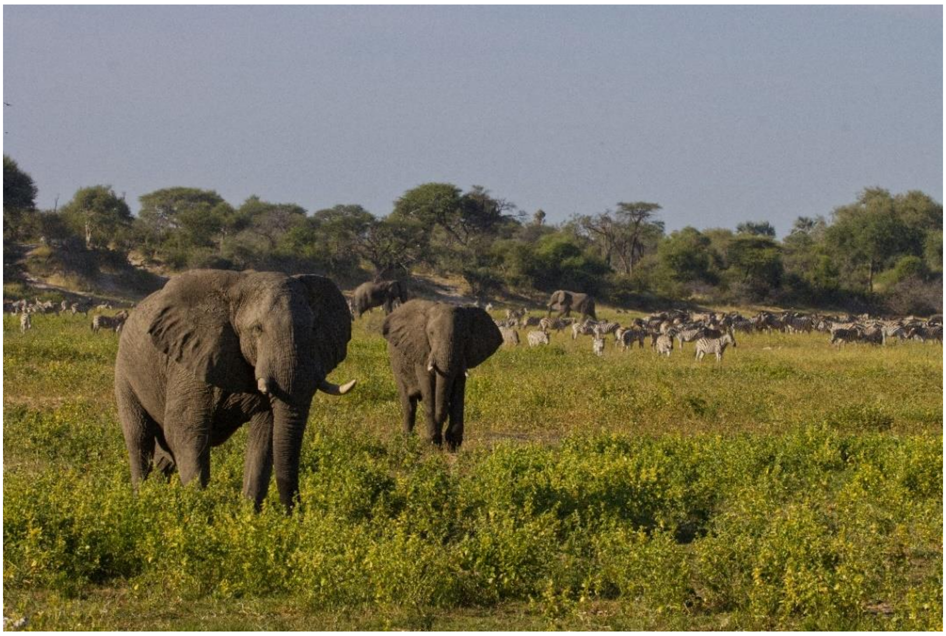
UNIVERSITY OF GOTHENBURG

DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

MOVEMENT PATTERNS AND SOCIAL DYNAMICS OF MALE AFRICAN SAVANNAH ELEPHANTS (*LOXODONTA AFRICANA*)

Following the steps of giants



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Sammanfattning

Populationer av vilda djur minskar över hela planeten. Konflikter med människor ökar medan de vilda landskapen minskar. Den afrikanska savannelefanten (*Loxodonta* africana) vandrade förr i de flesta delar av Afrika, men idag återstår enbart en bråkdel av dess historiska antal. Botswana är hem för 130 000 elefanter, ungefär 1/3 av Afrikas återstående antal. I sökandet av resurser har savannelefanterna traditionellt genomfört stora säsongsvandringar, dessvärre har fragmenteringen av landskapet gjort dessa rörelsemönster betydligt svårare att genomföra.

Savannelefanten är en starkt hotad art och även om det sociala livet hos de matriarkala familjegrupperna är väl studerade så har grupperna som hanarna kan bilda blivit desto mindre undersökta. Denna studies syfte var att fylla några av dessa luckor och bidra med kunskap gällande rörelsemönster och social dynamik hos tjurar för att bättre bevara arten och minska konflikter mellan människa och vilda djur.

Fotoidentifiering användes för att spåra individer i Makgadikgadi och Nxai Pans nationalparker i Botswana för att beräkna hur många dagar tjurarna spenderade i och utanför parken, samt hur det skiljde sig mellan olika åldersgrupper och säsonger av året. Dessutom undersöktes hanars sociala relationer för att öka kunskapen om dessa grupper.

Jag hittade att tjurar i genomsnitt stannade i 37 (KI 31-48) dagar inne i parken innan de lämnade under i genomsnitt 108 (KI 87-138) dagar. Dessutom indikerar resultatet att de yngsta hanarna stannade kortare perioder i och utanför parken under både regn- och torrsäsongerna jämfört med de äldsta tjurarna. Båda åldersgrupperna stannade en längre tid i och utanför parken under torrsäsongen jämfört med under regnsäsongen. Forskningen visade även att associationer mellan tjurar inte var slumpmässig även om de flesta relationer enbart varade en kort tid.

Resultaten visade att elefanters rörelse generellt ökar under regnperioden och att yngre elefanter tenderar att röra sig mer in och ut ur parken vilket kan öka deras risk att hamna i konflikt med människor boendes i närheten. De indikerar även att elefanter har föredragna sällskap. Samtliga av dessa fynd bör beaktas när beslut tas rörande bevarandet av arten.

Abstract

Wildlife populations are decreasing all over the globe. Conflicts with humans increase as the wild landscapes shrink. The African savannah elephant (*Loxodonta africana*) used to roam in most parts of Africa but only a fraction of the historical numbers remains today. Botswana is home to 130,000 elephants, about 1/3 of the elephants remaining in Africa. Savannah elephants have traditionally made large seasonal migrations for resources, but landscape fragmentation has made these movements much harder.

The savannah elephant is an endangered species and even if the social lives of matriarchal families are well-studied, the groups that the bulls may form have been less so. This study aimed to fill some of these gaps and contribute with knowledge about movement patterns and social dynamics of males to better conserve the species and decrease human-wildlife conflicts.

Photo identification was used to track individuals in the Makgadikgadi and Nxai Pan National Park in Botswana to estimate how many days the bulls stayed inside and outside the park, and how it differed between different age groups and seasons of the year. I also investigated the social dynamics of male associations to increase the knowledge about bull groups.

I found that a bull on average stayed for 37 (CI 31-48) days inside the park before leaving the park for 108 (CI 87-138) days. My findings also suggest that the youngest males stayed and left for shorter periods under both the wet and dry seasons compared to the oldest bulls. Both age groups stayed and left for longer periods during the dry season compared to the wet. The research also showed that bull association isn’t random even though most relationships will be short-term.

My results indicated that elephant movement generally increased during the wet season and that young bulls in general moved more in and out of the park, increasing their risk of conflict with people living in the surroundings. It also indicated that elephants do have preferred companions, and all these findings should be taken into consideration for the conservation of the species.

1. Introduction

1.1. A key player in the ecosystem

The role of keystone species in different ecosystems is well documented (e.g. Jordán, 2009; McNeill, 2023). The services can be made in numerous ways. Abandoned dens from wolves (*Canis lupus*) and warthogs (*Phacochoerus africanus*) create shelter for other opportunistic individuals of different species (Mech, 1971; Cumming, 1975). Beavers (*Castor fiber*) build dams which alternate streamflow and affect a variety of plants and animals (Naiman et al, 1988). Some of the effects are small and individual; others impact the entire ecosystem. The effects of elephants can be of both these kinds (Kerley et al., 2008; Haynes, 2012; McNeill, 2023). Despite their importance, the factors affecting the movements of migratory keystone species into and out of protected areas are poorly known.

Elephants are megaherbivores and keystone species with the ability to shape the landscape they live in, and thus, their population has a cascading effect on the ecosystem and the biodiversity of the area (Kerley et al., 2008; Haynes, 2012). Elephant movement creates large trails which are used by many other species (Haynes, 2012; Relfsson, 2023), including humans (*Homo sapiens*). Removal of trees by elephants creates open landscapes, and dung accumulation can alter the local pH of the soil and provide nutrients to the residents (Haynes, 2012). Elephants may influence erosion in their search for minerals and water, or alter vegetation since not all plant species are equally well adapted to survive the trampling of a giant (Sikes, 1971; Haynes, 2012). The elephant enables a variety of species to exist in different areas, and their removal from the ecosystem may cause a spatial homogenisation of plant communities, and a decrease in niche space for consumers (Pringle et al., 2016).

According to the recent Living Planet Report, the average population size for wildlife has decreased by 73% since 1970 (WWF, 2024). Conserving elephants may play an important role if we are to reach the objective of stopping the loss of biodiversity as decided by the Convention on Biological Diversity (Convention on Biological Diversity, 2022). Protecting elephants is also beneficial for a country from an economic point of view since the economic increase in tourism in a protected area, compared to an unprotected area, outweighs the costs of protection (Naidoo et al., 2016). However, it is important that this money does not end up in the pockets of foreign stakeholders, but that it increases the livelihood of the local communities in the range states to incentivize them to live alongside elephants and to decrease potential conflicts (Naidoo et al., 2016).

1.2. Historical numbers and ivory trade

The African savannah elephant (*Loxodonta africana*) is classed as endangered by the IUCN (International Union for Conservation of Nature) since the species has been reduced by more than 50% over the last 75 years (Gobush et al., 2022). Exact historical numbers for the species are hard to estimate, but 200 years ago, prior to the European colonisation of Africa, it is believed that 20 million elephants roamed the continent (Milner-Gulland & Beddington, 1993). This includes both the African savannah and forest elephants (*Loxodonta* cyclotis). A century later, the number had decreased to approximately 4 million African elephants, and by the 1970s, only 1 million remained (Douglas-Hamilton, 1987; Milner-Gulland & Beddington, 1993). A major reason for the disappearance of elephants was the hunt for ivory (Douglas-Hamilton, 1987).

The trade of ivory has a long history. Cultures around the globe used the material for primarily decorative and ornamental items, e.g. the keys on the piano or the balls in billiards (Shamos, 2002; Baker et al., 2020; Gobush et al., 2022). The demand was especially high in Europe, the USA, and Asia (Martin et al., 1986; Nishihara, 2003, 2012). The decrease in the elephant population coincides with the price of ivory which increased from an average of $5.45 (United States dollar) per kg in the 1960s to $74.42 in 1978; and finally ended above $100 per kg in the 1980s (Parker,1979; Douglas-Hamilton, 1987). The rising price for ivory in combination with habitat destruction, drought, disease, and poaching for meat, led to an increase in elephant mortality during the 70s and 80s (Douglas-Hamilton, 1987). The international commercial trade of ivory was banned in 1989 by CITES (the Convention on International Trade of Endangered Species of Wild Flora and Fauna) due to the rapid decline in the African elephants (Gobush et al., 2022). Since then, two CITES-sanctioned sales have been held, one in 2002 and one in 2008, where Botswana, Zimbabwe, South Africa, and Namibia sold ivory to Japan and China (Gobush et al., 2022). During the sanction in 2008, Botswana sold 43,153 kg of ivory for the price of $7,093,551; the proceeds were reported as going exclusively to conservation actions for elephants and rural communities, and to development programs in connection with the elephant range (Wijnstekers, 2011).

1.3. The status of the African savannah elephant

In 2006, a new surge of poaching started due to an increase in ivory demand, making the population suffer another blow where the numbers decreased by approximately 100,000 individuals between 2007 and 2016 (Wittemyer et al., 2014; CITES, 2016; Thouless et al., 2016). During the years that followed the CITES sanction in 2008, Botswana had an annual export quota of 600-800 tusks and other hunting trophies (Thouless et al., 2016). This continued until the country banned trophy hunting in 2014, and one year later, Botswana declared a zero quota for the export of elephant hunting trophies (CITES, n.d., referenced in Thouless et al., 2016). The hunting ban was in 2019 exchanged to a hunting quota of circa 400 elephants each year (Bale, 2019; Mahr, 2019; Ministry of Environment, Natural Resources Conservation and Tourism, 2019).

In addition to poaching, the extension of human land use has caused the distribution of elephants to decrease from previously covering most of Africa, to today covering roughly 15% of its historical pre-agricultural range (Sikes 1971; Sayre, 1999; Chase et al., 2016). Traditionally, savannah elephants underwent extensive seasonal migrations in search of food and water (Kangwana, 1996). Elephant movement is influenced by the availability of water, making their movements easy to predict during the dry season but more random when the resources are abundant (Wittemyer et al., 2008). The human increase in population size and use of land has caused fragmentation and a reduction of elephant movements, making extensive migrations much harder (Kangwana, 1996). They do, however, still need a large area of land, and this is causing an increase in human-elephant conflict and conflicts between different human interests (Redpath et al., 2015; Chase et al., 2016; Thouless et al., 2016; Gobush et al., 2022).

The total number of African elephants, including both the savannah and the forest elephant, was estimated to be 400,000 individuals in 2016; 2% of the numbers 200 years ago, and declining in most regions (Milner-Gulland & Beddington, 1993; Thouless et al., 2016). The average generation time is about 25 years which makes the recovery of the population very slow (Wittemyer et al., 2013). Botswana is home to the world’s largest remaining population with an estimated 130,000 savannah elephants, but the national estimates have differed by up to 80,000 individuals since 2006 and a better understanding of this population is crucial for the survival of the species (Thouless et al., 2016; Schlossberg et al., 2019). Most of these savannah elephants are found within the Kavango-Zambezi Transfrontier Conservation Area, where the shared savannah elephant population moves between the countries of Angola, Botswana, Namibia, Zambia and Zimbabwe (Thouless et al., 2016).

About 25 years ago, savannah elephants returned to the area of Makgadikgadi Pans and Nxai Pans National Park in Botswana (Chase et al., 2015). Since then, the numbers have rapidly increased with an average of 16% annually during 2001-2014, reaching an estimated population of 2,242 (95%-confidence interval (CI): 1367-3117) savannah elephants in 2014 (Chase et al., 2015). The highest number of elephants was in the western part of Makgadikgadi where 801 (CI 478-1123) elephants were estimated (Chase et al., 2015). The theoretical maximum rate of increase in a population, excluding immigration, is estimated to be 6.2-7% per year (Calef, 1988). A likely explanation for the much higher increase in the Makgadikgadi and Nxai Pan is due to immigration and range expansion (Calef, 1988; Chase et al. 2015).

1.4. Bulls and social associations

The social lives of savannah elephant males and females differ in many ways. Female elephants live in matriarchal herds together with the young, while the males leave the herd during their adolescence (Evans & Harris, 2008). The matriarchal herds have been well-researched but the groups that the males may form have been less so (Evans, 2006; Allen et al., 2020). Because the males are the sex that disperses (Dobson, 1982), they are sometimes seen as replaceable and reproductively redundant, and this is often used as an argument to support legal trophy hunting of old males (Baker, 1997), translocations and culling. The desire to get hands on the largest tusks and take down the largest elephant, both legally and illegally, is putting hard pressure on old males and causes changes in the population's composition and morphological evolution (Chiyo et al., 2015).

Since the savannah elephant recently returned to the Makgadikgadi where this research took place, most sighted elephants are bulls while the females are more likely to be found closer to a reliant water source as the Okavango delta (Stokke & du Toit, 2002; Evans, 2019; Agell, 2021). We know relatively little about the social dynamics of bulls but previous research in the area by Pitfield (2017) concluded that long-term group formations were not based on age class and that the proportion of long-term companions increased with age.

To better protect the elephants and decrease conflicts with humans, it is important to investigate the elephants' land use and movement patterns as well as social dynamics. Bulls move further from perennial water sources during the dry season than female herds do (Stokke & du Toit, 2002). Adult males roam widely during this period, probably to avoid bulls in musth, i.e. bulls in the periodic state of sexual activity, who remain close to the females (Stokke & du Toit, 2002). When bulls enter musth, meaning “intoxicated”, their level of testosterone and aggression increases (Poole, 1987; Poole, 1996; Merriam-Webster, n.d.). Bulls usually become sexually mature around the age of 17 but do not compete for oestrous females before they reach 30 (Poole, 1982; Poole, 1994). The duration of the state of musth is age-related, where young bulls last in musth for days to several weeks, while older bulls usually are in musth for numerous months (Poole, 1987). The musth is triggered by females and therefore seldomly observed in bull areas like the

Makgadikgadi (Poole, 1982; Pitfield, 2017). The older bulls usually leave the area before entering the musth and are in less association with other males during this period (Poole, 1982). Males are non-territorial and if not in musth, they roam widely between different "feeding hotspots" during the dry season (Stokke & du Toit, 2002; Ngene et al., 2009).

Previous findings suggest that the bulls stay on average 47 days in the park and leave for roughly 238 days before returning (Pitfield, 2017). Adolescents are more aggressive to non-elephants, i.e. vehicles or other animals, when alone compared to when in the company of older bulls (Allen, 2021). The bull areas are therefore likely to be a valuable place for bulls to build bonds when not in musth and constitute a possibility to share company and obtain knowledge; a place where older bulls can calm the behaviour of the younger and the young can feel protected by the old. The fact that old bulls are not replaceable, but crucially important for bulls of all ages and the population as a whole is supported by several pieces of evidence. First, the selective hunting of older bulls influences the composition and morphological evolution of the population (Baker, 1997). Second, all age groups have the most stable bonds with individuals of the oldest age class (Pitfield, 2017). Third, young bulls are less aggressive to non-elephants when in the company of older bulls (Allen, 2021). My study helps us understand how the movement patterns of the bulls look and the value of these social behaviours.

1.5. How to track individuals

By identifying individuals and noting the place and time of observations we can map the movement of individual bulls and learn more about how long different elephants stay in the area, when they are absent, what groups they are forming, and how they are behaving (Whitehead, 2009). With this information, we may predict behaviours, calculate population growth in the national park, and better manage and conserve the species. GPS (global positioning system) collars are used to track elephants, but this is both an invasive and potentially dangerous undertaking (Kulits et al., 2021) as well as a hugely expensive operation that limits sample size.

By applying photo identification, where the time and place of a photograph can be used as mark and recapture data, we can track individuals and thus get knowledge about populations, their movement, and utilization of Makgadikgadi and Botswana (Lettink & Armstrong, 2003; Whitehead, 2009). The method is mostly used on species with distinct patterns like zebras (*Equus quagga*), giraffes (*Giraffa spp.*), or harbour seals (*Phoca vitulina*) (Berger-Wolf et al., 2017; Isaksson, 2022). Since African savannah elephants don't have distinct patterns, they can be more challenging to separate from each other. To identify them, ecologists usually use sex, tusk shape, rips, tears and holes on the ears, and any other unique markings that may stand out (Kulits et al., 2021). However, many of the markers being used to identify the individuals change over time; thus, a known individual may be misidentified as a new individual. A less changeable feature that could be seen as a more reliable source, and be used to identify individuals, is the wrinkles around the elephant's eyes (Chui & Karczmarski, 2022). However, using wrinkles does require high-resolution photographs, whilst the traditional way is more easily applied from a distance or with less sharp images (Chui & Karczmarski, 2022). To date, 1,391 bulls have been uniquely identified using photo identification by the organisation Elephants for Africa with whom this study has been made.

2. Aims

2.1. Length of stay

Use photo-identification to collect information about individual savannah elephants and investigate how long they are staying in the Makgadikgadi Pans and Nxai Pan National Parks and if the length of stay differs between different age groups.

2.2. Preferred or random association

Analyse whether associations of bulls are preferred or random.

3. Material and method

3.1. Study area

The research was taking place inside the Makgadikgadi Pans and Nxai Pan National Park, with most data collected in the western part of Makgadikgadi. The parks are located in the central parts of northern Botswana, southeast of the town of Maun and the Okavango Delta, and on the western boundary of the Makgadikgadi Pans National Park lies the Boteti River (Figure 1). The region is exposed to a high level of human-wildlife conflicts, perhaps the highest in all of Botswana (Brooks & Bradley, 2010). The water in the river is collected in the mountains of Angola before it runs through the delta and arrives in Makgadikgadi (Bartsch et al., 2019). During a period when the river was dry for almost 20 years, a fence was constructed in 2004 to decrease the interactions between wildlife inside the park and livestock (Hazelhurst & Vander Kolk, 2006). In 2009 the river was once again flooded causing the previously electrified fence to malfunction and since then, the fence has broken in many places creating possible pathways for animals to pass between the park and the surrounding communal areas (Pitfield, 2017; Evans, 2019). Coinciding with the resurgence of the river was the savannah elephant (henceforth referred to as elephant) range expansion southwards to the Central Kalahari Game Reserve, leading to a population increase in the study area (Thouless et al., 2016; Evans, 2019).

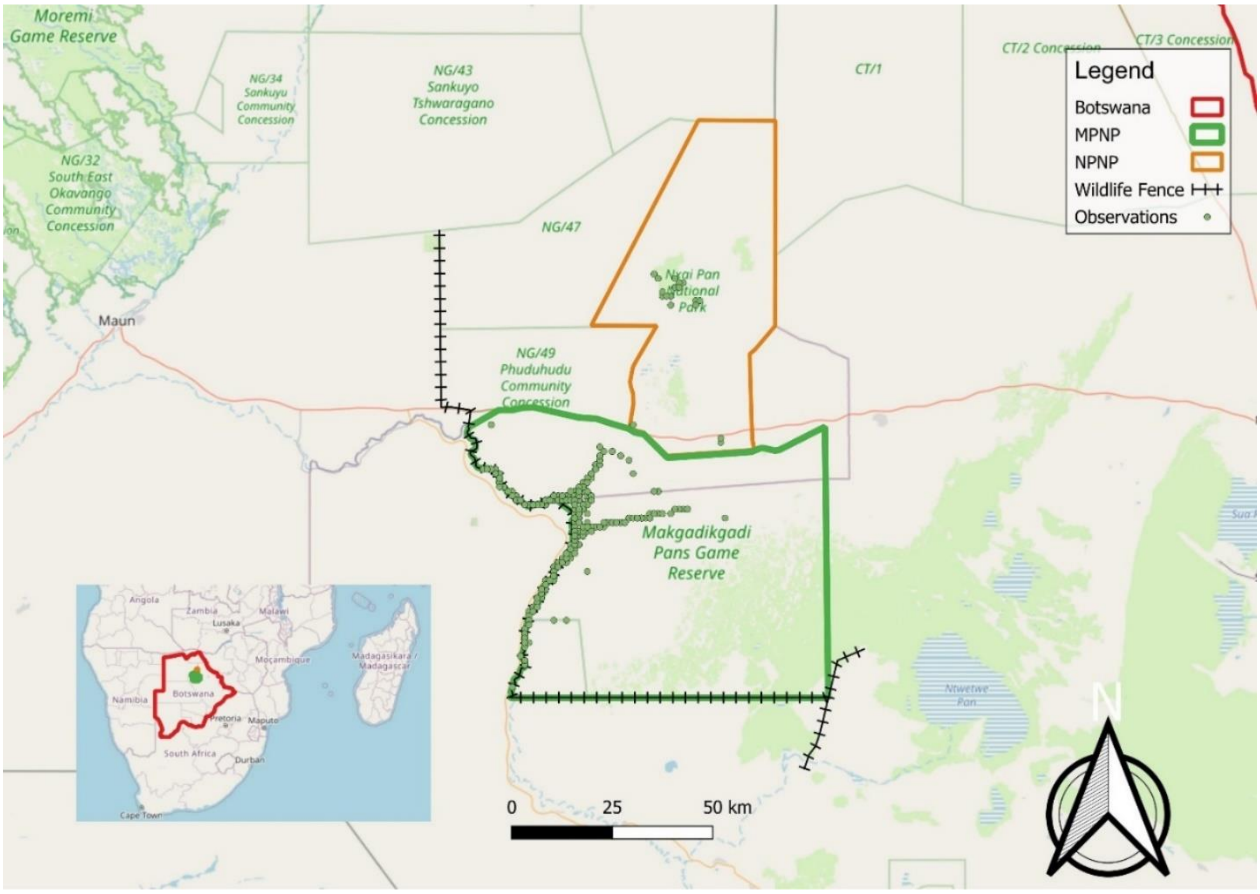


Figure 1: Map of the study area. Note that the wildlife fence continues, only the parts connected to the research area are shown on the map. The map was made in QGIS 3.34.10.

The research group Elephants for Africa has been based in the park since 2012, researching the predominately male population (Evans, 2019; Figure 2). The total size of the study area is roughly 7,500km^2, consisting of the 4,900km^2 in the Makgadikgadi Pans National Park, and 2,590km^2 in the Nxai Pan National Park (Chase et al., 2015).

Rain occurs mostly during the wet summer season reaching from October/November to April/May, and the dry winter season goes from May/June to September/October (Chase et al., 2015; Allen, 2021). The climate in the park is semi-arid and during the dry season, the daily temperature can reach 28^{o}C while the nights can create occasional ground frost (Thomas & Shaw, 1991; Kgathi & Kalikawe, 1993). The wet season is much hotter where the daily temperature may exceed 40^{o}C causing potential evapotranspiration while the nights don't usually go much below 20^{o}C (Thomas & Shaw, 1991; Kgathi & Kalikawe, 1993).


Figure 2: A bull and cow outside my tent on Valentine's Day just before mating; note the difference in size.

3.2. Collecting data

The research was done from a vehicle in the Makgadikgadi Pans National Park, and we made sure to always keep a safe distance to avoid interfering with the elephants. A DSLR (Digital single-lens reflex) camera was used to document the identification characteristics of the elephants (Section 3.2.3. & Appendix 2). The photos were linked to a GPS location of the observation, and notes were taken so that photos of different individuals didn't get mixed together. Many different groups may gather at resources making it difficult to separate one group from another. Therefore, when photographing along the Boteti River, short-term interactions that appeared only at water resources were not documented; only the groups that arrived at the river after we had arrived and set up were recorded. Once the elephant(s) had arrived, I focused on one group at a time and recorded the ages before the individuals were photographed. The guidelines established by the organisation Elephants for Africa on how to estimate the sex and age of the elephant were followed (Section 3.2.1. and 3.2.2.). When all the data on one group had been collected, I moved on to the next group (Section 3.2.4., Appendix 3 & Appendix 4). Collected data was entered into the database containing information about the observation, the individual, and the group. New sightings were entered to later be matched with known elephants or registered as new individuals. Characteristics of an elephant were described and entered by hand together with photos to enable potential matches to be made in the future.

3.2.1. Cow or bull?

The first step to identifying an individual bull is to be able to separate the sexes. Different characteristics will distinguish elephant males from females at different stages of their lives (Table 1). The differences become more noticeable with age and will be apparent as the bull goes into becoming independent and sexually mature (Evans & Harris, 2008). Some of the most distinct characteristics are the sharp forehead and narrow face of the female compared to the round and wide head of the bull, and males' much larger body size (Figures 2 & 3).

Table 1: Some of the characteristics that differentiate bulls from cows

Differences	**Males**	**Females**	**Reference**
Age 0-10	No obvious differences between the sexes		(Lee & Moss, 1995)
Age 10	Size dimorphism becomes distinct		(Lee & Moss, 1995)
Age 10-20	Goes into adolescence, i.e. process of independence & sexual maturity	Height difference becomes apparent	(Evans & Harris, 2008)
Age 25	Continues to grow	Growth rate decreases	(Laws and Parker, 1968, referenced in Moss, 1996)
Age 50	A shoulder height of 360 cm and weight of 7,000 kg	Maximum 270 cm and may weigh 3,000 kg	(Moss, 1996)
Age 60	Tusk growth rate increases throughout life, mean combined weight of 109 kg	Linear tusk growth, mean combined weight of 17.7 kg	(Kunz, 1916; Laws, 1966; Moss, 1996; Henley and Henley, 2008, referenced in Henley, 2012)
Age 65	Bull on average 60-70 cm taller than cow		(Lee & Moss, 1995; Figure 2)
Head	Broader between eyes and more rounded	Pointier forehead and eyes closer together	(Moss, 1996; Figure 3)
Genitals	Penis and testicles are enclosed in a sheath, opening forward	The vulva looks like a sheath but opening downwards	(Moss, 1996)
Body shape	The hip and waist are evenly shaped	Sides extending beyond hip, round shape	(Moss, 1996)
Breast	Looks like female's before her first calf	Breasts are developed once pregnant	(Moss, 1996)

Figure 3: On the left side we have cows and their young, on the right side there are bulls. It can take some practice before separating the two.

3.2.2. How old is the elephant?

Since the elephant will continue to grow as long as it lives, the first indication of the age is its size (Croze 1972; Lee & Moss 1995; Moss, 1996). Some features to look at are the shoulder height, length of the back, and size of the footprint (Croze 1972; Lee & Moss 1995). As mentioned above, bulls leave the matriarchal group when they are between 10-20 years old (Evans & Harris, 2008). Between the ages of 10-15, the shape of the male head will become sloping rather than angular, tusks get thicker, and the shoulder height becomes taller than females of the same age (Moss, 1996). The bull becomes sexually mature on average at the age of 17 and reaches the same height as females over 40

(Poole, 1994; Moss, 1996). When between the ages of 20-25, he is taller than all the females but still lean and narrow in head shape (Moss, 1996). From 25 years and up, the head starts shaping like an hourglass, wide at the base of the tusks and between the eyes, the head keeps getting larger and so does the height of the shoulders (Moss, 1996; Figure 4). At the age of 40+, the bull is like a tower over the females with a shoulder height of more than 3 meters but can even grow to become 4 meters (Wood, 1982; Shrader et al., 2006).

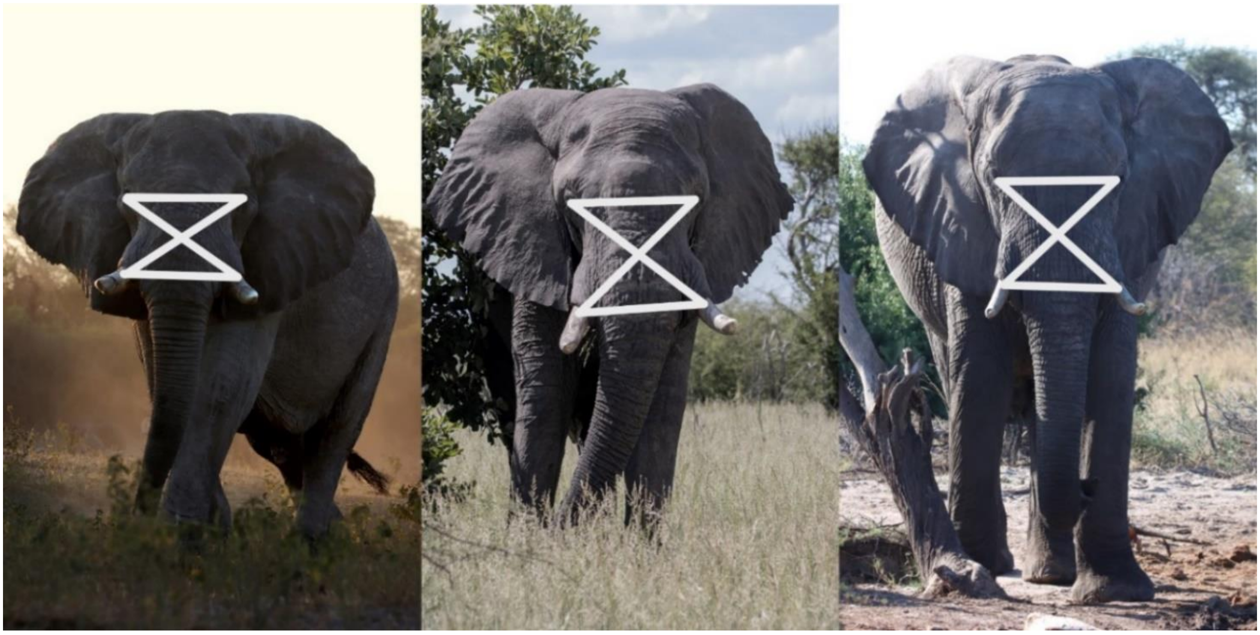


Figure 4: The older the bull, the wider and more compressed the 'hourglass' becomes. From left to right you have the oldest to the youngest.

3.2.3. Who is it?

Photos and descriptions of characteristics for every identified individual are saved as a digital archive in the database, making it possible to manually search for features to match different observations. Douglas-Hamilton (1972) introduced the method of looking at the ears to reliably recognize individuals, which today is widely used for elephant research. By observing notches, cuts and holes in the ears, the pattern of the blood vessels, and the size and shape of the tusks, one can distinguish an individual; characteristics that become more distinguishable with age (Douglas-Hamilton, 1972).

The tusks are elongated incisor teeth that continue to grow throughout the elephant's life (Ngure, 1996). Usage in feeding or fights with other elephants may wear down the tusk or cause it to break. Since one of the tusks is usually used more than the other, the master tusk often becomes blunter (Douglas-Hamilton, 1972). This creates a great variety of shapes which is helpful when identifying individuals. However, since the tusk will continue to grow throughout life, one cannot expect the shape to remain. An elephant may have lost the complete tusk a couple of days after an observation or grown out a new one if some time has passed (Figure 5). The tusks are in other words of great help to identify an individual, but it is a feature that will change as time passes.

Figure 5: This male elephant came into musth (note swollen glands and temporal secretions in the photo to the left) during which he broke his left tusk within the period of 7/5-24 and 14/5-24 when the photos were taken.

The primary feature to look at when identifying an elephant is their ears. Since they are big and floppy, they tend to get stuck in things creating notches and holes in unique patterns. We get V notches, U notches, N notches, M notches, key notches, small notches, large notches, notches with a flop, lobe notches, slits, round holes, linear holes, triangle holes and so on (Figure 6). Since the ears cannot mend themselves, almost every elephant has a unique set of notches and holes that we could search for in the database to find if the individual has been photographed before.

This method is enough most of the time, but the features of the ears and tusks may change and if that is the case, the wrinkles around the eyes are an excellent way to ensure that the identification is correct (Chui & Karczmarski, 2022).

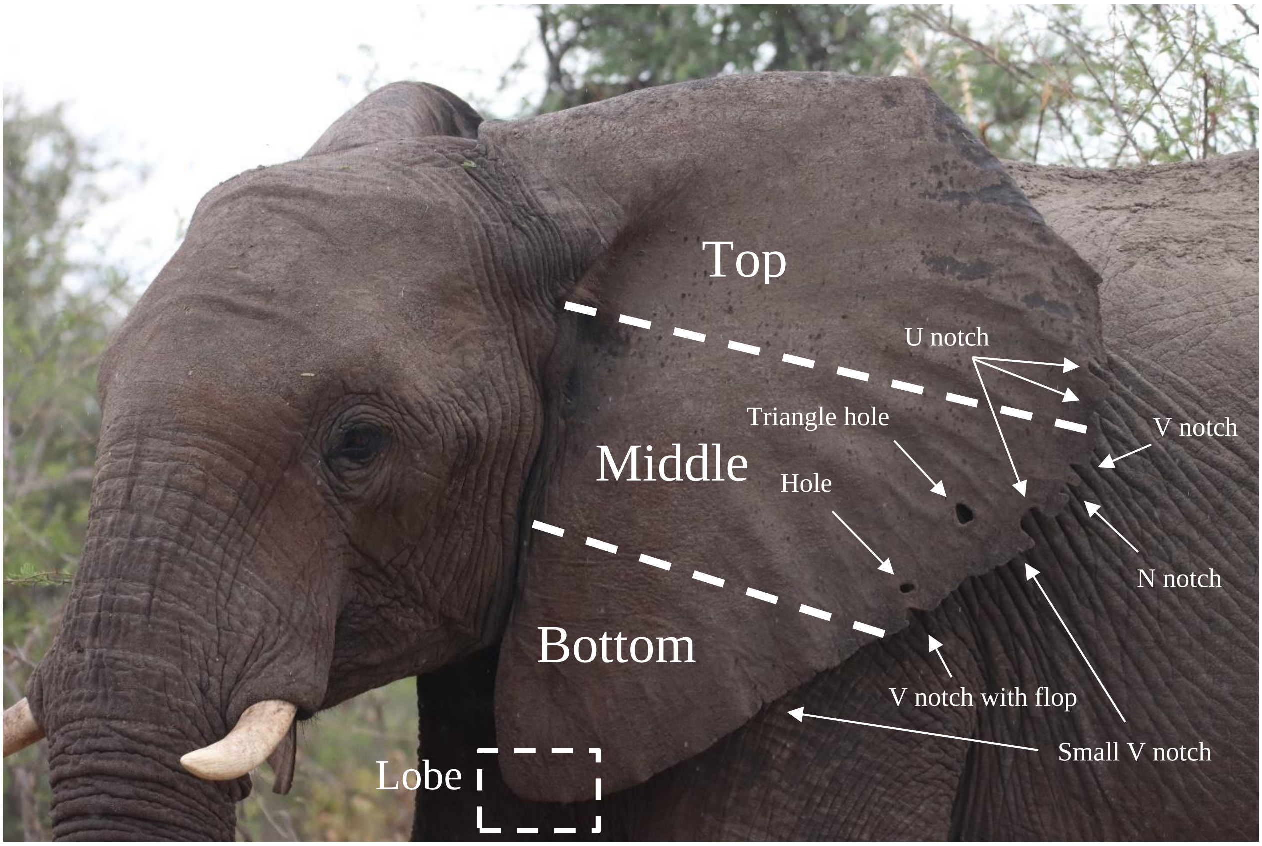


Figure 6: The unique set of markings in the ears is the main feature used to identify individual elephants, even the absence of notches could be used since this is very rare for an elephant. Eye wrinkles and characteristics of the tusks could also help identify them.

3.2.4. What is a group?

The two criteria I have used to define the membership of a group are spatial proximity and behaviour. In other words, the members of a group are spatially close to each other and engaged in the same behaviour. What distance I regarded as close differed depending on habitat, where the members could spread out more in an open habitat like the *Vachellia* savannah and still be considered as associating, whilst they must be much closer to each other in a riverine forest. The direction of movement was also considered where elephants moving in the same speed and direction were recorded as a group, whereas individuals in proximity but moving in different directions were not.

3.3. Analysing

The data collected during the time the author was in the field (January-May 2024), together with historical data (2012-2024), was used as mark and recapture data to estimate the elephants' length of stay and social dynamics by using the MATLAB program SOCPROG, developed by Hal Whitehead (Whitehead, 2009).

3.3.1. Estimating the probability of reidentifying individuals

The lagged identification rate estimates the probability of re-identifying an individual given the time lag since last identified (Gowans et al., 2000; Whitehead, 2007; Pitfield, 2017). This was done to calculate the bull's periods of presence in, and absence from, the study area, and how it differs between different age groups and during different seasons. In this study, the dry season was set as May to October, and the wet season as November to April. SOCPROG has several models that can be fitted to the lagged identification rates, some of which estimate demographic effects such as emigration, reimmigration, and mortality. The models estimated up to 4 parameters; these were population size, number of days in the study area, number of days outside the study area, and mortality. Note that mortality is in this study a collective term for mortality, permanent emigration and misidentification.

The parameter starting values of the model could be adjusted to improve the model, this was shown to impact the result of some analyses. I experimented with trying the default start parameters and with values that would represent the previous findings (Chase et al., 2014; Pitfield, 2017), both of which showed imprecise confidence intervals. After some more experimenting, the start parameters were set to 100 for population size, 100 for days in the park, 100 for days outside the park, and 0.5 for mortality rate. I used these start parameters in analyses made on the whole population as well as on specific age groups since they gave the most precise estimates and kept the starting values consistent throughout the study. However, the optimal value for each start parameter might not have been found due to time constraints.

When running the analyses, SOCPROG provided the QAIC (Quasi-Akaike Information Criterion) for the different models. By comparing the ΔQAIC, i.e. the difference between the QAIC values of different models, I got an indication of how well the data supported the different models and this helped me choose which model(s) to use. The model with the lowest QAIC got a ΔQAIC of 0. The QAIC of this model was subtracted from the QAIC of the other models to obtain their score. A score in ΔQAIC of 0-2 indicated substantial support for the model, 4-7 indicated considerably less support, and >10 meant essentially no support (Burnham & Anderson, 2002). The first analysis was done using all the models to be able to compare the QAIC. The model that got the lowest score, i.e. suited my data the best, was then run again with 1,000 bootstrap replications. A bootstrap replication is a resampling with replacement from the collected data; doing this 1,000 times gave an estimate of uncertainty by showing how the model varies when some subsets of the data were included or excluded (Whitehead, 2008).

SOCPROG also provided a function that could restrict the data to only include certain parts in an analysis. This function was used when analysing specific age groups or periods of the year.

3.3.2. Estimating if associations are preferred or random

Similar to the lagged identification rate, the standardised lagged association rate is the probability of re-associating two individuals in a given time lag (Whitehead, 1997; Whitehead, 2007). By using a standardized version, we can estimate the association rate for re-associating individuals and account for migration or other demographic effects (Whitehead, 2008; Farine, 2013). The standardised lagged association rate can then be compared to the null lagged association rate, which estimates the association rates if the population is associated randomly (Whitehead, 2008). Moving averages were used to make the plotted association rate smoother. This is done by making a series of averages instead of plotting all the data points. Different models could be fitted to the association rate and just like with the identification rate, ΔQAIC of the models was used to select the one(s) that best suited the data (Whitehead, 2009). When fitting models to the association rate, SOCPROG provided parameters that could be used to estimate different social structures (Whitehead, 2008). The different models provided slightly different parameters and depending on the model, different equations had to be used (Table 2). The three different models that I used were "Casual acquaintances", "Preferred companions and casual acquaintances" and "Two levels of casual acquaintances".

"Casual acquaintances" is a model that uses an initial association rate (a2) and a rate of the decay of the association (a1) to estimate how the association rate changes over time (td). The model equation of the model looks like this: $a2 \times exp^{-a1 \times td}$

"Preferred companions and casual acquaintances" are similar to the first model but also assume that some companions are preferred (a2) and that their association rate doesn't decay. There is also an initial association rate for casual acquaintances (a3), and this has a rate of decay (a1) that influences the association rate over time (td). The equation of the model is as following: $a2 + a3 \times exp^{-a1 \times td}$

"Two levels of casual acquaintances" assume in turn that the associations consist of two types of acquaintances. One has an initial association rate for a short-term relationship (a3) that decays (a1) over time (td). The other relationship has an initial rate for long-term associations (a4) with a long-term decay (a2). This model looks like this: $a3 \times exp^{-a1 \times td} + a4 \times exp^{-a2 \times td}$

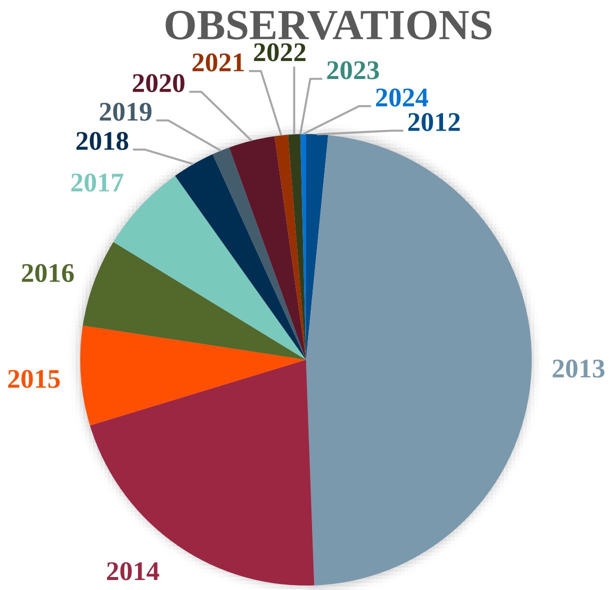
Table 2: Different estimations possible to do with the parameter values provided by the standardised lagged association rate (Whitehead, 2008).

Model	**Social structure**	**Equation**
Casual acquaintances (CA)	Duration of association	$(\frac{1}{a1})$
Preferred companions and casual acquaintances (PC+CA)	Length of short-term associations	$(\frac{1}{a1})$
	Gregariousness = Typical number of associations	$(\frac{1}{a2+a3})$
	Typical unit size = Number of preferred companions	$(1 + \frac{a2}{(a2+a3)^2})$
	Rate of observed with a preferred companion (Ratio of PC)	$(1/\left(\frac{Unit\ size}{Gregariousness}\right))$
Two levels of casual acquaintance (2LVLCA)	Length of short-term casual acquaintances	$(\frac{1}{a1})$
	Length of long-term casual acquaintances	$(\frac{1}{a2})$

4. Results

The dataset used for all analyses consisted of uniquely identified individuals. The database also contains temporary individuals who are yet to be matched with existing IDs or converted into new ones. Because I didn't know if the temporary individuals had been observed before, it would make no sense to include them in the lagged identification rate; but perhaps in the lagged association rate since this part of the study doesn't look at a specific ID, but rather the relationship between different age groups. I decided to only keep the uniquely identified individuals and keep a consistent dataset for all analyses, but the pros and cons of this decision are discussed in section 5.1.2..

The mean number of observations was 2.2 observations per elephant (continuously referring to the savannah elephant). Most of these observations were made in 2013 and 2014 when the organisation started collecting IDs, but it has continued throughout the study period (Figure 7). A few individuals were observed >15 times over the years but most elephants were seen once or twice. About 6% of the observations were registered with an unknown (UK) age, these were still included in the study as a part of "All", i.e. all elephants no matter the age. Besides belonging to "All", all individuals except the ones with unknown age are classified into one of four age groups "<21", "21-25", "26-35" or "36+". In this study, most of the bulls were under the age of 21, but all four age groups were well represented (Figure 7).



N	Obs	<21	21-25	26-35	36+	UK
1391	3007	873	673	830	458	173

Figure 7: The dataset for the analyses consisted of 3,007 observations of 1,391 elephants over 12 years. Most of these observations were made in this period's first half, but IDs have been collected in all years except 2023. The observations were categorized into one of five age groups, a few had unknown age (UK) and were only used in analyses as part of the whole population.

4.1. Length of stay

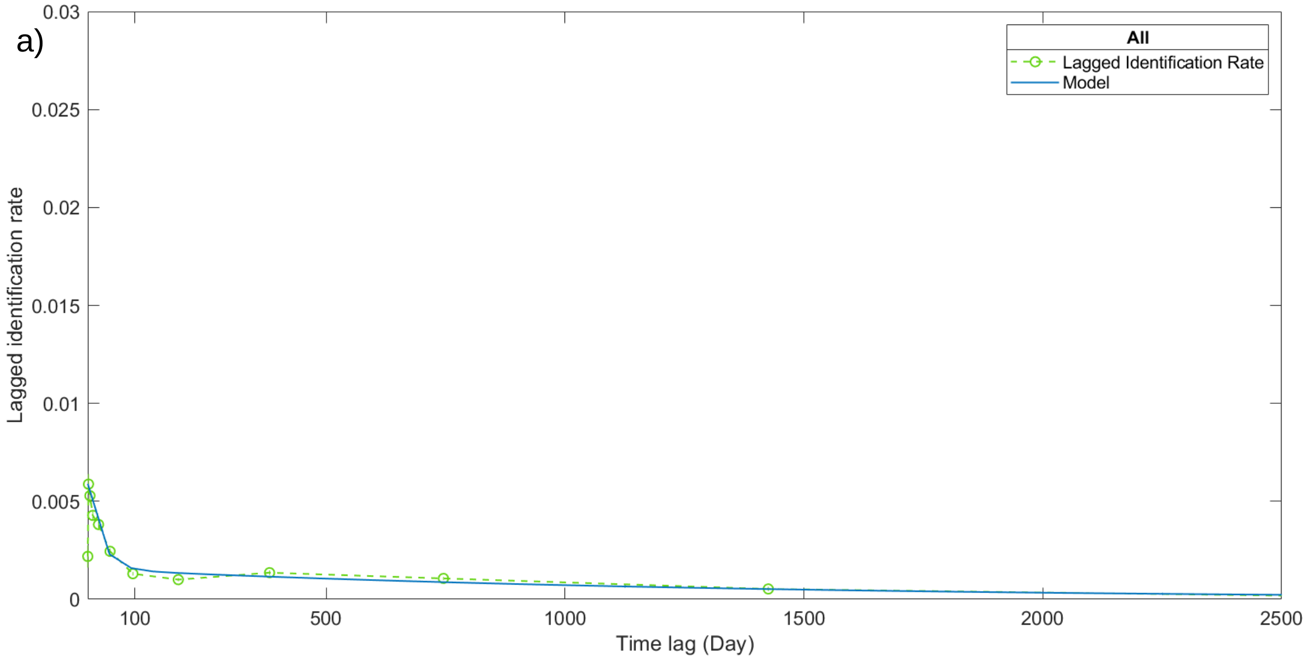
4.1.1. Estimating movement patterns

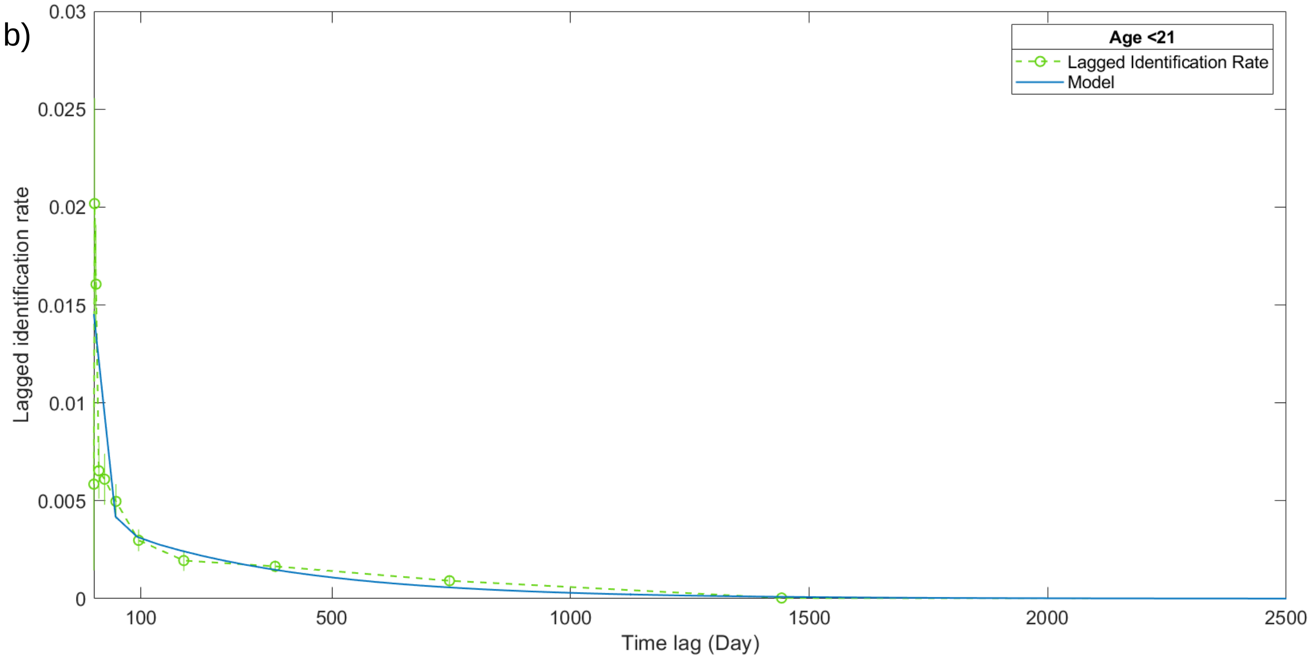
Analysing lagged identification rates helped us estimate elephants' lengths of stay in the park. The ΔQAIC was used to evaluate how well my data fitted the models and the results showed that the model "Emigration + reimmigration + mortality" had substantial support in all analyses (Table 3). This model included parameters for population size, days inside the park, days outside of the park, and mortality rates, which in the study include permanent emigration and misidentification. The other evaluated model was named “Emigration + reimmigration” and excluded the parameter for mortality rate. This model scored lower in the analysis for the age group 36+, meaning that the model was a better fit for this age group. However, since the model including mortality had the lowest ΔQAIC in the other and substantial support in all analyses, I decided to use this model consistently throughout the study.

Table 3: The ΔQAIC indicated that the model including mortality had substantial support from the data in all analyses.

ΔQAIC	Emigration + reimmigration	Emigration + reimmigration + mortality
All	>10	0
<21	>10	0
21-25	>10	0
26-35	4	0
36+	0	1
Wet season	>10	0
Dry season	>10	0

All the graphs showed a steep decline in the lagged identification rate during the first 100 days before the curve evened out to slowly decrease over time. The parameter for mortality rate was always very low but existed, making the probability of reidentifying an elephant continue to decrease over time. Since the sampling period was set to “Day”, the information extracted from the analysis is the mean each day. Thus, the mean time spent in the park before leaving was 37, with a 95-percentage CI reaching between 31 and 48 days. The mean time outside the park was 108 days with a 95-percentage CI stretching between 87-138 days. The mortality rate for the population is estimated to be 0.000764, which means that the probability that an individual dies or leaves permanently is 0.0764% per day (Table 4). The estimations of these four parameters are included in the equation that makes the model that is plotted as a line in the following graphs (Figure 8).


a)
All
Lagged Identification Rate
Model
Lagged identification rate
Time lag (Day)
0.03
0.025
0.02
0.015
0.01
0.005
0
100
500
1000
1500
2000
2500


b)
Age <21
Lagged Identification Rate
Model
Lagged identification rate
Time lag (Day)
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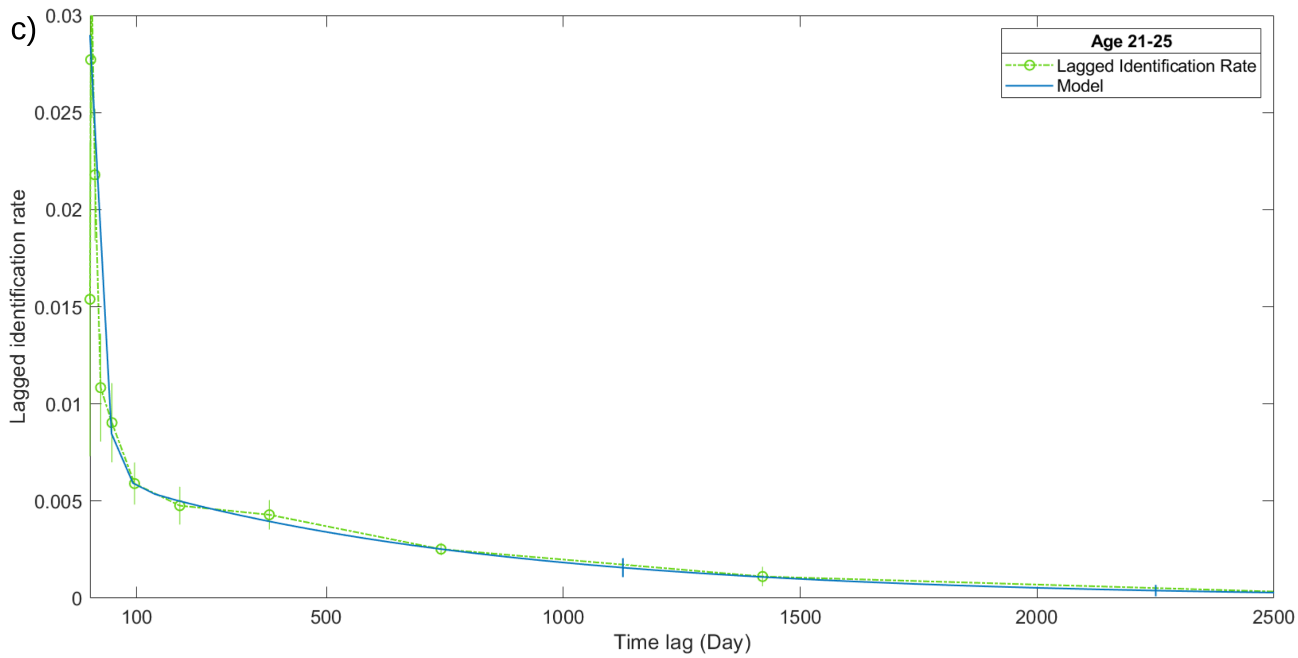
0.02
0.015
0.01
0.005
0
100
500
1000
1500
2000
2500


c)
Age 21-25
Lagged Identification Rate
Model
Lagged identification rate
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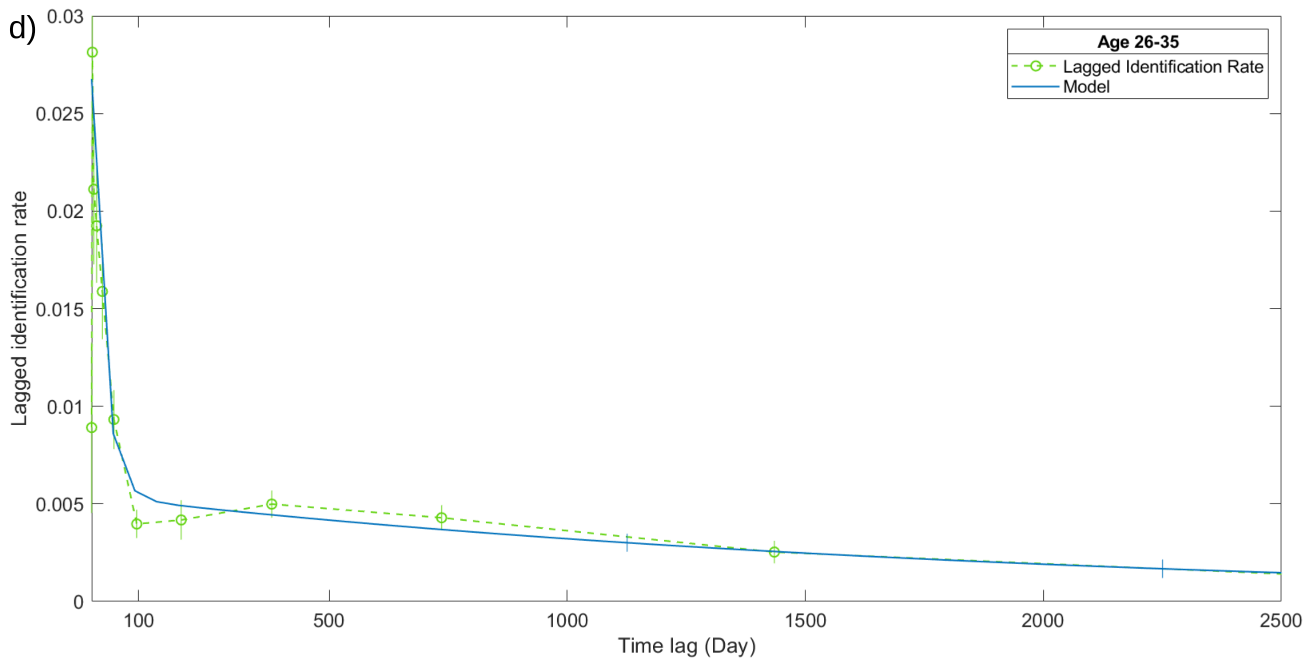
1500
2000
2500
Time lag (Day)


d)
Age 26-35
Lagged Identification Rate
Model
Lagged identification rate
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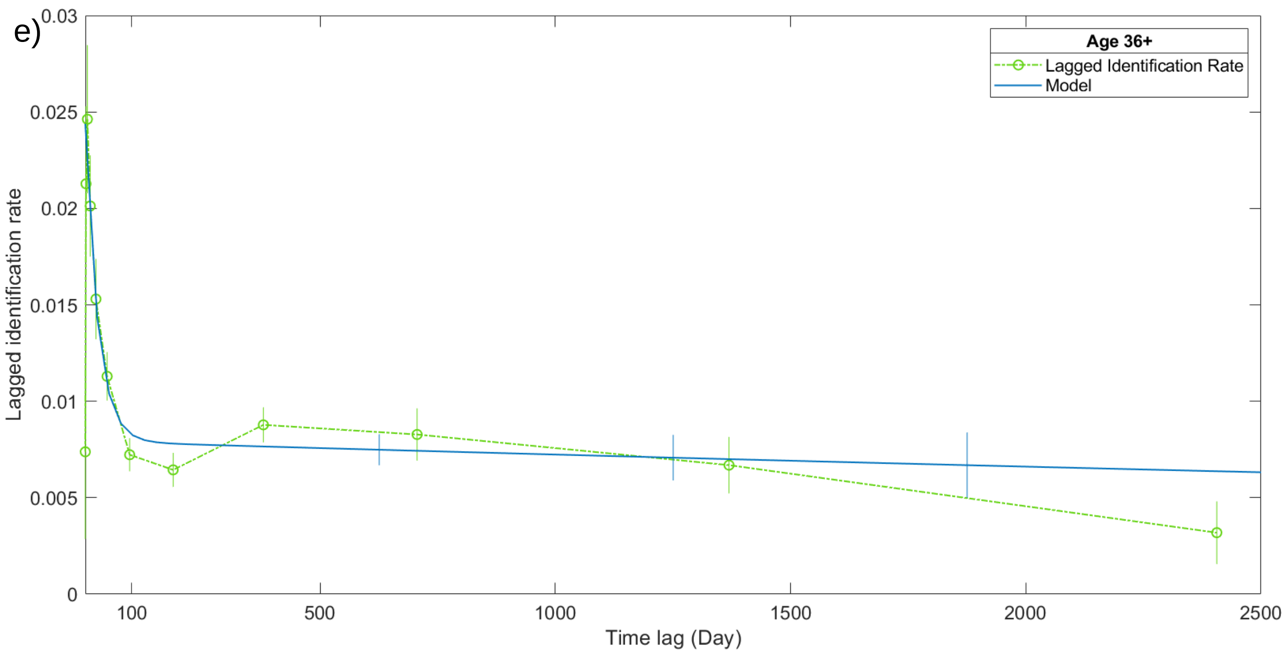
0.01
0.005
0
100
500
1000
1500
2000
2500
Time lag (Day)



e)
Age 36+
Lagged Identification Rate
Model
Lagged identification rate
Time lag (Day)
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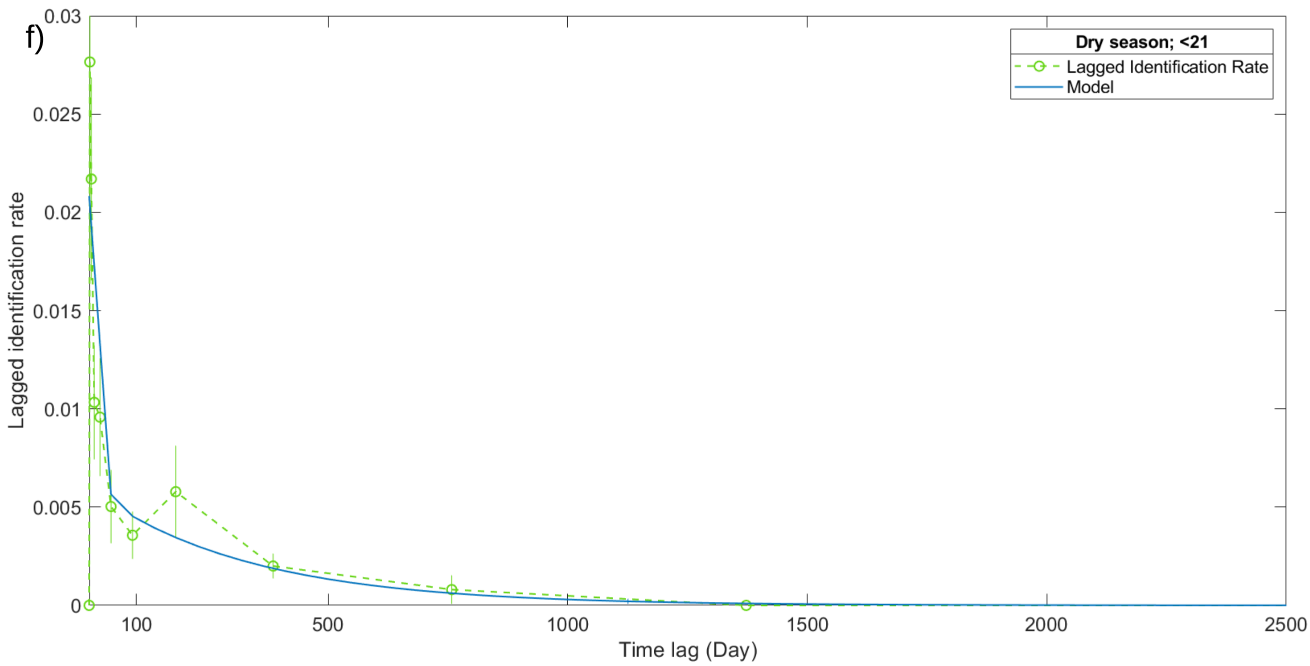
0.02
0.015
0.01
0.005
0
100
500
1000
1500
2000
2500



f)
Dry season; <21
Lagged Identification Rate
Model
Lagged identification rate
Time lag (Day)
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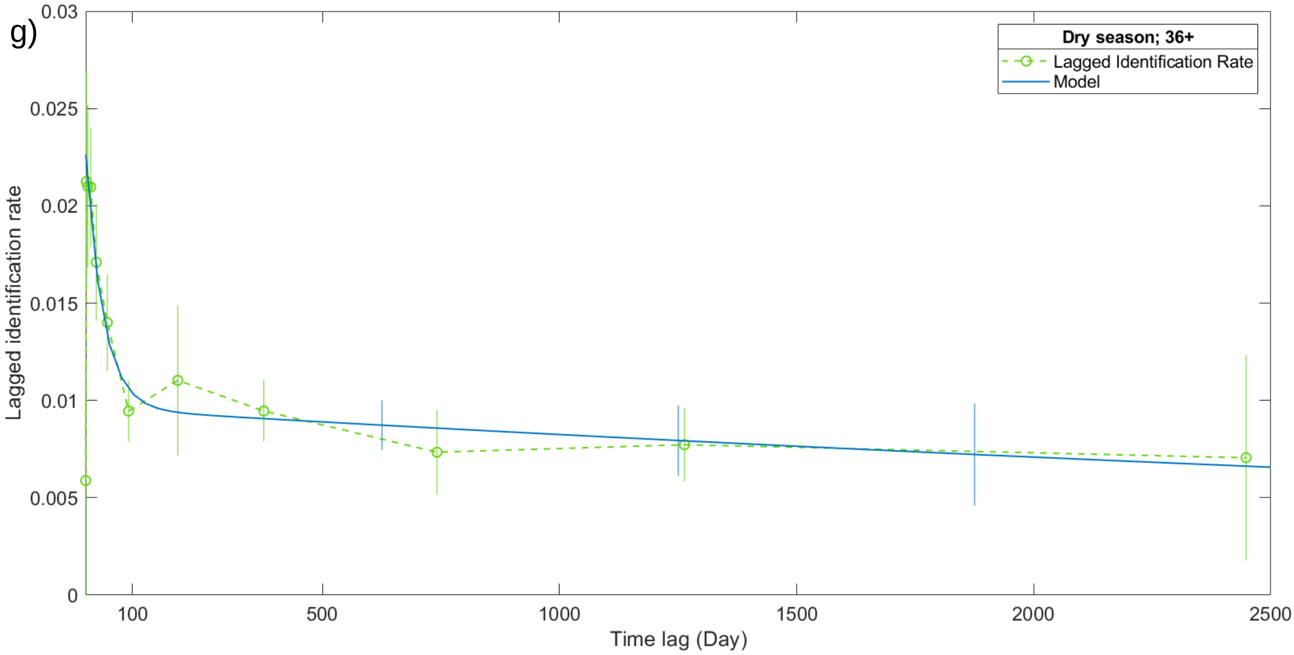
0.025
0.02
0.015
0.01
0.005
0
100
500
1000
1500
2000
2500


g)
Dry season; 36+
Lagged Identification Rate
Model
Lagged identification rate
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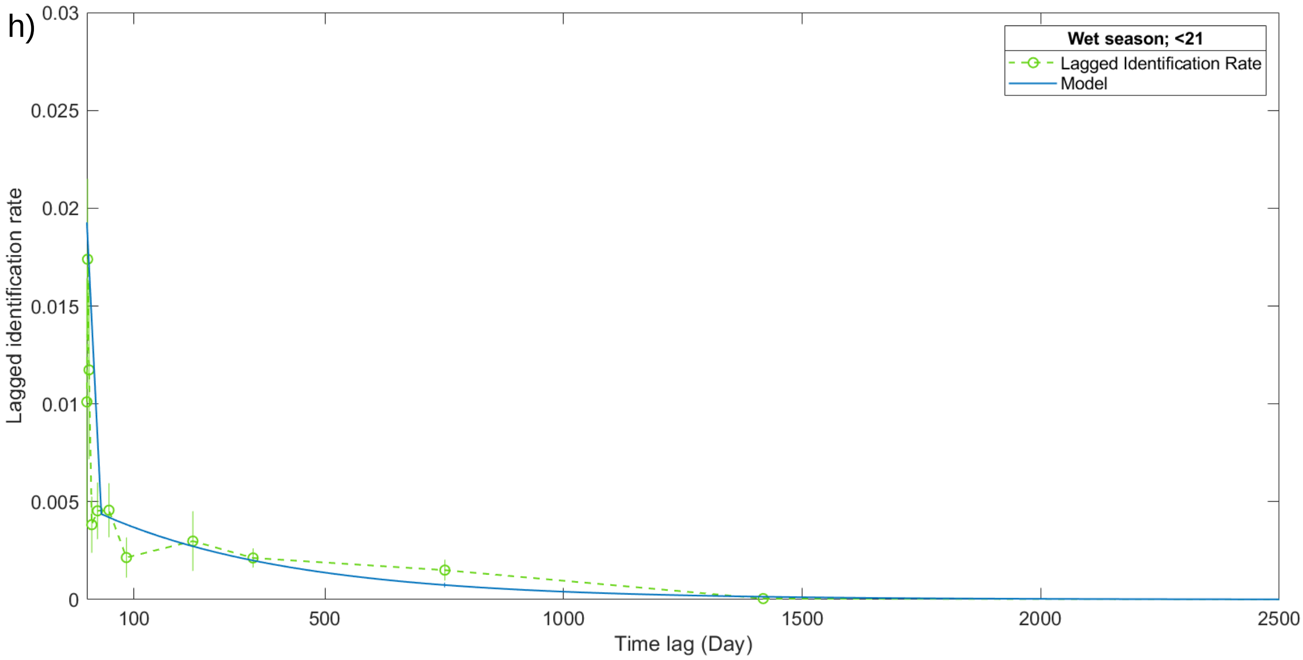
0.015
0.01
0.005
0
100
500
1000
1500
2000
2500
Time lag (Day)


h)
Wet season; <21
Lagged Identification Rate
Model
Lagged identification rate
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0.005
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2000
2500
Time lag (Day)

i)

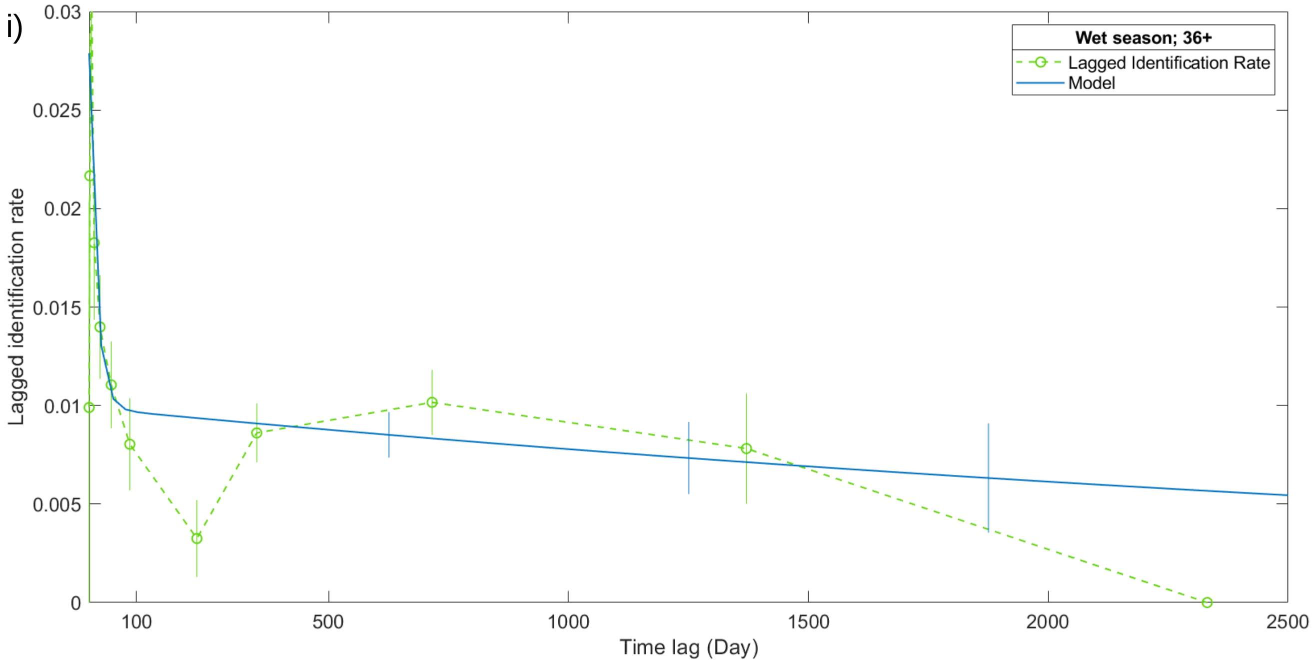


Figure 8: The lagged identification rate, i.e. the probability of reidentifying an individual after a time lag, is plotted for different age groups and seasons of the year. The identification rate is plotted on the Y-axis and the time lag since the first observation is plotted on the X-axis. Each data point, called "Lagged Identification Rate" in the graph, represents the average lagged identification rate between two time lags, and the point is placed at the mean of these time lags. The data point also includes a bar showing the standard error of the lagged identification rate.

a) The lagged identification rate for all individuals decreases rapidly for the first 100 days before becoming more stable at about 0.002, meaning that about 1 in 500 is the same individual after 100 days.

b) The lagged identification rate for elephants under the age of 21 stabilises beneath 0.002.

c) The probability of reidentifying a bull between the ages of 21 and 25 decreases fast for the first 100 days and is almost zero after 2,500 days.

d) The elephants between the ages 26 and 35 are more likely than the younger elephants to be reidentified over long time lags.

e) The lagged identification rate for males aged 36 and over was higher than for the other age groups. The probability to reidentify an individual was after 2,500 days still over 1 in 200. Possible explanations for the higher identification rate will be analysed in the discussion.

f) The probability of reidentifying an individual of the age group <21 will during the dry season decrease from about 0.025 to 0.005 within the first 100 days after the first observation. The probability decays at a slower rate after about 100 days but will reach 0 after about 4 years.

g) The probability to reidentify an individual of the age group 36+ is likely to remain between 0.5-1% over the 7 years plotted.

h) The lagged identification rate is slightly lower during the wet season compared to the dry, but the rate of decay is also lower making the identification rate reach 0 at a later stage.

i) The probability of reidentifying an individual of the age group 36+ during the wet season seems to decrease at a higher rate both in the initial stage, but also over long periods compared to the dry season.

In addition to the graphs, the analyses provided estimates of the parameters and a confidence interval (Table 4). The information is the same as what is visualised in the graphs, and it helps us observe differences between age groups and/or seasons. This means that each day during the wet season, the average number of elephants (N) of age

36 or above (36+ Wet) is estimated to be 34 (CI 22-61) and they stay on average 22 (CI 10-239) days in the park (Days in).

Table 4: From the lagged identification rate, I got information about the population size (N), how many days the elephants stayed in and out of the park, and the mortality rates which also include permanent emigration and misidentification.

Category	N	(95-% c.i.)	Days in	(95-% c.i.)	Days out	(95-% c.i.)	Mortality	(95-% c.i.)
All	165	(152-184)	37	(31-48)	108	(87-138)	0.000764	(0.000590-0.001054)
<21	66	(34-91)	23	(6-64)	67	(22-166)	0.002579	(0.002067-0.003426)
21-25	33	(23-52)	27	(11-62)	101	(48-189)	0.001236	(0.000623-0.002109)
26-35	36	(29-47)	31	(22-39)	127	(86-189)	0.000520	(0.000281-0.000843)
36+	40	(31-50)	39	(25-56)	85	(54-132)	0.000090	(-0.000184-0.000375)
Wet season	182	(139-225)	15	(10-26)	27	(18-46)	0.000843	(0.000488-0.001159)
<21 Wet	43	(30-92)	5	(2-27)	20	(9-51)	0.002462	(0.001951-0.003081)
36+ Wet	34	(22-61)	22	(10-239)	43	(22-133)	0.000238	(-0.000152-0.000911)
Dry season	150	(132-177)	53	(41-67)	117	(71-161)	0.000961	(0.000652-0.001352)
<21 Dry	45	(25-77)	19	(7-48)	51	(16-168)	0.002984	(0.001534-0.005189)
36+ Dry	44	(33-61)	64	(28-128)	89	(32-305)	0.000152	(-0.000330-0.000829)

4.1.2. Estimating social dynamics

Association rates were used to decipher the relationships of bulls. This was done by estimating the probability that two associating bulls would associate again some time later. I used the ΔQAIC of three different models and the look of the graphs to evaluate how well the models fitted my data. Only models that had substantial support from the data, i.e. an ΔQAIC between 0-2, were used for estimations and calculations (Table 5). The model "Preferred companions and casual acquaintances" was the most used, followed by the model for "Casual acquaintances" and the least used "Two levels of casual acquaintances".

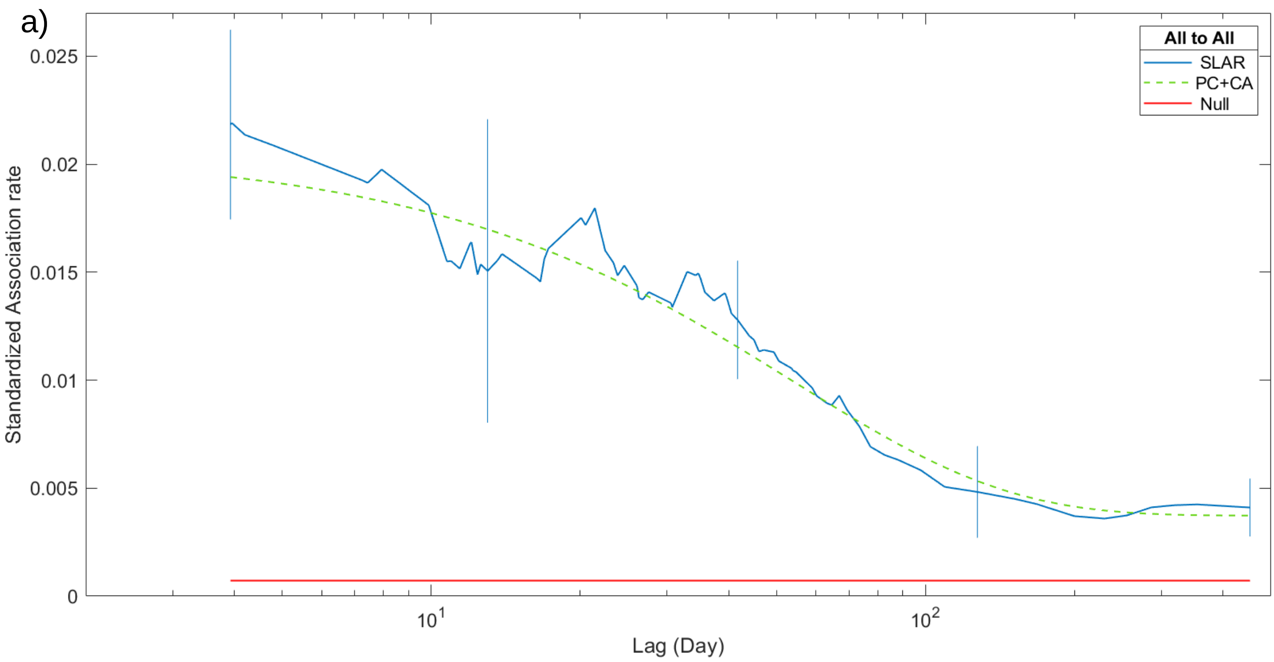
The analyses investigate the relationships between different age groups of the perspective from one group to another (Figure 9). "All" indicates that associations of individuals from all age groups to all age groups are considered. This therefore shows the average probability that a bull of any age group will be reassociating with another bull of any age group after a given time lag (Figure 9a). The relationship "<21 to All" examines the probability that a male under the age of 21 will be reassociated with a bull of any age after a time lag (Figure 9b). Finally, the relationship "All to <21" estimates the probability that a bull of any age will be reassociated with a male under the age of 21 (Figure 9f).

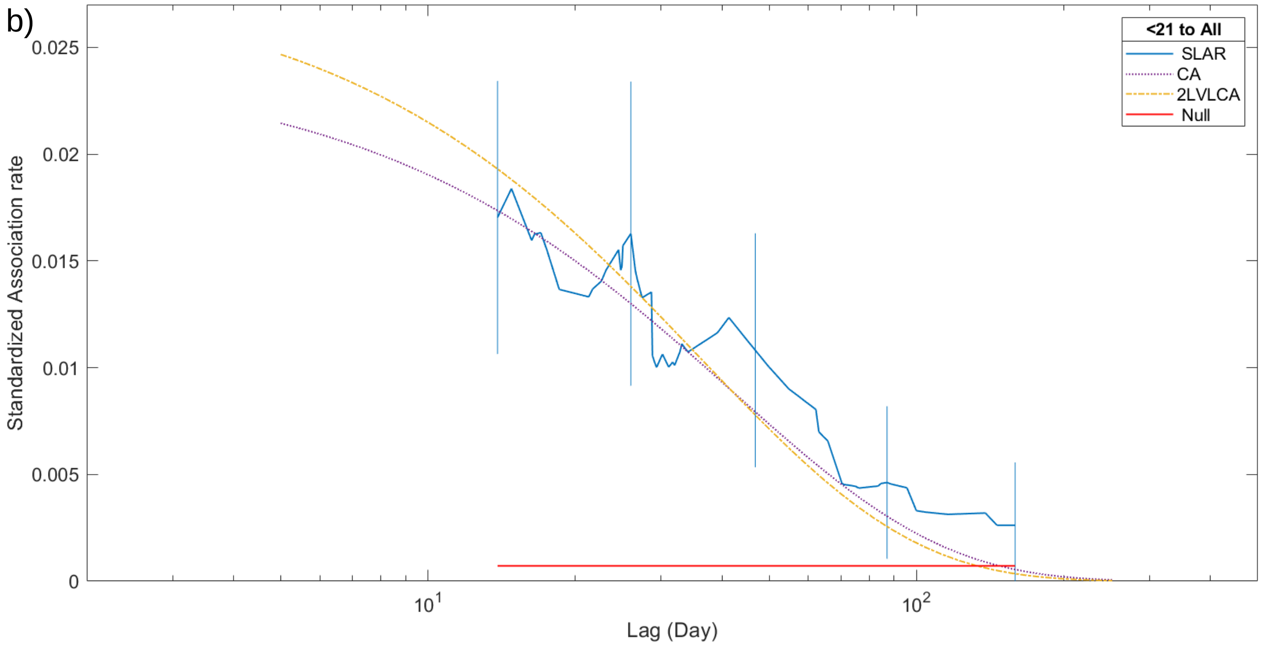
All relationships had at least one model that was a good fit except for this last-mentioned group, the relationships of "All to <21". The ΔQAIC showed significant support for all three models but none aligned with the data when looking at the graph (Figure 9f). The likely explanation for this is that the data doesn't fit any of the models. Therefore, any further estimations made from this relationship were disregarded.

Table 5: The ΔQAIC indicates how well the data supports the three models, “Casual acquaintances” (CA), “Preferred companions and casual acquaintances” (PC+CA) and “Two levels of casual acquaintances” (2LVLCA). A score between 0-2 implies substantial support, 4-7 suggests considerably less support and over 10 means essentially no support.

ΔQAIC	CA	PC+CA	2LVLCA
All	>10	0	>10
<21 to All	0	>10	1
21-25 to All	>10	0.5	0
26-35 to All	3.5	0	7.5
36+ to All	>10	0	>10
All to <21	0	1.5	3.5
All to 21-25	>10	0	1.5
All to 26-35	0	>10	4
All to 36+	0.5	0	4.5
Dry; All	0	>10	4
Wet; All	0	10	1.5

The model used for the association rate between all individuals was the “preferred companions + casual acquaintances”. The association rate decreased with time until it stabilised after a bit more than 100 days above the null lagged association rate which could be seen as “the line of random association” (Figure 9a). An association rate that stabilises above the null indicates non-random associations, i.e. that the individuals have some preferred associates. However, in some graphs, the association rate fell below the null which implies random associations, interpretations and potential reasons for this are discussed in section 5.1.2..




b)
<21 to All
SLAR
CA
2LVLCA
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Standardized Association rate
Lag (Day)
0.025
0.02
0.015
0.01
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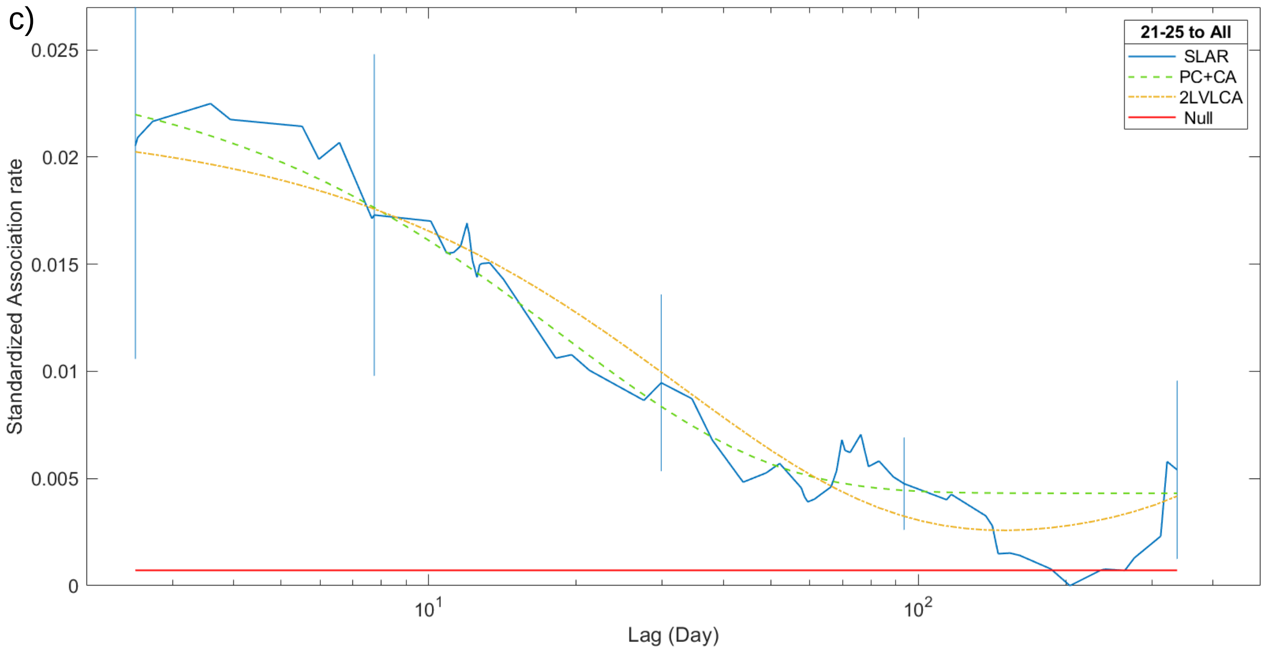
0
10^1
10^2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21-25 to All
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PC+CA
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Lag (Day)
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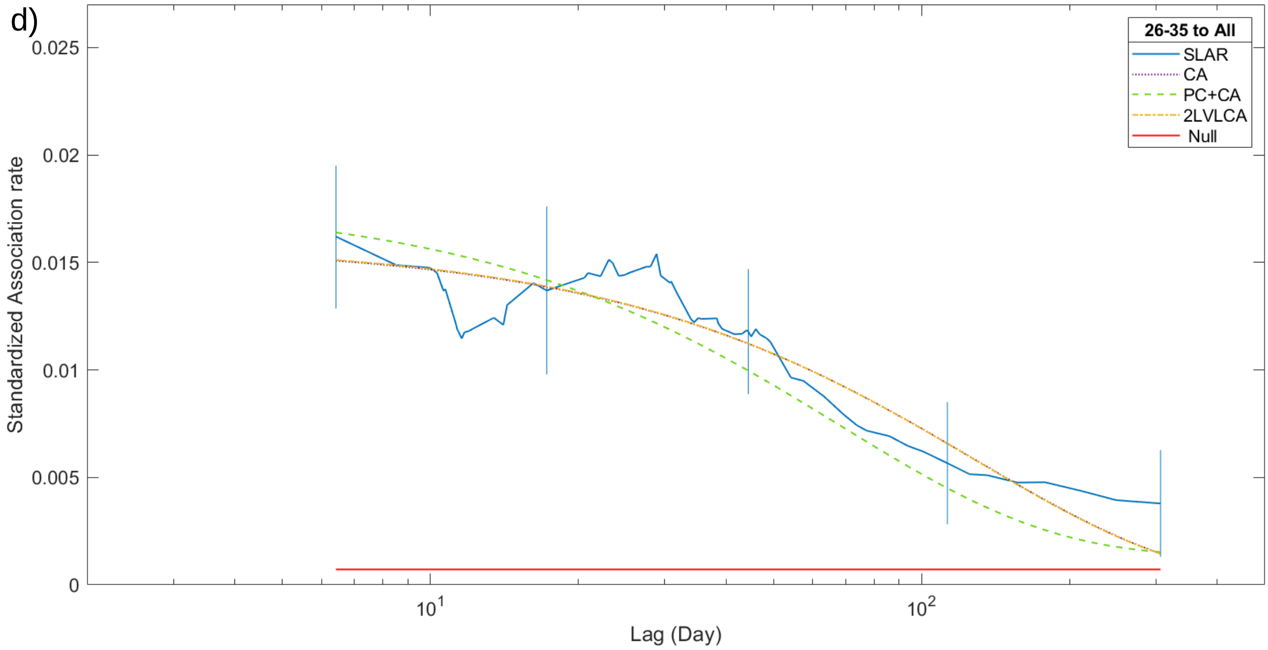
10^1
10^2



d)
26-35 to All
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CA
PC+CA
2LVLCA
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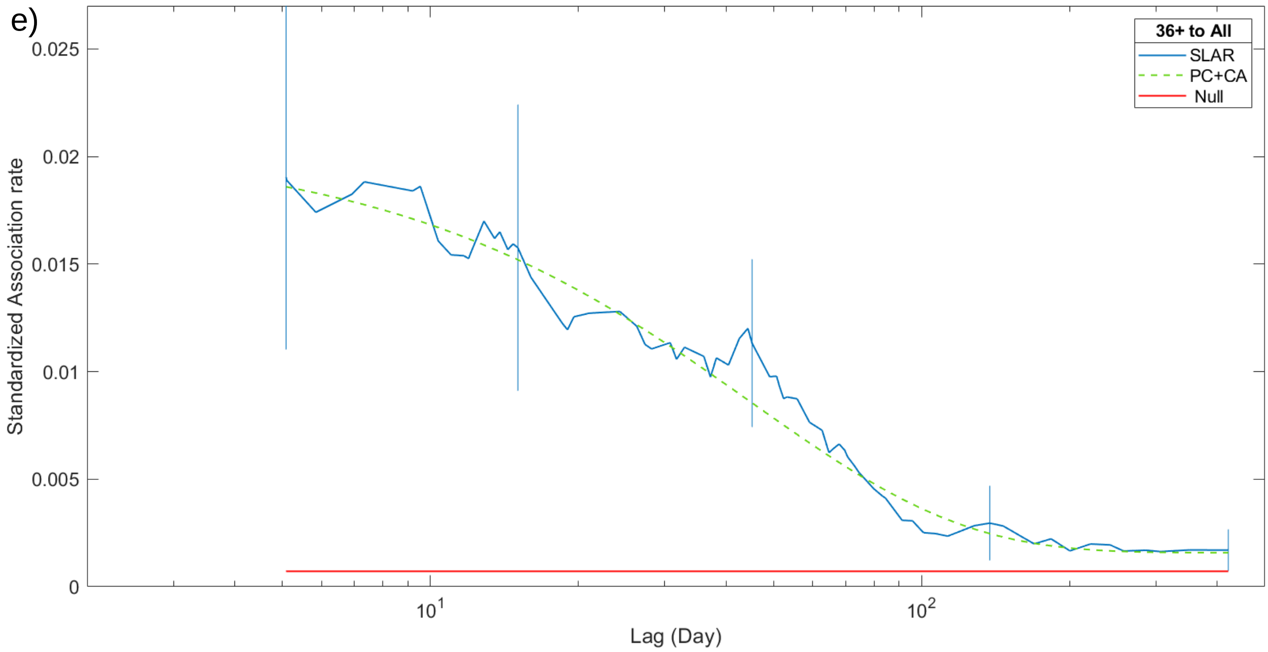
0
Standardized Association rate
10^1
10^2
Lag (Day)



e)
36+ to All
SLAR
PC+CA
Null
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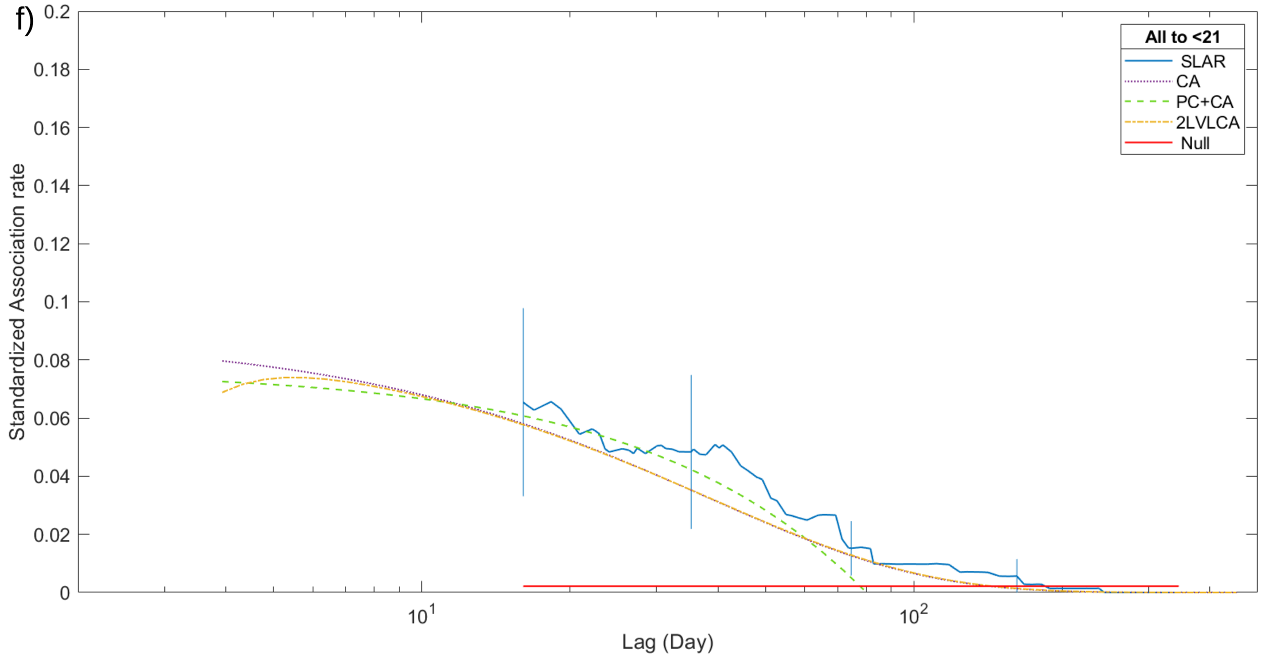
0.015
0.01
0.005
0
Standardized Association rate
10^1
10^2
Lag (Day)

f)


All to <21
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PC+CA
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Null
Standardized Association rate
Lag (Day)
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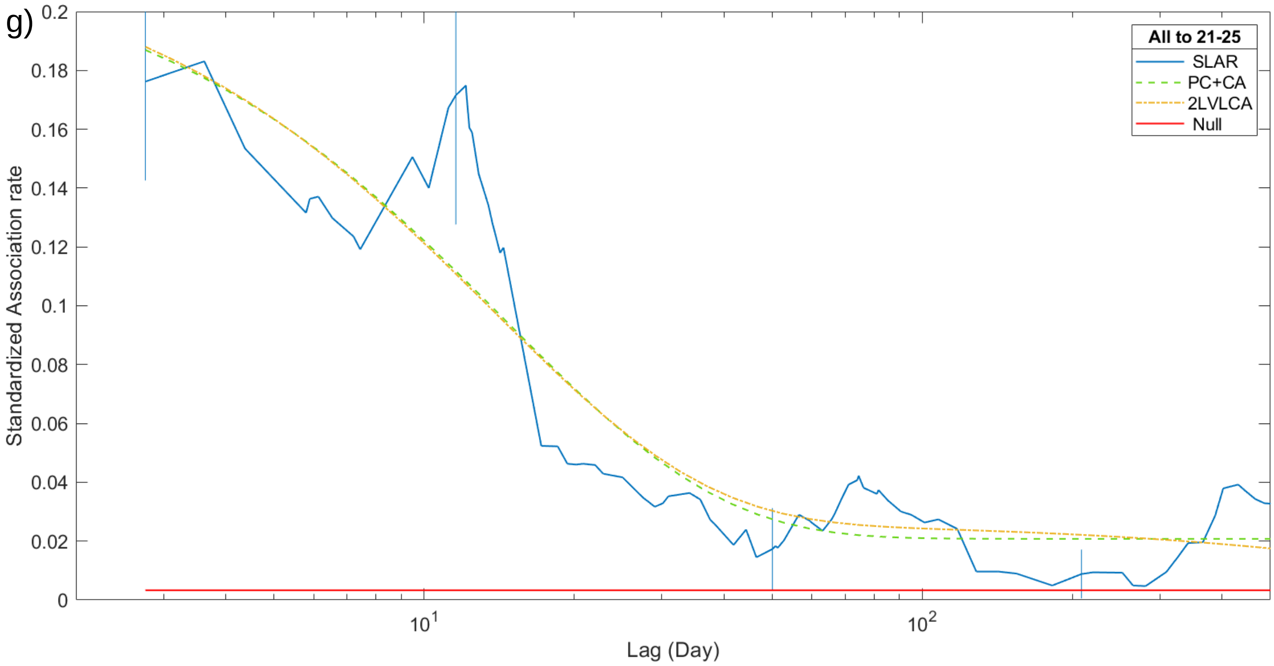
0.1
0.08
0.06
0.04
0.02
0
10^1
10^2

g)


All to 21-25
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PC+CA
2LVLCA
Null
Standardized Association rate
Lag (Day)
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0.04
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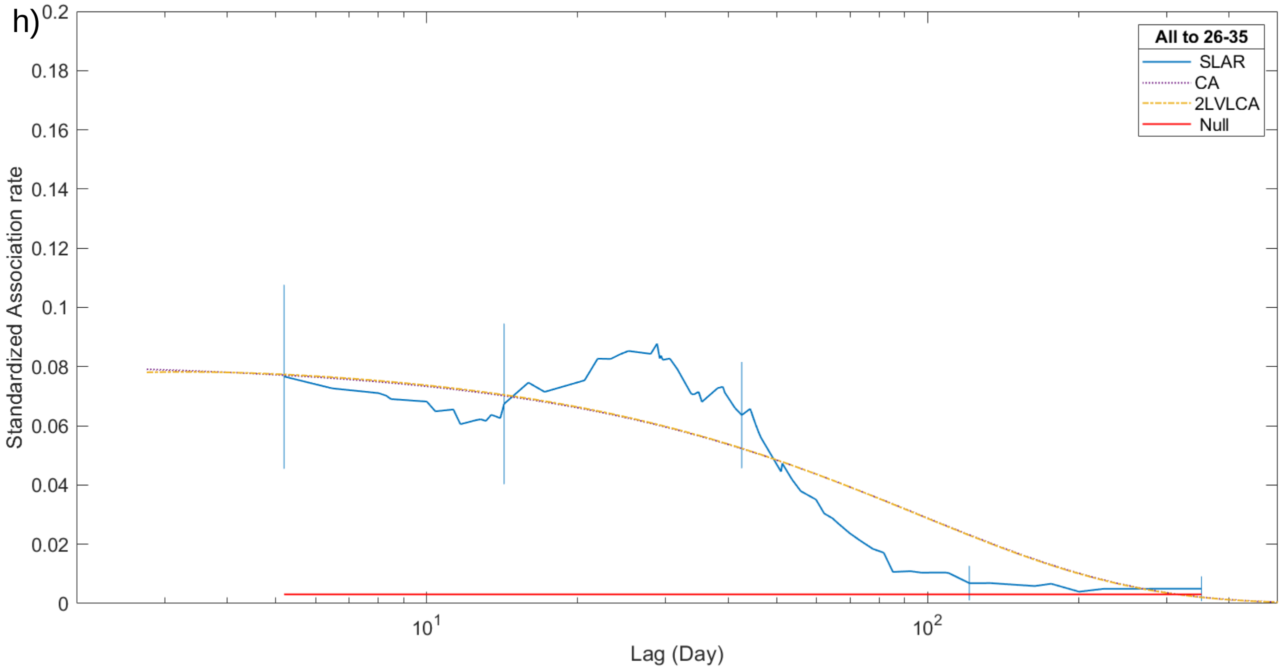
0
10^1
10^2



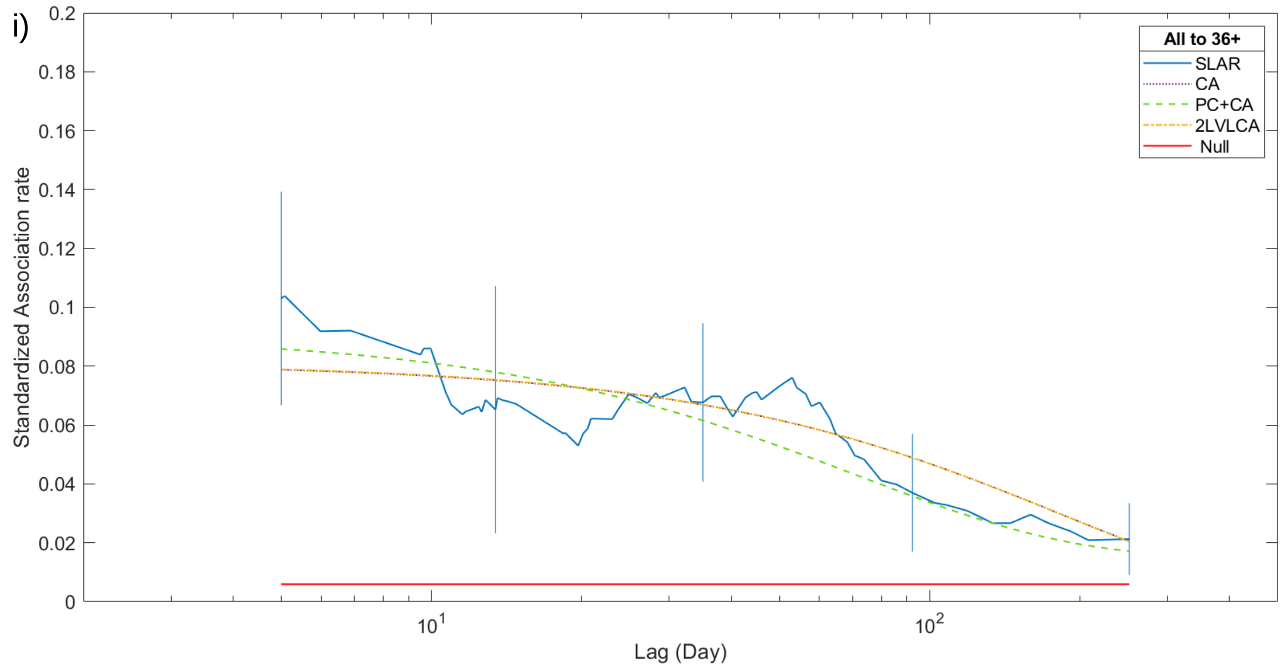


Figure 9: The graphs demonstrate how the average probability of reassociating two individuals of two age groups changed over time. The standardized association rate was plotted on the Y-axis and the time since the first observation was plotted on the X-axis. The line labelled as "SLAR" is the calculated association rate of the data used. The line called "Null" is the null lagged association rate and demonstrates the rate of association that should be observed if associations were random. The other potential lines are the models, and all models with a ΔQAIC less than 10 were included. The model "Casual acquaintances" was marked as "CA" in the graphs and this model assumed that all associations decayed at the same rate. "Preferred companions and casual acquaintances" were labelled as "PC+CA" and this model assumes that some associations decay over time, but that some persist without decay. The third model was the "Two levels of casual acquaintances" which in the graphs were marked as "2LVLCA" and this model assumed that there are two types of acquaintances. Note the smaller scale on the Y-axis in a-e compared to f-i.

a) Standardized lagged association rates of all individuals. It shows a decrease in the association rate before stabilising after about 100 days above the null lagged association rate, indicating non-random association.
b) This graph shows the probability that an elephant of the age group under 21 would reassociate with an elephant of any age.
c) The standardised lagged association rate for elephants of age group 21-25 to individuals of all ages.
d) The probability that an elephant of the age group 26-35 would reassociate with an elephant of any age. All three models are plotted in this graph and the models for “Casual acquaintances” and “Two levels of casual acquaintances” show an almost identical curve.
e) The association rate between age groups “36+” and “All” stabilised above the null, indicating non-random association.
f) None of the models were a good fit for the data on the relationship between elephants of any age and those under the age of 21.
g) The probability of reassociation started high but decreased rapidly and evened out at a rate of about 0.02, i.e. 2% chance of reassociating.
h) This graph shows how the association rate changed over time between elephants of all ages and the elephants of age 26-35.
i) The association rate of all elephants to those over the age of 36 indicates that the associations are non-random.

The parameters provided by the analyses for association rates were then used to estimate the length of associations and the number of acquaintances and companions (Table 2, 6 & 7). The average length of short-term associations for the different age groups was estimated from all three models.

The model “Preferred companions and casual acquaintances” provided parameters that were used to calculate the average gregariousness and unit size of the age groups. The gregariousness was the typical number of associations for the average elephant, while the unit size estimated the number of preferred companions. These numbers were in turn used to estimate the ratio between decaying acquaintances and non-decaying companions. A two in this ratio would indicate that there were twice as many casual acquaintances as preferred companions. A ten would mean that the casual acquaintances were ten times as many (Table 7).

Table 6: Length of short-term associations estimated from the three models, the numbers in *bold are from the model with the lowest QAIC.

Days	CA	PC+CA	2LVLCA
All	223	***54**	1
<21 to All	***42**	0	0
21-25 to All	250	19	***34**
26-35 to All	128	***68**	1
36+ to All	107	***45**	0
All to 21-25	182	***15**	14
All to 26-35	***96**	1	1
All to 36+	183	***72**	0
Dry; All	***350**	1	1
Wet; All	***243**	0	0

Table 7: The typical number of associations (Gregariousness), the number of preferred companions (Unit size) and the ratio between the two (Ratio of PC) were calculated for the relationships where the model "PC+CA" had a ΔQAIC <2.

PC+CA	Gregariousness	Unit size	Ratio of PC
All	49	10	5
21-25 to All	41	8	5
26-35 to All	56	5	11
36+ to All	48	5	10
All to 21-25	5	1	3
All to 36+	1	1	1

5. Discussion

5.1. Length of stay

5.1.1. Movement patterns in the park

The first part of the study was to investigate male movement patterns in and out of the national park and how it differed between age groups and seasons of the year. The lagged identification rate had a drastic decline in the first 100 days before the steepness decreased and slowly went down to zero after long time lags (Figure 8a). This indicates that an individual is most likely to be reidentified shortly after an observation, but that the probability decreases fast before it stabilizes at longer time lags. According to my result, the model using a parameter for mortality rate fitted the data for all analyses the best. The model indicates a continuous decrease in the identification rate after long periods. Since elephants, in general, have a very low mortality rate, a likely explanation for the continuous decline is the possibility of permanent emigration, or the increased risk of missed identification after long periods (Whitehead, 2008).

My study suggested that the typical bull stayed in the park for 37 (CI 31-48) days before he left for about 108 (CI 87-137) days. This was less than the 47 days in and 238 days out that was found by Pitfield (2017). Unfortunately, no confidence intervals were included in Pitfield's study making the results hard to compare. However, the confidence interval of the number of days in the park in this study overlaps with Pitfield's average while the days out of the park do not. It may be that the additional data collected has adjusted the result and now offers a more correct answer or that the movement pattern has changed. However, when running the analysis with the same model as Pitfield used, the outcome changes to 50 (CI 41-65) days inside the park before leaving and 277 (CI 220-379) days outside before returning. The result would in other words be much closer to his findings and my confidence interval would have overlapped his average.

The overall lagged identification rate, i.e. the probability of reidentifying an individual, stabilizes beneath 0.002, indicating that the likelihood of reidentifying an elephant after 100 days is about 0.2% or 1 in 500. The fact that this group has the lowest rate is logical since it includes all individuals, making reidentification rarer (Figure 8a).

The identification rate of the youngest age group flattens out around 0.002-0.004 while it for the oldest age group stabilises at a 2-4 times higher probability (Figure 8a & 8e). This indicates that older bulls are reidentified at a higher rate than young bulls. The explanation could be that the older bulls stay for longer or return more frequently. It could also be that the identifying characteristics of the bulls in these age classes change less than they do for the younger bulls, making the old elephants easier to recognize and reidentify (Chui & Karczmarski, 2022). When analysing an age group, subsets are used to remove the observations that aren't classed as the age group of interest. Since estimating ages is more difficult on younger savannah elephants, there is an increased risk of falsely rejecting observations belonging to a younger or older age group. For example, an elephant at age 20 may look similar to one at age 22. The two should be separated into different age groups but one observation of the elephant might be placed in the age group "<21" while another observation is placed in "21-25". If this happened, it would decrease the estimated identification rate of the age groups compared to if both observations were placed in the right age group. It would also impact the lagged identification rate of the age group that the second observation has been classed as the identification rate would go down if one observation has been misplaced but might go up if both were placed in the same wrong group by mistake. However, since the risk of misidentifying the age decreases with age, the number of mistakes could decrease as well, making the lagged identification rate more accurate with age. It is not likely that estimating the wrong age of bulls would explain the difference in lagged identification rate, but it could play a small role.

The parameters for mortality rate were higher in younger age groups than in older (Table 4). This means that more young elephants disappear from the study due to mortality, permanent emigration or misidentification. It may indicate that the younger savannah elephants die at a higher rate and that the old and large bulls manage the challenges of life better than the younger elephants do. Possible explanations for this are their larger size and higher position in the hierarchy which would help them compete over resources, or their life experiences collected through the years that would decrease the energy spent on gathering information about foraging areas (Evans & Harris, 2008). But note that it is equally likely for all three explanations, or a combination of them, to cause the increase in the parameter for mortality rate for the younger elephants. However, an individual is only included in the analysis of an age group as long as he is estimated to be that age. The lagged identification rate of the individual will start over once he is estimated to a new age group and will disappear from the younger age group which is likely to play a big part in the higher mortality rate of the younger age groups. Due to this, the parameters for the mortality rate are the most trustworthy when all age groups are included, followed by the age group "36+" since no elephant will grow out of this group.

The local population size may be slightly larger in the wet season. This would make sense since the area has more resources in this period and can sustain more animals. The lower number of days inside and outside of the park during the wet season compared to the dry season could suggest that the elephants move more during the wet season, and either stay for long periods or are absent for long periods during the dry season. This would support the hypothesis by Wittemyer et al. (2008), that savannah elephants move more randomly during the wet season when the resources are abundant and that they are more likely to stay close to known water sources during the dry season when resources are scarce.

A comparison was made between the youngest and oldest age groups to take a closer look at how the seasons affect different age groups (Table 4). The number of days in the park differed between the groups during both seasons. The young elephants stayed for fewer days during both the wet and the dry season compared to the older elephants. They also stayed outside the park for fewer days before returning during both seasons compared to the old elephants. This is a sign of the elephants' movement pattern and indicates that younger bulls in general move in and out of the national park more than old bulls do. Both age groups seemed to move more during the wet season compared to the dry season.

5.1.2. Social associations among the elephants

The second part of the study was to investigate bull relationships to examine whether associations were random or not. Similar to the lagged identification rate, the probability of elephants reassociating decreased rapidly during the first 100 days before it evened out. This indicates that the savannah elephants are likely to have many short-term associations during their time in the park. The pattern illustrated in Figure 9a is categorised by Whitehead (2008) as "constant companions plus casual acquaintances". He mentions three social systems that could produce this pattern where the association rate declines but stabilizes above the rate for random association. One is that the elephants could be forming permanent groups that socialize with other groups for about the 100 days shown in the graph (Whitehead, 2008). This would mean that there are subgroups within the observed groups that stay associated for longer periods, but that these subgroups leave the other subgroups after on average 100 days. The second scenario indicates that the savannah elephants have casual, but preferred, companions with whom to socialize. These relationships would last about 100 days, but the elephants are more likely to reform these than associate with a new elephant at random (Whitehead, 2008). The third and final suggestion is that the bull groups could have permanent core associations that last for longer, and "floaters" who move between different groups (Whitehead, 2008).

Most of the graphs of the relationships from specific age groups to all groups show a similar shape. The exceptions are the graphs of "<21 to All", "All to <21" and "All to 26-35" where the model of the association rate stabilises at the null or maybe even below, i.e. at the line for random association (Figure 9b, 9f & 9h). If the association rates do stabilise there, a potential explanation could be that the savannah elephants under age 21 only have casual acquaintances with whom they socialise for about 100 days before breaking up. The association may reform later but it is equally likely to be a new companion. This could potentially suggest that the age group <21 is a big part of the "floaters" mentioned in the paragraph above (Whitehead, 2008). Another explanation could be that the association rate of this age group should, as for the others, stabilize above the null, but due to misidentifications or other factors, the reidentification of these individuals may have been less successful over long periods.

In the study done by Pitfield (2017), he found that a great majority of the associations were short-term relationships, with a smaller proportion of preferred companions that increased with age. My results supported the hypothesis that the great majority were short-term associations, however, I did not find that the proportion of preferred companions increased with age (Table 7). My result of "X to All", i.e. how many associations an individual of age group X has with individuals of any age group, suggested that the number of preferred companions may decrease with age. At the same time, the number of associations increased, making the proportion of preferred companions decrease compared to some of the younger age groups. Pitfield (2017) notes that many associations may be missed due to elephants' ability to communicate over large distances, which is also the case in my study. After spending time with elephants, I hypothesised that both the number and the proportion of preferred companions would increase with age, but this was not supported by my results.

The dataset I used consisted of uniquely identified individuals while the available database also contained temporary individuals, that is bulls who have been photographed but not possible to identify as an existing individual or converted into a new one. One could argue that the temporary males should have been included in this part of the study since a lot of the associations of the uniquely identified bulls will be missed by not including all individuals. However, since I don't know if the temporary individuals have been observed several times, if they are one of the unique bulls or if they are a first new observation, adding these could potentially cause more harm than help if not properly investigated and this couldn't be done due to time constraints. It should also be noted that most of the elephants that were observed weren't possible to photograph even if the ages of the individuals and the size of the groups were recorded. However, since only the photographed individuals are used in these analyses, most of the associations have been missed, including long-distance communication and missed opportunities for identification. This means that the true number of associations is likely to be much higher than my results suggest. Nevertheless, by using a consistent data set I have hopefully provided a fair demonstration of the associations, even though the numbers of associations are likely to be highly underestimated.

All the models in the relationship "All to <21" had a relatively low ΔQAIC, but none of the lines followed the graph (Figure 9f). This indicates that none of the models was a good fit for this particular dataset and the estimations made from these models were therefore rejected.

The results of Table 6 demonstrate that the two younger age groups show longer short-term associations with other individuals (relationship "X to All") than the other groups have with them ("All to X"). The results also demonstrate that the two older age groups have shorter short-term associations with the other groups ("X to All") than the other groups have with the older age groups ("All to X"). This supports Allen's (2021) findings that associating with other bulls is more beneficial for younger males. The relationship of "All to 36+" in Table 7 indicates that all bulls associated on average with one of the 36+ males and had him as a preferred companion. However, only 1 out of 10 males that an individual of the 36+ age group associated with became a preferred companion. The results align with the findings by Chiyo et al. (2011) that most male-male relationships are weak and random with a few exceptions. The researchers found that bulls are associated with bulls of similar age for sparring, an activity more common among younger males; and that older bulls provide valuable knowledge as well as influence the cohesion of male social groups (Evans & Harris, 2008; Chiyo et al., 2011).

5.2. Conclusion and future research

In this thesis, I have explored the movement patterns of bull savannah elephants in the Makgadikgadi Pans and Nxai Pan National Park. I found that a bull stayed on average 37 (CI 31-48) days in the park before leaving for 108 (CI 87-138) days. I found that savannah elephants stayed both inside and outside of the park for longer periods during the dry season, indicating an increased movement during the wet season. Younger elephants stayed fewer days both inside and outside of the park compared to older elephants, suggesting that younger elephants moved more in and out of the park. Most bull associations were shown to be short-term relationships, but the average male associated with a few companions for longer periods. The study provides information to increase the knowledge about the poorly researched elephant bull societies and works as a step to better conserve the species and decrease potential conflicts with humans. Combining these findings with the ones of Allen (2021) and Pitfield (2017) suggests that younger males are likely to have a greater risk of getting into conflicts with humans and that this risk would be increased during the wet season but may be prevented to some degree by conserving older elephants to associate with.

Looking forward, more data needs to be collected to increase the accuracy of the results even more. A potential leap in the research would be if the process of matching individuals could be made smoother by making it more automatic. The process is at the moment done by manually searching for characteristics of the elephant which could very well be described differently by another researcher, leading to potentially missing the match. The database should nevertheless be cleaned up to make it easier to find potential matching observations in the future. If given more time, an attempt would have been made to find the optimal start parameters for each age group to increase the precision of the result. The last suggestion for further research would be to make a new estimation of the total number of elephants in the park. The last estimation was made 10 years ago and since then, more elephants have arrived and more female groups are present, changing the demography of the African savannah elephant in the Makgadikgadi Pans and Nxai Pan National Park.

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Appendices

Appendix 1: Popular science summary - Movements and Social Bonds of Savannah Elephant Bulls

Two hundred years ago, Earth looked vastly different. The human population was around one billion, and Africa was home to approximately 20 million elephants. Since then, the human population has increased by over 800%, while African elephant numbers have plummeted to about 400,000, representing just 2% of their population in the early 1800s. Today, elephants represent only about half the total biomass of domestic cats, highlighting the staggering impact of habitat loss and population decline.

Despite the African savannah elephant (Loxodonta africana) being endangered and facing a challenging future, some regions have seen population growth, including Botswana. Botswana holds about 130,000 savannah elephants, which is the largest single population globally and constitutes nearly one-third of Africa's total elephant population. This makes it a critical area for species conservation. The Makgadikgadi Pans National Park in Botswana, a semi-arid region, has only recently been recolonized by elephants in the last three decades. Elephant bulls are typically the first to explore new areas, establishing what is known as a "bull area" where females are scarce. While elephants generally live in matriarchal herds, previous research has primarily focused on these female-led groups, with male bulls historically thought to live solitary lives as adults.

However, recent studies indicate that elephant bulls often form social groups, where younger males benefit from the knowledge and protection of older bulls. Although we are beginning to understand these social bonds, much remains unknown about their dynamics and behaviours.

This study aimed to bridge this knowledge gap by investigating bull movement patterns in and out of the park, assessing seasonal variations, and examining if movement patterns differed among age groups. I also looked at social relationships between bulls to determine whether their associations were random or if they had preferred companions.

In the dry area of Makgadikgadi, competition for water and food intensifies during the dry season, from May to October. My findings revealed fewer bulls in the park during this time, with less movement in and out of the park compared to the wet season, spanning November to April. Results suggested that younger males moved more frequently than older males, who tended to stay within or outside the park for extended periods. The numbers were estimated to be approximately 165 elephants (95% CI: 152–184) in the park daily, with bulls remaining around 37 days (95% CI: 31–48) within the park before leaving and spending an average of 108 days (95% CI: 87–138) outside before returning.

I also found that social bonds were important among these bulls. Most male interactions were not random; instead, some bulls showed a preference for particular companions. While most relationships were short-term, a few bulls were observed together over extended periods, indicating that some bonds might last months or even years.

My research highlights the extensive movement patterns of Makgadikgadi's elephant bulls, which may increase the likelihood of human-wildlife conflicts. Studies indicate that young bulls are less aggressive when associating with older bulls, underscoring the importance of considering male associations and the role of elder bulls in conservation efforts. Incorporating these insights may improve our chances of reversing the downward trend in wildlife populations and preserving these majestic animals for the future years of this planet.

Appendix 2: How to take a good ID photo

An important mindset for photo identification is quality over quantity, you don't need that many photos if the quality is good and it doesn't matter how many you have if the photo is out of focus or badly exposed. The optimal light would be slightly cross-lighted, i.e. from the side but shining on the feature that you want to record. If the photo is backlighted (i.e. light is coming from behind the elephant), the photograph could be very artistic, but it tends to result in showing very few details, it could however show holes and notches that could otherwise easily be missed. A front-lighted photo (i.e. light coming from behind the camera) may lead to great details, but it could also result in great reflections making features hard to distinguish. A cross-lighted photo with the light on the body part photographed will give you a good chance of capturing a highly detailed and sharp photo. However, when photographing wildlife, you may at times simply have to do the best you can with the light and photo opportunity that is given to you. The features we want to capture are the ears, the tusks and the head, ideally one from each side, one from the front, and one of the whole body. It is important to take the surroundings of the elephant into account. Since the elephant is dark in colour, a dark surrounding will usually give the camera no problem in capturing the details of the body. If the surroundings are bright, e.g. the sky, then the exposure of the photo may be lower to adjust to the sky, we should in that case try to overexpose the photo to keep the details of the elephant in place.

Appendix 3: Physical condition score

The score for physical condition was based on a visual assessment of the shape and size of the elephant where a larger and rounder body form was considered a sign of better condition. The condition was scored between 1-5 in increments of 0.5 where 1 was very poor, 2 was poor, 3 was moderate, 4 was good, and 5 meant that the individual was in excellent condition. The score was recorded for future studies, but not used in this thesis.

Appendix 4: Group confidence scores

The Group confidence score is a score of how certain the observer was of recording all the individuals in a group. It is a score between 1-3 where 1 indicates certainty that all individuals were recorded, if scored 2 the observer is fairly confident that all individuals were recorded, and a 3 means it is likely that not all were recorded. This score was also collected for future studies but was not used for analysis in this one.