HiP), with over 700 elephants, started a porcine zona pellucida (pZP) immunocontraception program in 2014 with the aim of reducing the population growth rate from 7.7% (2014-2016) to between 2 and 3%, but the program has not yet been formally assessed. In this study, I aimed to (1) evaluate the effectiveness of the 8-year program at the park, by measuring its effect on the population growth rate, and (2) explore potential factors affecting contraception efficacy. The proportion of infants within breeding herds was used to estimate growth rate. The proportion was determined using on-the-ground observations of breeding herds collected during six weeks of fieldwork in October and November 2022 and compared to previous years. The infant proportion in breeding herds and population growth rate were estimated as 0.156 and 7.16% respectively, only slightly less than the 2016 values of 0.167 and 7.7%. A critical assessment suggests that the key reasons for reduced contraception efficacy are consistency of individuals being contracepted and population coverage of breeding-age females. Approximately 75% of all reproductive-age females in the park are associated with collared herds (GPS collars are used to help locate herds for darting), but herd size variation due to fission-fusion social dynamics limited the role of collars in improving efficacy. An average 14% of reproductive-age females were missed each year due to failure to locate some collared herds. Despite high annual coverage of females in any one year, the estimated probability of a reproductive-age female being darted consistently (every year) between 2018 and 2022 was estimated at only 0.355 due to multiplied probability effects. Records also suggest that HiP has been significantly under-darting every year, except for 2022, due to inaccurate darting targets. That this program has not reduced the growth rate as planned suggests that the use of porcine zona pellucida (pZP) immunocontraception in larger elephant populations may be limited by important practical aspects of implementing and maintaining the number of contracepted females. Further research is required to assess its potential at the scale of populations such as HiP's elephants, which currently totals an estimated 1100 individuals. Given the management goals of the program, HiP will need to consider whether to continue the program with adjustments to improve efficacy or explore other options to manage overpopulation, especially in the short term.

Keywords: *Loxodonta africana*, immunocontraception, porcine zona pellucida, overpopulation

Introduction

Status of African savanna elephants (*Loxodonta africana*)

The African savanna elephant, now defined as a separate species from the African forest elephant, (*Loxodonta cyclotis*) has been listed as endangered on the IUCN Red List since 2020 due to the major decline in its population in the last century (Gobush et al., 2022; Roca et al., 2001; Rohland et al., 2010). As recently as 1979, the population in Africa numbered an estimated 1.3 million, but as of 2015, only an estimated 415 428 elephants remain across the continent (Douglas-Hamilton, 1980; Thouless et al., 2016). This rapid decline has primarily been driven by extensive poaching for ivory, peaking in the 1970s and fuelled by the availability of automatic rifles and rising ivory prices in the global marketplace (Wittemyer et al. 2014; Douglas-Hamilton, 1987; Milner-Gulland & Beddington, 1993). The Convention of International Trade in Endangered Species (CITES) attempted to bring this under control in 1989 when the international trade of African elephant ivory was banned and, as a result, some populations have stabilised; nevertheless, poaching for ivory continues to affect elephant populations across most of the continent (Chase et al., 2016). Central, West, and East Africa, three of the four elephant regions on the continent, have seen a major surge in poaching since 2006, and many of their already vulnerable populations have been heavily impacted (Thouless et al., 2016; Wittemyer et al. 2014).

While poaching continues to garner extensive international attention, habitat loss and fragmentation have also played major roles in the decrease in African elephant numbers. Agricultural expansion throughout Africa has taken over much of the species' natural habitat with elephants now occupying only 15% of their historic range (Chase et al., 2016). As a result, human-wildlife conflict (HWC) has increased, involving crop raiding, property damage, and loss of lives on both sides (Knickerbocker & Waithaka, 2005). In addition to population declines, HWC has led to an increase in fencing and so has reduced the movement of elephants through the landscape (Osipova et al., 2018).

Southern Africa presents a very different scenario to the rest of the continent. Several countries in this region are experiencing population declines, e.g., Angola, Mozambique, and Zambia, but most populations in Namibia, South Africa, and Zimbabwe are stable or increasing, especially within well protected fenced reserves (Armbruster & Lande, 1993; Thouless et al., 2016). As a result, 70% percent of all African elephants are now found in southern African reserves, representing 42% of the species' total extant range (Thouless et al., 2016). This has led to parks facing the relatively new problem of elephant overpopulation. Even though the recovery of elephants is positive for the overall population, negative impacts at a local scale have led to heated debates regarding elephant population management (for further details on these see (Dickson & Adams, 2009)).

Wildlife population management, such as that of elephants, is based on the intricate balance between animals, humans, and habitat (Decker & Purdy, 1988; Giles, 1978). The interplay between these three elements determines the need for animal population control. If the impact of an animal species on the habitat and/or humans is seen as negative, and the consequences are significant enough, then population control may be necessary. Management techniques can include habitat manipulation (e.g., provision of water sources), mechanical (e.g., fencing), behavioural (e.g., deterrents), biological, genetic, direct population control, which includes culling and translocation, and contraception (Saltz et al., 2021). Each technique has its own advantages and disadvantages and ethical considerations which depend on the local context and species.

Elephant overpopulation and its consequences

In response to poaching and HWC, the majority of elephants in southern Africa are confined to protected reserves (Thouless et al., 2016). This has benefits for anti-poaching and tourism, and many populations have done well, but elephants are a migratory species and with large home range requirements. Both breeding herds and bulls roam widely, with recorded home ranges in southern Africa of up to 10 700km^2 and 12 800km^2 respectively, and migrate seasonally across the landscape (Guldemond, 2006). Rainfall, habitat heterogeneity, and water and food availability affect their movement, especially during the dry season when resources are limited (de Beer, 2007; Guldemond, 2006). Fencing significantly limits this natural movement, restricting their home ranges and preventing natural migration and dispersal at both the ecological and evolutionary scale required for the species (Guldemond, 2006; van Aarde et al., 2008). Due to this restriction, their impact on vegetation is highly concentrated, with little to no seasonal variation in distribution to allow for habitat recovery (Pretorius et al., 2019; van Aarde et al., 2008).

Due to their large size and behaviour, elephants have a significant impact on local habitats and biodiversity by influencing multiple ecological processes and patterns, including species composition and distribution, habitat structure, and soil composition, among others, and have been found to be greater drivers of local vegetation change than rainfall (Hayward & Zawadzka, 2010; Kerley & Landman, 2006). As a result, they are widely regarded as both a keystone species (Owen-Smith, 1987; Paine, 1969) and ecosystem engineers (Haynes, 2012; Jones et al., 1994, 1997; Power et al., 1996). At a small scale many of these impacts may be beneficial but are thought to be density dependent, and so become negative when population density increases, such has been found in savannah woodlands, with elephants causing high rates of tree fall and death across sub-Saharan Africa (Cumming et al., 1997; Guldemond & van Aarde, 2008).

As there is no current evidence of density dependent population regulation in small reserves, even at densities of 4 elephants per sq. km, reducing elephant numbers artificially has to be considered, particularly where damage to ecosystems and loss of biodiversity already occurs before the carrying capacity is reached (Gough & Kerley, 2006). This has led to the conclusion that elephant numbers need to be managed within fenced reserves. Whether this conclusion is correct has been a topic of debate for many decades, with some arguing that there is too much focus on the negative impacts of elephants (Guldemond, 2006). Studies have shown that the ‘destructive’ behaviour of elephants can also have positive impacts on the environment, including the creation of refuges for small vertebrates and insects, increasing understory biomass and richness, and improving the quality of browse for other herbivores (Coverdale et al., 2016; Kohi et al., 2011; Pringle, 2008). In addition, the overall impacts of other grazers and browsers are often underestimated (Kerley et al., 2008; O'Kane et al., 2011, 2014; Wiseman et al., 2004). There are also insufficient records detailing the state of habitats before elephant numbers declined, so an accurate baseline to which we can compare is lacking. While substantial changes in the environment are expected after the introduction of a megaherbivore, they should not automatically be considered negative.

In addition to the ecological debate on the negative/positive impacts of elephants, there is also the ethical debate regarding the best management options for populations. The ethics of different elephant management techniques have been discussed extensively since the 1960s, with topics including the decline in Africa's elephant populations and the knock-on ecological impacts, the behavioural impacts on such a long lived, highly social species, and the trade of elephant products (Dickson & Adams, 2009). While the development of contraception may provide a more ethical non-lethal solution to elephant management, it is still a major disruption of biological and ecological aspects of fertility with the potential for physiological and behavioural effects and impacts on welfare; these still need to be considered in a thorough assessment of all options (Kerley & Shrader, 2007; Lötter et al., 2008; Perdok et al., 2007).

Managing elephant populations - methods to control numbers

Management of elephant population numbers can be achieved in three ways: by culling, by removing individuals or groups through translocation, or by reducing birth rates with contraception (van Aarde et al., 2008). Through the 1980's and 1990's culling was the main method of population control across many managed areas in southern Africa, e.g. Kruger National Park (KNP) culled over 14 500 elephants between 1967 and 1996 to maintain their numbers at around 7000 individuals (van Aarde et al., 1999). This number was calculated by local scientists to prevent future destruction of vegetation in the park, but culling was stopped after multiple reviews and debates regarding both the ethics of culling, and that evidence showed adaptive management to be better than a program dictated by population numbers (Carruthers et al., 2008). Despite the significant revenue generated from culling products (potentially over R 5 million for 800 Kruger elephants yearly), the decision to cease culling was made (Grant, 2005; Slotow et al., 2008). Public opinion and the consequent loss of tourism, as well as the CITES ban, has outweighed the benefits of this method for almost all parks in southern Africa, except for the control of problem individuals (Slotow et al., 2008; van Aarde et al., 2006).

In South Africa translocation as a management method has helped to establish the majority of elephant populations, with over 800 elephants transferred to more than 58 reserves between 1979 and 2001 (Garaï et al., 2004). However, this method is not routinely used to manage overpopulation due to insufficient available space and the significant costs involved (Grobler et al., 2008). This might be changing, though, as translocation methods have improved, and the plight of the African elephant brings in more funding, as evidenced by the mass translocation of 520 elephants across Malawi by African Parks (*500 Elephants: An Extraordinary Journey*, 2023), but it is still most likely not an option for most southern African parks.

Reducing population growth rate through contraception

Growth rate of populations is determined by age of sexual maturity, age of first and last offspring, interval between offspring, and mortality (Hauenstein et al., 2022; Mackey et al., 2009). Contraception can effectively decrease growth rate by prolonging the interval between offspring and, in the last few decades, has emerged as an effective management tool to reduce both populations within fenced reserves and free-ranging elephant populations. By reducing the population growth rate, rather than removing individuals from the population, proponents argue that it is a more ethical alternative to culling and potentially an effective tool for longer-term control of population numbers. The use of contraception in wildlife has its origins in the management of domestic and agricultural animals, with surgical sterilisation being commonplace as early as the 15th century, followed by the development of hormonal (chemical) contraception in the 1960's and then immunocontraception in the late 1990's (Lueders et al., 2016). Each method of contraception has its advantages and disadvantages and can be evaluated against the characteristics of an ideal wildlife contraceptive outlined by Bertschinger et. al (2008) (see Table 1).

Table 1. Characteristics of an ideal wildlife contraceptive and evaluation of different methods for elephant population control (summarised from Bertschinger et al., 2008; Kirkpatrick et al., 2011)

	Surgical		Hormonal		Immunological	
	Gonadectomy	Vasectomy	Steroid implants	GnRH super-agonist implants	GnRH vaccine	pZP vaccine
Reversible	No	No	Yes	Yes	Yes	Yes
Passes through food chain	No	No	Yes	No	No	No
Serious known side effects	Yes	No	Yes	Yes	Yes/No	No
Duration	Permanent	Permanent	6-12 months	3 years	5-7 months	12 months
Safe in pregnancy	N/A	N/A	No	No	Yes	Yes
Remote delivery	No	No	No	No	Yes	Yes

Surgical contraception of elephants involves either the removal of the reproductive organs (gonadectomy - castration or ovariectomy) or a part of the reproductive tract (vasectomy or tubal ligation). Gonadectomy has significant physical and behavioural effects, so vasectomy/tubal ligation is generally preferred (Bertschinger et al., 2008). All these procedures are irreversible and require anaesthesia, significant equipment, and a large team of vets and assistants, and are generally seen as too costly, with a high risk for the individual animal, and impractical for widespread use except for small populations (Delsink, 2006; Rubio-Martínez et al., 2014; Stetter et al., 2006; Zitzer & Boult, 2018).

In 1996, hormonal contraception with oestradiol implants was trialled in female elephants in Kruger National Park (Whyte & Grobler, 1998). Contraception was successful with all females still effectively contracepted after 12 months, but there were significant physiological side effects that led to important social impacts. The cows were in oestrus for almost the entire 12 months and so were harassed continually by bulls. This led to the separation of young calves from their mothers and potentially two infant deaths. Hormonal contraception was therefore not trialled again due to being "unacceptable both on humane and ethical grounds" (Bertschinger et al., 2008; Whyte & Grobler, 1998).

Gonadotropin-releasing hormone (GnRH) super-agonist implants or depots are another form of hormonal contraception that work by supressing the hypothalamic-pituitary axis and has a similar effect to gonadectomy (Asa & Moresco, 2019). This method has been used successfully in female cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*), and leopards (*Panthera pardus*), as well as male cheetahs, but it is known to have several negative health and behavioural side effects and implantation is necessary every three years (Asa & Moresco, 2019; Lueders et al., 2016). This method has not been trialled in elephants.

Currently, two types of immunocontraception are available for elephant contraception, the GnRH vaccine for potential use in both males and females, and the porcine zona pellucida (pZP) vaccine for use in females. The GnRH vaccine stimulates the production of specific antibodies against GnRH. These neutralise the GnRH produced by the hypothalamus, preventing the release of stimulatory hormones from the pituitary. In African elephants, the GnRH vaccine has been used successfully to regulate aggressive behaviour and musth in bulls since 2003. Later in 2017, the vaccine was tested as a form of contraception on a group of 11 bulls, two of which were wild (Bertschinger & Lueders, 2018). After 12 months, all 11 bulls were infertile, but there were also significant physical side effects where some bulls became permanently infertile (Bertschinger & Sills, 2013; Lueders et al., 2017, 2018). In females, the GnRH vaccine has been shown to induce anoestrus and therefore prevent pregnancy, but due to the need for regular treatments, it is only practical for captive females. If a long-acting form was produced, the GnRH vaccine would be preferable to the pZP vaccine, as females would not go into oestrus and therefore would not be harassed by bulls at regular intervals (Bertschinger et al., 2008).

Immunocontraception of elephants with pZP: the answer to managing overpopulation?

Immunocontraception with pZP was first developed for fertility control of mammals in the 1980s and is achieved by the production of antibodies by the host individual in response to introduced foreign antigens. These antibodies then block fertilisation as long as the level of antibodies in the blood, i.e., titres, are high enough, which is assisted by combining the antigens with an adjuvant, an ingredient added to the vaccine that helps enhance the immune response of the individual. Immunocontraception only blocks fertilisation, therefore, it does not affect an ongoing pregnancy or natural hormonal cycles and is reversible in the absence of the vaccine. The method was first trialled in wild horses (*Equus caballus*) and has since been shown to be effective in over 90 species including white-tailed deer (*Odocoileus virginianus*) (Kirkpatrick et al., 1997), elk (*Cervus elaphus*) (Shideler, 2000), bison (*Bison bison*) (Duncan et al., 2013), the American black bear (*Ursus americanus*) (Lane et al., 2007), and African elephants (Kirkpatrick et al., 2011).

Mechanism of action

The zona pellucida is a glycoprotein capsule that surrounds all mammalian eggs. When a sperm binds to one of the receptors found on the capsule, a reaction is triggered that allows that sperm to release its nuclear material into the egg. pZP immunocontraception is achieved using porcine zona pellucida proteins derived from pig ovaries (as is standard for most mammals)(Bertschinger et al., 2018). When injected, the immune system produces antibodies to the porcine proteins. The antibodies then bind to the elephant's own zona pellucida capsule receptors and prevent sperm attachment and therefore egg fertilisation. Adjuvants are used to enhance the immune response to ensure that antibody levels remain above the threshold necessary for contraception.

In African savanna elephants, the standard protocol to induce immunocontraception involves an initial darting with 400µg pZP and 0.5ml of Freund's Complete Modified Adjuvant (FCMA), a booster dart 3-5 weeks later with 200µg pZP and 0.5ml of Freund's Incomplete Adjuvant (FIA), and then a repeat annual booster every year thereafter (Delsink & Kirkpatrick, 2012). The 6-week booster 'primes' the immune system and, along with the adjuvants, helps to boost the immune response to the vaccine (Castiglione et al., 2012). There used to be a second 5-7 week booster, but this has since been deemed unnecessary (A. Delsink, personal communication, January 13, 2023).

Elephant immunocontraception programs in South Africa

Elephant immunocontraception programs have now been initiated at over 20 different reserves across South Africa (Bertschinger et al., 2018). The most important programs in terms of the establishment of pZP contraception efficacy of wild elephants in fenced reserves are Kruger National Park in 1996, the Greater Makalali Private Game Reserve in 2000, and Tembe Elephant Park in 2007 (Bertschinger et al., 2013; Delsink et al., 2006; Fayrer-Hosken et al., 2000a).

Elephant immunocontraception with pZP was first field tested in Kruger National Park, South Africa in 1996 after successful trials in zoo elephants in the United States and Canada (Fayrer-Hosken et al., 1999). The aim of this trial was to determine the efficacy of the pZP vaccine in free roaming elephants. In the first phase, 41 adult, non-pregnant female elephants were selected and collared for the trial, with 21 receiving 600µg pZP with the adjuvant synthetic trehalose dicorynomycolate (TDCM), and the other 20 a placebo. The vaccinated elephants received boosters (200µg pZP with TDCM) after six weeks and six months. Of the 19 vaccinated females (two collars failed), nine were pregnant at the 12 month follow up, one of which was in the last trimester and therefore pregnant at the start of the trial, and so was excluded. Of the 20 unvaccinated females, 18 were found and 16 were pregnant, proving a significant difference in pregnancies between the vaccinated (44%) and unvaccinated (89%). A second phase started shortly afterwards with a different booster schedule. Ten elephants were vaccinated with 400µg and then received boosters of the same dose 2 and 4 weeks later. This trial was more successful than the first, with only 2 of the 10 elephants falling pregnant in 10 months (80% efficacy). No behavioural aberrations were recorded during both these trials and a separate third trial proved reversibility (Fayrer-Hosken et al., 2000b).

The next step was to test immunocontraception as a tool to reduce elephant population growth in a small, fenced reserve (Delsink et al., 2006). The Greater Makalali Private Game Reserve is a 24500ha reserve is based in the Limpopo Province of South Africa with a well-known small population of 47 elephants, 18 of which were adult females (>12years), making it ideal for the trial. All of these females were vaccinated in 2000 with 600µg of pZP with FCMA and received 2 boosters of the same dose with FIA at 3-week intervals. A third booster was given 12 months after the first vaccination. At this time different booster dosages of 600, 400 and 200µg were trialled to test efficacy. Two females were added to the program in 2001 as it was decided to include females aged 8 to 12yrs. In 2003 the primary vaccine dosage was reduced to 400µg and the boosters to 200µg to reduce costs and because it was not likely to reduce efficacy. In 2004 it was decided to allow females to have their first calf before adding them to the program and that they would only receive annual vaccines after calving, no boosters at 3-week intervals (Bertschinger et al., 2018). By the end of the program in 2006, the vaccine efficacy was 100% with no births from contracepted females since 2003. In addition to proving vaccine efficacy, this program reconfirmed that the vaccine had no effect on pregnancies; it showed that darting from the air was better than from the ground as even though it caused more stress, it was much quicker and so overall caused less disturbance; no adverse effects on behaviour were observed; and granulomas that developed at the vaccine site resolved spontaneously (Delsink et al., 2007).

Following the success at Makalali, Tembe Elephant Park in Northern KwaZulu-Natal initiated a contraception program in 2007 (Bertschinger et al., 2013). In addition to having a much larger population, the elephants on the reserve were not individually known and so presented a new question regarding pZP immunocontraception – could it be used to control population growth in a reserve without individually identified elephants? At the time, the 30,000ha reserve had an estimated 200 elephants with a population growth rate of 9%, and a unique sand forest habitat that needed protection. A total of 76 adult females were identified during the immunocontraception darting from a helicopter and 71 received a single booster after 20 weeks. Between 2008 and 2014, 60 to 65 females received annual boosters and the number of calves born during these years were 8, 10, 5, 3, 3, 4 and 4 respectively, a reduction from the 10 to 14 calves born annually between 2004 and 2007 (Bertschinger et al., 2018). This meant a decrease in annual growth rate to 1.5% by 2014 and so demonstrated that pZP immunocontraception could be successful in reserves with elephant populations of around 200 and that are not individually known.

The next step for pZP contraception: Hluhluwe-iMfolozi Park

Hluhluwe-iMfolozi Park (HiP) is a 96 000-ha conservation area in the province of KwaZulu-Natal on the east coast of South Africa. The park was created in 1989 by the joining of three reserves: the Hluhluwe and the iMfolozi (formerly known as Umfolozi) Game Reserves, which were in individually proclaimed in 1895; and the Corridor Game Reserve. These were later consolidated in 2012 into HiP (M. T. Beest et al., 2017). It has all the 'big 5' and a wide range of vegetation types ranging from lush forests in the north to semi-arid thorn savannah in the south.

Elephants were absent from the area for almost 100 years before being introduced to HiP between 1981 and 1996. 174 orphaned juvenile elephants between the ages of 2 and 5 were sourced from Kruger National Park's culling operations over the 15-year period, with an additional 10 adult bulls introduced in 2000. The young population quickly grew with growth rate of 4.7% between 1990 and 1996, which increased to 6.7% between 2004 and 2014 as the population matured. In 2014, the population was estimated at 698 individuals (0.73/km^2), of which 144 were independent males, and with the oldest female around 38 years old. Other than removal of problem animals and the translocation of one herd to another park, there had been no elephant population management at HiP up until 2014 (D. J. Druce et al., 2017; le Roux et al., 2017).

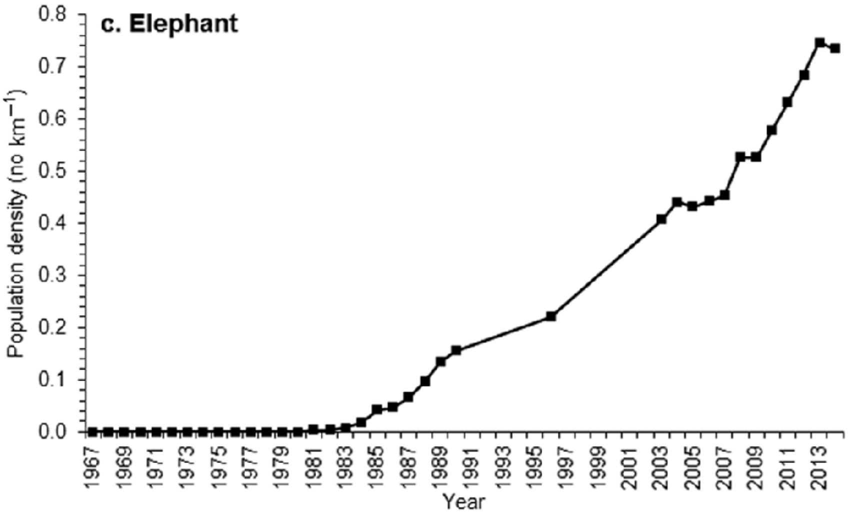

Figure 1. Elephant population density in Hluhluwe-iMfolozi Park from 1967-2013. Reproduced from Cromsigt, Archibald & Owen-Smith (2017) with permission.

Due to the rapid growth of the population, an immunocontraception program with pZP was initiated in 2014 (D. J. Druce et al., 2021). The primary aim of the program was to reduce the average annual growth rate from 6.6% (2014-2016) to between 2-3%. Initially, HiP aimed to contracept an estimated 35% of the breeding cows but increased their contraceptive coverage target to 100% of breeding cows in 2018, with 407 individuals darted in the year 2022. Twenty-six adult cows have tracking collars and so can be individually identified when darted, but otherwise it is unknown whether every individual adult cow is contracepted each year. Adult cows are darted with the vaccine from a helicopter annually at the end of the dry season.

To evaluate the success of this initial phase of the program, baseline data on the elephant population was collected in 2016 (Kuiper, 2017; Kuiper et al., 2018). Using spatially-explicit capture recapture models (Elliot & Gopalaswamy, 2017; Kuiper, 2017) based on ground observations, aerial census, and calculated growth rate, total population size was estimated to be 732 individuals in 2016. An infant proportion of 14% was used to calculate an average annual growth rate of 6.58% between 2014 and 2016. To date, there has been no official follow up of the program and its effects on population size and growth.

Study Aims and Objectives

The aims of this study are to (i) evaluate the effectiveness of the 8-year pZP immunocontraception program at Hluhluwe-iMfolozi Park in terms of reducing the elephant population growth rate, and (ii) determine potential reasons for reduced contraception efficacy in this population. I address these aims by exploring the following questions: (1) has the park achieved the goal of reducing the population growth rate to 2-3%?, (2) what are the potential reasons for reduced efficacy?, and (3) is there evidence to support these proposed reasons?

To achieve this, ground observational data of the infant proportion in the population were collected and used to calculate the current (2020-2022) annual population growth rate (see Methods). Potential reasons for reduced efficacy were critically evaluated, specifically focusing on data describing immunocontraception implementation consistency and the degree of population coverage. Results are compared to previous successful immunocontraception programs and suggestions are made regarding future implementation of immunocontraception both at HiP and in reserves with elephant populations of the same size or larger. Future research opportunities based on the findings of this study are also outlined.

Rationale

The findings from this study are important for several reasons. First, at a local scale, the annual growth rate calculation for 2020-2022 will assist the park in assessing the success of the contraception program and its effects on population size. This is an important step in the adaptative management of elephants within the reserve and will help guide future decisions regarding the program. Secondly, at a regional scale, an assessment of the HiP program and its potential issues will help establish the viability of using immunocontraception as a tool to manage the growth rate of elephant populations larger than 100 individuals within fenced reserves. A broader viability assessment is the next logical step in assessing pZP immunocontraception as a population management method and will frame future research both with regards to immunocontraception and elephant overpopulation management in southern Africa. Thirdly, the findings will be of value to other reserves where it can act as a blueprint for evaluating similar elephant immunocontraception programs elsewhere in southern Africa. More generally, this study will contribute valuable insight into the methods and their utility to the ongoing debate around elephant population management in Africa.

Methods

Study Site

Hluhluwe-iMfolozi Park is a 96 000 ha reserve in the KwaZulu-Natal province of South Africa located between 28°00’-28°26’ S and 31°43’-32°09’ E (Figure 3). It consists of two sections, Hluhluwe in the North and iMfolozi (previously known as Umfolozi) in the South, with the ‘Corridor Road’ dividing them. Elevation in the park ranges between 45m above sea level (asl) at the confluence of the iMfolozi rivers and 750m asl in the north-west of Hluhluwe (Howison et al., 2017). The park receives most of its rain in the summer months between October and March, with a mean annual rainfall of 975mm in Hluhluwe and 627mm in iMfolozi (Howison et al., 2017). The park has three major rivers - the Black and White iMfolozi in the South and the Hluhluwe River with its tributaries in the North. These occasionally stop flowing and consist only of pools in dry years, but usually the furthest distance from a water source in the park is between 8 to 10 km (Howison et al., 2017).

Temperatures in the park are on average higher in iMfolozi, with mean minimum and maximum temperatures of 10 and 33°C, compared to 12 and 25°C in Hluhluwe (Howison et al., 2017). The vegetation in the park is diverse due to its geographical position (at the transition of coastal lowlands to upland plateau), and the climactic and topographical differences between iMfolozi and Hluhluwe (Figure 2a and b). It consists of predominantly savannah and thicket, with central areas of open grassland, and patches of scarp forest in Hluhluwe (2018 Vegmap, SANBI). There are tarred and dirt tourist roads as well as permission-only management tracks that can be used for wildlife viewing. The only area inaccessible by car is the 30 000 ha Wilderness Area in the South of the park. The main research camp is situated in Hluhluwe, near the main tourist camp, Hilltop.

Figure 2a: Elephants in the lush and hilly Hluhluwe section of the park (Image: E. Fagan).

Figure 2b: In comparison to the Hluhluwe vegetation seen in Figure 2a, a cheetah in the savanna vegetation of iMfolozi (Image: E. Fagan).

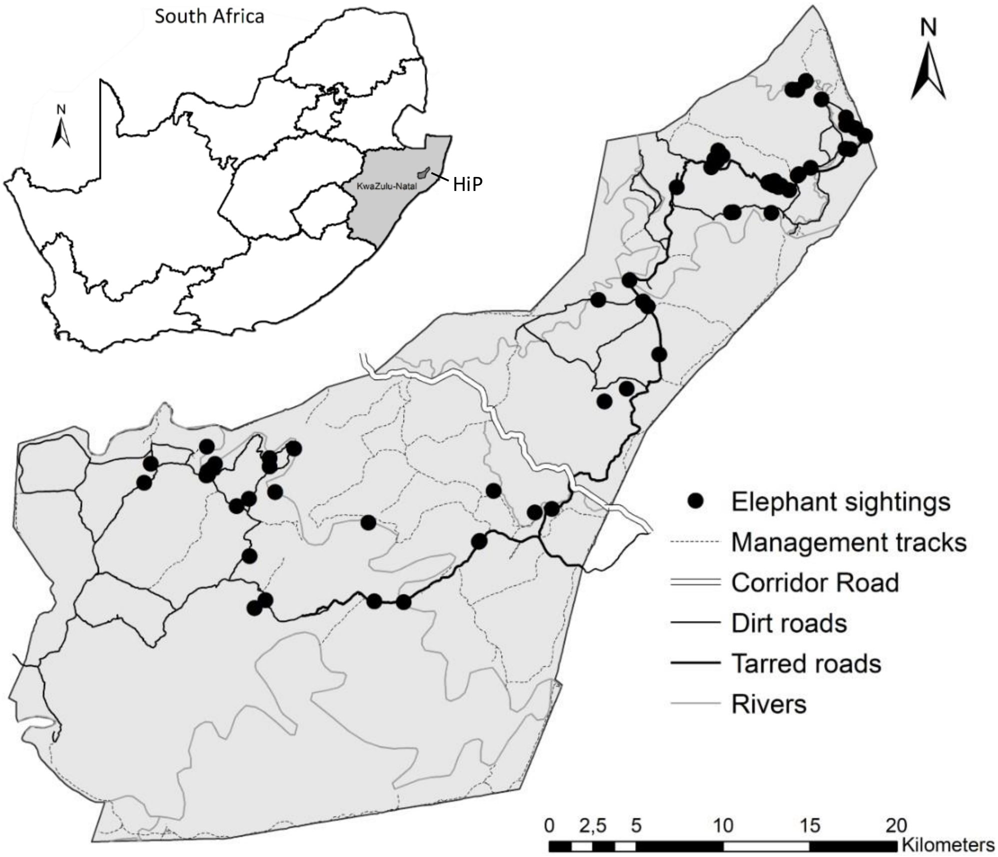

Figure 3: Map showing the location of HiP in the KwaZulu-Natal province of South Africa and the location of elephant sightings from fieldwork in 2022. The white road is Corridor Road which separates Hluhluwe in the north from iMfolozi in the south. Each black circle represents an individual elephant sighting.

Field monitoring of elephants in HiP

To determine the proportion of infants within breeding herds in HiP, fieldwork was conducted from 26 September - 1 November 2022 at the end of the park's dry season. Two weeks were spent at the southern iMfolozi section and three weeks at Hilltop Research Camp in Hluhluwe to ensure wide coverage of the park. A minimum of one observation session was conducted per day between 07h00 and 18h00. When possible, a second session was also carried out. Observations were made from within the field vehicle, and Pentax (DCF 9x32 BC) binoculars were used when necessary. Effort was made not to disturb herds during observations. A total of 2681km were driven between 3 October and 1 November 2022; the first week was spent driving with a conservation monitor in the park to ensure comfort and safety around 'big 5' animals. Sightings of elephant herds were usually by chance, but a VHF (very high frequency) receiver was also used to track and identify breeding herds that were collared. This included 16 old collars (4 were not working) fitted to adult females, and 6 new collars that were fitted to adult females on 17 October 2022. Two social media sightings groups, where regular tour guides, tourists, researchers, and wildlife monitors reported animal sightings, assisted with locating breeding herds during the observation sessions. The geolocations of all personal sightings, collar signals and triangulations, and social-media-reported sightings were recorded on the Avenza Map® mobile application (Avenza Systems Inc., 2022). Data recorded at each sighting included: date, time, GPS location, number of individuals in four defined age classes, number of adult bulls (>16 years), identities of individuals present (collared females), and sighting quality (1-10). Age classes followed those used in the 2016 baseline study: infant (<2 years), intermediate (2-8 years), subadult (8-12 years), and adult (>12 years) (Kuiper et al., 2018; Lee & Moss, 1995). Ages were based on relative shoulder height, and infants were distinguished by a lack of visible tusks (Laws, 1966). Bulls of 12-16 years were classified as subadults. Sighting quality was rated out of 10 to reflect the confidence in data accuracy. A good quality sighting (rating ≥ 7) indicated confidence in accuracy regarding counting, sexing, and ageing of the whole herd. A poor quality sighting indicated that there was low visibility, the herd was moving too fast, or only part of the herd was seen. A total of 67 sightings were recorded, with 46 rated as ≥ 7, good quality (Figure 3). Only five herds out of these good quality sightings were collared, and only one herd was seen more than once.

A priori power analysis

An a priori power analysis was conducted using R (R Core Team, 2021) for sample size estimation based on the mean and variation in the infant proportion data from the 2016 baseline study (Kuiper et al., 2018). My goal was to collect enough observations of breeding herds to be able to detect a biologically significant change in the proportion of infants in 2022 compared to 2016, with reasonable power. I considered a change above 20% (e.g., an infant proportion changing from 15% to 12%) to be biologically significant and power of 80% to be adequate. With a significance criterion of $\alpha = 0.05$, and a power of 0.80, the minimum sample size of elephant herd observations needed to detect a 20% decrease in infant proportion is $n = 30$ (Figure 4). Thus, my obtained field sample of $n = 46$ (see Results) was adequate to test the effectiveness of the immunocontraception program.

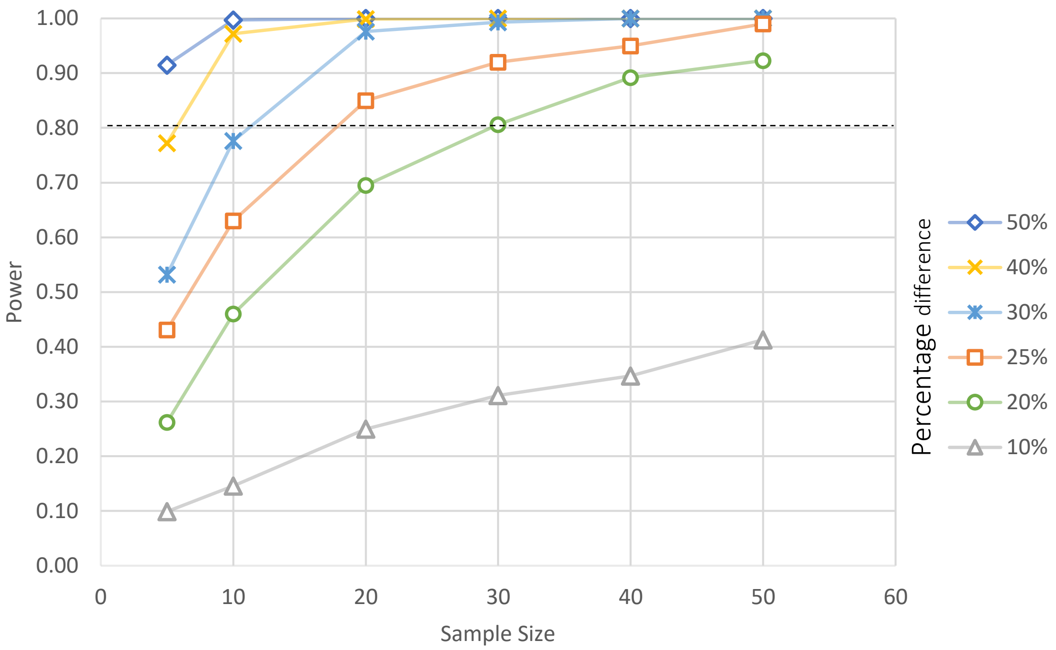

Figure 4. A priori power analysis showing the power associated with % difference from an infant proportion in breeding herds of 0.167 with varying sample sizes.

Aim 1: Determination of annual population growth rate from infant proportion

The annual growth rate of the elephant population is needed to determine immunocontraception efficacy. Building on previous work (Kuiper, 2017), I developed further equations for estimating the population growth rate based on the proportion of infants in the population, as described below. The advantage of this method is that the actual population size is not needed, as demonstrated in the simultaneous equations below. The method takes advantage of the following:

- Infants are classified as those without visible tusks and are conservatively classified 2 years or younger.
- The proportion of infants (p) therefore represents the proportion of the population that was born in the previous 2 years.
- Due to minimal recorded natural mortalities and no immigration or emigration of elephants to or from the park, it is assumed that the effect of mortality and migration on population growth rate is negligible.

Using the standard equation for population growth:

$$N_t = N_{t-2}(1+r)^2 \tag{1}$$

where N_t = current population total, N_{t-2} = population total 2 years ago, and r = annual growth rate.

Solving for *r* using the above equation:

$$r = \sqrt{\frac{N_t}{N_{t-2}}} - 1 \tag{2}$$

Next, the proportion of infants in the current population reflects the growth in the previous 2 years. Therefore, the current population is equal to the population 2 years ago plus the number of infants in the current population.

The number of infants in the current population = $N_t \times p_t$, and therefore:

$$N_t = N_{t-2} + N_t \times p_t \tag{3}$$

where N_t = current population, N_{t-2} = the population size 2 years ago, and p_t = the proportion of infants in the current population.

Solving for N_{t-2} using the above equation:

$$N_{t-2} = N_t(1 - p_t) \tag{4}$$

Now if we substitute N_{t-2} in eq. (2) with $N_t(1-p_t)$ as per eq. (4):

$$r = \sqrt{\frac{N_t}{N_t(1 - p_t)}} - 1 \tag{5}$$

$$r = \sqrt{\frac{1}{1 - p_t}} - 1 \tag{6}$$

Therefore, the average estimated annual population growth rate over the previous 2 years can be determined accurately using the proportion of infants in the current population.

This equation and the current proportion of infants based on field data were used to calculate the population growth rate for the period 2020 to 2022. For all calculations, it was assumed that the proportion of independent adult bulls within the total population remained 0.174, the same as in 2016 (D. J. Druce et al., 2017; Kuiper et al., 2018). This is based on the assumption that the total population and the number of independent adult bulls should grow at relatively the same rate.

To complement the 2016 and 2022 ground field observation data on the proportion of infants in breeding herds, estimates of total group size and the number of infants for every separate elephant group observed from the helicopter during the annual contraception operations (2016-2022) was determined.

Aim 2: Critical evaluation of reduced immunocontraception efficacy

Potential factors influencing immunocontraception efficacy at HiP were explored using field data, park records, and associated literature. PZP dose and manufacturer, adjuvant dose, type and manufacturer, dart type, and dart preparation were excluded as potential causes of low efficacy as they were all the same as in previous successful programs (Bertschinger et al., 2018; Delsink & Kirkpatrick, 2012).

As discussed in more detail below, the most likely explanations for lower-than-expected contraception efficacy centre on issues with (a) vaccination consistency and (b) population coverage. Consistent boosters are needed to keep antibody levels above the threshold necessary for contraception, and a significant proportion of females in the population needs to be darted to reduce growth rate. The factors affecting these two issues are as follows:

(a) Consistency
  - Cows must be darted at the same time every year
  - The same cows must be darted every year

(b) Population coverage
  - Targets for the number of reproductive females to be darted must be accurate and met.
  - Subadult females 8-12 years (not only adults) should be included in the program as they may be reproductive (Mackey et al., 2006)

These two factors were considered candidate explanations for low efficacy and were critically evaluated regarding which factors or combination of factors were likely at play on HiP.

1. Consistency - Time interval between boosters

For immunocontraception to be effective, boosters need to be given at the same time every year to ensure antibody levels remain above the threshold necessary to prevent conception (Delsink & Kirkpatrick, 2012; Fayrer-Hosken et al., 1999). This is especially true for cows that are added to the program using only annual boosters (no 6-week booster), as the risks of below threshold antibody levels are higher (immune system is not ‘primed’), and they do not receive the initial higher pZP dose. With these cows, a delay of a few months, especially in the first few years of treatment, may be enough for levels to drop below threshold (J. van Altena, personal communication, January 20, 2023). Even though there is no published data showing antibody level response with the currently recommended pZP immunocontraception program, we can assume that they remain at adequate contraceptive levels due to the success of previous programs. To investigate the impact of timing on contraception efficacy at HiP, records were examined to see if there were any significant delays in the giving of boosters between 2014 and 2022.

2. Consistency - Was there consistent darting of the same individuals?

In all the previous immunocontraception programs, except for the one at Tembe Elephant Park, all elephants were individually known. This means that there was 100% certainty that each individual cow received an annual booster. HiP's elephants are not individually known due to the much larger population size, and the total number of cows is unknown. Collars are used on HiP to improve the chances of darting the same individuals each year, but do not guarantee this. Darting records were analysed to identify how often collars were missed and the variations in herd size (as explained below, if herd structure is stable across years, there is a higher chance of consistency). The impact of GPS/radio collaring elephant herds on improving contraception coverage and efficacy was also investigated.

2.1. Missing collared herds

To improve darting consistency, one cow in each of the 20 breeding herds included in the 2015 and 2016 booster groups was fitted with a VHF and GPS collar. As of the end of 2022, 3 collars had fallen off, and 3 were not working. Six additional herds were collared in 2022 but were not included in this analysis. Using data collected from the annual darting operations, I investigated the number of collars missed per year. These records were also used to estimate the number of individuals associated with each collar and therefore the number of individuals potentially missed per year. The minimum number of individuals per collared group represents the core (also known as tier 2) herd, while larger group sizes represent aggregations of core herds (Wittemyer, Douglas-Hamilton, et al., 2005).

To assess the impact of missing herds on immunocontraception, the percentage of reproductive-age females missed per year due to the missing of collared herds was calculated. For this, I combined data on (1) estimated population size, (2) the proportion that potentially reproductive females constitute of this population size, and (3) the number of females darted each year, for each year between 2016 and 2022. This required a combination of field data and extrapolation. To estimate population sizes, I used the robust mark-recapture population estimate for 2016 of 732 (Kuiper, 2017), and then projected that forward using estimated growth rates. For this, I used the mean estimated growth rate estimated from infant proportion data in 2016 and 2022. The proportion of reproductive-age females was assumed to be the proportion of adult females plus half the proportion of subadults as half of the subadults are assumed to be male (elephant populations generally have a sex ratio of 1:1 (Kuiper, 2019)). To estimate the number of reproductive-age females in the population in each year from 2016 to 2022 I calculated the number in 2016 using the proportion of reproductive-age females in 2016 and then the number in 2022 using the proportion from field data in 2022. For 2017 to 2021, I used linear interpolation to estimate the number of reproductive-age females for each year.

2.2. Herd size variation

Herd structure also plays a role in contraception consistency. If herd structures are relatively stable, in that each herd has a constant number of members, then darting the same individuals each year is likely guaranteed. Observations of the total group size associated with each collared female from helicopter observations during darting operations each year were used to investigate annual herd sizes for each collared herd. The records relating to the first two groups of elephants to receive contraception (Group 1 and Group 2) were also examined to see how herd size variation affected contraception efficacy. The number of individuals darted per collared herd for both the initial and booster were compared. The minimum number across both darting operations for each herd represented the number effectively contracepted as it was assumed that the core herd would be consistent.

2.3. The impact of collars in improving contraception efficacy

Collars have been used at HiP to improve the efficacy of their contraception program. By placing collars on individual cows in different breeding herds, the contraception darting team can record which breeding herds are darted each year, and so can infer consistency for those herds and can use the collars to find breeding herds across the reserve to ensure good coverage of the population. To assess the value of collars, records were analysed to see (a) how many of the females that were darted were associated with collared herds and (b) the percentage of the total number of reproductive-age females that these females constituted.

3. Population coverage - Cow selection for darting

When darting elephants from the helicopter for contraception either the vet or an assistant identifies which elephants need to be darted. The identifier needs to be able to distinguish bulls from cows and age them. All potentially reproductive-age females need to be darted which includes all cows >8 years old, assuming an age of sexual maturity of 8 years (Mackey et al., 2006) to achieve contraception of the whole population. Even in reserves where the age of sexual maturity is older than 8 years, a drop in age sexual maturity should be anticipated - this often occurs in response to interventions that reduce the number of calves in an environment with high resource availability (van Aarde et al., 2008). In most implementing reserves, cows are allowed to have their first calves before being contracepted, so all adult females (>12 years) are darted as well as subadults (age 10 – 12 years) and any younger cows with a calf at foot (Bertschinger et al., 2018). This is because it is assumed that cows aged 10 and above have either had their first calf or are already pregnant with their first (J. van Altena, personal communication, February 4, 2023).

The success in darting all reproductive-age females is dependent on the skill of the identifier. Inexperienced identifiers often focus on more easily distinguished adult and subadult females, meaning that younger cows are missed. This means multiple calves can still be born every year despite regular darting and consistency. To investigate the effect of the identifier on darting numbers, I compared the darting numbers from 2022, when a different person was used as the identifier, to previous years. I also compared darting numbers to the estimated number of reproductive-age females in each year (as per the method outlined in section 2.1). This was only done for years 2018 to 2022 as those were the years that the park planned on darting 100% of the population (D. J. Druce et al., 2021).

4. Population coverage - Annual darting targets

HiP estimated the number of reproductive-age females per year based on calculated growth rate and assumed contraception efficacy. This was used to help inform the number of darts they needed for yearly boosters. This method can be useful but has limited accuracy as many assumptions are made - initial population size, calculated growth rate, proportion of reproductive-age females in the population, and contraception efficacy rates. To estimate whether targets were (a) accurate, and (b) met, I compared the numbers of reproductive-age females calculated for darting over the years and the numbers darted with the numbers based on the calculated growth rate for 2020 – 2022 (see section 2.1). Comparisons were only made for the years 2018 to 2022 as these were the years that HiP was aiming to dart 100% of reproductive-age cows (D. J. Druce et al., 2021). The probability of a reproductive-age female being darted consistently between 2018 and 2022 was calculated by multiplying together the probability that a reproductive-age female would be darted each year i.e., the percentage that darted females constituted of the estimated number of reproductive-age females.

Projected population trajectory

In order to estimate the future trajectory of the HiP elephant population, I modelled population growth for the period 2020-2028 under the revised growth rates estimated from the 2022 infant proportion field observations. I used the 2016 population size as a starting point as this was considered the most recent accurate population estimate. The total population in 2020 was calculated using the growth rate for 2014-2016 (7.7%). The growth rate for 2020-2022 was then used to project the estimated total population size between 2020-2028. The growth estimated from the proportion of infants could be used because the HiP elephant population is still relatively young, with very little old age senescence (with very few individuals over the age of 40, given the juvenile re-introduction history; Dominy et al., 1998). Population size was projected to 2028, after which senescence would start playing a more significant role.

Results

Growth rate determination from infant proportion in breeding herds

Infant proportion in breeding herds

A total of 46 good observations (sighting quality ≥ 7) were used to calculate an average infant proportion of 0.156 (SD = 0.073), i.e., infants made up 15.63% of breeding herds in 2022.

A power analysis was conducted based on data from 2016 and the sample size (number of good sightings) in 2022. It supported the use of a sample size of 46 (>0.80 power) to detect a decrease (between 2016 and 2022) in infant proportion of 18% or more. Therefore, if contraception was working to reduce population growth as planned, the difference in the infant proportion would have been detected (i.e., Would be 5.74% at a population growth rate of 3% - see calculations further on).

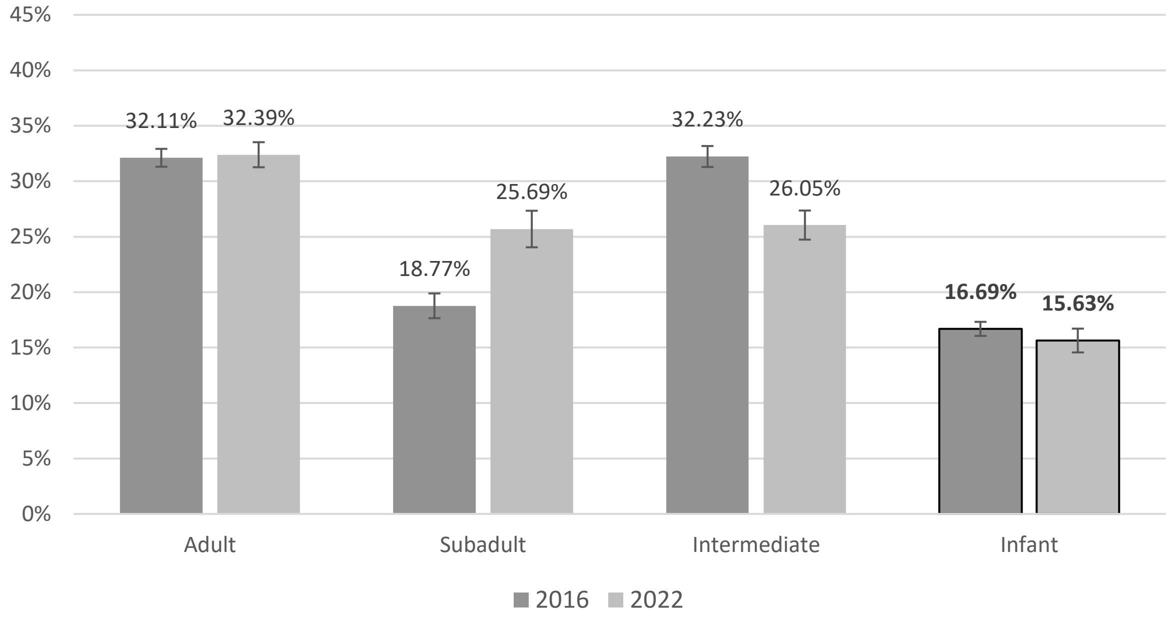

Figure 5. Breeding herd age distribution from fieldwork in 2016 and 2022. Age groups are adult (>12 years), subadult (8< × < 12 years), intermediate (2< × < 8 years) and infant (<2 years). Standard error bars are shown.

Age distributions in 2016 and 2022 were similar for both adults and infants (Figure 5). The percentage of subadults and intermediates in breeding herds were noticeably different, but if summed were very similar: 51% in 2016 and 51.74% in 2022. These two age groups are more difficult to distinguish, especially for novice identifiers, which may explain the different proportions but similar totals. Infants are easily identified from vehicle monitoring by their lack of tusks and so the ability of identifiers should not affect the result (though this may be different for observation from the air; see later).

A two sample t-test was performed to compare mean infant proportions in 2016 and 2022. There was not a significant difference in mean infant proportions between 2016 (Mean = 0.167, SD = 0.054, N =

72) and 2022 (Mean = 0.156, SD = 0.073, N = 46); t_{76} = 0.84, p = 0.40. The data were similarly distributed as shown in Figure 6 (the data fulfilled the assumptions of normality and homegeneity of variance).

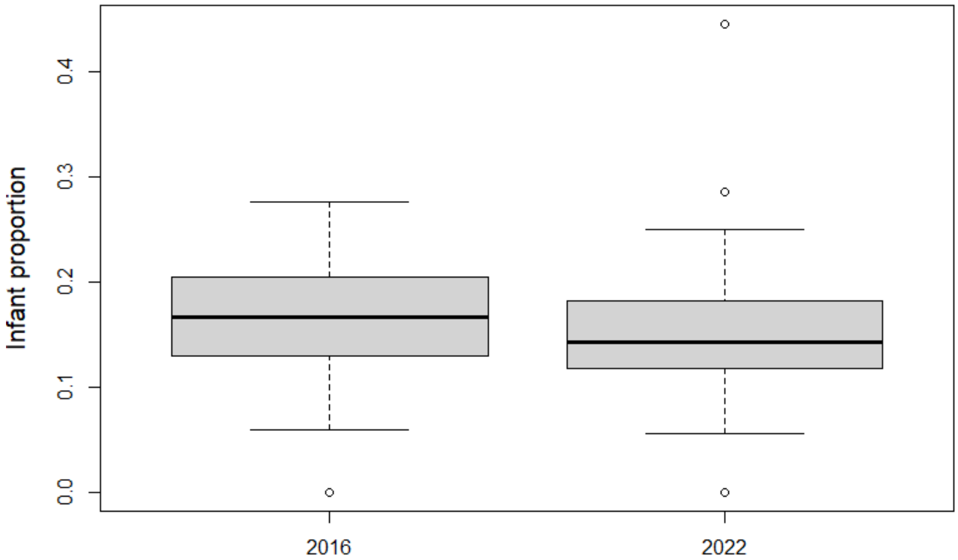

Figure 6. Box plot showing the distribution of data for infant proportion in breeding herds between this study and the baseline study done in 2016 (Kuiper et al., 2018).

Annual Growth Rate Determination

Using the equations for estimating growth rate from the proportion of infants (see Methods):

1. Corrected growth rate in 2016 using eq. (6) and the infant proportion in the total population (0.1379):

$$r_{2016} = \sqrt{\frac{1}{1-0.1379}} - 1$$
$$r_{2016} = 0.077$$

   Annual growth rate for between 2014 and 2016 was 7.7%.

2. Calculation of ideal infant proportion if goal of 3% growth rate was achieved:

$$r = \sqrt{\frac{1}{1-p_t}} - 1$$

$$r + 1 = \sqrt{\frac{1}{1-p_t}}$$

$$(r+1)^2 = \frac{1}{1-p_t}$$

$$\frac{1}{(r+1)^2} = 1 - p_t$$

$$p_t = 1 - \frac{1}{(r+1)^2} \tag{7}$$

$$p_t = 1 - \frac{1}{(0.03+1)^2}$$

$$p_t = 0.0574$$

If annual growth rate was 3% then infant proportion would be 0.0574.

For the following calculations it was assumed that proportion of independent adult bulls was still 0.1735 in 2022 as it was in 2016 (see section 2.1 Methods).

3. Calculation of growth rate in 2022 based on the proportion of infants in breeding herds (0.1563):

   Proportion in total population = (1-0.1735) x 0.1563 = 0.1292

$$r_{2022} = \sqrt{\frac{1}{1-0.1292}} - 1$$
$$r_{2022} = 0.0716$$

   Annual estimated population growth rate in 2022 was 7.16%.

4. Minimum and maximum (+/- 1 SD) growth rates in 2022 based on standard deviation of 0.0727 associated with infant proportion:

   Minimum proportion in total population = (1-0.1735) x 0.0836 = 0.0691

$$r_{2022Min} = \sqrt{\frac{1}{1-0.0691}} - 1$$
$$r_{2022Min} = 0.0365$$

   Minimum growth rate for 2022 was 3.65%.

   Maximum proportion in total population = (1-0.1735) x 0.2290 = 0.1893

$$r_{2022Max} = \sqrt{\frac{1}{1-0.1893}} - 1$$
$$r_{2022Max} = 0.1106$$

   The maximum growth rate for 2022 was 11.06%.

Infant proportion data collected during the annual contraception operations

Figure 7 below shows the estimated proportion of infants in breeding herds based on estimates of total group size and the number of infants for every separate elephant group observed from the helicopter during the annual contraception operations (2016-2022). Over 6 years, from 2016 to 2021, the observed proportion of infants remained fairly consistent over time, at around 0.2. While estimates of group size and infant numbers from the air may be less reliable than ground observations, this stable infant proportion (2016-2021) supports and validates the lack of a significant change in infant proportions found when comparing 2022 to 2016 ground observations (Figure 6).

The large drop in estimated infant proportion in the 2022 helicopter data (estimated at 0.08; Figure 7) is most likely due to the fact that the observer that collected the 2016-2021 data was not available in 2022, and the replacement observer may have been stricter in what they counted as an infant. The observer in question did confirm that this could explain the difference (L. Muller personal communication, February 6). It is of course, possible that the infant proportion did drop between 2021 and 2022, but this is unlikely given the argument for poor contraception consistency discussed below, and the fact that the 2022 infant proportion estimate from ground observations (likely more reliable) was still high (see above).

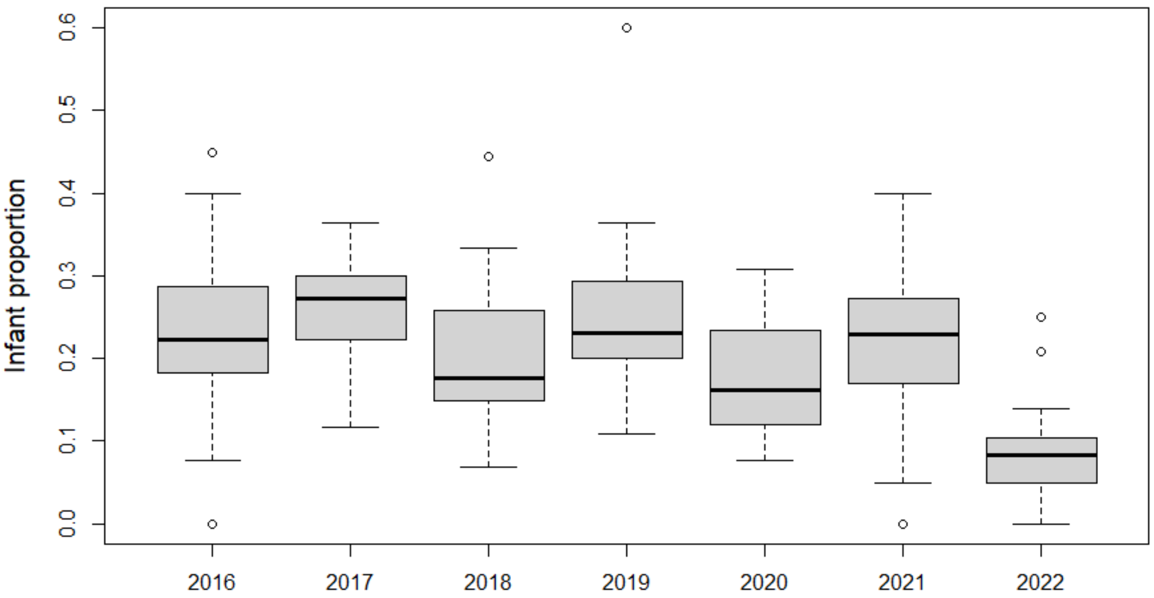

Figure 7. Box plot showing the mean and variation in the proportion of infants in elephant groups observed from the helicopter during annual contraception operations.

Causes of reduced immunocontraception efficacy

Effectiveness of pZP immunocontraception depends on the host's immune response and the resultant formation of antibodies. Antibody levels need to remain above the threshold necessary to prevent conception. Yearly boosters maintain these above-threshold levels. If there is any delay, or a booster is missed, antibody levels may fall below the threshold. Individuals who receive multiple years of consecutive boosters are more likely to maintain these antibody levels for longer, as well as those that receive a ‘priming’ booster 6 weeks after the initial pZP dose.

1. Time interval between boosters

Two groups of elephants required 6-week boosters: Group 1 in 2014 and Group 2 in 2015. Neither of these group’s 6-week boosters were delayed more than a week. There were no significant delays in the giving of annual (2016-2022) boosters either. The time intervals of annual boosters were found to be relatively consistent, with an acceptable maximum duration of 14 months (months between annual boosters from 2016: 13, 11, 12, 12, 10, 14).

2. Darting consistency

2.1. How often were collared herds missed?

Of the 20 herds that were collared between 2014 and 2022 (identified using BH codes, where BH stands for breeding herd), only 4 were darted consistently (BH003, BH087, BH119 and BH163) as shown in Table 2. Two herds (BH071, BH103) that lost their collars had perfect records except for the years their collars were off. Technically they could have been darted when they were uncollared but were no longer identifiable from the helicopter. The breeding herd with the worst record was BH355, which had been missed 5 times out of 9 attempts and therefore was probably not contracepted for most of the program. The herds that missed one or more boosters early on had a higher risk of not being contracepted, such as BH170, compared to those that were missed after receiving multiple boosters consistently, such as BH044. This is because herds that are darted consistently over many years take longer to reverse than those that have received only a few annual boosters. Each year an elephant receives a booster, the immune response increases due to priming, so the greater the number of consecutive boosters, the higher the resultant antibody levels, meaning that it will take longer for these levels to fall below the threshold necessary for contraception. Four herds (BH132, BH170, BH324 and BH347) did not receive 6 week boosters and so would have both taken longer to establish antibodies above threshold for contraception due to a lack of priming of the immune system, and also would have had a higher risk of being not contracepted if a booster was missed subsequently.

Table 2. Contraceptive darting records for the 20 collared breeding herds (2014-2022) and the number of times each herd has been missed. Y = darted, B = 6-week booster, N = not darted, NC = not collared (i.e., collar fell off) and UC = uncollared (i.e., not yet collared)

BH	Oct-14	Nov-14	Dec-15	Jan-16	Sep-16	Oct-17	Oct-18	Oct-19	Oct-20	Aug-21	Oct-22	Missed
071	Y	B	*	NC	NC	NC	NC	NC	NC	NC	NC	0
103	Y	B	*	Y	Y	Y	Y	Y	Y	Y	NC	0
126	Y	B	*	Y	Y	N	Y	Y	Y	Y	N	2
128	Y	B	*	Y	Y	Y	Y	N	N	N	NC	3
140	Y	B	*	N	Y	Y	Y	Y	Y	Y	Y	1
177	Y	B	*	N	Y	Y	Y	Y	Y	N	N	3
178	Y	B	*	Y	Y	Y	N	Y	Y	Y	Y	1
003	UC	UC	Y	B	Y	Y	Y	Y	Y	Y	Y	0
044	UC	UC	Y	B	Y	Y	N	Y	Y	Y	Y	1
087	UC	UC	Y	B	Y	Y	Y	Y	Y	Y	Y	0
119	UC	UC	Y	B	Y	Y	Y	Y	Y	Y	Y	0
132	UC	UC	N	N	Y	Y	Y	Y	Y	Y	N	1
157	UC	UC	Y	B	N	Y	Y	Y	Y	Y	Y	1
163	UC	UC	Y	B	Y	Y	Y	Y	Y	Y	Y	0
170	UC	UC	Y	N	N	Y	Y	Y	Y	Y	Y	2
327	UC	UC	Y	B	Y	Y	N	Y	Y	Y	Y	1
331	UC	UC	Y	B	Y	N	N	Y	Y	Y	Y	2
355	UC	UC	Y	B	N	N	Y	Y	N	N	N	5
324	UC	Y	UC	UC	Y	Y	Y	Y	N	Y	Y	1
347	UC	UC	UC	UC	Y	N	Y	Y	Y	Y	N	2

*These herds did not need boosters yet

2.2. How many individuals were missed per year as a consequence of missing collared herds?

At least one collared herd was missed every year except in 2014. Given the fission-fusion dynamics of elephant family groups on HiP (see Methods section 2.1 and Figure 8 below), the total number of individuals associated with each collared herd varied across the 8 years of darting. The minimum, maximum and mean size of the group associated with each collared individual (across the years of contraception each herd was observed) was estimated. Based on this and the particular collared herds missed each year, the minimum, maximum and average number of individuals that were potentially missed each year were estimated (Table 3). The minimum number of missed individuals per year between 2015 and 2022, was 4 and the maximum was 140. On average, 38 individuals were missed per year due to the missing of collared herds (this number does not include all the individuals not darted per year, just those potentially missed because collars were missed during the darting operations).

Table 3. Number of collared herds missed per darting operation with associated minimum (Min), maximum (Max), and average (Ave) number of reproductive-age females of all the missed herds combined based on darting records of herd size

Darting date	Number of collared herds missed	Estimated number of cows missed per year		
		Min	Max	Ave
Dec-15	1	4	15	11
Jan-16	4	18	49	34
Sep-16	3	13	57	34
Oct-17	4	36	87	61
Oct-18	4	29	140	72
Oct-19	1	4	9	7
Oct-20	3	14	50	29
Aug-21	3	12	35	23
Oct-22	5	37	112	73
	Mean:	19	62	38

Using the estimated number of reproductive-age females for the years 2016 to 2022 based on calculated growth rate and proportion of adult and subadult females in the population (see Methods section 2.1), the average percentage of reproductive-age females missed per year due to the missing of collared herds was 13.42% (SD 7.30%) as shown in Table 4.

Table 4. Estimated percentage of reproductive-age females in the total population missed per year due to the missing of collared herds

Darting date	No. of individuals missed per year	Estimated no. reproductive-age females	Reproductive-age females missed per year
Jan-16	11	251	13.45%
Sep-16	34	251	13.71%
Oct-17	34	279	22.47%
Oct-18	61	308	24.18%
Oct-19	72	336	2.00%
Oct-20	7	364	8.14%
Aug-21	29	392	6.04%
Oct-22	23	421	17.35%
		Mean:	13.42%

2.3. What percentage of reproductive-age females are associated with collared herds?

As shown in Table 5, an average of 81.04% (SD 10.56%) of the reproductive-age females that were darted were associated with collared herds. These darted females also constituted 63.12% (SD 9.98%) of the total number of reproductive-age females in the population. This means that approximately 76.54% (63.12% darted/year, 13.42% missed/year) of reproductive-age females are associated with collared herds at HiP.

Table 5. The number of reproductive-age females associated with collared herds (RAFCH), that were darted each year from 2016 to 2022. Also shown is the percentage that these RAFCH constituted of the total number of females darted and of the total estimated number of reproductive-age females (RAF) in the population

Year	Total darted	RAFCH	Percentage RAFCH of total darted	Estimated no. of RAF	Percentage that RAFCH constituted of estimated no. of RAF
2016	191	148	77.49%	251	58.96%
2017	176	164	93.18%	279	58.78%
2018	272	253	93.01%	308	82.14%
2019	276	246	89.13%	336	73.21%
2020	290	209	72.07%	364	57.42%
2021	249	198	79.52%	392	50.51%
2022	407	256	62.90%	421	60.81%
		Mean:	81.04%	Mean:	63.12%

2.4. Herd size variation at HiP

The number of individuals in each collared herd varied greatly from year to year within and between groups. The 6 breeding herds with the highest number of individual darting records (i.e., were not darted as part of a larger group or together with another collared herd) were BH044, BH178, BH324, BH003, BH177 and BH119. For all of these herds, there were large fluctuations in the number of individuals observed in the herd (Figure 8). BH044 had the largest range of 47, then BH178 with 42, while BH177 and BH119 had ranges of only 4.

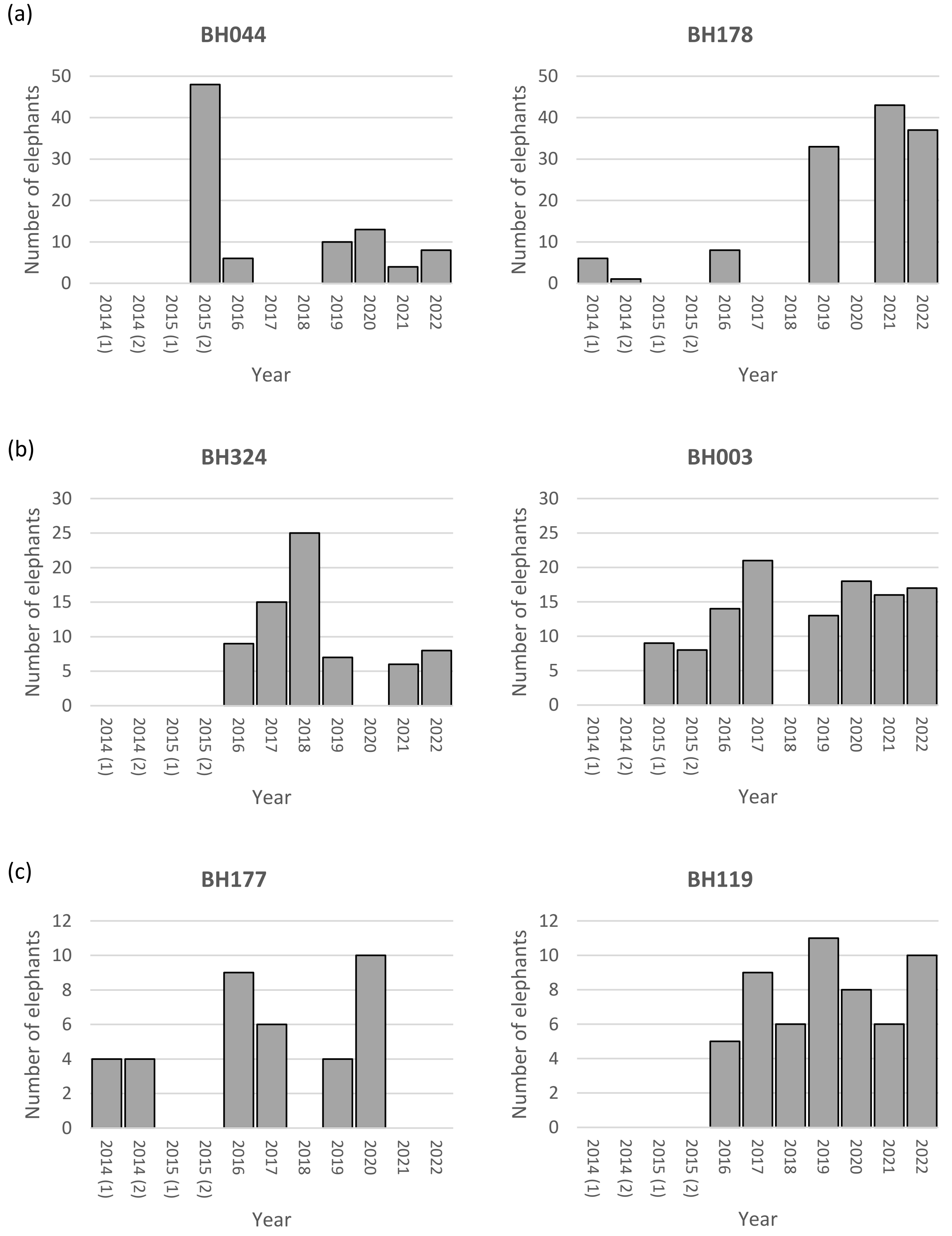

Figure 8. Number of elephants in collared breeding herds recorded during immunocontraception darting operations from 2014 to 2022 at HiP. These 6 breeding herds had the most individual records. In the years without records the herd was either not yet part of the contraception program or missed. Out of these 6 herds, BH044 and BH178 (a) had the most variation, then BH324 and BH003 (b), then BH177 and BH119 (c).

2.5. The impact of herd size variation on number effectively contracepted

Group 1, which consisted of seven collared breeding herds and four individually known breeding herds, was darted with an initial and 6-week booster in 2014. In October 58 cows associated with these breeding herds were darted with the initial pZP dose, and in November 51 cows received follow up boosters. Only 45 were effectively contracepted due to herd size variation as shown in Table 6.

Table 6. The number of adult females darted per breeding herd with an initial pZP dose on 04 October 2014 and a booster 6 weeks later on 16 November 2014. Seven collared breeding herds (BH) were targeted. Four additional herds (BH359/011/043) were identified and darted during the operation. The total number contracepted are those that received both doses

Group 1	Initial (04-Oct-14)	6-week booster (16-Nov-14)	Total contracepted
BH071	2	7[a]	2
BH103	4	5	4
BH126	14[a]	11	11
BH128	9	4	4
BH140	9	9	9
BH177	4	4	4
BH178	6[a]	1	1
BH125	2	2	2
BH359	Not recorded	Not recorded	-
BH011	8[b]	8[b]	8[b]
BH043	8[b]	8[b]	8[b]
Total	58	51	45

[a] Darted as part of a larger group

[b] BH011 and BH043 counted together

In Group 2, 72 cows received an initial dose and 157, more than double, were darted during the second round. Despite this large number, only 65 cows were effectively contracepted as shown in Table 7.

Table 7. The number of adult females darted per breeding herd with an initial pZP dose on 04 December 2015 and a booster 6 weeks later on 20 January 2016. Eleven collared breeding herds (BH) were targeted. The total number contracepted are those that received both doses

Group 2	Initial (04-Dec-15)	6-week booster (20-Jan-16)	Total contracepted
BH003	9	8	8
BH044	9[b]	48	6[d]
BH087	18[c]	26[a]	18[c]
BH119	Not recorded	Not recorded	-
BH132	Not darted	Not darted	0
BH157	9[b]	3	3
BH163	Not recorded	Not recorded	-
BH170	Not recorded	Not darted	0
BH327	18[c]	56[a]	18[c]
BH331	15	56[a]	15
BH355	12	16	12
Total	63	157	62

[a] Darted as part of a larger group

[b] BH044 and BH157 counted together

[c] BH087 and BH327 counted together

[d] BH044 total assumed to be 6 as BH157 core herd is 3

3. *Annual coverage of reproductive-age females at HiP*

In 2022, 407 cows were darted compared to 249 in the previous year (Figure 9). It is highly unlikely that the number of cows increased by almost two thirds in 1 year without any migration into the park. This could be due to four main reasons: a) the darting inclusion criteria was broader than in previous years, i.e., younger elephants were included, b) more elephants were simply found while flying, c) the 6 new collars added in 2022 allowed them to find more elephants, or d) the target was closer to the actual number of reproductive-age females.

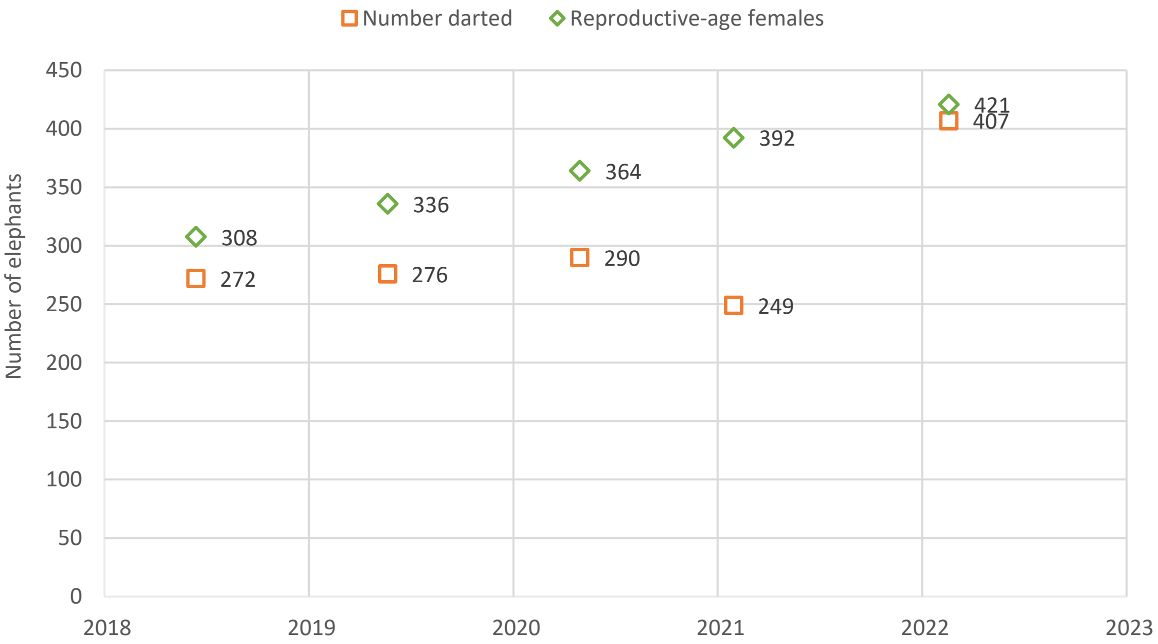

Figure 9. Total number of cows darted per year based on darting records and the estimated number of reproductive-age females in the total population each year (see Section 2.1 in Methods).

4. *Accuracy of HiP annual darting targets*

As shown in Table 8, darting targets from 2018 onwards were all lower than the average estimated number of reproductive-age females in the population, except for in 2022. All targets were high enough to include at least 80% of reproductive-age females or more. In 2022 the highest percentage of reproductive-age females were darted - over 95%. It should be noted that it is assumed that 10% of females darted are assumed to be below breeding age (Kuiper, 2017), meaning that these values are lower in reality. The numbers darted each year were also all lower than the darting targets except for in 2018.

The probability of a reproductive-age female being darted in a year is equal to the percentage that darted females constituted of the estimated total number of reproductive-age females. To calculate the probability of being darted consistently (every year) over the five years from 2018-2022, all the probabilities were multiplied together (88.31 x 82.14 x 79.67 x 63.52 x 96.67), giving an estimated probability of 0.355.

Table 8. Comparison of darting targets, numbers darted, and average estimated number of reproductive-age females (RAF) based on the calculated growth rates (see section 2.1 in Methods)

Year	Darting target	Number darted	Estimated no. of RAF	Percentage target of estimated no. of RAF	Percentage darted of estimated no. of RAF
2018	260	272	308	84.42%	88.31%
2019	285	276	336	84.82%	82.14%
2020	300	290	364	82.42%	79.67%
2021	338	249	392	86.22%	63.52%
2022	416	407	421	98.81%	96.67%

HiP elephant population trajectory

Based on annual population growth calculated for the period 2020-2022, by 2028, when mortality from senescence will begin to affect the population, the estimated number of elephants in the park will be 1713. This would mean a density of 1.78/km (Figure 10).

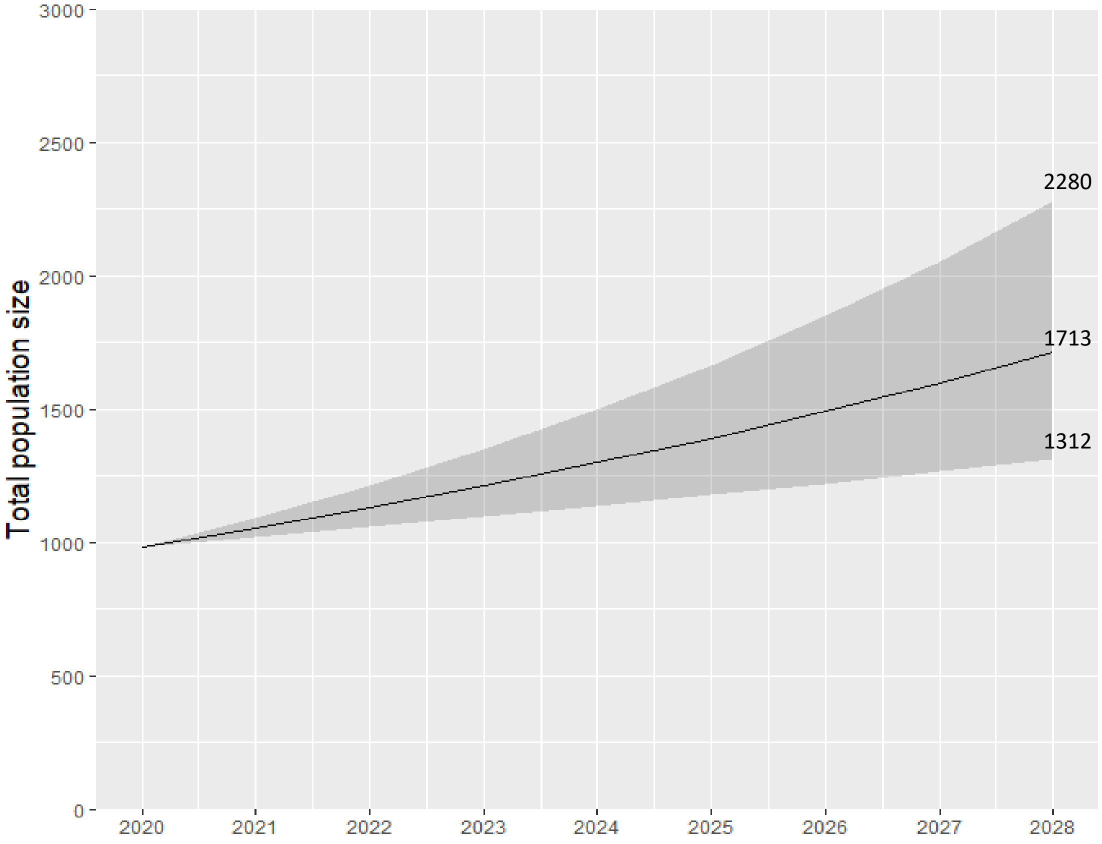

Figure 10. Graph showing the HiP elephant population trajectory from 2020 to 2028 with a confidence band based on the minimum and maximum estimated growth rates (see Methods: Projected population trajectory).

Discussion

Across fenced reserves in southern Africa, there is a pressing need to manage the overpopulation of elephants. Immunocontraception with pZP is successful in reducing the growth rate of elephant populations in small reserves with up to 250 elephants (Bertschinger et al., 2013; Delsink et al., 2006; Fayrer-Hosken et al., 2000a). Following success in a number of reserves, Hluhluwe-iMfolozi Park (HiP) in South Africa, started an immunocontraception program in 2014 to reduce the annual population growth rate from 6-7% to 2-3%; at the time the park supported a population of 700 elephants (D. J. Druce et al., 2021). This study aimed to assess the efficacy of HiP's contraception program. Using the proportion of infants within breeding herds to calculate the change in population growth rate from 2016 to 2022, the results suggest that the annual population growth rate from 2020 to 2022 was 7.16%, only slightly lower than the 2016 growth rate of 7.7%, indicating that contraception has not reduced the growth rate as expected. This is despite HiP following the same implementation protocol as a number of previously successful programs implemented in South African reserves. Currently, the population totals an estimated 1100 individuals (1.15 individuals/km^2) and will likely surpass 1700 individuals (1.78/km^2) by 2028 if the growth rate remains constant over the next six years (Figure 10). Given the findings, potential reasons for reduced contraception efficacy in this population were investigated. The findings presented here suggest the two major factors affecting the efficacy of the program are consistency and population coverage, both key to an effective immunocontraception program.

Elephant population growth in HiP

The estimated growth rates of the elephant population in HiP of 7.7% in 2016 and 7.16% in 2022 align with maximum growth rates reported in South Africa. The maximum annual population growth rate of elephants in this region was originally thought not to exceed 7% (Calef, 1988), but recent studies have shown that rates are often >10% (Mackey et al., 2006) and can even exceed 16% (Mackey et al., 2009; Slotow et al., 2005; van Jaarsveld et al., 1999) e.g., Mabula Game Reserve 15.3%, Pilanesberg Game Reserve 10.6%, and Pongola Game Reserve 11.8%. These high growth rates are most often seen in the early stages after re-introduction of elephants into a new area and can lead to a population doubling in as little as 10 years (Mackey et al., 2006, 2009). As there is no evidence of density dependence, these populations can quickly exceed estimated maximum densities within reserves (Gough & Kerley, 2006). Mortality due to predation and drought can reduce these growth rates, but within southern Africa, are not high enough to stabilise populations (Woolley et al., 2008). Elsewhere in Africa this is not the case, with adult elephants being removed from the population via human predation and poaching and associated knock-on impacts on the survival of remaining orphans (Moss, 2001; Ottichilo et al., 1987; Parker et al., 2021; Wittemyer, Daballen, et al., 2005). Population growth rates can, however, recover in these areas to rates of 7% if protection from poaching is increased (Foley & Faust, 2010). The estimated growth rates for 2016 and 2022 for HiP are also almost identical to the projected growth rate of 7.7% for the period 2003-2025 for HiP by Mackey (2006), and therefore support the method of calculating growth rate from infant proportion within breeding herds; although the impact of immunocontraception on the growth rate is unlikely to follow the predictions made for other small reserves due to the larger population size and reduced efficacy (see Mackey et al. 2009).

The role of consistency in immunocontraception efficacy

Key to successful immunocontraception programs is maintaining antibody levels above the threshold necessary to prevent conception. To achieve this, reproductive-age females need to be darted every year with boosters, as demonstrated by Fayrer-Hosken et al. (1999). This consistency can easily be assured in smaller populations where individuals are known, but it is undoubtedly more difficult in larger populations such as on HiP. In large populations where individuals are not known, GPS/VHF collars can be used to locate breeding herds, which helps guarantee some consistency if every collared herd is found and all breeding-age females are darted every year. At HiP, this has been attempted with 26 collars placed on females in separate breeding herds, which covers approximately 75% of all reproductive-age females; unfortunately, at least one collared herd has been missed every year since 2015 (Table 3), and only four collared herds have been consistently darted every year (Table 2). High variation in herd size, due to the fission-fusion society dynamics in the park, has also reduced consistency as it is only possible to guarantee that the minimum number of individuals darted per collared herd are effectively contracepted, i.e., if 10 are darted one year, and 20 the next, only 10 (the minimum) have been darted consistently over the two years (Figure 8, Table 6 & Table 7). This suggests that even though the collaring of herds can improve consistency, it only does so for only the core herd associated with each collar. Immunocontraception programs of other species with pZP have not faced the same challenges because 1) target populations have been much smaller (e.g., Duncan et al. 2013), 2) individuals of the species were easily recognisable or were tagged (e.g., Rutberg 2012), and 3) group structures were more stable or carefully monitored (e.g., Fertility control" 2020). These three factors clearly need to be assessed for any future immunocontraception program so that high levels of efficacy can be achieved.

The effect of missing collared herds becomes an even greater issue when new females have been added to the program (darted for the first time) without receiving either a higher initial dose of pZP or a 6-week booster, as their immune systems have not been primed. This is the case when a reserve decides to increase the percentage of immunocontraception coverage a few years into the program, such as at HiP, where coverage was increased from 35% to 100%. The newly added females have a reduced immune response to boosters than those that are primed and so take longer to build up their antibody levels (Figure 11). Therefore, if a booster dose is missed in the first few years, these 'new' females have a higher probability of being below the antibody threshold necessary for effective contraception (J. van Altena, personal communication, January 20, 2023). And so, by adding females to the program in this way, it is more likely that efficacy will be reduced and will need to be taken into consideration for future large scale immunocontraception programs. It is important to note that consistency may become less of an issue in the near future with the development of longer lasting contraception and is an active area of research (Behert & Fraker, 2016; Fraker et al., 2002; Miller et al., 2009).

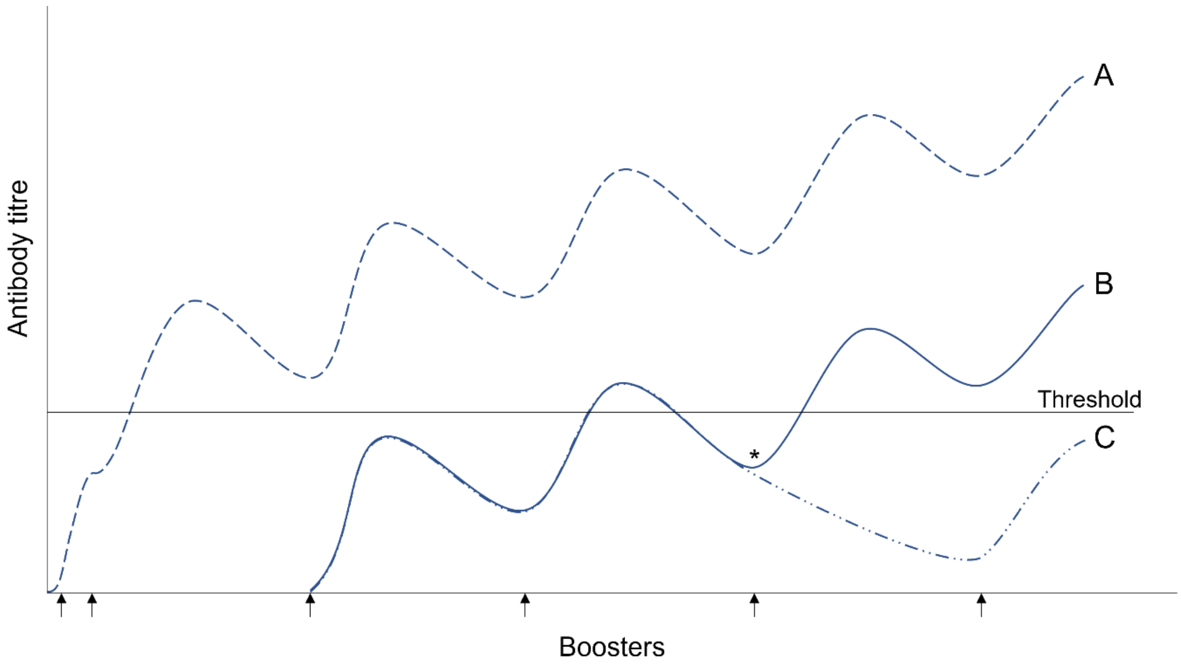

Figure 11. Visual representation of the difference in antibody levels in A) an elephant that received a higher initial dose of pZP + 6-week booster and annual boosters thereafter, B) an elephant that was added to the program with annual boosters, and C) an elephant that was added to the program with annual boosters but missed booster (*) in the third year. The threshold level necessary for contraception is indicated (figure by author)

The role of population coverage in immunocontraception efficacy

The percentage of the population contracepted, along with other factors such as number of offspring born per year, age of sexual maturity, age at first and last calving, and intercalving interval will determine the effect on population growth rate. This was modelled for elephants by Mackey (2009) to show the relative effects of contracepting 25%, 50% and 75% of the population over 20 years in small reserves. In these scenarios, annual population growth rates declined by 1.3%, 2.8%, and 4.9% respectively, compared to populations not treated with contraception, under the assumption that contraception was 100% effective, which, in practice, can only be achieved if all elephants are individually known. Where this is not the case, it becomes a question of probability: what are the chances of darting the same individual consistently over subsequent years? In large populations, darting a high percentage of reproductive-age females is important because the probability of darting the same individual every year quickly declines with a decrease in percentage coverage over time. Reliable yearly estimates of the number of reproductive-age females in the total population are vital for 100% darting efficacy because these estimates directly inform the darting targets i.e., the number of reproductive-age females that need to be darted to achieve a particular percentage coverage. If the yearly estimate is incorrect and the target is too low, both coverage and consistency decrease. For example, if your target covers 90% of the total population each year rather than 100%, then over five years there is only a 60% chance that a reproductive-age female will be darted every year (0.90 compounded over 5 years); at 80% coverage, there is only a 33% chance of the same female being darted every year over five years. The reason for incorrect estimates of the number of reproductive-age females in any population is because this number is calculated based on a number of assumptions. If recent population data is available e.g., size, sex ratios, age distributions, then fewer assumptions need to be made, but this data is not often readily available, especially for large populations that may require significant effort and expense to count. This study's estimates for the number of reproductive-age females in the population were consistently higher than the targets set for darting, suggesting that HiP has significantly under-darted in the years that they aimed to dart 100% of reproductive-age females (2018-2022). Only the number darted in 2022 came close to the estimated number of reproductive-age females calculated for that year (Figure 9). Based on the estimated percentage coverage for 2018-2022, the chances of HiP having darted the same female consistently over the last five years is only approximately 57%. This is far too low for an effective immunocontraception program. This concept applies to any large scale immunocontraception program if the species is not individually recognisable.

Recommendations for the elephant management program at HiP

Over the last eight years, HiP has expended extensive effort and funds to give their pZP immunocontraception program the best possible chance of working. Despite this, HiP still has a rapidly growing elephant population. The question is, can contraception efficacy on HiP be improved through changes in implementation, or is the main determinant of the program's success the size of the population and the different set of challenges associated with this?

To improve coverage and consistency, more accurate darting targets based on the number of reproductive-age females in the population is needed. This requires (1) regular population counts, (2) annual population growth rate data; and (3) accurate estimates of the proportion of reproductive-age females in the population. Population counts, although expensive and resource intensive, provide vital estimates of population size and of the proportion of bulls in the total population, which is necessary for the calculation of growth rate from infant proportion in breeding herds. Advances in technology such as the use of drones and AI identification of individuals is likely to reduce these costs in the near future. The annual population growth rate can be calculated from either total population counts or infant proportion counts in breeding herds as demonstrated in this study and Kuiper (2017). If the main limiting factor to this is cost, volunteer groups in the park that already assist with species monitoring could also be tasked with recording infant proportion in breeding herds, either throughout the year or for a shorter, intensive period, as was done in this study. The proportion of reproductive-age females in the total population can also be estimated from counts, immunocontraception darting records, or field work such as reported in this study. The darting of all collared herds also needs to be a high priority to improve consistency of the program. This could also be supported by ground-based darting of missed herds if helicopter time was too costly given the allocated budgets. Identification of collared herds is also key, and an identifying feature of collars e.g., colour banding allowing for individual identification without functioning VHF or GPS, could be trialled. This would address the issue of the identifier in the helicopter seeing a collar but not being able to identify the herd due to a lack of VHF or GPS signal and would allow for collars to retain their value even after their batteries have died. An increase in the number of collared elephants in breeding herds will also improve both coverage and consistency, although the ethics and impact on tourism would need to be considered but would unlikely outweigh the alternative – an ineffective immunocontraception program and so potential translocation or culling.

HiP also acknowledges that immunocontraception is only the third priority intervention for management of elephants in the park currently (D. J. Druce et al., 2021). The live removal of elephants and protected area expansion are both higher priorities, but these are limited by available opportunities. While immunocontraception will buy time for these other management interventions, it is not a standalone method for managing the population and there are concerns regarding the longer-term consequences, such as an ageing population, potential social behavioural effects due to fewer calves in the population, the accumulation of aluminium darts and the costs (R1000-R1500/elephant)(Delsink et al., 2002; H. C. Druce et al., 2013; Kirkpatrick, 2007; Matthews et al., 2011).

Can immunocontraception with pZP provide an effective management tool for large elephant populations in fenced reserves?

What is evident from this study is that the larger the population, the more difficult it is to ensure consistency and coverage in immunocontraception programs. And so, despite there being ways to potentially improve the program at HiP, it is possible that the population is already too large to ensure contraception efficacy with the current implementation protocol, irrespective of the fact that it has worked in smaller populations. With the addition of more elephant collars, the park could improve efficacy, but any park with an elephant population size equivalent to that of HiP or larger would need to collar a large proportion of their herds at the start to ensure adequate population coverage for immunocontraception efficacy. This is likely to be unfeasible for many parks and reserves due to the prohibitive costs involved (e.g., R18 000-R23 000/elephant depending on collar type together with the costs of the immobilisation team and drugs (D. Druce, personal communication, February 11, 2023)) and is clearly impractical for very large populations that number in the thousands. Where immunocontraception is unlikely to be effective in large elephant populations, barring translocation and culling, there are only two options to decrease density: range expansion by increasing reserve size, or establishing corridors to promote source-sink dynamics (Pulliam, 1988; van Aarde et al., 2006). Sinks (areas with declining populations) could be reserves suffering from poaching or smaller reserves with successful contraception programs, while sources would be reserves that are too large to implement immunocontraception.

Conclusions

In summary, the eight-year pZP immunocontraception program at Hluhluwe-iMfolozi Park has not reduced the elephant population growth rate from 6-7% to 2-3% as planned. Annual population growth rate for the period 2020-2022 was 7.16% based on infant proportion in the population, only slightly less that the estimated growth rate of 7.7% at the start of the program. Contraception efficacy was reduced by several factors including the missing of collared herds, herd size variation, and inaccurate darting targets for the population. It is possible that HiP can increase the efficacy of their program by improving the accuracy of darting targets, ensuring every collared herd is darted every year, and by placing more collars on elephants in breeding herds. It may be that the population size of HiP is already too large for immunocontraception with pZP to be effective, and that until a longer-lasting contraceptive is available, pZP should only be used in reserves with elephant populations in the range of 200-250 elephants.

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Appendices

Appendix I: Data from field work at Hluhluwe-iMfolozi Park (26 September - 1 November 2022)

Sight ID	Date	Time	GPS South	GPS East	Group	Adult	Subadult	Intermed	Infant	Unknown	Collars	Sighting Quality
1	27/09/2022	16:09	-28.278030	31.941572	2	1	0	0	1	0	NA	6
2	29/09/2022	17:45	-28.309260	31.902646	15	5	4	4	2	0	NA	8
3	30/09/2022	15:25	-28.277555	31.942010	12	5	3	3	1	0	bh119	7
4	01/10/2022	17:25	-28.243618	31.800415	7	3	1	2	1	0	NA	8
5	03/10/2022	14:45	-28.285395	31.822760	9	5	2	2	0	0	NA	5
6	04/10/2022	16:20	-28.239517	31.803846	12	3	0	0	1	8	NA	6
7	04/10/2022	16:25	-28.237617	31.804902	7	3	0	0	1	3	NA	4
8	04/10/2022	17:17	-28.240280	31.802769	16	5	4	4	3	0	NA	8
9	04/10/2022	17:35	-28.238993	31.833240	3	1	1	1	0	0	NA	9
10	05/10/2022	08:03	-28.255741	31.822449	11	5	0	3	3	0	NA	5
11	05/10/2022	16:56	-28.252241	31.836077	17	7	3	4	3	0	NA	9
12	05/10/2022	17:30	-28.229667	31.845902	17	7	3	5	2	0	NA	7
13	06/10/2022	06:30	-28.308216	31.831035	10				2	8	bh178	3
14	06/10/2022	08:47	-28.251584	31.949131	0						bh119	2
15	06/10/2022	12:46	-28.228673	31.800711	18	5	3	7	3	0	NA	7
16	07/10/2022	06:57	-28.234671	31.833217	9	3	2	3	1	0	NA	10
17	07/10/2022	10:07	-28.247418	31.768260	15				2	13	NA	4
18	07/10/2022	16:17	-28.241524	31.801031	11	4	2	3	2	0	NA	9
19	07/10/2022	16:49	-28.243290	31.801365	10	3	1	4	2	0	NA	7
20	08/10/2022	11:46	-28.237519	31.771590	18	4	3	8	3	0	NA	5
21	09/10/2022	09:46	-28.268063	31.884433	0						bh331	1
22	10/10/2022	17:15	-28.083906	32.061914	6	2	1	2	1	0	NA	10
23	10/10/2022	17:35	-28.083906	32.061914	7	4	0	1	2	0	NA	8
24	10/10/2022	17:52	-28.083906	32.061914	8	3	4	0	1	0	NA	7
25	11/10/2022	09:48	-28.156100	32.029000	15	7	0	6	2	0	NA	Other
26	11/10/2022	17:50	-28.152740	32.003440	9	2	1	3	2	1	NA	8

27	11/10/2022	18:12	-28.142580	32.019527	3	1	0	1	0	1	NA	2
28	12/10/2022	09:18	-28.107402	32.072089	17	6	6	2	3	0	NA	7
29	13/10/2022	11:01	-28.107256	32.073546	8	4	1	2	1	0	NA	6
30	13/10/2022	16:19	-28.078063	32.067808	13	5	2	4	2	0	NA	8
31	13/10/2022	17:07	-28.048772	32.119086	17	7	4	4	2	0	bh119	8
32	13/10/2022	17:22	-28.058073	32.131753	18	6	7	4	1	0	NA	8
33	13/10/2022	17:35	-28.062038	32.131847	6	2	1	2	1	0	NA	9
34	14/10/2022	11:55	-28.087502	32.107354	9	2	5	1	1	0	NA	7
35	14/10/2022	12:16	-28.088264	32.106661	18	5	5	5	3	0	NA	10
36	13/10/2022	17:41	-28.094270	32.044020	9	4	1	0	4	0	NA	10
37	14/10/2022	16:29	-28.079843	32.063531	5	2	1	1	1	0	NA	9
38	14/10/2022	17:37	-28.074553	32.133906	10	5	3	2	0	0	bh347	6
39	15/10/2022	08:39	-28.080500	32.065071	6	3	1	2	0	0	NA	6
40	15/10/2022	09:06	-28.095831	32.102348	16	3	7	5	1	0	NA	7
41	15/10/2022	15:15	-28.259527	31.816082	4	1	1	1	1	0	NA	7
42	15/10/2022	16:40	-28.243613	32.800476	16	6	2	4	4	0	NA	9
43	16/10/2022	09:09	-28.312416	31.825372	47	15	8	17	7	0	NA	7
44	16/10/2022	09:52	-28.308865	31.887436	39	11	11	10	7	0	NA	6
45	17/10/2022	05:32	-28.153572	32.026641	14	4	3	5	2	0	NA	7
46	18/10/2022	16:09	-28.074366	32.131434	14	4	4	3	3	0	NA	7
47	18/10/2022	16:22	-28.063791	32.136719	79	28	25	21	5	0	bh163	7
48	18/10/2022	17:17	-28.067687	32.141569	13	5	3	4	1	0	NA	6
49	19/10/2022	08:07	-28.075262	32.065574	7	2	1	2	2	0	NA	8
50	20/10/2022	06:24	-28.039175	32.110967	6	1	2	2	1	0	NA	7
51	20/10/2022	06:58	-28.043771	32.103956	17	5	4	6	2	0	bh126	7
52	20/10/2022	07:34	-28.043856	32.106529	15	5	4	4	2	0	NA	8
53	22/10/2022	15:00	-28.093123	32.093662	21	8	6	4	3	0	NA	7
54	23/10/2022	11:23	-28.107587	32.093070	19	3	4	5	2	5	NA	6
55	23/10/2022	16:43	-28.094240	32.096835	28	8	9	9	2	0	NA	9
56	23/10/2022	16:55	-28.094240	32.096835	35	12	10	8	5	0	NA	9
57	26/10/2022	11:26	-28.093317	32.094441	19	5	7	5	2	0	NA	7

58	27/10/2022	15:15	-28.260989	31.979389	6	2	1	3	0	0	bh087	4
59	28/10/2022	11:07	-28.262846	31.970530	18	5	7	4	2	0	bh003	7
60	28/10/2022	16:03	-28.091936	32.091440	7	2	2	2	1	0	NA	7
61	28/10/2022	16:07	-28.093369	32.098052	9	3	2	3	1	0	NA	8
62	28/10/2022	16:09	-28.090987	32.094757	13	5	5	2	1	0	NA	6
63	28/10/2022	16:38	-28.091631	32.092402	9	2	4	1	2	0	NA	8
64	29/10/2022	09:04	-28.205228	32.006600	49	17	16	10	6	0	NA	7
65	29/10/2022	16:34	-28.084275	32.113467	16	3	6	5	2	0	NA	9
66	30/10/2022	10:07	-28.198749	32.018127	28	7	7	9	5	0	NA	6
67	30/10/2022	15:46	-28.180935	32.034958	24	6	6	8	4	0	NA	8