What studbooks can tell us about captive breeding programmes: a case study of cheetahs (*Acinonyx jubatus*)

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Table of Contents

List of Figures

List of Tables

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Abstract

The success of captive breeding programmes demands planning and communication among zoos, national parks, conservation organizations and political institutions. To avoid inbreeding and enhance the likelihood of finding suitable partners, target individuals may need to be transported from one institution to another to allow biological (genetic) matching. The collaboration among institutions involved with the reproduction and reintroduction of threatened species in their natural environment can be mapped and analysed by social network analyses using studbook data. The cheetah (*Acinonyx jubatus*), considered as vulnerable by the IUCN Red List of Threatened Species, is a species which has been participating in captive breeding programmes for relative considerable time and can be a good model of study. Although this species has a low wild population density, it has been managed for many years and still has a significant sample of individuals for population and conservation studies, both in the wild or captivity. A general bibliometric review was first conducted with the intention of examining the nature of studbook studies published from 1988 to 2016 on different animal species. Furthermore, International Cheetah Studbooks were used to extract historical data, which was then processed and analysed to investigate the relationship between the transfers of individuals and the position of captive breeding institutions in social networks. Using UCINET software, measures of centralities, density and reciprocity from the collaborative network of institutions were calculated and several maps expressing the transfers between institutions were created using Netdraw to evaluate their patterns in relation to geographical, economic and biological factors. Lastly, longevity and reproductive success were also investigated using statistical analysis such as generalized linear models (GLM) in R software (R Core Team). Results showed that groups of institutions were formed regarding the exchange of animals, and some were highly connected as geographical regions of the world (America, Europe and Africa). Longevity of cheetahs can be partially explained by factors including many transfer-related variables. Reproductive success was not significantly affected by GDP per capita or climate category from the facility location. Breeding recommendations need to be followed by institutions to maximise the conservation value of the species; this will generate genetic improvement for future reintroductions in the wild and the avoidance of extinction. In conclusion, although there is some effort in protecting and managing zoo species through studbooks, conservationists should make maximum use of such datasets to inspire the creation of new tools for the best conservation management of species which need more care and attention such as the cheetah.

Chapter 1 General Introduction

1.1 The role of zoos and the captive breeding programmes initiative

The history of wild animal keeping (including zoos) comprises several thousands of years since the Neolithic and, perhaps, initiated with animals being domesticated for food by ancient civilizations, although at that time zoos were not established institutions nor had this denomination (Kisling, 2001). Ancient illustrations show the uses of animals mainly for religious purposes (e.g., sacrifices and adoration). However, companionship, gifts, hunting and display of power were some of other reasons why ancient civilizations such as Assyrians, Phoenicians, Romans, Greeks and Chinese kept animals in captivity (Rees, 2011). In the last thousand years, emperors and kings, who were the individuals that could afford the extravagances of transportation, maintenance and exhibition of animals, extended this habit of keeping wild animals during the medieval age (Kisling, 2001).

The menageries – that preceded modern zoos centuries ago – evolved from the simple purpose of exhibiting animals in cages as a way of demonstrating status for the aristocracy or royalty (Kallipoliti, 2011) to institutions that have responsibility for the conservation of species (EAZA, 2013). The transition between menageries and modern zoos was a result of many factors, but mainly because of the new scientific perspective on the natural world acquired by the society during the 19th century (Kleiman et al., 1996). Human activity since this time has caused a massive impact on wildlife survival - including some extinctions – by for example, polluting and destroying animals' habitats, spreading invasive species and diseases. Thus, scientists started to care about the future of animals from about the 1930s, but only gaining significant momentum in the 1980s, which led to a significant change in the role of zoos (Fraser & Wharton, 2007).

Entertainment is still the main reason why the public go to zoos, but today zoos suffer pressure to also work as educational organizations, disseminating knowledge about the biology of species, human influences on species survival and, most importantly, how people have individual responsibility to change harmful attitudes/behaviours toward animals and nature (Patrick et al., 2007; EAZA, 2013). Moreover, the scientific community considers zoos as potential site for several kinds of research (Kleiman, 1992; Fernandez & Timberlake, 2008). Most modern zoos have attempted to change their function, as previously described, to stop being only a place for wildlife exhibition or people's entertainment (Hutchins, 1988; Moss & Esson, 2010). This change combined with the ongoing human induced extinction crisis (Conde et al., 2013; Wakchaure & Ganguli, 2016) and growing ideas of animal welfare led zoos to change their role to be more conservation driven organizations with focus on sustainability (WAZA, 2011).

The term "sustainable" is defined as the conscientious use of a resource avoiding its damage and over depletion (WAZA, 2011). It means making use of a source to attend population's needs, but at the same time, respecting, defending and supporting its source so that future generations are also able to benefit from it (Lacy, 2013; Dickie, 2009). Applying these terms and definitions into a zoo context, a sustainable zoo would be the one which cares about wildlife by avoiding unnecessary recruitment from the wild to replace their animal pool. Finally, the last step for zoo sustainability would be to reintroduce species into their natural habitat and above all, to invest more money and effort preserving what is left in nature; however, this is probably the most difficult step, since reintroductions requires long-term monitoring of the animals and work with local people (Tribe & Booth, 2003).

The initiative of creating programmes for reproduction of animals in captivity appeared from the International Union for the Conservation of Nature (IUCN). To be successful, captive breeding requires much attention and planning by zoos and people with different expertise from all around the world (Kleiman et. al, 1996; Ballou et. al, 2010; Conway, 2011). It must follow some biological/genetic regulations, because successful captive breeding is more than just putting together mature sexual partners. Animals need to be matched genetically to ensure that the genetic goals (such as maintaining founder diversity) of the captive breeding programme are met (Foose et. al, 1986).

These goals are usually focussed on maintaining genetic diversity in the captive population, especially founder diversity. When a genetically important animal does not match genetically with its partner or does not breed, it is then transferred to another location to be paired with a more appropriate individual (Asa et al, 2010). Therefore, there is the constant need for communication between institutions to create an efficient breeding programme in captivity. In addition, the welfare of animals during this process should be an element to be considered so animal health and behaviour are not unduly affected by the stress suffered during exchanges (i.e. transportation), and future reproduction, the main reason for captive breeding transportation, can be achieved more easily (Linhart et al., 2008).

Many zoos act together to captively breed a species in a metapopulation, and this is established to allow dynamic animal exchange between *ex-situ* institutions. The reason for joining captive individuals of a single species into a metapopulation is that, normally, no single zoo, can for financial or logistical reasons, hold enough individuals of a specific species to maintain the species genetically diverse/healthy (Foose et. al, 1986; Conway, 2011). In addition, zoos need to meet species' requirements to express appropriate behavioural activity, parental care, disease resistance, exhibit mate choice behaviours, reproductive patterns and physiological responsiveness to environmental cues (Lacy, 2013). Therefore, the success of captive breeding programmes depends on the sum of the efforts of the zoos involved in collaborations over a long-term time scale.

1.1.1 A brief analysis of the cheetah captive breeding programme

Cheetahs have been kept for centuries in India and were used for hunting but were never successfully bred in captivity there, although one record of mating was recorded as reported by Divyabhanusinh (1996). Mughal emperors had the habit of keeping a large number of cheetahs for the practice of hunting gazelles and blackbuck antelopes (*Antilope cervicapra*), especially Akbar the Great (1556–1605) (Charruau et al., 2011), who owned about 9000 animals during his lifetime.

The first cheetah in a zoo collection was recorded at the Zoological Society of London in 1829 (Marker-Kraus, 1997). Due the low reproductive efficiency in zoos (Marker-Kraus, 1997), free-ranging *Acinonyx jubatus* are imported from African countries – mainly from Namibia (Marker-Kraus, 1990). The captive population ideally would be self-sustaining and would not require any wild-caught individuals to keep the gene pool healthy and diverse. Nevertheless, capturing wild individuals is still a strategy for minimizing the effects of inbreeding and genetic drift for this species in captivity (Marker-Kraus, 1990), although this number has been decreasing considerably with time and has reached the official mark of zero wild-caught animals in 2016.

Captive breeding programmes are careful to avoid pairing mates with high genetic relatedness when reproducing cheetahs in captivity, but animals originating from captive populations are less genetically diverse than their wild counterparts (Frankham, 2008). Furthermore, the behaviour, welfare and management of a species exert a large influence on its reproductive success in captivity, which cannot be ignored; however, most of the research on cheetahs has only considered genetics (Chadwick, 2014).Since 1969 the creation of international studbooks is helping scientists to gather information about captive individuals (including kinship) to create safety net populations (Leus, 2011). The first official studbook was published in England around 1791 and was called “General studbook for thoroughbred horses”, however, the first studbook for a wild species was the European Bison (*Bison bonasus*), established in 1932 (Glatston, 1986). Captive cheetahs have only attracted attention from conservationists on the 1980s, when many other initiatives were implemented (i.e. regional and international studbooks, conservation plans, research incentives and the IUCN’s Conservation Breeding Specialist Group). The first international cheetah studbook was published in 1988. Presently, a detailed analysis of captive populations is found through the web-based software called Species360 (previously called ISIS), where credited institutions access and can collaborate adding information regarding their collection of captive cheetahs in the world, sharing knowledge and allowing easy-access of data for zoo personnel.

1.1.2 Genetic basis of cheetahs captive breeding programmes

Genetics exert a strong influence on the success of the species, especially in cheetahs since this species had a genetic bottleneck, which occurred around the end of the Pleistocene together with a mass extinction of large mammals that happened about 10,000 years ago (Menotti-Raymond & O’Brien; 1993). The genetic variability of cheetahs was affected by inbreeding after a temporal genetic bottleneck, which possibly resulted in the reduction of allelic variation and physiological problems observed in current individuals (O’Brien et al., 1985). These problems diminished the adaptability of individuals to survive, overcome environmental changes and to produce healthy offspring (Lacy, 1997).

The genetic management of current individuals kept in captivity for breeding purposes aims to maximise genetic variability through the reproduction of compatible animals (individuals with most divergent genotypes) and the maintenance of genes inherited from founders captured from the wild (Kleiman et al., 2010). Wild individuals are generally more genetically diverse because the population is usually much bigger than in captivity (Frankham, 1996), lowering the chance of fixation of common alleles. However, the decline of wild animals caused by human-animal conflicts, loss of habitat and its fragmentation has negatively affected the adaptability of wild individuals since the population is declining substantially and consequently its gene pool is also decreasing.

The level of genetic erosion and evidence for inbreeding associated with other information such as the population's structure and reproduction data has placed the cheetah in the same baseline of highly inbred mice or livestock (Menotti-Raymond & O'Brien, 1993). The danger involved with this genetic uniformity is the species' vulnerability towards the expression of recessive deleterious genes, in addition to the difficulty of surviving natural perturbations such as diseases outbreaks, for example (Dobrynin et al., 2015). When a population is large, deleterious alleles are still transmitted to following generations, but the expression of those genes is not so frequent because the probability of receiving deleterious alleles from both parents are lower. However, in small populations this probability increases and represents a risk for the population. In cheetahs, problems related to low levels of genetic diversityare: high mortality of juveniles, infertility, spermatozoid abnormalities and reduction of litter sizes (O'Brien, 1994). Generally, in captivity, the more generations coming from founders (the longer the time has passed) the lower the genetic diversity, especially if measures (i.e. management) for avoiding this effect are not put in practice.

Therefore, the zoos can play an important role in establishing effective breeding exchanges of individuals towards the maintenance of the genetic diversity of the species. Each breeding event should be strategically planned by the studbook keeper taking into consideration not only the individuals locations' logistics but also biological information from the individuals.

For example, the genetic makeup of one individual should be the most different as possible from its breeding partner, meaning that mating with kinshould also be avoided as much as possible. It is important to remember that although genetics is essential in captive breeding planning, it is not the only factor that should be considered for the management of the species: behaviour, welfare and other specific areas must also be considered to achieve the best results in reproducing species in captivity.

1.2 Cheetah's natural history

Cheetahs are recognized as being the fastest animal on land, reaching speeds greater than 100 km/h (Hudson et al., 2011; Grohe et al., 2018), due to their many morphological adaptations such as long limbs (Hudson et al., 2011), large organs such as lungs and heart for better oxygenation (O'Brien et al., 1986), specialized inner ear (Grohe et al., 2018), semi-retractable jaws (O'Brien et al., 1986), flexible spine (Hayward, 2005), stabilizing tail, slim body, foot pads, and "tear marks" (Becker, 2010; Cheetah Conservation Fund, 2018). Cheetahs' adult weight is between 30 to 72 kilograms (Hayward, 2005) and they measure between 1 to 1.5 meters approximately plus the tail which adds 60 to 80 centimetres more to their length (Cheetah Conservation Fund, 2018).

Currently, wild cheetah's distribution occupies several African countries and Iran. Figure 1 shows the countries ranged by cheetahs according to the Cheetah Conservation Fund website (2018). Historic range was much larger centuries ago (Charruau et al., 2011); however, the decrease in population has happened gradually due to several factors such as environmental changes, human activity, low genetic diversity, amongst others.

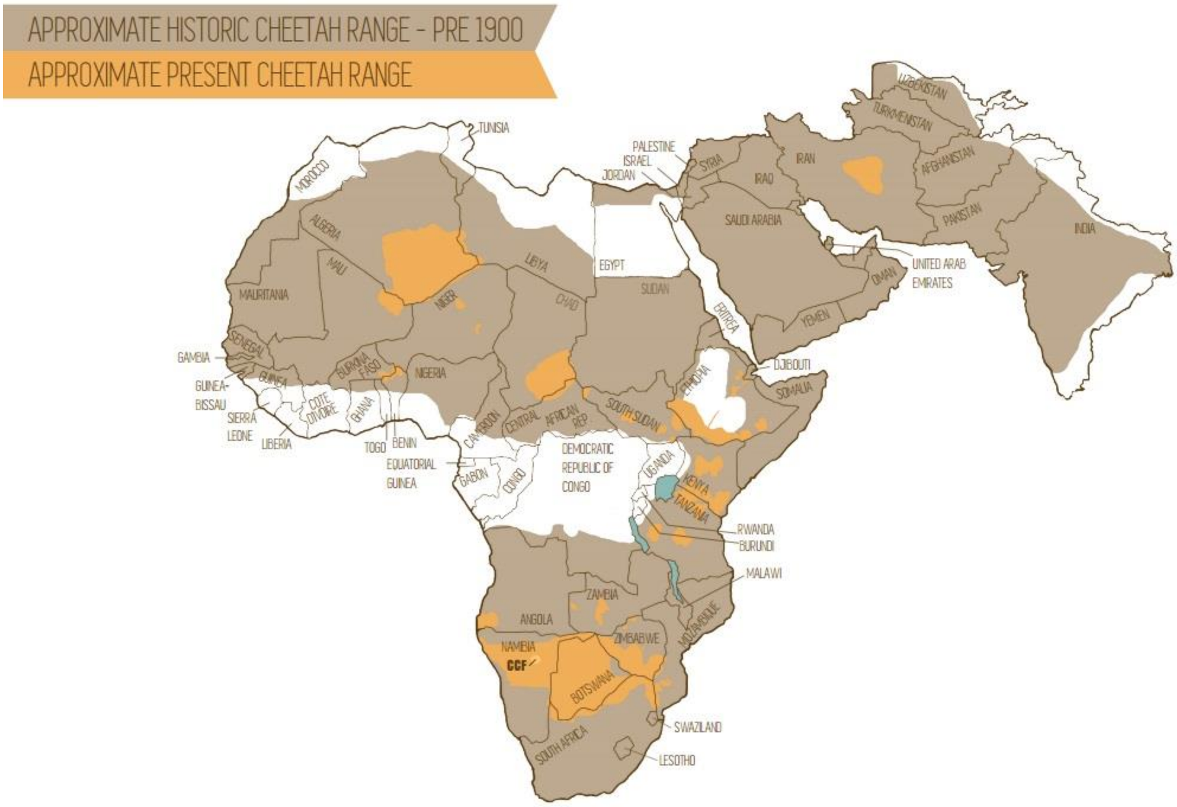


Figure 1. Current distribution of wild cheetahs (*Acinonyx jubatus*). Extracted from the Cheetah Conservation Fund website (2018).

Cheetahs are considered vulnerable to extinction by the IUCN's Red List of Threatened Species since 1986 (IUCN Red List of Threatened Species, 2018). The loss of their habitat (Klaassen & Broekhuis, 2018), especially caused by farming and land fragmentation has sharply declined the number of cheetahs in the wild (Marker-Kraus & Kraus, 1997). Direct killing or capture in response to livestock depredation (Marker et al., 2003; Marker-Kraus &

Kraus, 1997) also contributed to the decrease in animal numbers together with cub mortality. The subspecies *A. j. venaticus*, known as the Asiatic cheetah and currently found only in Iran, is considered critically endangered since the wild population is estimated to have currently less than 50 individuals (Durant et al., 2017).

The number of mature *Acinonyx jubatus* in the wild is believed to be less than 7000 individuals. About 4000 individuals make the largest subpopulation, which comprises mostly southern African countries such as Namibia and Botswana (IUCN Red List of Threatened Species, 2018). The population of wild cheetahs in Namibia is generally located in farmlands, outside conservation areas. The reason for cheetahs staying outside protected areas is due to competition with large predators such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), which usually kill cheetah cubs, compete for territory and feed on the same prey (Marker-Kraus, 1997; Durant, 1998; Caro & Stoner, 2003; Winterbach et al., 2013). To avoid encounters with larger predators, which are mainly nocturnal hunters, cheetahs usually hunt during the day, characterizing this species as mostly diurnal (Caro, 1994). However, Hetem et al. (2018) have shown that this species can also display activity during the night using biologging technology, with this behaviour explained in relation to temperature regulation.

Hunting behaviour of cheetahs in most instances is structured by stalk and chase (Hilborn et al., 2012). A review study by Mills et al. (2004) has compared cheetah's different habitat use and predation patterns and has discussed their preferences for medium-sized prey such as impalas (*Aepyceros melampus*), Thomson's gazelle (*Eudorcas thomsonii*) and springbok (*Antidorcas marsupialis*) (prey weight usually between 23 kg – 56 kg; Hayward, 2005), although some other larger (especially juveniles) and smaller animals such as zebra (*Equus burchellii*) and Grey duiker (*Sylvicapra grimmia*), respectively, for example, are also hunted. Prey size and species preferences also depend on the hunting group characteristics (e.g.

sex, size). This study has also shown that open savannas provide best hunting success than other habitats with thicker bush, despite having longer chase distances, since the vegetation may obstruct the sprints developed by those animals during animal chases.

Cover vegetation, nevertheless, was proved by Mills et al. (2004)to be useful to cheetahs when stalking prey and to prevent kleptoparasites from stealing their food. Therefore, the best habitats reported for cheetahs might be the open ones with some cover in the periphery. Broekhuis (2018) examined the recruitment of wild cheetah cubs based on the quantity of tourists, predators and habitat. The results showed that the type of habitat and abundance of tourists have a stronger negative effect on the recruitment of cheetah cubs than predator abundance. Therefore, it is recommended that animal breeding programmes use heterogeneous environments and tourist numbers should be limited for the best management of captive, reintroduced or wild cheetah.

Wild male and female cheetahs behave differently when they achieve sexual maturity (Krausman & Morales, 2005); female cheetahs usually reach sexual maturity between 2 to 3 years old (Brown, 2011). The females separate themselves and live solitary lives with big home ranges. Males usually form a coalition of 2 or 3 brothers and less often with non-related males which stay together during their whole lives (Caro, 1993). They prefer to stay in areas where females' home ranges overlap (Laurenson, 1993) to increase success of mating, which can occur during the whole year. Males do not participate in caring of the offspring, therefore, after mating, the males leave the female on her own (Caro, 1994). If fertilized, the gestation period lasts for about three months (Brown, 2011; Vernocchi et al., 2018) and the litter size is usually between 3 to 5 cubs, although it can vary until approximately 8 cubs, the highest of any big cat, a biological characteristic that could have evolved due high cub mortality to increase fitness of this species (Nowell, 1996). In captivity, the average litter size is around 3 cubs. When the cubs reach approximately one year and a half of age (their independence), the mother leaves and the sibling group stay together for approximately 6 more months, until the female cubs leave the male brothers' coalition and establish their own home ranges (Nyhus et al., 2017).

Female cheetahs are polyestrus with cycles of approximately 12 days (Krausman & Morales, 2005). Estruses in captivity seem to be enhanced by the provision of food, although the excess of the same can impair it due to obesity (Laurenson et al., 1992). Wild female cheetahs protect their litter in lairs during the first two months of age from predators and environmental conditions (Laurenson, 1993). Abandonment of cubs in the nature occurs in general due prey scarcity but in captive environments can be a result of human disturbance and noise (Laurenson, 1993). Therefore, zoos must also consider and adapt maternal behaviour from the wild into their contexts to boost the reproduction success of this species in captivity including, for example, nest boxes for the mothers to move their litter to temporarily, providing a reclusive area for the mothers, etc (Laurenson, 1993).

Studies have discussed the viability of cheetah sperms in assisted reproduction (Crosier et al, 2009) and the quality of sperm. Due the high level of inbreeding, the offspring is subject to express deleterious genes which can cause many health problems for the population. For this reason, cheetahs have been bred in captivity with the help of zoos and, artificially, through 'frozen zoo' techniques (Clarke, 2009). These methods are needed since the captive population is not self-sustainable and needs genetic maintenance/input from wild individuals. Sperm from wild individuals has already been collected and stored in the past (Crosier et al., 2009). Reproductive technology such as cryopreservation of gametes in parallel with the assistance of efficient planned breeding based on pedigree are considered the optimal strategies used to manage small populations of mammals in captivity (Bainbridge & Jabbour, 1998).

1.3 Studbooks

Captive breeding programmes usually use studbooks to assist the decision-making processes of which individual will breed with another. Studbooks have been used for centuries in managing the breeding of racehorses, but in zoos, their first application was less than 100 years ago (Glatston, 1986). These books usually contain the genealogical data pertaining to a captive population of a certain species, and thus permit breeding decisions to be made in relation to genetic goals such as maintaining genetic diversity and avoiding inbreeding (Glatston, 1986).

The loss of genetic diversity is a consequence of adaptation to captivity due artificial selection, genetic drift (random fluctuations of alleles) or inbreeding (decrease of heterozygosity) and has been considered as a strong indirect barrier for the reintroduction of potential animals into their natural habitats (Frankham, 2008). It creates a fragile population with the risk of extinction, if population growth rate is negatively affected, and reduces the ability of it recovering in response to environmental change. Therefore, a studbook holder (manager) has a fundamental role in selecting individuals to improve reproductive success in a genetically appropriate manner (Willoughby et al., 2015). Furthermore, a studbook holder should analyse the reproductive and mortality data to determine if there are any specific temporal problems affecting the animals.

Some successful programmes for rebuilding the wild populations of threatened species, through captive breeding, have already been undertaken by zoos; for example: the Przewalski's horse (*Equus przewalskii*), the California condor (*Gymnogyps californianus*) and the black-footed ferret (*Mustela nigripes*) (Willoughby et al., 2015). However, successful reintroduction of threatened animal species is still difficult and a challenging process that demands a lot of attention from the scientific community, and inter-zoo communication (Conde, 2013).

The International Cheetah Studbooks are, essentially, datasets collected across the years that contain extensive information about population management of captive cheetahs around the world. These annually released studbooks offer a great opportunity to conduct wildlife and conservation science since they provide substantial and detailed information about the captive cheetah inventory such as births, deaths, transfers, wild caught individuals and animal releases. In addition, pedigree, demographic history and some genetic information can be found in these documents, facilitating the maintenance of this species *ex-situ*. The Cheetah Conservation Fund website provide eighteen International Cheetah Studbooks (from 1999 to 2016) on their website (https://cheetah.org/research/by-type/international-studbooks/).

International Studbooks are managed (held) by a person who plans carefully each possible mating between two suitable individuals using the data generated from genetic management software such as ZIMS (Species 360, 2018). This studbook keeper gathers information on the status of cheetahs from registered institutions, which keep those animals for breeding in captivity, and are distributed around the world. Due to historical reproductive problems related to low genetic variance in cheetahs, pairings need to be methodically examined before being accomplished to avoid kinship and behaviour incompatibilities (Asa et al., 2010). Dr Laurie Marker – founder and executive director of Cheetah Conservation Fund (CCF) in Namibia – is the current international studbook holder for cheetahs (International Zoo Yearbook, 2017; WAZA, 2018).

After choosing the most appropriate partners for reproduction, the studbook keeper creates a recommendation report for breeding individuals and the consequent animal transfers that should be undertaken by zoos and other breeding institutions to achieve the captive breeding conservation plan. However, the communication between and contact with hundreds of institutions is not always an easy task to accomplish and sometimes it can be difficult to track captive population changes from one year to another. Moreover, indirect factors may be influencing the relationships between the captive breeding establishments; for example, the political alliances between countries, the wealth of zoos or even the geographical region where the institution is located. In the early days of studbooks communication of studbook data often depended on zoos sending their data to the studbook holder on a floppy disk by mail, but recently the advent of cloud-based software such as ZIMS has allowed data gathering to be conducted in real time (Species 360, 2018).

Social network analysis is a useful tool in the present case, because it can help scientists to visualise animal transfers (through graphical information representation), which are done every year for the species' management and can compare the modifications or patterns in the network structure along time (Haythornthwaite, 1996). In addition, specific social network measures highlight the most active institutions of the network and permit a deep analysis of their participation in a captive breeding programme. Furthermore, simulations can be performed to allow insights about the importance of an institution in determined contexts. For instance, if an institution is removed from the network (e.g. due to a disease outbreak), how the other participant facilities would be organized and linked in response to this change in the captive breeding network.

1.4 Social network analysis

The metapopulation of zoo animals can be considered a social network with interactions occurring between zoos when animals are exchanged for breeding programmes. Social network analyses (SNA) can facilitate the visualization of the inter-zoo exchanges involved in captive breeding programs and, potentially, highlight patterns of relationships followed by those institutions across the years of this activity (Tichy et al., 1979). Through the production of graphs, SNA express the interactions and associations between subjects (zoos) and have been used in many different areas such as social and computer sciences, biology, business and engineering.

The relationships (interactions or associations) between individuals or institutions are represented in SNA by ties (edges), which are lines or arrows that connect two subjects represented by nodes (Borgatti et al., 2013). The type of interactions can vary according to each network, and they can be oriented and weighted if the direction and quantification (strength) of the relationship, respectively, is considered (Haythornthwaite, 1996). The relationships existing in a social structure are represented in social network analysis by a matrix, which is the basis for the analysis (see Figure 2; Sueur et al., 2011). Each row in a matrix defines what is called the “actor”, which in the present case is an institution (zoo sending an animal for captive breeding). The columns represent the “receivers’’ of the interaction or association (zoo receiving an animal for captive breeding).

One can represent the relationships between the institutions from the extracted matrix data using specific software designed to graphically represent data in the form of nodes and edges (see Figure 3; Sueur et al., 2011). Each node represents an institution while each edge represents the relationship that exists between them (i.e. animal exchanges). Some characteristics of the relationships can be expressed in a graph (see Figure 4; Sueur et al., 2011) frequently called a sociogram, such as the direction (arrow orientation; that is, who sent the animal; Figure 4; Sueur et al., 2011), the strength (thickness of the line or arrow; that is, how many times animals were sent; Figure 4; Sueur et al., 2011) and the nature (positive or negative tie; usually used to express negative relationships such as distrust, dislike or avoidance for example, but not applicable to this study) of the relationship between two or more participants in the network (Sueur et al., 2011).

Binary matrix of Relationships Between individuals a to s

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*	*l*	*m*	*n*	*o*	*p*	*q*	*r*	*s*
a		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
b	1		1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
c	0	1		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
d	0	1	0		1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
e	0	0	1	1		1	1	0	0	0	0	0	0	0	0	0	0	0	0
f	0	0	1	1	1		1	1	0	0	0	0	0	0	0	0	0	0	0
g	0	0	0	0	1	1		1	0	1	0	0	0	0	0	0	0	0	0
h	0	0	0	0	0	1	1		1	0	0	0	0	0	0	0	0	0	0
i	0	0	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0	0
j	0	0	0	0	0	0	1	0	0		1	0	1	1	0	0	0	0	0
k	0	0	0	0	0	0	0	0	0	1		0	0	1	1	0	0	0	0
l	0	0	0	0	0	0	0	0	0	0	0		0	0	1	0	0	0	0
m	0	0	0	0	0	0	0	0	0	1	0	0		1	0	0	0	0	0
n	0	0	0	0	0	0	0	0	0	1	1	0	1		1	1	1	1	0
o	0	0	0	0	0	0	0	0	0	0	1	1	0	1		1	1	0	0
p	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1		1	0	0
q	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1		1	1
r	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1		1
s	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	

Figure 2. Example of a Binary Matrix of an unweighted network: either individuals are connected (value of relationship is 1; that is, they had an animal exchange), or they are not connected (value of relationship is 0). Extracted from Sueur et al. (2011).

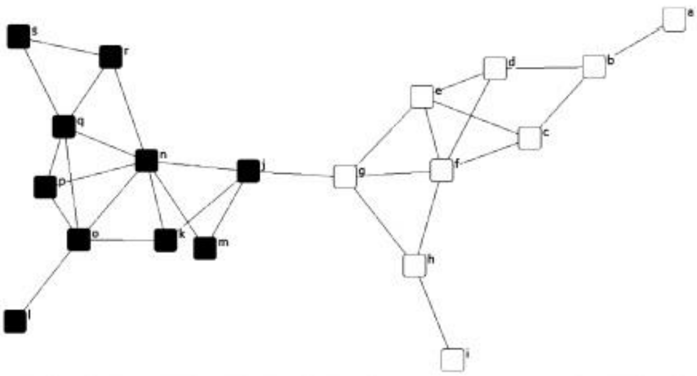


Figure 3. Example of a theoretical social network containing 19 individuals labelled from a to s. Extracted from Sueur et al. (2011).

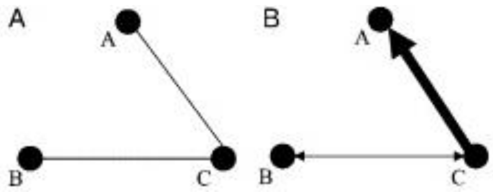


Figure 4. Graphical representation of (A) an undirected and unweighted three-node network, and (B) a directed and weighted three-node network. (B) Gives information about the strength and direction of interactions between individuals or institutions, while (A) does not. Extracted from Sueur et al. (2011).

Subtle information that is found in a data matrix can be interpreted more easily by the researcher from a sociogram (Brent et al., 2011). The global viewing of the connections among network members provides insights about the operation of the social structure. It is possible to see what role each entity (i.e. zoo) plays in the network and how influential it is for a determined situation depending on its attributes and position in the social network (Brent et al., 2011).

Centrality is a SNA measure of “importance’’ that an entity has in the network (Wey, 2008). According to Hanneman and Riddle (2005), “Actors who have more ties to other actors may be in advantaged positions.’’ There are many types of centralities but one of the most used is node degree. Node degree (Figure 5) shows how connected the entity (zoo) is according to the number of associations or interactions it receives (indegree) or it sends to others (outdegree).

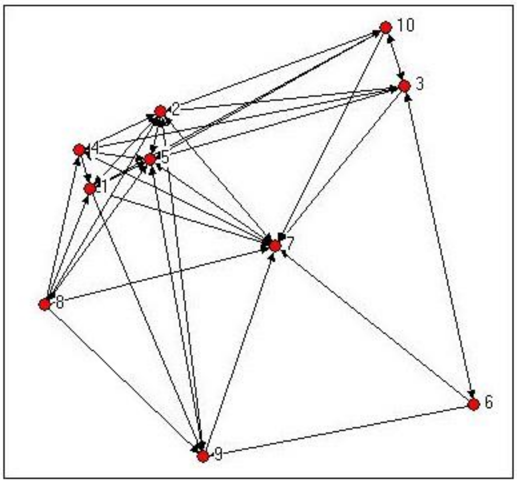


Figure 5. Example of a node in-degree and out-degree. Extracted from “Introduction to social network methods’’, Hanneman and Riddle (2005). Indegree is defined as the number of ties the actor emits (i.e. animals sent) and the outdegree is the number of ties the actor receives (i.e. animals received). The more ties an actor receives, the more ‘’prominent’’ it is; the more ties an actor emits, the more ‘’influential’’ it is.

1.5 Study aims

This project was developed with the intention of expanding knowledge about zoo management and wildlife conservation science (chapter one) in addition to investigating the rich information studbooks maintain through: (1) a bibliometric review of the use of studbooks (chapter two); (2) statistical analysis and modelling of longevity and reproductive data (chapter three); and (3) social network analysis investigation using the cheetah (*Acinonyx jubatus*) as a model of study (chapter four). Chapter five has final considerations, limitations found during the progress of the study and suggestions about how this research could contribute to wildlife management and conservation science as conducted by zoos.

The specific objectives from each research chapter are described as follow:

Chapter Two

The bibliometric review intends to investigate patterns in the research conducted with studbooks related to the taxa chosen for study, country of first author and respective wealth based on GDP per capita, institution type, scientific journal selected for publication and corresponding impact factors. It aims to compare these taxa using the most threatened ones published by the IUCN Red List of Threatened Species to assess if there are preferences for any taxa in the research conducted and why these preferences occur. In addition, the review intends to quantify the articles selected into categories and subcategories chosen by the author according to their scientific emphasis. This would provide awareness of scientific trend areas that need more development and would allow the identification of any study that possibly used social network analysis in their research. Therefore, the bibliometric review of articles not only contributes with more knowledge but also confirms the originality of chapter four from this thesis.

Some example of research questions related to this chapter are: Are there preferences for working with any specific taxa in research conducted with studbook data? If so, why is it the case? What are the main topics/subtopics related to the research conducted using studbook data from 1988 to 2016? What are the topics/subtopics that need more scientific development according to the least number of articles published using studbook data from the dataset considered?

Chapter Three

The influence on the lifespan of captive cheetahs from number of transfers done during their life, institution where the animal was born, individual's age during first transfer and the total distance travelled during life was analysed via Generalized Linear Models (GLMs). Some examples of research questions related to this chapter are: Does the number of transfers conducted during life affect the death age of cheetahs? Is birth place a variable that influences positively or negatively the death age of cheetahs? Does the age of first transfer have some influence on the death age of cheetahs? Does the distance travelled during life have any effect on the death age of cheetahs?

In addition, the influence on the reproductive success from the climate and the GDP per capita was analysed also via Generalized Linear Models (GLMs). Some of the research questions answered in the discussion are: Does the climate related to the institutions that breed cheetahs influence the number of cheetahs born there? Does the GDP (as a measure of wealth, education and access to technology) per capita of the country where the breeding facility is located has some influence on the number of cheetahs born in captivity?

Chapter Four

Social network analysis was used to examine the existence of patterns in transferring cheetahs for captive breeding purposes. This objective was undertaken using social network measurements of degree centrality, network density and node reciprocity. Examples of research questions answered in this chapter are: Which are the main institutions that exchange cheetahs around the world considering the indegree and outdegree centralities? Are there sub-networks formed according to geographical regions? How interconnected are the networks according to their density? Is there any change of structure of networks along the time? Are the networks weakly or highly reciprocated?

1.5.1 Why was the cheetah the species chosen for this research?

The cheetah was the species selected for the development of this project due the following reasons:

1) The international studbooks from this species have been published for many years consecutively (since 1988), and therefore they contain a high amount of continuous data, which provides a good source for the social network analysis that focuses mainly in looking at patterns of relationships along time.

2) Despite cheetahs having vulnerable status in the wild, which requires special attention, there is a relatively large global population of this species in captivity. Therefore, the historical and current data provides a good sample size for the conduction of this research, especially regarding lifespan and reproductive success modelling.

3) The international studbooks used in this project (from 1999 to 2016) were available online for download, differently from most data related to the management of captive animals which usually has restrict access to the zoo community.

4) Several studies have indicated the difficulty in breeding this species in the wild and captivity, justifying the low genetic diversity found along cheetah generations, which probably started by a genetic bottleneck in the late Pleistocene. This low genetic diversity highlights the importance of a well-planned and effective genetic management of those animals.

5) Cheetahs are also one example of species which has been involved in reintroductions to its natural habitat along the years. The participation of captive institutions was instrumental for the success of the individuals during the whole process. Therefore, there is a demand for research that provides more understanding of the species' biology and captive behaviour for the future benefit of the species in terms of welfare and survival assessment.

6) Even though the reintroductions of the animals into their habitats can be sometimes problematic due to difficulty in adaptation to the environment Ccheetahs have been selected for this research because they have the potential to restore the deficit of wild individuals in the future and to have breeding outcome from captive facilities improved.

Chapter 2 Bibliographic analysis of studies using studbooks from 1988 to 2016

2.1 Introduction

The need for zoo studbooks has increased with time, because human activity has impacted drastically on the survival of many wild species (Mallinson, 2003; Lees & Wilcken, 2009). The extinction of species can occur due a variety of environmental factors, intrinsic biological traits aside from anthropogenic threats including: habitat degradation and fragmentation, illegal trafficking, poaching, pollution, livestock production, logging, habitat exploitation and innumerable other activities. In parallel, zoos have been paying more attention over the years to their conservation, education and research-driven roles in addition to being entertainment venues (Rees, 2011; Schwartz & Flesness, 2014). A single zoo does not play those roles effectively by itself, though; it depends on good communication and collaborations with other zoos (Lovejoy, 1980; Dickie, 2009).

Often a regional level of zoo collaboration in captive breeding programmes is not enough to achieve self-sustainable populations of endangered species and a management plan at the international level is needed (WAZA magazine, 2011). Ideally, zoo populations should not need wild-caught individuals to improve genetic management, but sometimes this still is an alternative for some species, which cannot achieve self-sustainability even with international cooperation. Animal management plans and breeding programmes appeared as a strategy to minimise the damage that has been done to wild populations through the careful breeding of species *ex-situ* for demographic increase. In addition, such programmes try to avoid captive adaptation, use genetic information for the selection of individuals for breeding and sometimes prepare the animals for a reintroduction to their habitat. Much progress has been made by zoos since their beginning, but new tools, ideas and methods are needed to fulfil their objectives (Leus et al., 2011).

Those regional and specific programs such as SSPs (Special Survivor Plans), EEPs (European Endangered Species Programmes) and others were created with careful conservation objectives, aiming for self-sustainable animal populations in the wild and a genetically healthy insurance metapopulation in zoos (Lees and Wilcken, 2009; EAZA, 2018). The organization of regional zoo associations also divided-up the job of trying to optimize the captive management of wild species along with promoting better communication between institutions. Such captive breeding programmes are managed by a studbook keeper who is responsible for gathering all the information provided by regional captive breeding programmes (Glatston, 1986).

The publication of studbooks helps captive animal management through the registering and organization of important individual animal data. They represent a set of data stored for the monitoring of demographic and genetic changes, which have happened over time from a determined species. Information such as date of birth, date of death, transfers done between institutions, locations where the events took place, pedigree and other data can usually be found concentrated for easy handling and analysis (WAZA, 2018). This allows zoo biologists to study many characteristics of a population over time to make a management plan for the benefit of an endangered species, such as maintaining genetic diversity and stabilizing population size with recommendations for age/sex structure (Glatston, 1986; Ballou et al., 2010). Furthermore, studbooks help to keep the information of an individual without the risk of it being lost during a transfer from one animal collection to another (Olney, 1980).

The 1970s and 1980s were important decades for many scientific disciplines. It was around this time that personal computers and the internet emerged for academic purposes (Leiner et al., 2009; Kleinrock, 2010). Together with the necessity of developing a better communication within the research community, zoo management programmes and academics were also trying to improve strategies for animal conservation through demography and genetics approaches – a period in which studbooks took an important step forward (Flesness, 2003).

The initial construction of studbooks was made through the use of questionnaires, which needed to be manually answered and mailed to the central institution by a specific date. However, that requirement was not always followed with accuracy by the zoos and data collection turned out to be, sometimes, a difficult task (Glatston, 1986). The development and emergence of software in the field of animal conservation has facilitated the way in which zoo professionals communicated with each other and had access to biological data and population trends through the spread of zoo animal data within the zoo community. Studbook keepers and programmes coordinators were required to type their records into computerized systems.

The proposal started with Professor Ulysses Seal in 1974 from ISIS (International Species Inventory System), which later was called International Species Information System and that today is called Species 360. ISIS released software such as ARKS (Animal Records Keeping System), MedARKS (Medical Animal Records Keeping System) and SPARKS (Single Population Animal Records Keeping Software), which have brought advances in recording husbandry, veterinary and management data from zoo animals (Flesness & Mace, 1988). Nowadays, one of their latest products called ZIMS for Studbooks allows gathering and sharing studbook records globally and online for the member institutions. Therefore, collaborations are easily established between zoos and data can be constantly updated (Species 360, 2017).

The World Association of Zoos and Aquariums (WAZA) website (2018) recognizes more than 1000 studbooks of different taxa, however, it does not specify the proportion for each of the animal classes. Oberwemmer et al. (2011) recognizes that 1027 different species have active studbooks and the vast majority of them are vertebrates (96.3%), mainly including mammals (48.8%) and birds (31.8%). About 41.5% of the species of mammals and birds included in the statistics before are classified by threatened by the IUCN Red List of Threatened Species (Oberwemmer et al., 2011). According to the Species 360 website (2018), there were 238 studbooks in ZIMS for studbooks until April (2018), which have been transitioned from other sources and amongst them, 132 were studbooks from mammals, 79 from birds, 19 from reptiles, 5 from fish, 2 from amphibians and only one was from an invertebrate species. The International Zoo Yearbook also from April (2018) also identify 130 active international studbooks of 142 species/subspecies.

Studbooks for domestic species described as “a written record of the pedigree of a purebred stock, esp. of racehorses” have existed for longer than studbooks for wild species (Princée, 2016). In fact, studbooks for wild species began around 1932 with the European bison (*Bison bonasus*), 141 years later than the first studbook containing the pedigree of Thoroughbred horses (1791). Domestic animal studbooks, differently from the wild studbooks, focus on the selection of characteristics or genes within breeds, for example, for the quality of milk production by cattle (Glatston, 1986) or racehorses of a pure lineage that have a good characteristic for improvement of race performances (e.g. conformation traits).

Therefore, in domestic species it is common to see the expression “studbook admission”, meaning the process in which horses are selected based on physical traits and pedigree data to be included in the studbook – the recognized book of animals that can reproduce with the purpose of racing or keeping the lineage. Studbooks for wild species do not want to improve or alter any characteristics of the animals, but instead, their aim is to maintain the original genetic diversity from founder individuals and to avoid inbreeding (Glatston, 1986;

Ryder, 1986). Thus, zoo studbooks aim to maintain genetic diversity, whereas domestic animal studbooks are used to reduce genetic diversity.

Studbooks are rich sources of data useful for a wide range of different biological areas. However, data have been used mostly for demographic and genetic analysis. An investigation of the areas of study utilising studbooks data in their research would be appropriate for this thesis since it would show the originality of using social network analysis in the study of zoo animal management and captive breeding programmes.

The present study aims to analyse quantitatively research, which has been undertaken using data from studbooks. It intends to investigate the studies that used studbooks since 1988 until 2016 in their methodology through a bibliometric analysis with the objective of finding publishing patterns and providing guidance for future research, including the chapters that follow in this thesis (Chapter 3 and 4). Therefore, this chapter focuses on articles collected for investigation and not the studbooks *per se*. The main topic/subtopic of research from each article is identified according to the judgment of the author of this thesis and some other characteristics were extracted from the papers for a descriptive analysis such as the main taxonomic class, order and species used, and their respective threat category delimited by the IUCN Red List of Threatened Species. This objective helps to understand if there are any preferences for species or threat level in published studies using studbook data.

This chapter also intends to investigate if there are any relationship between the number of articles published per year and the countries' economic development via GDP per capita evaluation and main author's institution. It is interesting to explore an economic temporal analysis to determine if the wealthier countries publish more than others and if so, what are the possible reasons for this. The journals impact factors and human use of domestic species were also considered in the study.

2.2 Methodology

The collection of data was done on 18th April 2017 using the scientific papers database Web of Science© through the software Endnote X7 (Thomson Reuters, New York, NY, USA), where the word “stud$book*” was searched in the field “Title/Keywords/Abstract” to obtain the initial pool of articles for this study. This methodology was based on Goulart et al. (2009) and Azevedo et al. (2010), whose studies generated interesting results and confirmed that this is a good quantitative method for the evaluation of studies in a determined scientific area. The word chosen for the search in the database was selected to make the dataset very specific and avoid irrelevant articles for the purpose of this research.

The outcome of this search from the Web of Science© was 234 multidisciplinary articles, which were filtered according to the following criteria: 1) only research articles were included: technical notes, conference proceedings, pathological case reports, book chapters, review papers, summaries of captive breeding programmes or studbooks *per se* were rejected; 2) only articles written in English were considered; 3) only articles concerning animal science were considered; 4) only articles that used studbook data were considered; articles that mentioned the word “studbook” but did not effectively use studbook data were excluded; 5) articles that did not explicitly cite the use of studbook data were also rejected; however, articles that did not mention the word studbook but used ISIS data (software used for the input of animal records, also called Species360) were included in the research; 6) livestock studies for studbook admission were excluded; and 7) any articles from the year 2017 were excluded from the dataset (as we wished to use complete years in the statistical analyses). For horses, studbooks have the function of organising and recording information about pedigree and identification as part of standardising racehorse registrations, since they need to be inspected and included in the studbook to be recognized and to participate in race competitions

(Weatherbys, 2017). Studbook admission events select horses based on specific criteria such as genealogy and morphology (Bodo et al., 2005).

Initially, the title and abstract of papers were read to confirm their appropriateness to the objectives of this research and, if they could not provide enough information for selection, the methodology and/or conclusion were used to select the articles and to complete the categories chosen for this review. The full article was only read if considered necessary for the purpose of this review. A total of 135 articles resulted from the selection that formed the dataset of this research. The scientific papers were then categorized by: Year of publication, First author's country, First author's institution type (i.e. university, zoo, private company, research centre, institute or other), Journal of publication, Animal type (i.e. zoo or domesticated), Class (i.e. Mammalia, Aves, Reptilia, Amphibia or Actinopterygii/Sarcopterygii), Order, Species, Subject area (i.e. behaviour, computer modelling, demography, environmental studies, evolution, genetics, livestock science, morphology, pathology, physiology or population management) and Subtopic (i.e. body condition, breeding value, disease transmission, familiarity, fertility, genealogy, genetic disorder, genetic diversity, genetic structure, heritability, pedigree, performance, phenotype, recommendations, reintroductions, reproductive biology, reproductive success, sex allocation, software development, status, studbook, survivorship and viability). If an article had more than one author, only the first author was considered for the analysis. Moreover, if more than one subject could be identified in a same article, only the main subject was recorded according to the content of the research. The subtopic specified more about the subject approached in the paper. When the paper did not specify the scientific name of the target species, the latter was found according to the common name cited in the text of the paper.

For the classification of animals according to their risk of extinction, IUCN Red List of Threatened Species data was used to evaluate their threat level for the publication year of study. If there was no report of threat level for the year published, the immediate preceding year reported available was used to define in which category the species was located. If a subspecies classification was not found in the inventory, the species classification was used instead to categorize the threat level. Articles that did not specify the scientific name of the species in the study were also considered, but the species scientific name was included based on their popular names and research from other databases such as IUCN Red List of Threatened Species. The number of threatened species for each taxon and year was also imported from the IUCN website. The World Bank® databank was used to extract information of Gross Domestic Products (GDP) from each country and year published. The data were used to investigate the association between number of articles published and the GDP per capita using a generalized linear mixed model (GLMM). Journal Impact Factors were acquired from InCites Journal Citation Reports ® (Clarivate Analytics, 2017) for every article that was included in our dataset. After all the data had been entered into a spreadsheet, they were checked for normality (Shapiro-Wilk test) and statistically analysed using Minitab 16.2.4 and R using statistical tests such as a GLMM and chi-squared tests. Most of the data did not have a normal distribution and, for this reason, non-parametric statistical tests were applied whenever appropriate.

2.3 Results

The number of scientific papers using studbooks had alternating peaks of increase and decrease along the years, but has, in general, been increasing since 1988 (Figure 6) and reached a cumulative value of 135 articles in 2016. A Spearman's rank correlation was run to confirm the association of the variables "Number of articles published" and "Year". There was a strong positive correlation, which was statistically significant ($r=0.87$, $N=26$, $p<0.001$). The relationship between Gross Domestic Product (GDP) per capita of each country per year of publication and the number of publications using studbooks were investigated through a Generalized Linear Mixed Model (GLMM) and the result showed a significant association ($p<0.001$) between the variables. One important peak (2015) should be highlighted for its significant increase in number of publications from previous year (N=11 or 183%). The addresses of first authors' institutions (Figure 7) were predominantly universities (65.19%), followed by zoos (17.78%) and research centres (5.93%).

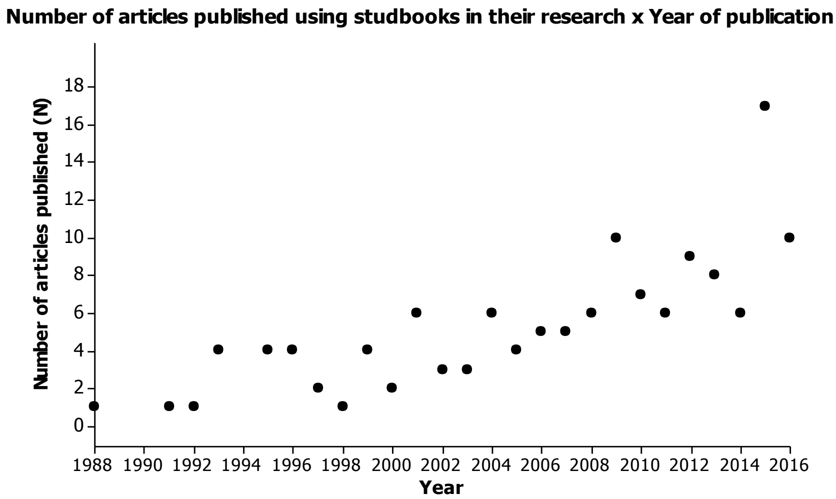


Figure 6. Scientific article production concerning studbooks in research (1988-2016 using data from the Web of Science©).

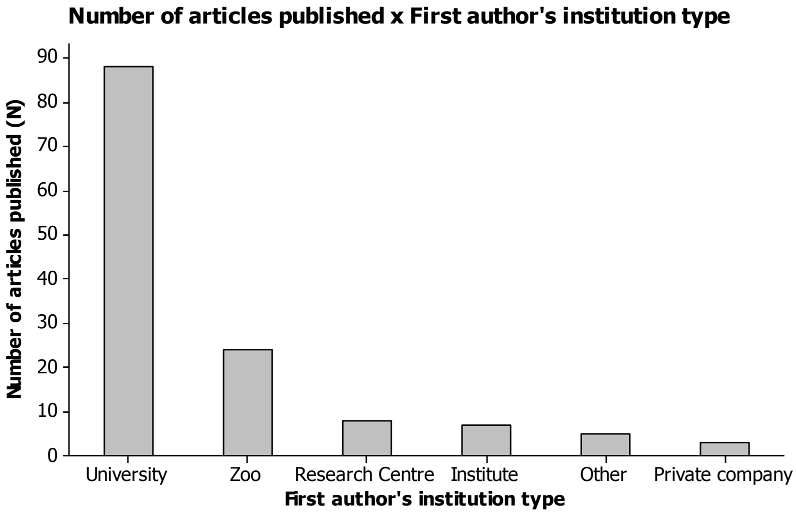


Figure 7. Number of papers published using the keyword "stud$book" (data from the Web of Science©) with respective first author's institution type.

Table 1. Worldwide scientific production concerning studbook research between 1988-2016 by country.

Country	**Number of articles**		**Total number of articles***	**%§**
	Zoo species	*Domesticated species*		
AUSTRALIA	*3*	0	*3*	2.22
AUSTRIA	*0*	1	*1*	0.74
BELGIUM	*4*	0	*4*	2.96
BRAZIL	*1*	0	*1*	0.74
CANADA	*1*	0	*1*	0.74
CHINA	*1*	0	*1*	0.74
CZECH REPUBLIC	*1*	1	*2*	1.48
DENMARK	*2*	1	*3*	2.22
FINLAND	*0*	3	*3*	2.22
GERMANY	*3*	3	*6*	4.44
HUNGARY	*0*	1	*1*	0.74
ICELAND	*0*	1	*1*	0.74
IRAN	*0*	2	*2*	1.48
ISRAEL	*2*	0	*2*	1.48
JAPAN	*1*	0	*1*	0.74
NETHERLANDS	*3*	9	*12*	8.89
NORWAY	*0*	1	*1*	0.74
POLAND	*2*	5	*7*	5.19
PORTUGAL	*0*	7	*7*	5.19
SOUTH AFRICA	*3*	1	*4*	2.96
SPAIN	*3*	8	*11*	8.15
SWEDEN	*3*	3	*6*	4.44
SWITZERLAND	*6*	0	*6*	4.44
UNITED ARAB EMIRATES	*1*	0	*1*	7.41
UNITED KINGDOM	*9*	1	*10*	0.74
UNITED STATES	*36*	1	*38*	28.15
Total	**85**	**49**	**135¤**	**100**

*Total number of articles published using studbooks in their research per country.
§Percentage of total number of articles in the database (N=135).
¤The total number of articles includes one paper published from United States that does not use either zoo or domesticated species.

Table 1 presents worldwide scientific article production using studbooks for their research from 1988 to the year 2016 per country and reveals 26 countries that published articles using studbooks. United States led the number of publications with 28.15%, followed by Netherlands with 8.89% and Spain 8.15%. However, when we look at the publications per animal type separately; that is, zoo (N=85) or domesticated (N=49) species, the top countries changed completely. United States (42.35%), United Kingdom (10.59%) and Switzerland (7.06%) turn to be in the higher rank of publications for zoo species, while Netherlands (18.37%), Spain (16.33%) and Portugal (14.29%) dominate the top ranks for domesticated species. One article could not be categorized between zoo and domesticated species, but was also published by United States, totalizing 135 articles. If we extrapolate the categories to regions, the contribution of each region is as follow: Europe (16 countries; 60% of papers published), North America (2 countries; 28.89% of papers published), South America (1 country; 0.74% of papers published), Asia (5 countries; 5.19% of papers published), Oceania (1 country; 2.22% of papers published) and Africa (1 country; 2.96% of papers published).

Table 2. Number of threatened species registered by the IUCN Red List of Threatened Species according to their taxon. Numbers between brackets represent the number of articles from our database published with only threatened species for that specific year/taxon.

Year§	**Number of threatened species registered by IUCN for each taxon per year listed***				
	Mammalia	*Aves*	*Reptilia*	*Amphibia*	*Actinopterygii/Sarcopterygii*
1996	1,096(2)	1,107(1)	253	124	734
1997	-	-	-	-	-
1998	1,096	1,107	253	124	734
1999	-	-	-	-	-
2000	1,130(1)	1,183	296	146	752
2001	-	-	-	-	-
2002	1,137(2)	1,192(1)	293	157	742
2003	1,130(1)	1,194	293	157	750
2004	1,101(2)	1,213(2)	304	1,770	800
2005	-	-	-	-	-
2006	1,093	1,206	341	1,811	1,171
2007	1,094(4)	1,217	422	1,808	1,201
2008	1,141(3)	1,222	423	1,905	1,275
2009	1,142(3)	1,223	469(1)	1,895	1,414
2010	1,131(2)	1,240(1)	594	1,898	1,851
2011	1,138(1)	1,253	772	1,917	2,028
2012	1,139(2)	1,313(1)	807	1,933	2,058
2013	1,143(5)	1,308	879	1,950	2,110
2014	1,199(1)	1,373(1)	927	1,957	2,222
2015	1,197(11)	1,375(1)	944	1,994	2,271
2016	1,194(5)	1,460	1,079	2,068(1)	2,359

**Source:* IUCN Red List of Threatened Species. Accesed on 13/09/2017.
*Threatened species = Species classified as "Critically Endangered" (CR), "Endangered" (EN) or "Vulnerable" (VU) by the IUCN Red List of Threatened Species.
§The IUCN Red List of threatened species only had data available from the year 1996 onwards; some years were not available (1997, 1999, 2001 and 2005). The absence of numbers in brackets means that no paper included in our dataset studied the taxon on that respective year.

Table 3. Number and percentage of taxonomic orders studied from the articles database extracted from the Web of Science© for zoo and domesticated species.

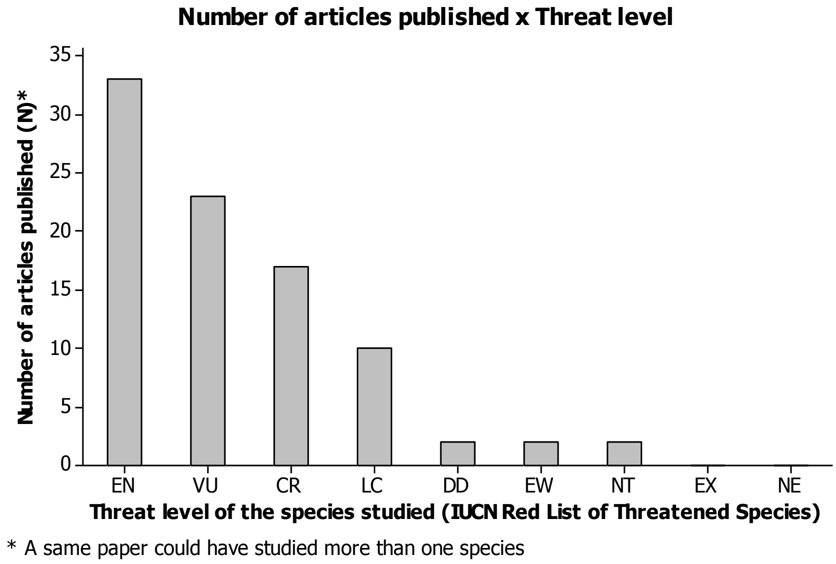
Order	**Zoo**		**Domesticated**		**Total**	
	N	**%**	**N**	**%**	**N**	**%**
Accipitriformes	4	4.65	0	0	4	2.96
Anseriformes	0	0.00	1	2.04	1	0.74
Artiodactyla	2	2.33	2	4.08	4	2.96
Carnivora	21	24.42	2	4.08	23	17.04
Caudata	1	1.16	0	0	1	0.74
Cetartiodactyla	11	12.79	0	0	11	8.15
Ciconiiformes	1	1.16	0	0	1	0.74
Dasyuromorphia	1	1.16	0	0	1	0.74
Diprotodontia	1	1.16	0	0	1	0.74
Gruiformes	3	3.49	0	0	3	2.22
Peramelemorphia	1	1.16	0	0	1	0.74
Perissodactyla	11	12.79	44	89.80	55	40.74
Primates	16	18.60	0	0	16	11.85
Proboscidea	3	3.49	0	0	3	2.22
Psittaciformes	2	2.33	0	0	2	1.48
Sphenisciformes	1	1.16	0	0	1	0.74
Squamata	2	2.33	0	0	2	1.48
Several	5	5.81	0	0	5	3.70
Total	**86***	**100**	**49**	**100**	**134****	**100**

Source: IUCN Red List of Threatened Species.
*An article studied more than one order but less than four orders to be included in the "several" category, therefore the total value of zoo studies shows 86 instead of 85.
**The total number of articles is 134 instead of 135 because it excluded the publication from United States which did not used either zoo or domesticated species.

The majority of studies conducted with zoo species used threatened species/subspecies (N=73; 82.02%) (Figure 8), while studies with domesticated species selected animals used for sport/entertainment (N=43; 87.76%), mainly the domestic horse (*Equus ferus caballus*) (Figure 9). A chi-squared test of goodness of fit was performed to determine if whether the IUCN categories were equally studied. The results show that the nine categories (EX, EW, CR, EN, VU, NT, LC, DD or NE) were not equally studied (X^2=115.169; N = 89; p<0.01). Therefore, animals from the categories "Endangered" and "Vulnerable" had a greater number of articles published, more than expected. In total, 85 articles used zoo animals and 49 articles used domesticated animals. Only one article worked with studbooks but did not use any zoo or domesticated species since its data came from a hypothetical species.

According with the IUCN Red List of Threatened species (2017), Actinopterygii/Sarcopterigyii are the main threatened taxonomic group, followed by Amphibia and Aves. However, most studies focused in studying Mammalia over the years (Table 2 and Figure 10). Also, regarding the groups evaluated by the IUCN Red List of Threatened Species until 2017, from the most studied group to the least studied in number of species are: fishes, birds, amphibians, mammals and reptiles (IUCN Red List of Threatened Species, 2017).

From the zoo animals, 54 was the number of species studied; from the domesticated animals, the number of species was much lower (N=5). One species of a goose could not be identified by its common name and its order was considered to be Anseriformes. The main species studied for zoo and domesticated animals were *Diceros bicornis* and *Equus ferus caballus*, respectively. Seventeen taxonomic orders were represented based on the species studied (Table 3); Carnivora was the order most studied for zoo species (24.42%), while Perissodactyla was the order most studied for domesticated species (89.80%). Overall, Perissodactyla was the order most studied when considered both zoo and domesticated species (40.74%).



List of threat categories defined by the IUCN Red List of Threatened Species in order of extinction risk: EX=”Extinct”, EW=”Extinct in the wild”, CR=”Critically endangered”, EN=”Endangered”, VU=”Vulnerable”, NT=”Near Threatened”, LC=”Least concern”, DD=”Data deficient”, NE=”Not evaluated”

Figure 8. Number of articles published using studbooks of zoo animals and their respective level of threat of extinction as described by the IUCN Red List of Species (1988-2016).

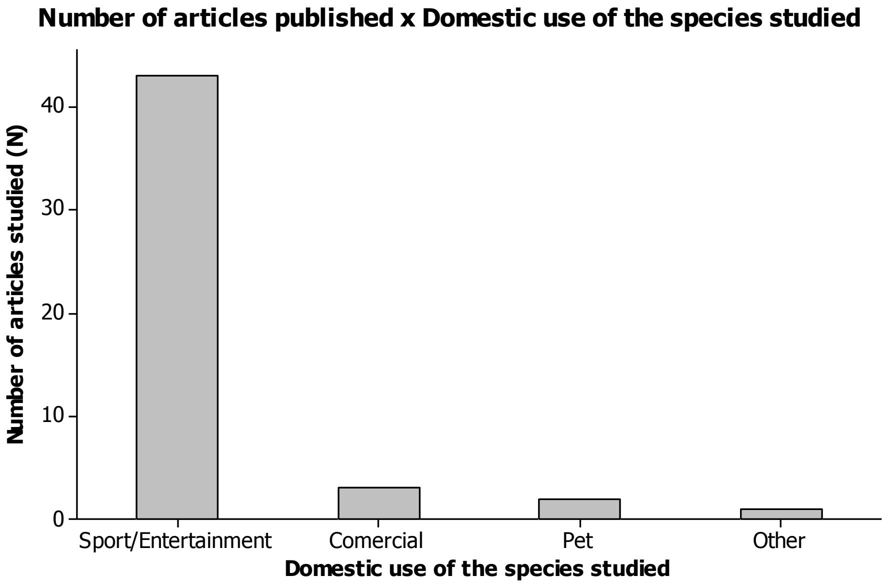


Figure 9. Number of articles published using studbooks of domestic animals and respective domestic uses of the species studied between 1988 and 2016.

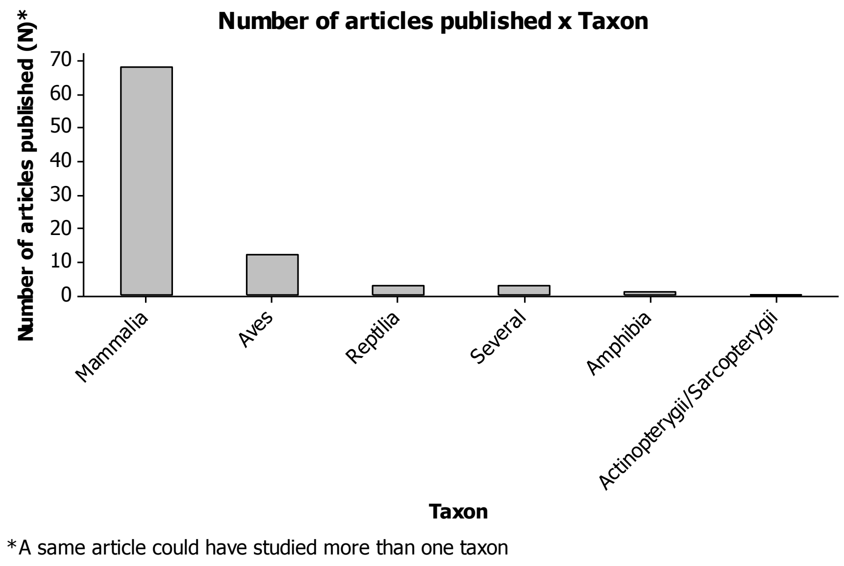


Figure 10. Number of articles published using studbooks 1998-2016 by respective taxon studied.

Table 4. Most frequently used scientific journals ranked for zoo animals and domesticated animals based on the bibliometric analysis of studies using studbooks for their research from 1988 to 2016. The number of articles published by the journals and their respective impact factors are shown in the table.

Journal	Impact factor*	Number of articles	%§
<u>*Zoo animals*</u>			
Zoo Biology	***0.813***	24	28.24
Biological Conservation	***4.022***	6	7.06
Conservation Genetics	***1.515***	6	7.06
Conservation Biology	***4.842***	5	5.88
Plos One	***2.806***	5	5.88
Ecology and Evolution	***2.440***	3	3.53
Animal Conservation	***2.835***	2	2.35
Applied Animal Behaviour Science	***1.771***	2	2.35
International Journal of Primatology	***1.285***	2	2.35
Journal of Zoo and Wildlife Medicine	***0.59***	2	2.35
Journal of Zoology	***2.186***	2	2.35
American Journal of Primatology	***2.005***	2	2.35
Other		24	28.24
Total		**85**	**100.00**
<u>*Domesticated animals*</u>			
Livestock Science	***1.377***	16	32.65
Journal of Animal Breeding and Genetics	***1.877***	8	16.33
Czech Journal of Animal Science	***0.741***	3	6.12
Equine Veterinary Journal	***2.382***	2	4.08
Animal Genetics	***1.815***	2	4.08
Acta Agriculturae Scandinavica Section a-Animal Science	***0.340***	2	4.08
Genetics Selection Evolution	***2.964***	2	4.08
Animal	***1.921***	2	4.08
Journal of Animal Science	***1.863***	2	4.08
Other		10	20.41
Total		**49**	**100.00**

**Source: InCites Journal Citation Reports on 18/09/2017.*
§Percentage of total number of articles in the database for zoo animals (N=85) and domesticated animals (N=49). The article that did not work with wild or domesticated species was published in the journal *Zoo Biology*.

The articles were published in many different journals (N=54): 35 for zoo species and 19 for domesticated species. Zoo Biology was the most utilised journal for zoo species (N=24) while Livestock Science was for domesticated species (N=16) as is indicated in Table 4. The mean journal impact factors (2016) was 1.728, but one journal did not have an impact factor for the year 2016 and the impact factor from 2015 was used instead only for that journal. For zoo species only, the mean impact factor was 1.842 (SEM=0.15) and for domesticated species it was 1.506 (SEM=0.08). Eleven main subject areas and 23 subtopic areas were used to classify the articles from our dataset. The majority of articles were found to be about Population Management (50.37%) and the main subtopic associated was Genetic Diversity (31.85%). Other subject areas and subtopics with respective number of articles published and relative percentages are shown in Table 5.

Table 5. Subject areas and subtopics approached in the 135 articles of the dataset extracted from the Web of Science©.

Category	**Number of articles**	**%§**
Subject area		
Population management	68	50.37
Genetics	21	15.56
Livestock science	18	13.33
Behaviour	9	6.67
Demography	5	3.70
Pathology	5	3.70
Physiology	5	3.70
Computer modeling	1	0.74
Environmental science	1	0.74
Evolution	1	0.74
Morphology	1	0.74
Total	***135***	**100.00**
Subtopic		
Genetic diversity	43	31.85
Reproductive success	12	8.89
Pedigree	9	6.67
Performance	9	6.67
Reproductive biology	9	6.67
Survivorship	8	5.93
Breeding value	7	5.19
Sex allocation	7	5.19
Status	4	2.96
Studbook	5	3.70
Reintroductions	4	2.96
Genetic structure	3	2.22
Phenotype	2	1.48
Fertility	2	1.48
Genealogy	2	1.48
Viability	2	1.48
Body condition	1	0.74
Disease transmission	1	0.74
Familiarity	1	0.74
Genetic disorder	1	0.74
Heritability	1	0.74
Recommendations	1	0.74
Software development	1	0.74
Total	***135***	**100.00**

§Percentage of total number of articles in the database according with their subject areas and subtopics as classified by the author.

2.4 Discussion

This study has shown that most studbook research concerning zoo animals, especially carnivore species, is conducted by university-based researchers in North America or Europe and the most commonly studied subjects are those related to animal management and genetic diversity.

From 1988 until 2016, the number of studies with studbook data grew gradually and peaked in 2015. This growth is probably based on the need for captive management programmes to boost their performance due the significant decrease of wild animals as a result of the ongoing extinction crisis. The reason for the peak in 2015 is uncertain but could be related to the advances in communication via the development of new software such as ZIMS (released first in 2011 but improved almost every following year), the better internet availability around the globe, the number of universities or even the increase, in general, of the publication pressure by world scientists.

The task of registering and keeping records from animals is restricted to professionals linked to zoological institutions unless there is some exception such as research. However, the majority of first authors from the dataset are from a university. This fact suggests that partnerships between universities and zoos have been made to support research using data from studbooks or that possibly zoos do not have enough staff, skills or time to conduct more in-depth research.

Scientific article production shows visible inequality in number of countries participating with publications per continent. Europe has 16 countries participating but does not lead the rank in number of publications. United States was first with 28.15% of the total number of publications by itself and when analysing only wild species, it represents 42.35% of the publications. This means that this country conducts/publishes more research containing zoo studbook data compared to others, although studbooks are only one of the components of animal management. A possible explanation for that could be their pioneerism in developing animal records through ISIS (now Species 360) and the high number of universities and scientists in the United States, which increase the chance of publishing more articles.

The Gross Domestic Product (GDP) per capita is also significantly associated with the number of publications. The GDP per capita influences on the fund amount designated for research indirectly. United States have usually been between the countries with highest GDP value of this dataset, together with United Arab Emirates, Switzerland and Norway for the year 2016, for example. Netherlands, however, publishes more articles with domesticated species than other countries (18.37%); this may reflect the importance of agriculture to this country's economy or their interest in horse racing or related business. Overall, the United States published most scientific papers using studbooks (28.14%). This to an extent reflects the wealth of North American universities and zoos, which are often better funded than their counterparts in other areas of the world (May, 1997).

This fact reinforces the dependence of investment and funding of studies to speed up scientific progress, especially in the field of animal conservation. Many countries with unstable economies have some of the most threatened animals in the wild and the greatest need for managing those species into zoos as it is the case, for instance, of the black rhino (*Diceros bicornis*), which was the main wild species studied from our dataset in this chapter. As science progresses, new tools and alternatives for caring for animals and managing species in captivity arise. Even though wealthier countries could still contribute developing science for those countries where science lacks, ideally, the host country of the threatened species would benefit more in terms of posteriorly reintroducing the species into the wild. This does not mean that only host countries should develop science towards their native species. Science should be expanded as much as possible to generate more knowledge and consequently better applications, but host countries would best benefit from such developments.

Considering the journals used to publish the studies, Zoo Biology was the journal most chosen for zoo species. Livestock Science led the rank in number of publications for domesticated species. However, both journals do not have high impact factors. The mean impact factor for zoo species was 1.842 (SEM=0.15) and for domesticated species was 1.506 (SEM=0.08). Both top rank journals have impact factors lower than their category means. The relatively low impact factors could probably reflect the specialization of the articles instead of poor quality science, since scientific articles of a specialised nature will be read and cited by fewer scientist (Seglen, 1997). A field too specialized could mean a slow progress of science in the area, since less scientists are able to understand, work, and apply the concepts involved in the field. This emphasizes the urgency for specialized scientists in generating maximum knowledge to the benefit of species, especially those which are critically endangered and demand more attention.

The IUCN Red List of Threatened Species describe as "threatened" species classified within one of these three categories: Critically endangered (CR), Endangered (EN) and Vulnerable (VU). Most studies published with studbook data from zoo species used threatened species. Even though Critically Endangered was not the category with the most studies, Endangered was the main category. Yet threatened species were the focus of most research, it is extremely important to distinguish what kind of animals was preferred for study.

The analysis indicated that most animals chosen for research were mammals. However, the number of threatened mammals is much lower than fish, amphibians and birds according to the IUCN Red List of Threatened species (IUCN, 2017). In addition, according to Oberwemmer et al. (2011), the number of mammals and birds identified and described until the article publication date was 9.1% and 3.3% of 62,574 species, which is a relatively low number in comparison to other taxa. This could reflect a paradox, in which the majority of animals containing studbooks are mammals, but they are not the taxa with the highest number of threatened speciesand neither the taxon with the higher number of species recognized and described. In general, mammals are a group of animals with bigger body sizes and this facilitates the study of these species besides attracting attention of researchers through empathy. Lindemann-Matthies (2005) summarizes some literature described to explain the higher interest that some children have toward mammals, which could include “human-like” appearance, culture, media and others.

The fact that most studbooks and research using studbooks are from mammals could reflect that some research has been developed not by necessity, but for other reasons such as, for example, personal interest in the species studied by the researcher. During the beginning of studbooks publications, the majority of animals studied were mammals due their strong public appeal (Glatston, 1986) and this seems to continue until present times as observed in other studies from Goulart et al. (2009) and Azevedo et al. (2006) for example.

Research and management plans ideally should not reflect personal preferences, favouring threatened species to avoid an uneven investment and to represent all the taxa proportionally to their conservation requirements (Leus et al., 2011). The low number of articles with studbooks from fishes or amphibians could also be related to their breeding system (e.g. explosive reproduction), making it hard to gather the necessary information. On another hand, given that most studies were applied in nature (as judged by their subject area) this could also suggest that research is been driven by conservation and not academic curiosity.

Population management was the subject area with the highest number of articles published and this was expected, since studbooks are extremely important for maintaining populations of species genetically healthy. Genetic diversity, similarly, was the most studied subtopic of the dataset. The aim of a studbook is, to have control of the genetics and demography of a species, therefore it was expected that these categories would appear more than others. Inbreeding is one of the main, potential, negative consequences of captive breeding programmes due the low founder genetic variability and must be controlled with care. Reproductive success occupies second place in subtopics most studied. Jarvis (1969) emphasized that reproduction is a vital topic of animal science and that captive animals allow for an easier investigation of some reproduction variables than wild animals. Pedigree and performance were common topics for domesticated species and occupied third and fourth places, respectively in the number of publications.

2.5 Conclusion

In conclusion, studbooks have allowed the expansion and better development of the animal management field to areas less explored, although population management and genetics are still the main research focus when considering this kind of data. The parallel growth of studies containing studbook data showed that multidisciplinary research areas have been interconnected due the great research potential offered by their information stored. Social network analysis, for example, as of our knowledge, has never been included in the context of zoo animal management and transfers as it is in chapter four. Therefore, studbooks could be better explored (Glatston, 1986; Jarvis, 1969). Additional data such as veterinary records, housing and transfer characteristics, for example, could be gradually added to studbooks allowing new paths of investigation and facilitating long-term historical analysis in the future. The more information provided the better, more conscious and well-designed could be the manipulation of animals *ex-situ*.

Ideally all studbook data should be made open access (online) as this will encourage researchers to use this vastly under-exploited resource. For example, Species360 platform ZIMS contains data on 22000 species, 10 million animals, representing 167 million husbandry and 75 million medical records both living and dead (Species360, 2018). This database is now becoming comparable in size with national human health databases, which have proved extremely useful for researchers studying population scale health effects. It is clear from the limited amount of research so far conducted with studbooks that scientists have only just begun to 'scratch the surface' and whilst some zoos might be protective over their data, this protectiveness should be weighed against the huge potential benefits for zoo animal conservation.

This study provided some base of areas that could be better developed with the use of studbooks and indicated the nature of publications done along the years. There is a positive relationship between the economy of a country and the number of publications with studbook data, which confirms the economic aspect of science and its dependence of investment/sponsorship. According to the results obtained, United States leads the publication rank of articles containing zoo studbook data while Netherlands leads the publication rank of articles containing domestic animals. Most of the research published had universities as the author's associated addresses instead of other types of institutions.

The taxonomic preference of study showed similar results with other publications involving zoo animals, although it is not the ideal result from a conservation perspective. Mammals and birds were the main classes of animals in consideration for studies with studbook data. More specifically, the orders Carnivora and Perissodactyla were the most studied for zoo and domesticated species, respectively. In the past, an explanation for this mammal preference could be the higher number of mammals and birds evaluated by the IUCN Red List for each taxon. In the recent years, however, the number of species registered for each category inverted, displaying the opposite pattern. Even though threatened species were the focus of study according to the articles from the dataset selected for this chapter, endangered and vulnerable species prevail over critically endangered species. In fact, those categories should be the focus of study due the extinction risk involved, but preferences should be toward critically endangered ones, which have a more imminent risk of disappearing. More research should be developed toward the understanding of mammals' "preference" in studies with zoo animals and to discover how it can be mitigated.

Chapter 3 Effect of studbook variables, climate and country's wealth on the longevity or reproductive success of captive cheetahs (*Acinonyx jubatus*)

3.1 Introduction

Although there are exceptions, in general, life in captivity has been increasing the lifespan of many species, especially those with fast life histories (Tidiere et al., 2016), due to managed conditions offered to animals such as diet, veterinary care (Longley, 2011) and protection against predators. Overall zoo animals can be considered to live under conditions of relaxed selection (Price, 2002; McPhee, 2004; Kleiman et al., 2010). However, in contrast to this, the captive environment can prevent animals from expressing natural behaviours (Hill & Broom, 2009) such as reproduction due contraception and lack of mate choice.

Reproductive decisions are normally made by studbook keepers for the best of the captive population (i.e. genetic health) rather than for the welfare of the individual (Charge et al., 2014). These factors can potentially have an impact on the welfare (Asa et al., 2010; Muller et al., 2011) and lifespan of determined species, especially those with slow life histories such as elephants (*Loxodonta africana, Elephas maximus*; Tidiere et al., 2016) or species where mate choice is very important such as cheetahs (*Acinonyx jubatus*). Asa et al. (2010) has discussed about the incorporation of mate choice under supervision of management programmes, therefore allowing the animals to express natural behaviours but still controlling the genetic outcome of the pairs chosen.

Understanding how animal longevity is affected by the functioning of the body, genetics and the environment is important for animal conservation, in particular for captive breeding programmes, which are trying to prevent species extinction resulting from the ongoing extinction crisis (Conde et al., 2013; Wakchaure & Ganguli, 2016). One almost inevitable consequence resulting from the management of captive breeding programmes is the relocation of an individual from one facility (i.e. zoo) to another. These transferences demand good communication between institutions and metapopulation planning is essential to establish a flow of genes, which avoids inbreeding and maximises the maintenance of the genetic diversity of the founder population (Conde et al., 2013). Nevertheless, the process of transferring individuals generates stress to the animals involved (Fazio & Ferlazzo, 2003; Wells et al., 2004; Teixeira et al., 2007; Minka & Ayo, 2009; Costa et al., 2013), especially if it involves long distances (Moberg & Mench, 2000; Dickens et al., 2010; Damtew et al., 2018).

The few studies conducted on the transport of non-domesticated animals (Montané et al., 2002) have confirmed the negative impact of transportation in the lifetime of an individual, especially over long distances (Dembiec et al., 2004; Snyder et al., 2012). Life in a new environment can also be stressful because animals will have new keepers, new management routines, a new enclosure and new social relationships (Dembiec et al., 2004; Pansini, 2006). The stress suffered in this period of transition is believed to impact on the survival rate of the animals, which decreases, generating chronic consequences or even causing their death. Studies of rhinos (*Diceros bicornis* and *Ceratotherium simum*) have shown that transporting them for captive breeding has a biological cost, which is, the animals will not breed or will have a delay in breeding that can be more than two years after transportation due to stress (Linklater et al., 2010).

The transportation of animals should meet international requirements developed by IATA (International Air Transport Association), CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) or other responsible organization from each country. Transport containers should be safely designed to hold and maintain the animals during the period of transference, sometimes including food and water provision or providing for other needs. However, these guidelines focus in dealing with the wellbeing of the animals whilst being transported, but the longer term or chronic impact suffered from transportation can have on animal's wellbeing should also be considered. Studies have demonstrated that traumatically stressful events can have a lifelong impact on the wellbeing of animals (Mirescu et al., 2004; Dickens et al., 2010) and as previously mentioned transporting animals is extremely stressful (Teixeira et al., 2007; Minka & Ayo, 2009; Costa et al., 2013).

The ideal age for transportation of young animals (i.e. simulating natal/innate wild dispersal) usually depends on their age of sexual maturity; that is, when they are able to live without their parents' support and reach reproductive stage or just before sexual maturity depending on the species (Howard, 1960; Sutherland et al., 2000) and wild behaviour should be used by zoos to guide this decision.

In the wild, generally female cheetahs (*Acinonyx jubatus*) become sexually mature around two-years-old (Wielebnowski & Brown, 1998; Pettorelli & Durant, 2007) and then separate themselves from relatives to live solitary lives (Laurenson et al., 1992; Federico & Bracchi, 2001). Male cheetahs leave their mothers when they are also about 2 years-old (Durant et al., 2004) and form coalitions mainly with brothers or occasionally with non-related individuals (Durant et al., 2015). Bertschinger et al. (2008) reported reproductive age for female captive cheetahs in South Africa to be around 2.5 or 3 years old and around 3.5-4 years old for males. However, some studbook records show that captive animals were transferred before the usual age of dispersal observed in wild cheetahs and this phenomenon could possibly lead to a negative effect on the longevity of animals and on their reproductive output. Therefore, the age of first transfer between zoo locations is an important topic for investigation.

The place where an animal is born has much influence on its life because of differences offered according to each institution's husbandry, wealth and qualified staff caring for the animals (Beattie et al., 2000). Studies have shown that the quality of the environment has an impact on animal health and wellbeing (Carlstead & Shepherdson, 1994). If zoo animal movement guidelines do not respect the timing needed for the animal development before its transportation, its welfare could be reduced, and its reproduction negatively affected (Moss, 1981).

Gender has also been investigated as a factor affecting longevity in animals with most frequently females having longer lifespans (Smith, 1989; Litzgus, 2006; May, 2007). These differences may arise because of hormones (Brown-Borg, 2007), genetics (Tower & Arbeitman, 2009), parasitism (Moore & Wilson, 2002) and life history of the species (Magalhaes & Costa, 2009), including reproductive events (Pettorelli & Durant, 2007). According to Eaton (1974), wild female cheetahs have higher survival rates than males. In a study from Pettorelli & Durant (2007), their dataset showed an average death age of 7.47±3.20 years for wild female cheetahs. Data from Cheetah Outreach (2017) reported male lifespan from Serengeti cheetahs with averages from 6 to 8.5 years and 6.9 years for females based on other studies (Caro, 1994).

Rees (2004) showed that Asian elephants (*Elephas maximus*) perform more stereotypic behaviours under lower temperatures in captivity. Princée & Glatston (2016) have suggested that climate could have an indirect influence on longevity and reproductive success of captive animals. Red pandas' (*Ailurus fulgens*) longevity was confirmed to be affected by different climate zones in their study. Therefore, the analysis of climate on the reproductive success of animals would benefit captive breeding plans, since it would be necessary to take the location of the breeding facility into consideration when recommending transfers to other facilities. This is especially important because zoos housing cheetahs are found on six continents.

One of most used climate classification is the Köppen-Geiger (Kottek et al., 2006; Rubel & Kottek, 2010; Alvares et al., 2013; Rubel et al., 2017), which is based on main climate, precipitation and temperature data to specify a code containing three letters that represents the climate of the location. The first letter of the code (A, B, C, D, E) represents the main climates: equatorial, arid, warm temperate, snow and polar, respectively; the second letter (W, S, f, s, w, m) refers to the precipitation of the location, which could be: desert, steppe, fully humid, summer dry, winter dry or monsoonal, respectively; lastly, the third letter (h, k, a, b, c, d, F, T) refers to the temperature of the environment, which can be: hot arid, cold arid, hot summer, warm summer, cool summer, extremely continental, polar frost or polar tundra, respectively. To summarize, a climate defined by Cfb, for instance, would indicate a place with climate that is warm temperate, fully humid and with warm summer. Figure 11 shows the global climate classification according to the Köppen-Geiger extracted from Kottek et al. (2006).

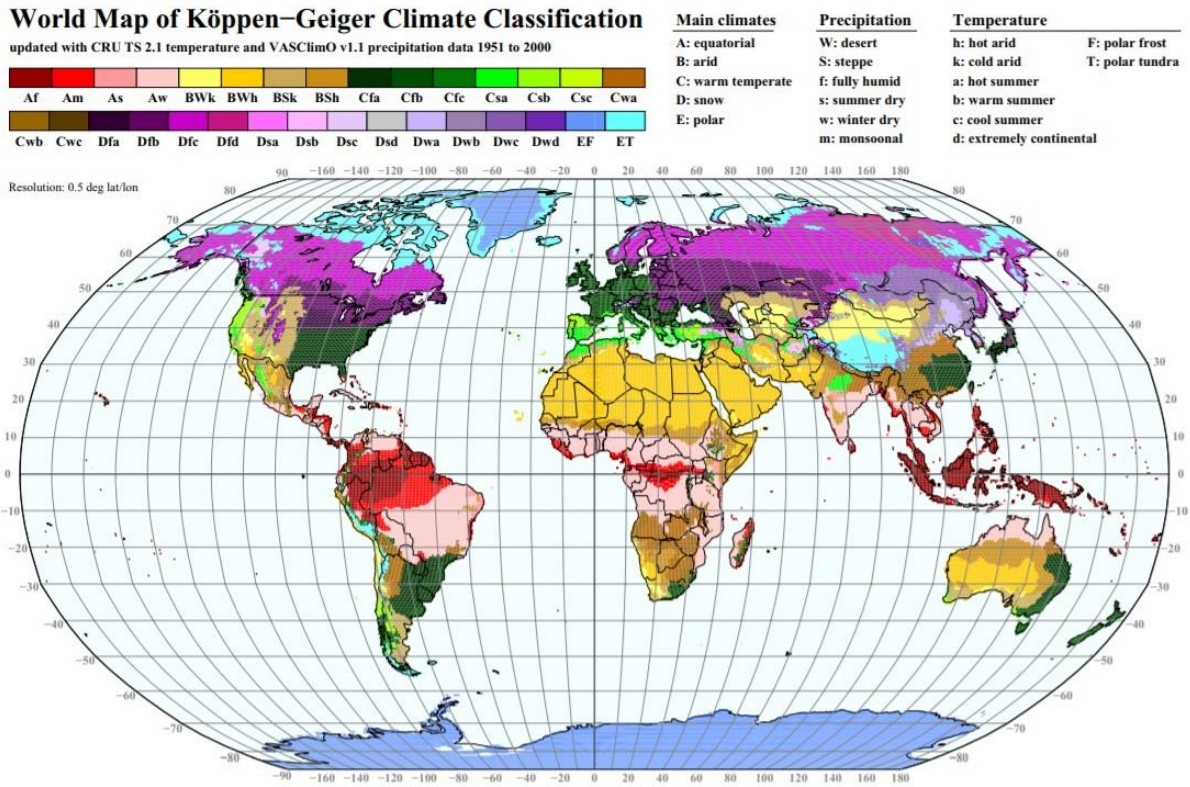


Figure 11. World map of Köppen-Geiger Climate Classification extracted from Kottek et al. (2006).

Until 2016, 119 facilities managed to reproduce cheetahs in captivity. Those facilities are widely spread across the world, as shown by Figure 12.

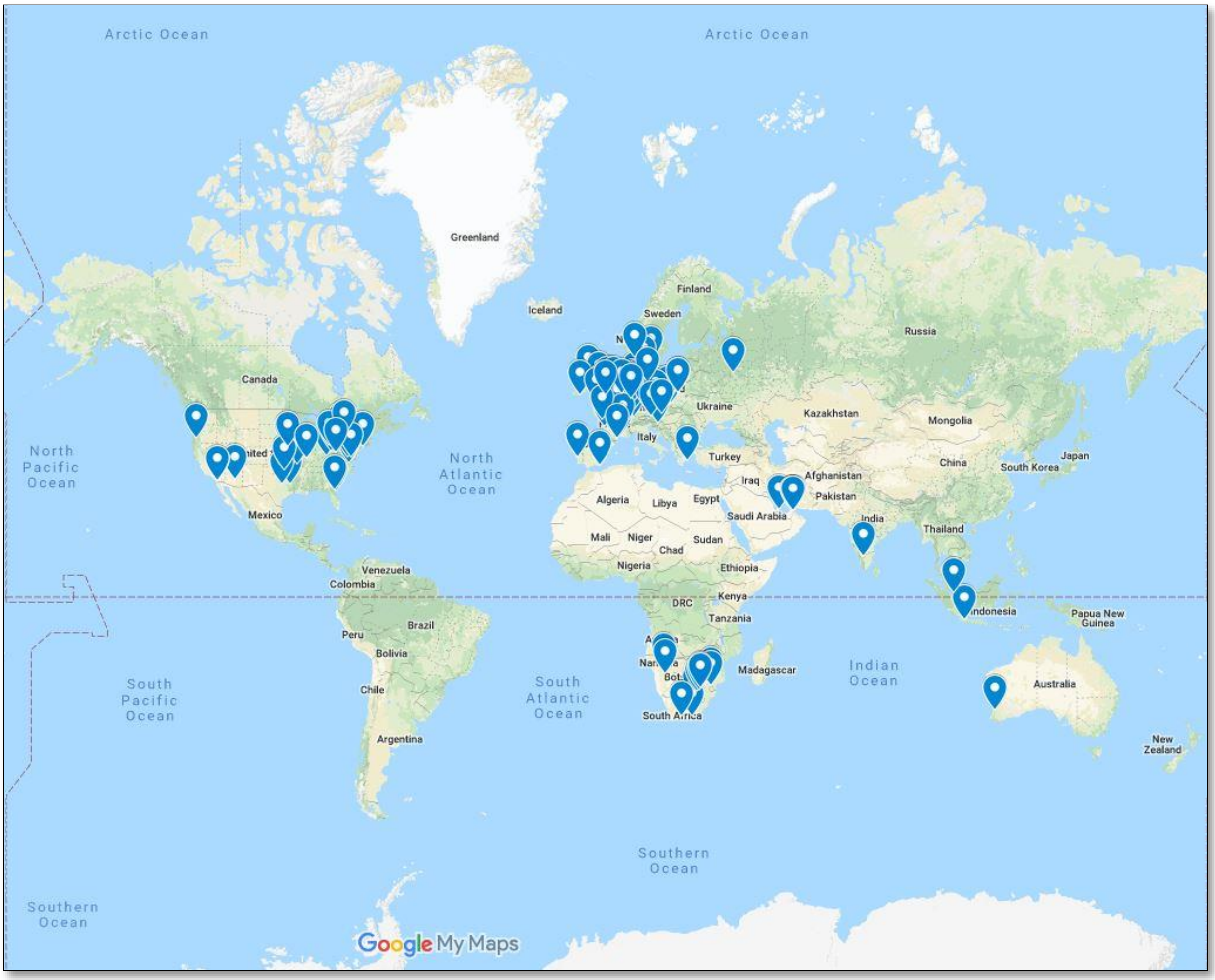


Figure 12. World map of the facilities that reproduced cheetahs in captivity from 1999 to 2016 according to international studbook information from the period mentioned.

The amount of money invested on animal husbandry and breeding is also a factor that can possibly affect the reproductive success of a species, since it can relate to better infrastructure conditions, care and qualified staff to look after the collection animals. Since the annual income of zoos are some data not easily accessible to researchers outside the zoo community, the GDP per capita of the country where this facility is located could indirectly infer some investment those facilities could be doing on them, since the higher the GDP per capita, the wealthier the country and consequently, the higher the chance of the zoos having more money to invest on their animals welfare/breeding. Leader-Williams et al. (2007) showed that there is a positive correlation between the number of zoo visits and the GDP per capita of a country. Thus, a country's GDP is a general proxy of a zoo's wealth and permits cross country comparisons to be made.

This study intends to investigate eighteen-years of studbook data from captive cheetahs (*Acinonyx jubatus*) to analyse how variables such as: gender, number of transfers performed during life, age of the first transfer between institutions, sum of the total distances travelled between captive breeding locations and birth place may affect their longevity in captivity. In addition, it intends to examine how climate differences derived from different facilities' locations and the GDP (Gross Domestic Product) per capita of the countries where the breeding facilities are located may affect the reproductive success of captive cheetahs.

3.2 Methods

Generalized Linear Models (GLMs) were the statistical tests chosen for the analysis of longevity and reproductive success data since the objective of this project was to identify the relationship between predictors and variables (longevity and reproductive success), which did not follow a normal distribution. Linear models were therefore excluded from the options due the sample residuals not being normally distributed. The two models were analysed separately because of the differences in stored data for each variable and differences in predictions.

3.2.1 Longevity analysis

The longevity of captive cheetahs was investigated using the section "Deaths" from eighteen International Cheetah Studbooks (years 1999-2016) available online at the Cheetah Conservation Fund website. First, a spreadsheet was created in excel containing information from historical data such as individual's IDs ("Stud#"), gender, date and age of death, number of total transfers during life by the individual, place of birth (names of the facilities where the animal was born) and age at first transfer. The number of transfers was verified throughout the transcription of data and input on the spreadsheets. Age of death and age at first transfer were calculated from basic subtractions from the birth dates and transfer dates available in the studbooks and were displayed in days, since many animals survived only for a short period of time. If an animal did not make any transfer during its life, the age at first transfer was replaced by "NA" and its total distance travelled during life consequently was zero.

The data were filtered according to the following conditions: 1) only captive animals were included, since the exact birth date of wild captured animals was unknown by the studbook keeper at the moment of individual registration; 2) animals with unknown gender or transfer dates were excluded from the data; 3) animals with mismatched or inconclusive dates of transfers or missing data were also excluded from the sample; 4) animals that survived less than 6 months were excluded from the sample since these animals are usually still very vulnerable, increasing the risk of death from different factors not included in this analysis and their inclusion would bias the data for the statistical analysis (GLM); and 5) any other records with inconsistent data were removed. This process resulted in 1100 observations but only 739 observations were considered for statistical modelling/analysis due the exclusions of NA values.

Another spreadsheet was created with the facilities' names where the cheetahs were transferred since birth until their death and the institutions' names were followed by their geographical location (coordinates), extracted using an add-on offered in Google Sheets called "Geocode cells", which allows you to determine the latitudes and longitudes of specific addresses. The facilities' addresses were taken from address catalogues provided by the studbooks. When the facility name was not present in the catalogue or the address was not listed there, the individual referred to in this data was excluded from the sample. Nevertheless, some coordinates were estimated, when possible, if the exact address was not given with precision. For instance, a facility with an address showing only municipality, district, city, was registered under the circumstances of estimated coordinates for those places.

Following this, the coordinates from the facilities that sent and received the animals during their transfers were saved in a ".txt" file, which was imported in R Studio (R Core team 2018) for the calculation of the distances between them. Using the package "geosphere", the shortest distances ("as the crow flies") were calculated through the Vincenty Ellipsoid method, which is more accurate than other methods that consider the Earth as a sphere. The script for this process is found in Appendix 1. Finally, the distances between all the facilities that an animal was transferred during life were summed to result in a final variable corresponding to the "total distance travelled during life," which was converted and displayed from meters to kilometres. This variable was added to the initial spreadsheet, described previously, containing the other information about the life history of our subject cheetahs.

With all the information ready for analysis, the data were imported again into Rstudio for data exploration. Normality was inspected using visual representations and Shapiro-Wilk tests; Spearman's correlation tests ($p<0.05$) were applied to confirm if there were correlations between the explanatory variables (collinearity) and, consequently, reinforce or not the suitability of the statistical test chosen (GLM). A GLM (Generalized Linear Model) procedure was chosen for the statistical analysis because the data was mostly non-parametric and independent (no repeated measures from the same observation).

The GLM function was used to model the death age of cheetahs (discrete variable), using as predictors the gender (categorical variable with two levels), the number of transfers done during life (discrete variable), place of birth (categorical variable with 104 levels), age at first transfer (discrete variable) and total distance travelled during life (continuous variable). Three models (m1, m2, m3) were created to predict the variable "Death age" and then the final model (m4) was developed. The first model (m1) included death age as the outcome variable and gender, number of transfers, age at first transfer and total distance travelled during life as predictors.

The “Poisson” family with a log link function was initially chosen to run the analysis (m1), since the outcome or response variable, “death age” is a discrete numerical variable and this family is typically used for count data (integers numbers; Coxe et. al, 2009). However, due to problems of overdispersion, the family used was changed to others such as Quasipoisson (m2) and lastly to Negative Binomial (m3), once both are used to correct models with this kind of problem because they allow means and variances to differ adding a dispersion parameter (Hilbe, 2007). This parameter, more specifically, adjusts the equation allowing variances to exceed the mean and lowering standard errors. Model 4 (m4) was created as a result of the output from model 3 (m3) and is considered the optimal model between the four developed.

Sometimes in model development it is necessary to exclude some explanatory variables due the variables’ coefficients not being statistically significant in the analysis of variance (ANOVA) method. This process happened after m3 was created, since gender was indicated as a non-significant variable. To make sure this variable should be removed, the command “drop1” was applied, which showed, in fact, the lowest AIC (Akaike’s Information Criteria) value for this variable. Model 4 (m4), the definitive model, was then created exactly the same way as m3, but without the variable “gender” this time. It was delimited as the definitive model because all the variables were found to be significant after running ANOVA test again. VIF (Variance Inflation Factor) was used to confirm the influence of the explanatory variables’ multicollinearity on the model using the conventional value of 10 as the acceptance limit for keeping the variable in the model. Analysis of variance (ANOVA) was also used for the comparisons of the final model with its null model (m4.null). The null model is the one that represents the null hypothesis, it is, the hypothesis that no explanatory variable contributes for the predictions of the answer variable, in this case death age.

M4 results demonstrated that birthplace had some levels as significant and others as non-significant (not all 104 levels appeared due the exclusion of observations with NA values when running the model). A model with and another without the categorical variable were used to test its significance as a whole. After a Likelihood Ratio Test check done comparing a model with and other without the variable "birthplace", the model which contained this variable proved to be the best. Therefore, birthplace is a variable that was kept in the model (m4) and analysed with due consideration.

In general, multiple regression procedures follow the example equation: $Y = \beta_0 + \beta_1X_1 + \beta_2X_2 + ... + \beta_kX_k$, where k is the number of explanatory variables, β are coefficients which represents the independent contribution of each variable to the prediction of the answer variable, X_{1-} X_k are the variables themselves and Y is the answer or outcome variable. Poisson regressions, nevertheless, uses a logarithm function, changing the formula to $\ln(Y) = \beta_0 + \beta_1X_1 + \beta_2X_2 + ... + \beta_kX_k$. When running a Poisson regression or an expansion of the Poisson regression that uses a log link function (e.g. Quasipoisson, Negative Binomial), the coefficients ("β") are easy to interpret if exponentiated at the end to obtain the proper contribution of each variable and to make it interpretable (Berk & MacDonald, 2008).

M4 contained a categorical variable ("birthplace") and for this reason dummy variables (artificial numerical variables coded as 0 or 1 to represent subgroups of a categorical variable) were necessary for the interpretation of the model, but R automatically creates dummy variables for categorical (factor) variables and no procedure was necessary to be taken for this step. Usually, when a categorical variable is used in a model in R, the software considers the first category in an alphabetical order or numerical order to be the reference level of comparison; that is, this category is not shown in the results because it was used as the intercept of the regression. However, if the researcher believes the reference level should be changed for another level with more meaningful relevance, one can do so using the function “relevel”. This method was applied in m4, changing the reference level from “Amersfoor” to “PretDW”. This decision was taken due the high success from “PretDW”, known as Ann van Dyk Cheetah Centre (South Africa), in reproducing cheetahs in captivity based on annual data from studbooks.

The script used in R for this statistical analysis can be found in Appendix 2.

3.2.2 Reproductive success analysis

Reproductive success data were extracted from the International Studbooks (1999-2016) and were input in a spreadsheet for analysis. Those data were calculated from the total number of cubs born in each facility minus the number of cubs that died in there before 1 month of age. Private facilities were not considered to this analysis since their locations are not made available in the studbooks. The GDP (Gross Domestic Product) per capita from the country where the facility is located was extracted for every year of occurrence from the World Bank databank (World Bank, 2018) and an average was calculated for each facility according to the number of years it appeared during the timeframe studied. Köppen-Geiger climate classification (Kottek et al., 2006; Rubel & Kottek, 2010; Rubel et al., 2017) was applied for the city of every breeding location using Climate-Data website (climate-data.org). Then, a scatterplot was created using R studio (R Core Team, 2018) for the visualization of any pattern of association between the variables.

Again, a GLM approach was applied in R using the full dataset (N=116) to investigate if the average GDP per capita (continuous variable) and the climate (categorical variable) affected reproductive success (discrete variable) of captive cheetahs. The same methodology, previously explained, for the longevity analysis was used to investigate normality and correlation of variables. Since reproductive success, a count variable, was used as the answer or dependent variable, the GLM family chosen initially for the statistical analysis of the model was the Poisson family (m.rep1). However, overdispersion was identified once more, changing the Poisson family to other families such as Quasipoisson and Negative Binomial (m.rep2 and m.rep3, respectively), which improved the regression. The reference level for the climate (categorical variable) was kept as the R default (alphabetical order). A null model called m.null was designed to compare which model answered for most variance in reproductive success.

A new model (m.rep4) was created containing only the independent variable “climate” to check for improvement, since AIC and BIC values from m.rep3 were bigger than the null model. This model was then compared with the null and confirmed to be the best fit.

Appendix 3 contains the script used in R for this statistical analysis.

3.3 Results

3.3.1 Longevity analysis

The normality tests showed that none of the numerical variables had a normal distribution (“deathage” w=0.9757, p>1.235e-12, N=1100; “ntransfers” w=0.7766, p>2.2e-16, N=1100; “agefirsttransfer” w=0.7644, p>2.2e-16, N=739; “distancetrav” w=0.666, p>2.2e-16, N=1100). Although Spearman’s rank correlation test has shown that most variables were correlated between themselves (ntransfers/agefirsttransfer r_s=-0.1091861, p=0.002958, N=739; ntransfers/distancetrav r_s=0.7685041, p<2.2e-16, N=1100; agefirsttransfer/distancetrav r_s=-0.0328861, p=0.372, N=739; ntransfers/deathage r_s=0.4625427, p<2.2e-16, N=1100; deathage/distancetrav r_s=0.3832989, p< 2.2e-16, N=1100; agefirsttransfer/deathage r_s=0.1245825, p=0.0006882, N=1100), the modelling was continued and re-evaluated using VIF values after the definitive model was chosen, which confirmed some correlation between the variables but with no values higher than 4. This is still accepted for modelling without much influence on the results since values are smaller than the conventional limit (borderline) of 10.

The models developed showed overdispersion patterns, which suggested the use of negative binomial models to explain death age. After m3 analysis via Chi square test in ANOVA, gender appeared as a non-significant explanatory variable and indeed this is confirmed as we compare the mean death age for male (Mean=3363.60, SD= 1569.63) and female (Mean=3357.56, SD= 1574.32) cheetahs from the study. In our study, the results suggest that differences in gender does not have an effect on the longevity of captive cheetahs and that the other variables used to explain and predict death age were more significant. Summaries from models 1, 2 and 3 can be found in Appendix 4.

The summary from m4 is showed below in Table 6. Birthplace had 27 significant levels and another 61 non-significant levels (not all 104 levels appeared due the exclusion of observations with NA values). Number of transfers, age of first transfer and distance travelled during life were all significant.

The BIC (Bayesian Information Criterion) values, such as the AIC values, from model m4 (13226.66) and m4.null (19598.11) were compared, revealing that m4 had the smallest value and therefore, the best fit. AIC values gave the same result, m4 (12798.37) was smaller than the m4.null (19588.1). Deviance differences were analysed between m4.null (1166.587) and m4 (754.3367), showing that m4 had a lower value, and therefore explained the variation better than the null model.

Table 6. Summary of the generalized linear model from m4 after removing the variable “gender” for captive cheetah (*Acinonyx jubatus*) longevity using studbook data.

	Estimate	Std. Error	Exponential Coefficients	z value	
(Intercept)	7.95	0.0574	2830	138.345	***
ntransfers	0.0604	0.0097	1.06	6.222	***
birthplaceAMERSFOOR	0.22	0.151	1.25	1.455	
birthplaceARNHEM	-0.345	0.18	0.708	-1.916	.
birthplaceBANHAM	-2.54	0.355	0.0792	-7.137	***
birthplaceBASEL	-0.0537	0.18	0.948	-0.299	
birthplaceBATTLECR	0.402	0.349	1.49	1.15	
birthplaceBELFAST	0.172	0.162	1.19	1.062	
birthplaceBROXBOURN	-0.164	0.163	0.849	-1.007	
birthplaceCALDWELL	0.466	0.18	1.59	2.591	**
birthplaceCHICAGOLP	0.405	0.15	1.5	2.704	**
birthplaceCHTAHEXP	-1.74	0.352	0.175	-4.957	***
birthplaceCINCINNAT	-0.169	0.131	0.844	-1.289	
birthplaceCLEVELAND	0.271	0.138	1.31	1.965	*
birthplaceCOLCHESTR	-0.697	0.25	0.498	-2.787	**
birthplaceCOLUMBUS	0.332	0.161	1.39	2.063	*
birthplaceDANIEL	0.381	0.347	1.46	1.096	
birthplaceDICKERSON	0.159	0.107	1.17	1.488	
birthplaceDUBBO	0.343	0.139	1.41	2.475	*
birthplaceDVURKRALV	0.0281	0.0887	1.03	0.316	
birthplaceEBELTOFT	-0.416	0.131	0.66	-3.165	**
birthplaceEDINBURGH	0.0304	0.349	1.03	0.087	
birthplaceFONTAINE	-0.316	0.25	0.729	-1.262	
birthplaceFORTWORTH	-0.218	0.205	0.804	-1.065	
birthplaceFOSSILRIM	0.142	0.0645	1.15	2.199	*
birthplaceFOTA	-0.0242	0.0848	0.976	-0.285	
birthplaceGLASGOW	0.461	0.349	1.59	1.322	
birthplaceHANNOVER	0.126	0.206	1.13	0.612	
birthplaceHERNEBC	-0.829	0.351	0.437	-2.364	*
birthplaceHILVARENB	0.233	0.0886	1.26	2.632	**
birthplaceHIMEJISH	0.218	0.206	1.24	1.06	
birthplaceHOEDSPRUI	0.0406	0.0638	1.04	0.637	
birthplaceHUIZENFD	0.0162	0.126	1.02	0.129	
birthplaceJACKSON	0.142	0.205	1.15	0.693	
birthplaceJADERBERG	0.344	0.25	1.41	1.377	
birthplaceKATOWICE	-1.24	0.35	0.289	-3.544	***
birthplaceKESSINGLA	-1.04	0.35	0.354	-2.964	**
birthplaceKREFELD	0.117	0.181	1.12	0.649	
birthplaceLAFLECHE	-0.354	0.35	0.702	-1.014	
birthplaceLAPALMYR	0.121	0.115	1.13	1.051	

birthplaceLETSATSI	-0.453	0.115	0.636	-3.949	***
birthplaceMAKTOUM	0.141	0.25	1.15	0.562	
birthplaceMARWELL	-0.107	0.133	0.899	-0.806	
birthplaceMEMPHIS	0.217	0.205	1.24	1.058	
birthplaceMONARTO	0.0747	0.205	1.08	0.365	
birthplaceMONTGOMRY	0.161	0.18	1.17	0.897	
birthplaceMOSCOW	0.48	0.179	1.62	2.683	**
birthplaceMUNSTER	0.189	0.101	1.21	1.88	.
birthplaceNADERMANN	-0.399	0.181	0.671	-2.209	*
birthplaceNEUWIED	0.476	0.163	1.61	2.925	**
birthplaceNISHIMURO	0.159	0.25	1.17	0.635	
birthplaceNISHINODA	-0.335	0.35	0.715	-0.957	
birthplaceNURNBERG	-0.109	0.15	0.897	-0.723	
birthplaceNZP-CRC	-2.82	0.357	0.0597	-7.903	***
birthplaceNZP-WASH	-0.117	0.179	0.889	-0.656	
birthplaceOAKHILL	0.437	0.125	1.55	3.501	***
birthplaceOLMENSE	-0.126	0.206	0.881	-0.613	
birthplaceOLOMOUC	-0.253	0.16	0.776	-1.586	
birthplaceORANA	-0.176	0.249	0.838	-0.708	
birthplaceOUDTSHORN	-0.0353	0.0771	0.965	-0.457	
birthplacePARYS	-0.257	0.135	0.773	-1.9	.
birthplacePEAUGRES	-0.0104	0.0947	0.99	-0.109	
birthplacePHOENIX	0.341	0.179	1.41	1.908	.
birthplacePRAHA	-0.156	0.18	0.855	-0.867	
birthplaceRHINOLION	-2.59	0.353	0.075	-7.333	***
birthplaceROCKTON	0.216	0.35	1.24	0.617	
birthplaceROSTOCK	0.0143	0.249	1.01	0.057	
birthplaceSAFAWILD	0.238	0.348	1.27	0.685	
birthplaceSAFRICA	-0.13	0.135	0.878	-0.965	
birthplaceSALZBURG	-0.229	0.115	0.795	-1.999	*
birthplaceSD-WAP	0.208	0.0826	1.23	2.515	*
birthplaceSHANGHAI	-0.0795	0.249	0.924	-0.319	
birthplaceSHARJAHBR	-0.0163	0.249	0.984	-0.066	
birthplaceSINGAPORE	-0.692	0.349	0.5	-1.983	*
birthplaceSTELLENBO	0.152	0.348	1.16	0.437	
birthplaceSTLOUIS	0.0374	0.251	1.04	0.149	
birthplaceSUSONO	-0.106	0.25	0.899	-0.425	
birthplaceTOKYOTAMA	-1.04	0.35	0.355	-2.96	**
birthplaceTOLEDO	0.282	0.15	1.33	1.882	.
birthplaceTORONTO	-0.093	0.139	0.911	-0.667	
birthplaceTSAOBIS	-0.0517	0.249	0.95	-0.207	
birthplaceVARADAY	0.486	0.35	1.63	1.387	
birthplaceVIENNA	-0.352	0.25	0.703	-1.409	
birthplaceWARSAW	-0.128	0.139	0.88	-0.914	
birthplaceWASSBRC	0.14	0.0662	1.15	2.118	*
birthplaceWHIPSNADE	0.265	0.14	1.3	1.894	.

birthplaceWILDS	-0.549	0.348	0.578	-1.575	
birthplaceWINSTON	-0.00175	0.112	0.998	-0.016	
birthplaceWUPPERTAL	-0.126	0.25	0.882	-0.504	
birthplaceYULEE	0.106	0.0736	1.11	1.439	
agefirsttransfer	0.0000915	0.0000191	1	4.787	***
distancetrav	0.0000106	0.00000408	1	2.599	**

Significance: "***" = p<0.001, "**" = p<0.01, "*" = p<0.05 and "." = p<0.1.

3.3.2 Reproductive success analysis

In total, 116 facilities reproduced cheetahs during the 18 years of studbook data and eleven climates defined the breeding facilities locations according with their city addresses: Af, BSh, BSk, BWh, Cfa, Cfb, Csa, Csb, Cwb, Dfa and Dfb. The average reproductive success per facility was 18.81 (SD=44.93) cheetahs and the average GDP per capita per country was US$36357.92 (SD=16730) for the whole period of 18 years.

Figure 13 shows the relation between the variables: reproductive success, average GDP of the facility's country and associated climate for the dataset. Each observation represents a facility and each colour symbolizes the climate referred to the city where the facility is located. The vertical and horizontal dashed lines represent the average GDP per capita and average number of cheetahs reproduced in captivity, respectively.

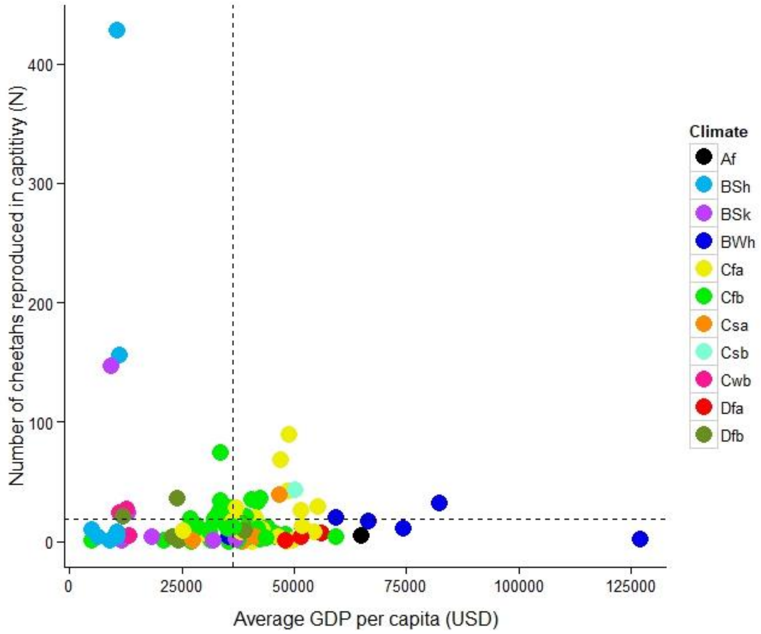


Figure 13. Relationship between the number of cheetah cubs born between 1999-2016 with the average GDP per capita (USD) per facility and climate for the facility according to Köppen-Geiger climate classification. The dashed lines represent the average values for GDP per capita and average cheetah reproductive success. The graph shows the full dataset with average GDP per capita (US$36357.92, SD=US$16730) and average cheetah reproductive success (N=18.81 animals, SD=44.93).

The normality tests showed that neither reproductive success nor average GDP per capita had a normal distribution ("repsuccess" w= 0.34404, p < 2.2e-16, N=116; "averagegdp" w= 0.89585, p= 1.788e-07, N=116). Spearman's rank correlation test showed that the numerical variables were not correlated between themselves (averagegdp/repsuccess r_s= 0.07224826, p= 0.4409, N=116). Model m.rep1 showed over dispersion, then m.rep2 (Quasipoisson) and m.rep3 (Negative Binomial) were developed to correct for this problem. M.rep3 proved to be the best between them to account for overdispersion after dividing the residual deviance by the degrees of freedom.

Average GDP was not significant and neither any of the 11 categories from climate of m.rep3, except for BSh. BIC and AIC values from the null model (m.null) were smaller than m.rep3, confirming that random variance was influencing reproductive success more than average GDP per capita and climate. BIC and AIC values from m.rep4 in fact decreased after the removal of average GDP variable.

Table 7. Summary of the generalized linear model from m.rep4 for captive cheetah (*Acinonyx jubatus*) reproductive success using studbook data and Köppen-Geiger climate classification of the cities from the breeding facilities.

	Estimate	**Std. Error**	**Exponentiated coefficients**	**z value**	
(Intercept)	1.6094	1.1757	5	1.369	
climateBSh	2.8597	1.2461	17.45714	2.295	*
climateBSk	1.6194	1.2389	5.05	1.307	
climateBWh	1.0531	1.2613	2.866667	0.835	
climateCfa	1.3181	1.1993	3.736364	1.099	
climateCfb	0.8626	1.186	2.369231	0.727	
climateCsa	0.55	1.2643	1.733333	0.435	
climateCsb	2.1518	1.6086	8.6	1.338	
climateCwb	1.3173	1.3395	3.733333	0.983	
climateDfa	-0.3567	1.3226	0.7	-0.27	
climateDfb	1.0531	1.2613	2.866667	0.835	

Significance: "***" = $p<0.001$, "**" = $p<0.01$, "*" = $p<0.05$ and "." = $p<0.1$.
Climates' legend: Af: equatorial, fully humid; BSh: Arid, steppe, hot arid; BSk: Arid, steppe, cold arid; BWh: Arid, desert, hot arid; Cfa: Warm temperate, fully humid, hot summer; Cfb: Warm temperate, fully humid, warm summer; Csa: Warm temperate, summer dry, hot summer; Csb:Warm temperate, summer dry, warm summer; Cwb: Warm temperate, winter dry, warm summer; Dfa:Snow, fully humid, hot summer; Dfb:Snow, fully humid, warm summer

3.4 Discussion

3.4.1 Longevity analysis

The number of transfers, age of first transfer and total distance travelled during life showed strong significance, indicating some positive influence on death age (i.e. increasing longevity). Their respective exponentiated coefficients, 1.0622068, 1.00009147 and 1.0000106 mean that for each one-unit increase in the variables, the expected death age increases by the amount of each respective variables' coefficients (the percentage is calculated from the subtraction of the coefficients from 1, the total representation of what explains death age).

Following the results from summary of m4, an increase in one unit in the number of transfers done by an individual increases about 6% its death age, which is a considerable amount of time (approximately 201 days or about 6 months) when thinking that captive cheetahs from the data used in this study lived in average 9.2 years old (SD=1573.67) and in average captive cheetahs have lived between 10-12 years old (Cheetah Outreach data, 2017), although some live until they are 16 or 17 and few have been reported to reach 20 years. In the wild cheetahs usually live a shorter life, approximately 7 or 8 years old and few reach 12 years.

Despite the significance of age of first transfer and distance travelled during life resulted in being significant variables, the percentage of influence from these variables on death age are <1%, and therefore they are not very relevant for the model. Some studies have argued that the duration of transportation is more important than distance when avoiding stressful events (Damtew et al.,2018), but in general, the longer the distance, the longer the duration of the transportation journey and the impact on the animal welfare will still be present.

The positive influence of the transfers in death age was much against our expectations, since the more transfers done in life would probably mean a bigger exposition to stress events and consequently an expected but not found diminished lifespan. This result possibly means that cheetahs could be dealing well with transportation situations and this resistance to stress could be beneficial to their longevity, as discussed similarly by Minois (2000).

It is well known that acute exposure to stress is normal for animals in nature, which have to be constantly alert to threats and decide between fight or escaping in threatening situations, but the stress from transportation or translocation activities is supposed to be extreme or chronic (Letty et al., 2007; Teixeira et al., 2007; Linklater et al., 2010). The methods used to reduce the impact of stress could be helping to mitigate this effect such as crate and transport training (Linhart et al., 2008). According to our results, cheetahs could be benefiting from these stressful events, possibly through the expenditure of energy accumulated in their bodies as per wild conspecifics (for wild conspecifics this occurs when sprinting long distances in prey hunts, for example (Williams et al., 1997; Marker, 2002; Broekhuis, 2007). Running, like stressful events, demands that the body's reserve of energy be managed (Williams et al., 1997) and the liver is an organ that stores and manages this energy (Berg et al., 2002; Minka & Ayo, 2009).

It is known that many captive cheetahs develop liver diseases, and some studies have indicated possible causes. For example, Setchell et al. (1987) suggested that some hormonal compounds present in soya beans from captive cheetahs' diet to be the major reason for liver diseases and infertility, for example. Some other authors associate the disease with FIP (Feline Infectious Peritonitis) (Pedersen, 2014) or VOD (Veno-occlusive Disease) (Gosselin, 1988; Leemans, 2015). The excess of vitamin A consumed from the diet in captivity is suggested to be toxic (Leemans, 2015).

If the hypothesis of the liver disease is related to cheetahs not being exposed to enough stress in their lives, then this would possibly mean that most cheetahs that suffer from this disease have not been under enough "beneficial" stress in their enclosures to allow them to spend their accumulated energy. The lack of exercises consequently may be related to liver diseases in captive cheetahs (Marker & Schumann 1998; Cheetah Outreach, 2017).

In contrast, another possible obvious explanation for number of transfers affecting positively on the death age of cheetahs is that old individuals are more susceptible to have had more transfers during its life, and consequently had travelled longer distances. Another point to consider is that the captive cheetahs from for this study were already born in captivity and are a selected population (offspring of survived founders), not representing fully wild cheetah phenotypes and genotypes and probably reacting differently from the transportation impact than a founder individual would react. Thus, it might be that cheetahs negatively affected by transportation have already been eliminated from the population.

Even though the variables cited previously have highly significant coefficients, their values are extremely low, except for number of transfers, indicating that the variables used in this study contribute very little to the variation in the longevity of captive cheetahs. There must be better variables explaining the variance of longevity in captivity. The addition of variables to the models should be made with care, since the inclusion of several unnecessary variables could be useless and even detrimental to the analysis. The inclusion of unnecessary variables increases the chances of them being correlated (multicollinearity) and this could affect the final result.

Birthplace, the only categorical variable used in this study, also showed some significant levels, indicating a possible contribution for the longevity variation of captive cheetahs, but again demonstrates low coefficients, confirming that this contribution is minimal compared to other variables, which might have more influence over the outcome variable and are not being considered in this study.

The categorical variable, nevertheless, have the coefficients compared to the intercept, it is, the reference level of the category, in this case “PretDW”. Therefore, the expected death age for “Banham", a strongly significative category for example, is about 92.1% (1-0.079) smaller than the expected death age of the reference variable, PretDW. Although the sample size for the study was enough to run the model, the number of observations for each facility included in “birthplace” might not be enough to conclude their relative contributions since most categories (facilities' names) do not appear many times in the study. Extensive amount of data would be required to best infer conclusions from the place where the animal is born to their captive longevity. This is something not possible for zoo animal populations at the present time due to small sample sizes result from the need to control population sizes in captivity as space in zoos is limited (Foose et. al, 1986; Hutchins et al., 2003; Conway, 2011).

3.4.2 Reproductive success analysis

The GLM demonstrated that average GDP per capita does not affect reproductive success of captive cheetahs significantly considering our dataset. It was expected that reproductive success would be bigger when GDP per capita was higher, since the investment in suitable husbandry practices and breeding would probably be higher. It was also expected that reproductive success was higher where climates were similar to the natural habitat of the species, and indeed BSh – the climate referred to most facilities in Namibia and in South Africa – showed to have a significative positive effect in reproductive success according to the final model developed (m.rep4) in relation to the reference level (Af). However, this effect has a high chance to be biased by extreme values, as it is noticeable from some influential observations in Figure 12.

The cheetah is still widely distributed across the African continent and some still survive in Iran. Therefore, the variations in climate also exist in this animal natural habitat, ranging from climates BWh (arid, desert, hot arid) in North Africa countries and part of Iran, for example, to some BSh (arid, steppe, hot arid) in South Africa countries and few variations on the East side of Africa.

The facilities with BWh countries included in this study were predominantly from Middle-East countries with high values of GDP per capita such as the United Arab Emirates and Qatar, except for one facility from Arizona in the United States. In general, the higher GDP per capita for this climate did not mean higher values of reproductive success in our sample, although two facilities had higher than average output with 20 and 32 cheetahs produced in captivity each for the period considered. One observation, “Alwabra” (Al Wabra Wildlife Preservation) had an extreme high value of average GDP per capita, but only two successful reproductions in captivity. Breeding facilities located in BSh countries such as Namibia, South Africa and India had in general, some of the lowest GDP per capita and all of them reproduced less cheetahs than the average during the period of the study except for two visibly extreme values from “PretDW” (Ann van Dyk Cheetah Centre) and “Hoedsprui” (Hoedspruit Endangered Species Centre).

Most facilities had GDPs per capita between USD25000 and USD50000, and some of those also achieved some of the highest reproductive success, especially if located in climates Cfa (warm temperate, fully humid, hot summer) and Cfb (warm temperate, fully humid, warm summer). The highest values were achieved by facilities located in Florida (US), Texas (US) and France, being the first and the second from Cfa climates and the third from Cfb climate. Furthermore, few facilities from other climates such as Csa (warm temperate, summer dry, hot summer), Csb (warm temperate, summer dry, warm summer) and Dfb (snow, fully humid, warm summer) also indicated relatively high values of cheetahs reproduced in captivity, but they were infrequent, and they were not enough to represent significantly their climate classification. The facilities located in climates defined as Af (equatorial, fully humid) or Dfa (snow, fully humid, hot summer) had number of cheetahs reproduced in captivity below the average although all of them had also GDP per capita higher than the average. Finally, the BSk (arid, steppe, cold arid) and Cwb (warm temperate, winter dry, warm summer) climates varied in number of cheetahs reproduced in captivity and GDP values, however, one facility from BSk (“Oudtshorn” - Cango Wildlife Ranch) was dissonant with the other observations.

Altogether, Figure 13 shows a variation in number of cheetahs born by facility during the period of study and the average GDP per capita, being difficult to determine a pattern of relationships between the variables. The fact that facilities from different climates of cheetahs' natural range countries are able to produce cheetahs in captivity shows that reproduction was not impeded by climate variationbecause of the climate variation. Alternatively, it is probable that breeding facilities have been taking good measures to offer suitable environment for animal adaptation and expression of reproductive behaviour. Another aspect that must be considered in this type of study is the recommendations for breeding advised by the studbook keeper, which could be trending more to one facility than another and consequently inducing that facility to have better reproductive success than others, although cheetahs have such low genetic diversity that most the recommendations would probably be to breed instead of to hold the animal.

The presence of extreme values (also called "outliers") as found from some observations in the plot does not necessarily mean one should exclude those observations from the dataset, but actually analyse the outcome very carefully with the intention of fully comprehend the behaviour of the developed models. In addition, since the model family chosen has a robust regression fit that account for overdispersion (Negative Binomial), the final model is already including most of the "contrasting" observations into consideration.

Variables related to husbandry such as enclosure size and group size might also have had an effect on the biology/behaviour of the species, including their longevity and reproduction success. Enclosure size, for example, has been described of being important in this scenario (McCusker, 1978) while other studies showed that the complexity and quality of enclosures are of bigger value for reproductive success analysis (Mellen, 1991). For captive cats, group size is also relevant, since large group size leads to low reproductive success (Mellen 1991) .

However, this depends on the biology of the species. As explained before, cheetahs live solitary lives (females) or in small groups (males) and the placement of small groups could, therefore, influence their longevity and reproductive success. Future studies with access to this kind of information could also include these variables in the models to analyse possible influences.

3.5 Conclusion

It is important to consider death age as a complex variable with many biological and external variables affecting its performance. However, this study used only available data from studbooks to investigate the performance of this variable under these circumstances and showed that the number of transfers, the age of first transfer and distance travelled during life are variables that affect positively on the age of death of an individual. Birthplace also resulted in some institutions with significant positive or negative contributions to longevity compared to the reference level. Building a statistical model with several variables results in a model difficult to interpret and increases the chances of the variables being associated. To definitively explain the behaviour of response variables, especially if they include many categorical variables or interactions of the terms is very difficult and requires a larger data-set. Therefore, models should contain an appropriate number of variables, but obviously this creates a trade-off between the model's statistical validity and its ability to usefully explain the situation under investigation.

Unfortunately, the model created in this study does not explain much of the variance in longevity of captive cheetahs. The low coefficients from most explanatory variables used in this study is proof that there might be better factors influencing the longevity of cheetahs in captivity. However, the number of transfers affecting on the death age of individuals is something that deserves more research and attention to confirm its effect. Future studies considering the hormonal monitoring from their faeces during transportation and using larger datasets with greater influence variables would best predict how longevity of captive cheetahs is affected, but historical data from studbooks is definitely something that should be more acknowledged in this type of analysis. For example, including veterinary records from ZIMS are obvious data to include in future models, however, such data are not available to non-zoo-based researchers and would require access from a member facility. The positive inference from these results for zoos is that transportation *per se* is not a problem for cheetahs; however, institutional variation is important and investigations into best practice should be made – so that it can be shared between facilities in the breeding programme.

Climate and GDP per capita were not demonstrated to significantly affect reproductive success of cheetahs from this study data analysis, although BSh climate had proven to be significant. This is probably an effect influenced by the extreme values observed from that climate. Longer studies would benefit of larger sample sizes and better inferences about the influences of those variables in the number of cheetahs reproduced by facility. Different climate classifications could also be used to confirm the results from this study together with the actual annual income of breeding facilities and previous experience by the facility in managing cheetahs in captivity, for example. The positive interpretation of these results for zoos is that neither wealth nor climate are predictors of reproductive success.

The two sections extracted from the cheetah international studbooks used for this chapter provided only limited information about longevity and reproductive success but generated good insights about the management of this species in captivity. The access to expanded husbandry knowledge would benefit the analysis once it would give the possibility of association between different variables not available to this researcher such as disease records, inbreeding coefficients, etc.

Chapter 4 Social network analysis of captive breeding programmes – using the cheetah (*Acinonyx jubatus*) as a model of study

4.1 Introduction

Social network analysis (SNA) is a method primarily used to examine complex social relationships and associations between subjects (Krause et al., 2007; Wey et al., 2008). It has attracted the attention of many scientists in recent decades because it provides a quantitative framework (Krause et al., 2007; Sueur et al., 2011; Farine & Whitehead, 2015; Croft et al., 2016), which allows researchers, for example, to investigate the dynamics of the social structure and the performance of entities, most commonly individuals or institutions (Sih et al., 2009; Sueur et. al, 2011). The use of SNA for the study of social organization is, therefore, important for identifying patterns of relationships and key individuals or institutions which might be acting as bridges (connectors between two separate groups, for example) and their removal could impact on the success of a network as a whole (Krause et al., 2007; McCowan et al., 2008; Brent et al., 2011; Makagon et. al, 2012; Wasserman & Faust, 2012).

Social network analysis allows scientists to examine direct and indirect social connections between the members of a determined network (Brent, 2015). These relationships can change over time and the investigation of the variation in social structure over time is fundamental for the understanding of the evolution of social patterns (Krause et. al, 2007; Wey, 2008). Within the field of biology, network analysis has been used in several studies, including areas such as the cognitive sciences (Falk & Bassett, 2017), epidemiological studies (Bell et al., 1999), socio-behavioural patterns (Coleing, A. 2009), gene expressions and cell biology (Zhu et al., 2007) etc. More specifically in conservation studies, network analysis has been used for the investigation of animal movement (Jacoby & Freeman, 2016), for husbandry and welfare of captive animals (Rose & Croft, 2015), monitoring and reintroduction of animals into the wild (Dunston et al, 2017) and prediction of infectious disease risk (Rushmore et al., 2013), for example. However, until recently no studies have considered the use of SNA for the management of transfers for captive breeding purposes.

Applying theories of SNA to that field would be interesting as it would provide an overview of the whole structure of breeding programmes across time (Snijders et al., 2017). It would also highlight the institutions that have been more active during the time specified by the studbooks or even the institutions located in important paths between other institutions. For example, it could indicate the institutions that have the most influence on the captive breeding of a certain species. Such results could possibly be found from centralities measures such as degree centrality and betweenness, for example. Furthermore, identifying the most prominent institutions (often referred to as "facilities") allows scientists to identify some of the factors that could be influencing those facilities performances such as geography, financial wealth, etc.

In addition, since the effectiveness in transferring recommended individuals by the studbook keeper could be compared with accomplished transfers between participating facilities, it is possible to create a network of expected versus real transfers, which would show the start and finish locations of an animal move through the direction of a tie between two institutions. Alternatively from other methods of representing data not easily understandable, visual representations can show complex phenomena and their dynamics allowing scientists to engage with big data in a more interpretable manner (Evagorou et al., 2015). Therefore, the use of visual representations such as sociograms as supplement of centralities measures from the social network analysis could be helpful if applied to animal management and conservation science, since the movements of individuals between the facilities could be tracked and monitored over time to avoid diversions from the recommended plans established by studbook keepers and to identify patterns that may influence the success of captive breeding.

Studbook keepers try to organise breeding transfers to maintain the maximum amount of founder genetic diversity in a population (Glatston, 1986; BIAZA, 2018). It means that this tool for visualization often for "big data" could facilitate the monitoring of breeding programmes or even allow the best biological outcomes while considering the geographic location of the individuals. While maintaining genetic diversity is a key aim of captive breeding, studbook keepers also need to consider the stress involved in moving an animal (i.e. its geography) because this can result in a biological cost such as delayed reproduction (Turner et al., 2002; Dickens et al., 2010).

This project uses interdisciplinary approaches including social network analyses to understand and to provide a tool for the improvement of the conservation work of zoos, especially captive breeding. The main objective of the study is to investigate how captive breeding relationships are established between captive breeding institutions such as zoos. The specific objectives include: 1) to identify which institutions are the most influential in the world for the specified species according to their centralities (indegree and outdegree) and network structures and why they are located in those important strategic positions; 2) confirm if there are local sub-networks formed according to geographical regions; 3) identify possible changes on the social network structure over time; and 4) investigate if there are political or economic factors affecting the prominence of zoos in social networks of transfers. It is predicted to find networks with transfers performed globally in favour of the recommendations for breeding and management plans, but it is also expected to find a low frequency of transfers across continents, since it is essential to consider the distance between the facilities' location to avoid stress derived from transportation.

4.2 Methods

4.2.1 Data Collection and processing

The data used for this study are freely available online and can be found at the Cheetah Conservation Fund website within "Research Library" until the publication date of this thesis: http://cheetah.org/research/by-type/international-studbooks/. There are 18 studbooks published and they contain extensive information about the captive cheetah inventory, usually including sections with historical data and current status, but only sections related to transfers of individuals were used for this Chapter. All transfers that occurred between two institutions were considered for captive breeding purposes in this study.

The data extracted from the studbooks were retyped and processed in Excel spreadsheets for every year available (1999-2016). The retyped data contained information about cheetahs' international identification (i.e., ''stud#''), sex, event (e.g., capture, birth, death or transfer), location of the event (facility name), date of the event (day, month, year), and birth origin (e.g., wild or captivity). Transfer information between locations (sender and receiver facilities) were recorded separately for each year of studbook along with the number of times a cheetah transfer from the sender to the receiver was done (Figure 14). Often, the same cheetah was transferred multiple times between a specific route, therefore, the number of transfers done between two zoos or facilities is not equivalent to the number of animals transferred.

ZooSour	ZooRec	Ntimes
FRA15	NLD8	1
USA25	USA26	1
FRA12	XXX9	1
USA82	USA48	4
USA28	USA14	1
NLD8	DEU6	2
USA42	USA5	1
ZAF25	ZAF10	11
GBR17	GBR18	2
GBR1	GBR12	2

Figure 14. Example of table data organization using the first 10 rows from the table of cheetah transfers for the year 1999. “ZooSour”, “ZooRec” and “Ntimes” are abbreviations for Zoo Source, Zoo Receiver and Number of times (a transfer from ZooSour to ZooRec occurred).

The institutions’ names were protected to avoid exposition whenever it was necessary to identify them through the use of a 3-letter code based on country of localization (ISO 3166) followed by random numbers. For example, the code “GBR” was used to represent United Kingdom, “USA” for United States, “DEU” for Germany and so on. The order of the numbers chosen to follow the code does not imply any rank or qualification for the facilities and they were chosen according to the nomination order by the researcher.

Regularly, a private or unknown facility appeared as a being either the source or the receiver of the animal, and those were described as “Private” or “Unknown” in the studbook data. However, it was not possible to identify their location, since their address was not given with other facilities in the addresses’ catalogues listed in the published studbooks. Due this limitation, the researcher could not imply if a facility called “Private” or “Unknown” in one year was the same as “Private” or “Unknown” in another year. For this reason, a repeated number were given for them every year, but this does not mean that “Private 1” from 1999 is the same as “Private 1” from 2007, for example.

Sometimes, multiple transfers were done on the same date/year by a private or unknown facility suggested that the animal came or went to the same place and, in this case, the same code was used. The codes used for private and unknown facilities were “PVT(number)” and “UKN(number)”, respectively. In addition, some facilities from the studbook were given a name by the studbook keeper but did not have their location listed in the address catalogue and did not provide any information about their identification. Those facilities received the code “XXX(number)” instead. When the names provided information for their identification, the address was found from online sources. Moreover, the data sometimes showed names that were none of the aforementioned options, but only had a country’s name. The nature of those facilities is uncertain, but it could perhaps mean the wild, or a facility from the country written that was not explicitly described on the address catalogue. For those cases, codes referred to the country cited without any number in front was given to represent them. For example, if “Namibia” appeared as a source (sender) or a receiver, the code “NAM” was used for its representation.

To create the networks for this study it was necessary to check in the table described previously (Figure 13) if the number of senders was the same of the receivers. If one of the columns did not have an institution from each other (i.e. the institution did not send or did not receive animals for the specific year), their names were added accordingly until both columns have the same number and names of institutions. For those additional interactions between institutions, however, the number of transfers written was null, since the transfers between those institutions did not happened in practice. This step was important to be undertaken for all annual data, since network modelling in this case requires a square (adjacency) matrix to run (Hanneman & Riddle, 2005), and therefore, it is necessary to make this equivalence for the creation of the appropriate number of rows and columns for future analysis.

4.2.2 Networks year by year

Using the software R with "reshape" package loaded, an adjacency (squared) matrix was created where the rows represent the institutions that transferred the animals, the columns represent the institutions that received animals and the filling values shows the number of times (''Ntimes'') a transfer from ''ZooSour'' to ''ZooRec'' was done. Although internal transfers could have happened in some years studied, they were not included in the matrix because the intention of this research is to show the transfers between institutions around the world for this specific species. For this reason, the main diagonal of the matrix expressed only values equal to zero. The script for this process can be found in Appendix 6.

The square matrices created in R were exported back in an Excel format. Posteriorly, these data were imported into UCINET to then be saved as UCINET format (*.##h and *.##d extensions), which was necessary to run the matrices in Netdraw later on for visualization. The centralities (Multiple Measures Method) were also calculated in UCINET for each breeding institution such as Degree (indegree/outdegree) for each active node, in addition to measures of network cohesion such as density and reciprocity.

The graphs displaying the network were then designed using the software Netdraw to delimit their nature – directed and weighted. The layout chosen for the display of the networks in Netdraw was the "Spring embedding" (distances + node repulsion + equal length edge), which gives you a good disposition of nodes and ties avoiding crossing of ties and nodes, but still allows you to move them for better visualization on space without losing or adding new visual information.

The direction of the arrows from the network graphs shows from which institution the animal was transferred to the institution where it was received; the weight, expressed by the thickness of the arrows, shows the number of transfers that occurred between them: the thicker the line, the more transfers occurred between that pair of facilities. Private, unknown, "not specified" institutions and places written only by country names were also included as nodes into the social networks since they could show the connections between those places with the other institutions, even though they could not be a zoo. The size of the nodes also varied according to their weighted outdegree centralities, meaning that bigger sizes represent facilities that had undertaken more transfers to another institution, and not necessarily with more connections. Finally, the colour of the nodes was based on attributes, in this study referring to the continent where the facilities which transferred or received cheetahs were located: blue for Europe, red for America, orange for Africa, green for Oceania, pink for Asia and grey for private institutions, unknowns or not specified facilities. The networks were saved into a JPG format for posterior analysis.

The methodology explained until here was repeated eighteen times for each of the studbooks released (from 1999 to 2016) resulting in eighteen different networks.

4.2.3 Growing network

In addition to individual networks created year by year, a single network was developed with the total values of nodes and transfers from all the years studied previously (1999-2016). The data obtained from each year's network was placed together to analyse the network formation along the years (adding data from previous networks) until it reached the sum of the years between 1999 – 2016, which represents the sum of all cheetah transfers done from 1999 until 2016.

The same methodology for processing the data and building the networks mentioned before was applied to the final network containing the sum of all the previous data and the results are discussed further in this Chapter. However, the private and unknown institutions were excluded in this case, since it was impossible to differentiate them from each other using only the data provided in the studbooks. The network map was not relevant to be displayed in this chapter due its complexity in visualization, but the social network metrics such as degree, reciprocity and density are shown and discussed in the next sections.

4.3 Results

4.3.1 Network year by year

The eighteen networks created according to the information provided by the studbooks for each year of study are displayed below (Figures 15-32).

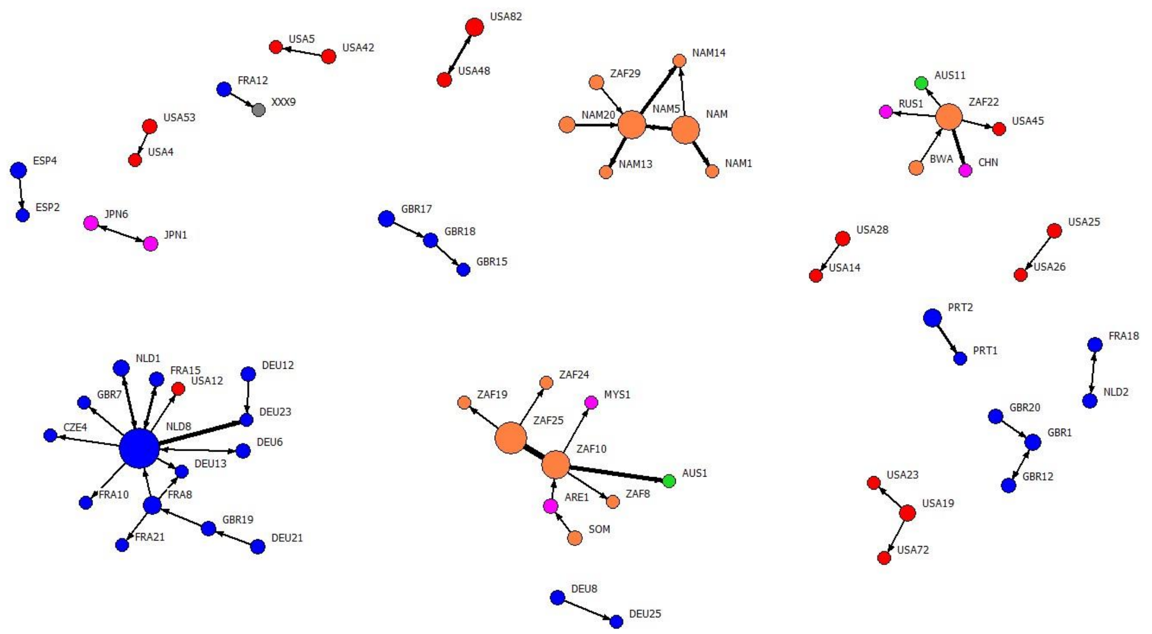


Figure 15. Graph representing the cheetah transfer network for the year 1999.

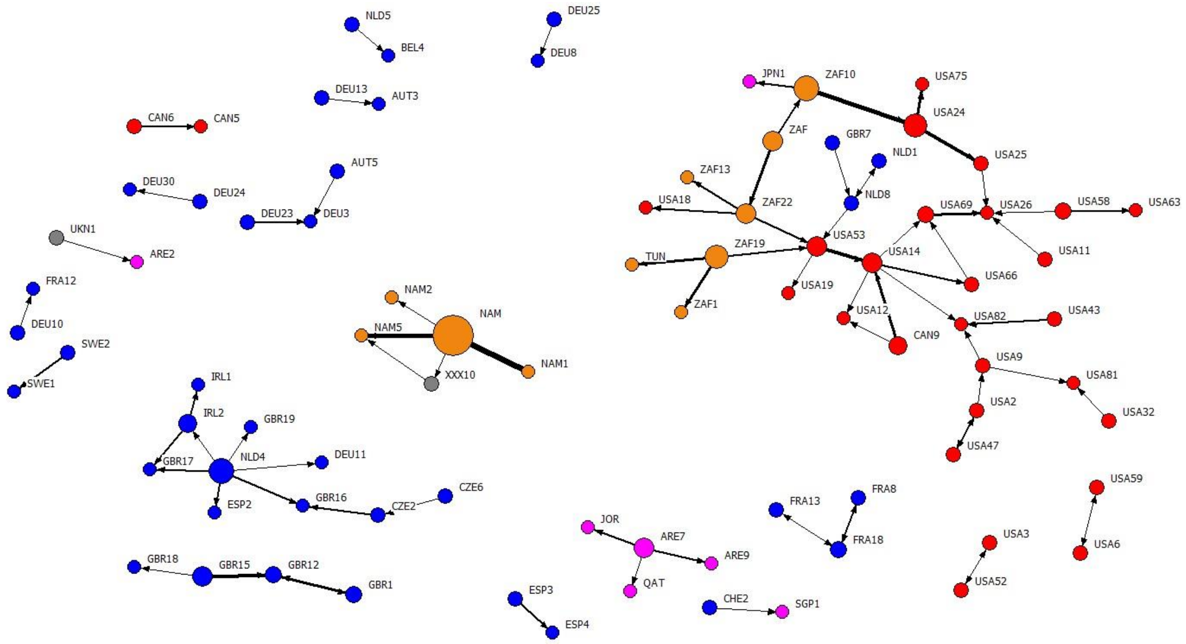


Figure 16. Graph representing the cheetah transfer network for the year 2000.

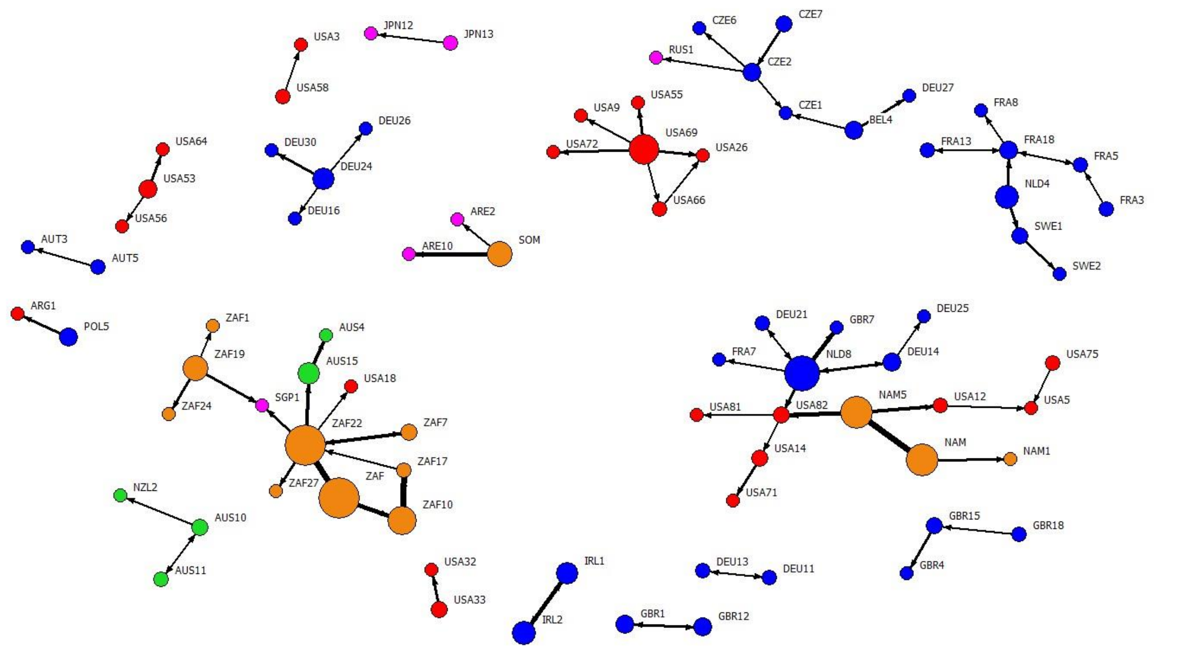


Figure 17. Graph representing the cheetah transfer network for the year 2001.

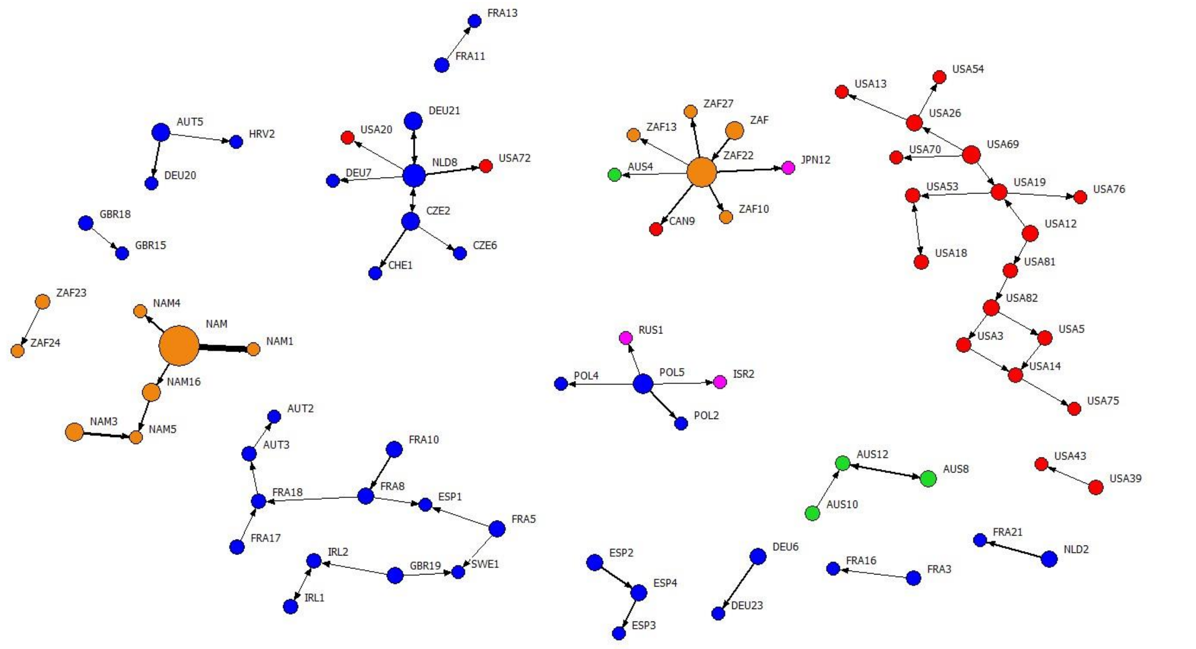


Figure 18. Graph representing the cheetah transfer network for the year 2002.

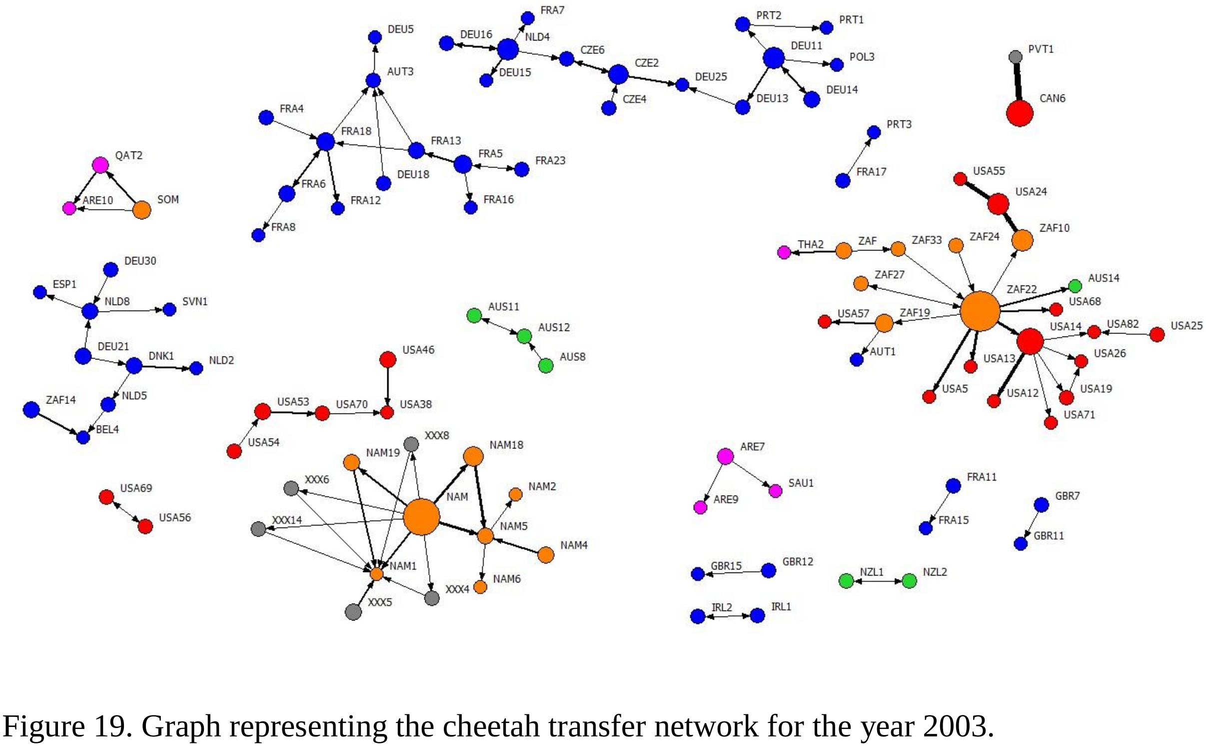


Figure 19. Graph representing the cheetah transfer network for the year 2003.

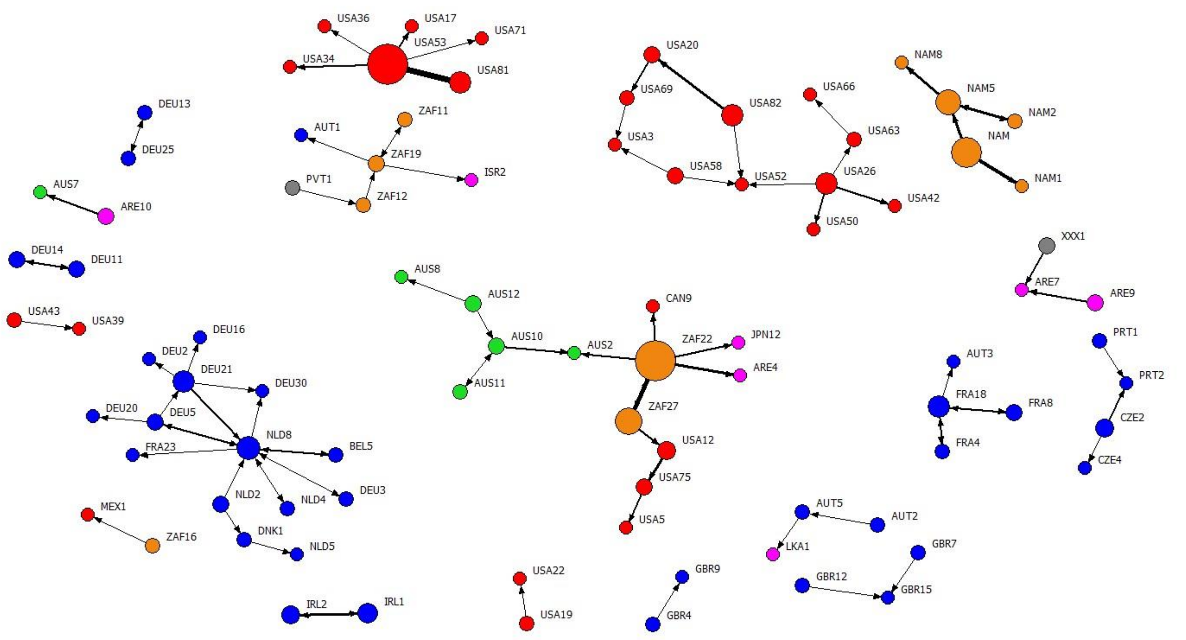


Figure 20. Graph representing the cheetah transfer network for the year 2004.

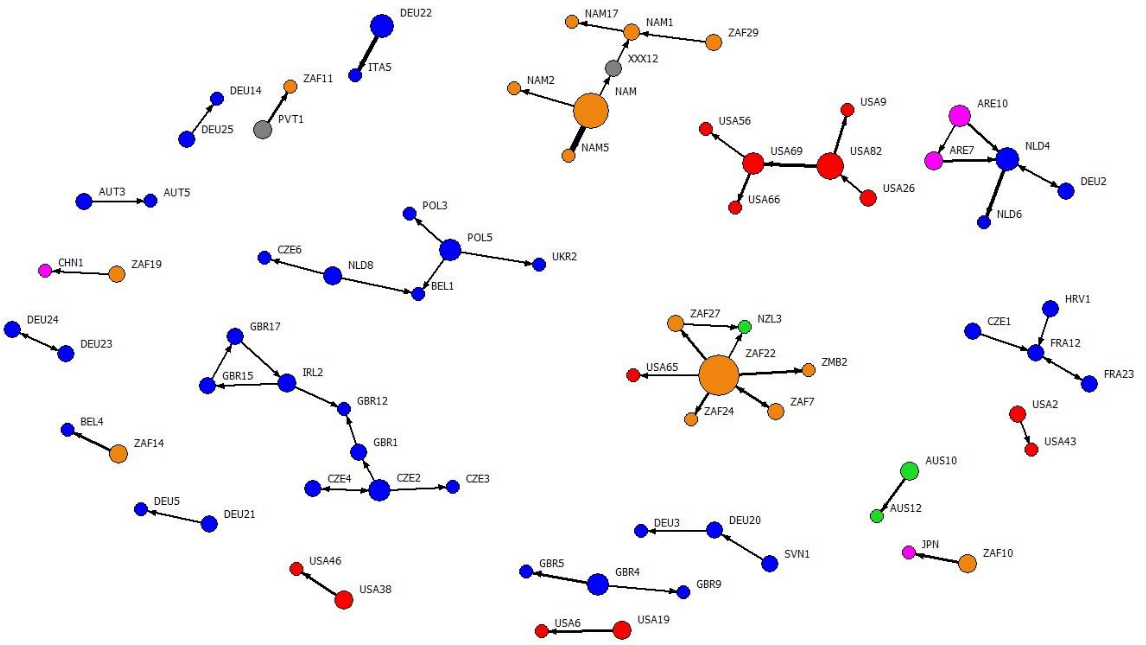


Figure 21. Graph representing the cheetah transfer network for the year 2005.

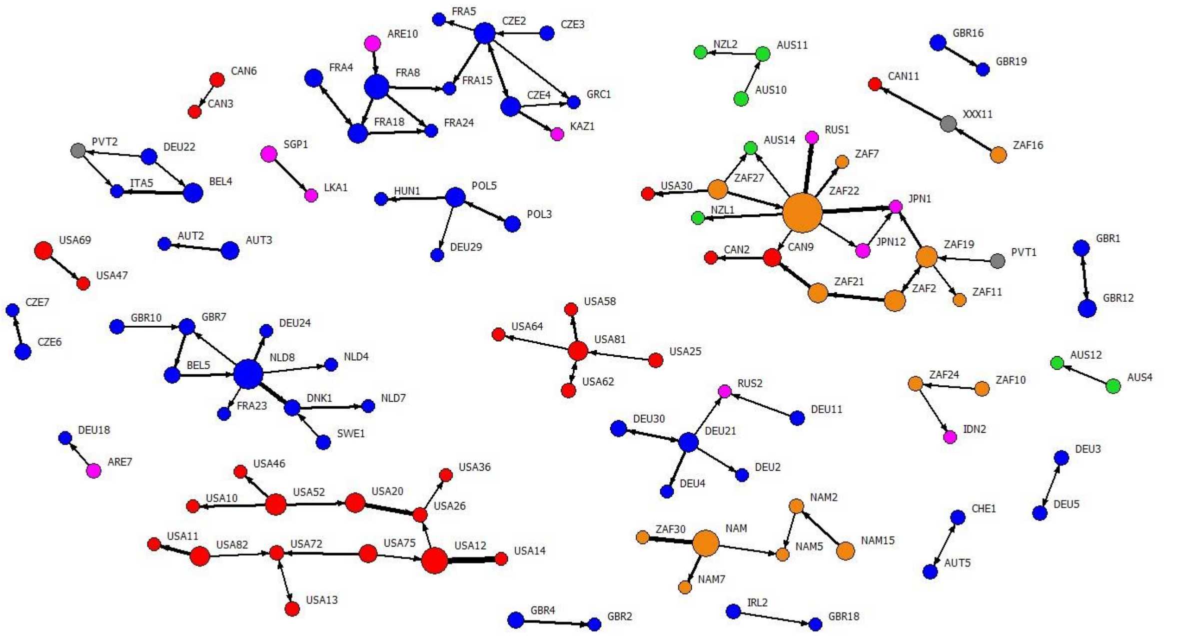


Figure 22. Graph representing the cheetah transfer network for the year 2006.

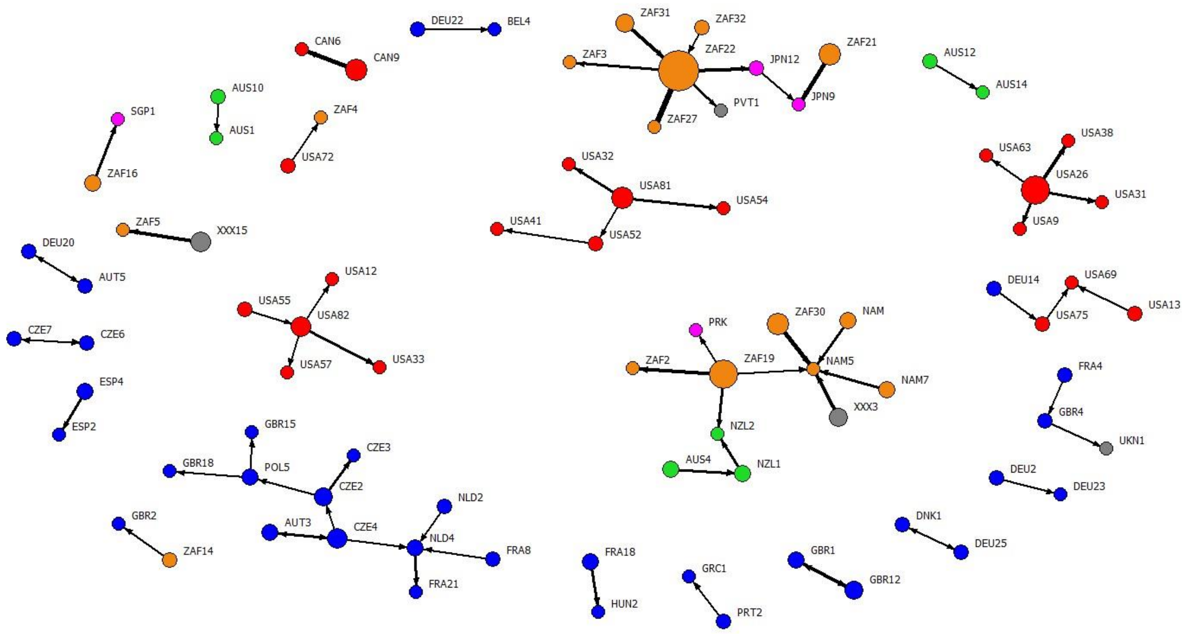


Figure 23. Graph representing the cheetah transfer network for the year 2007.

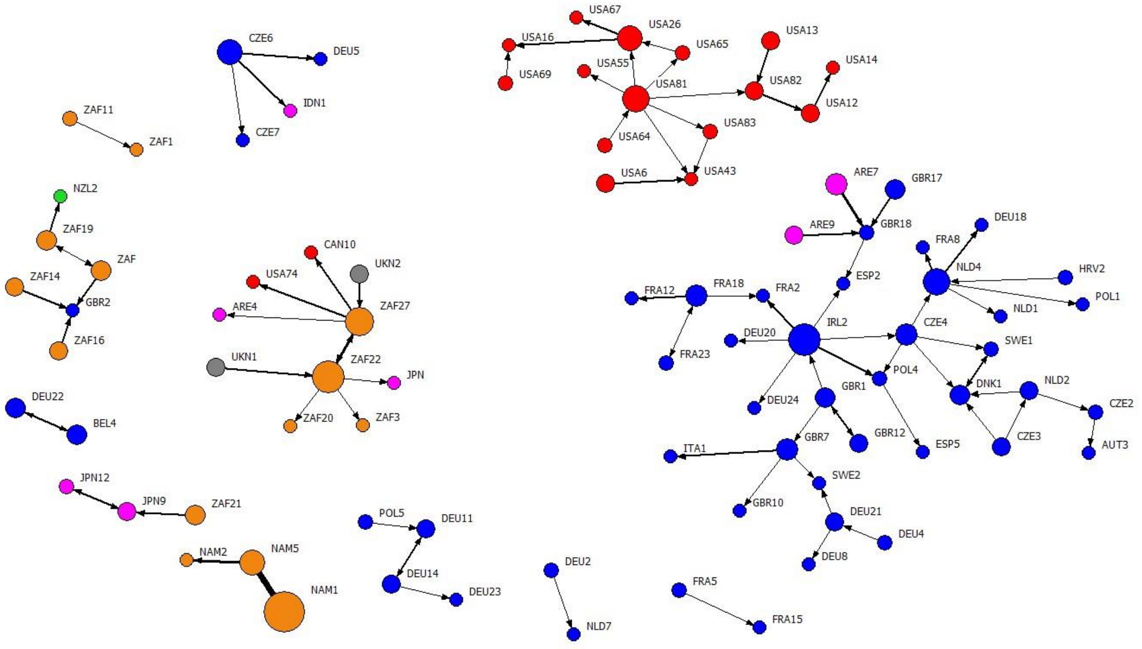


Figure 24. Graph representing the cheetah transfer network for the year 2008.

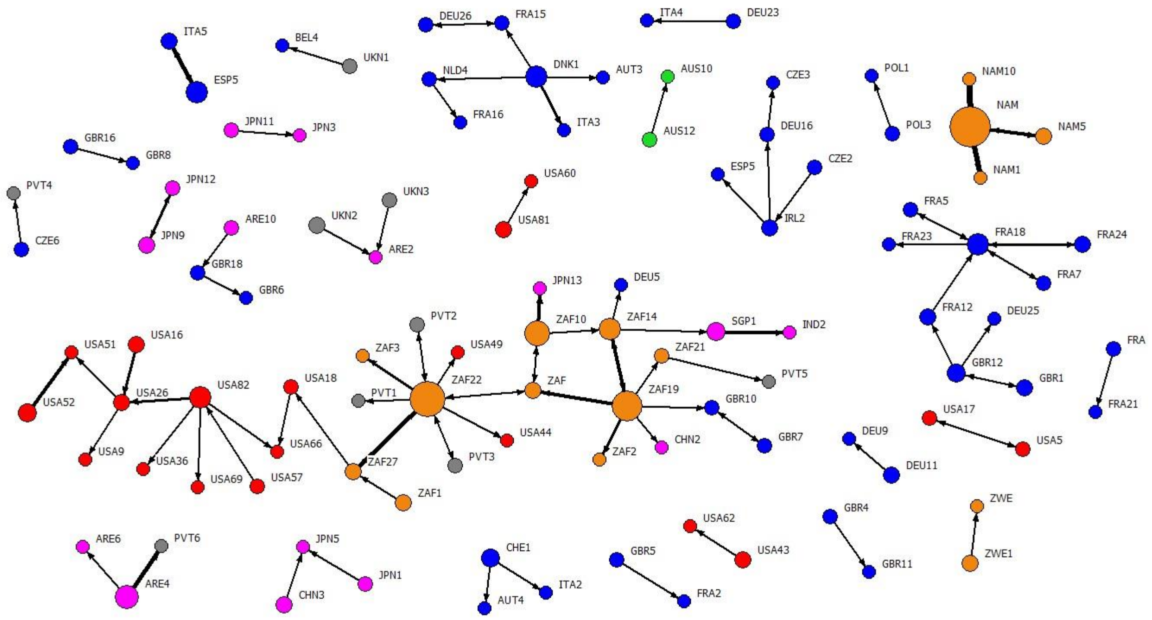


Figure 25. Graph representing the cheetah transfer network for the year 2009.

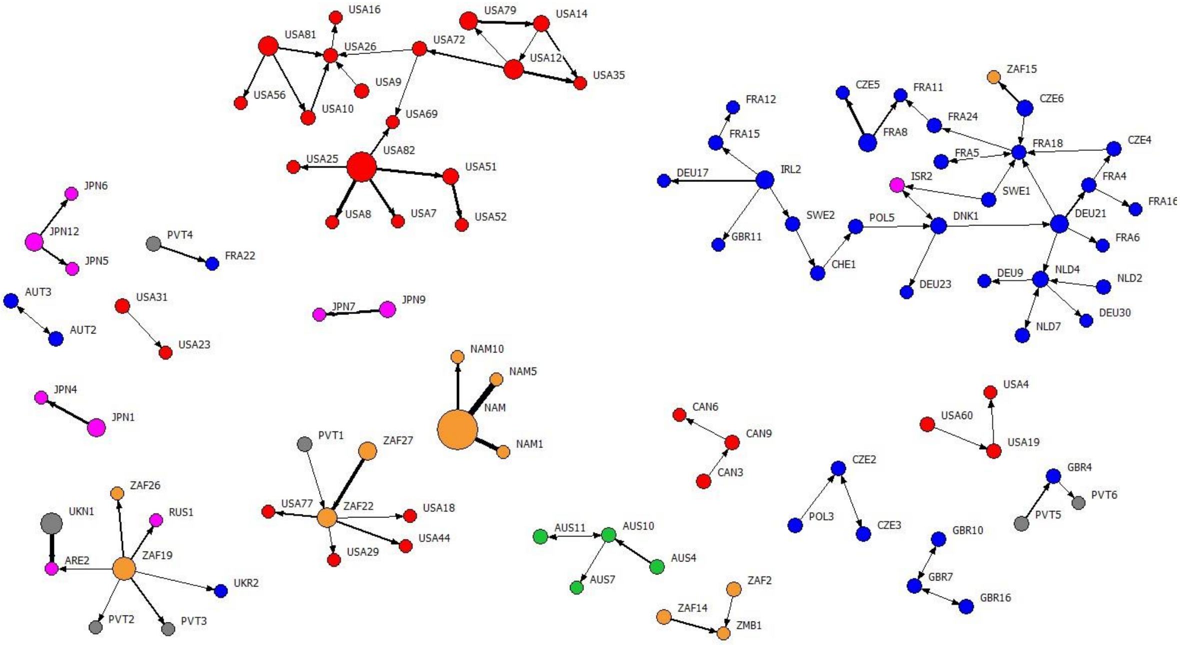


Figure 26. Graph representing the cheetah transfer network for the year 2010.

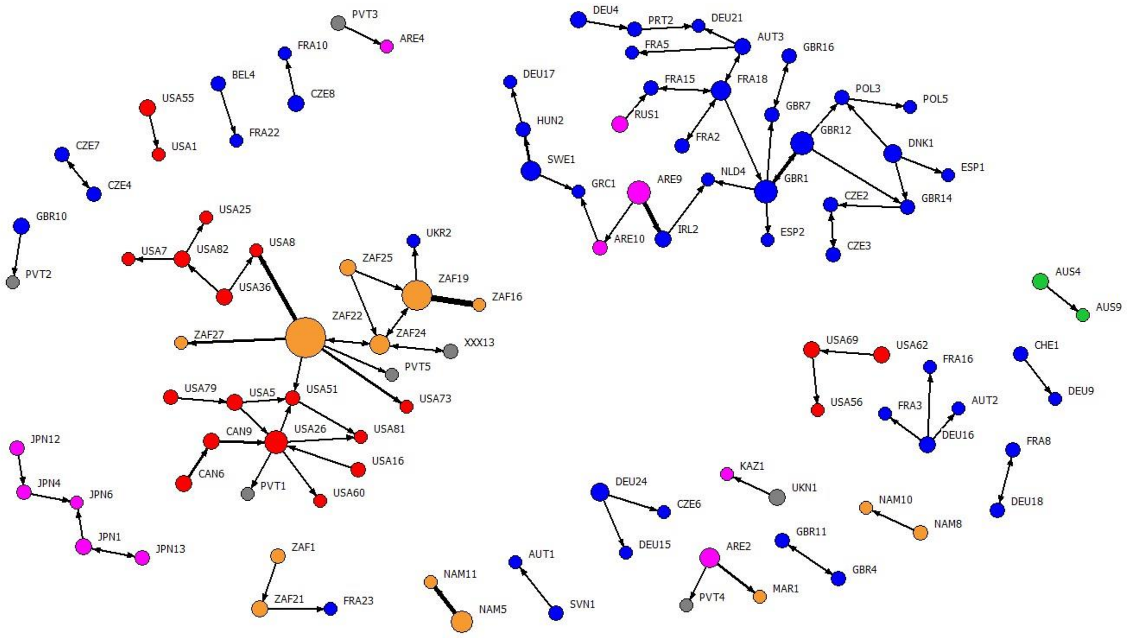


Figure 27. Graph representing the cheetah transfer network for the year 2011.

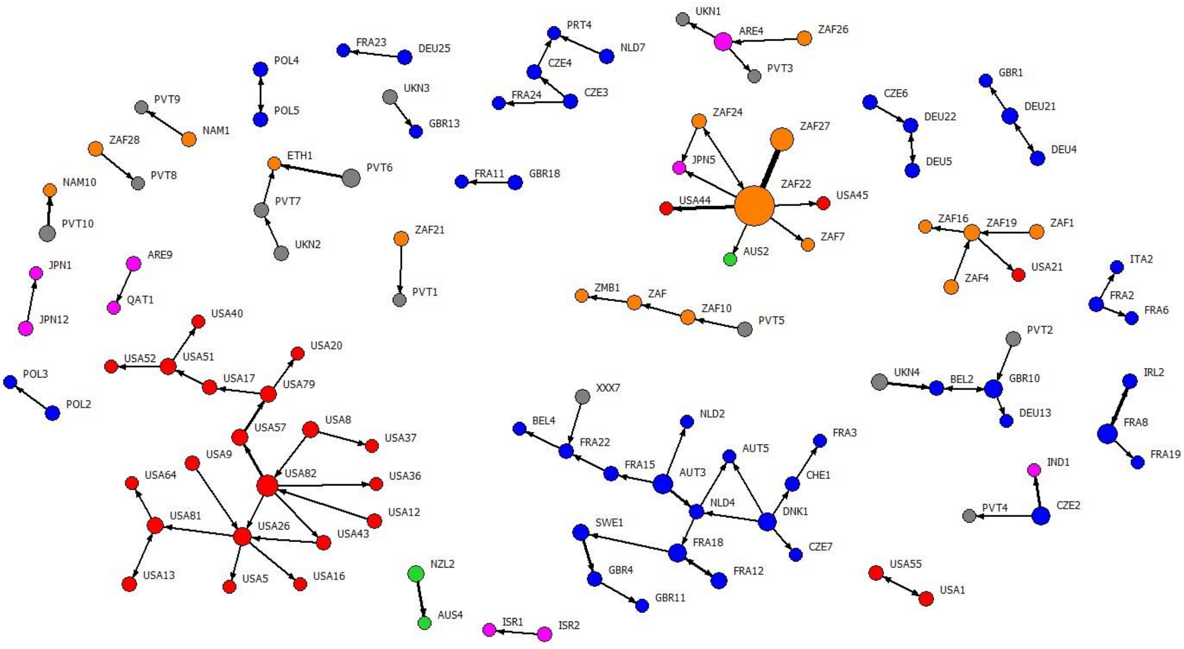


Figure 28. Graph representing the cheetah transfer network for the year 2012.

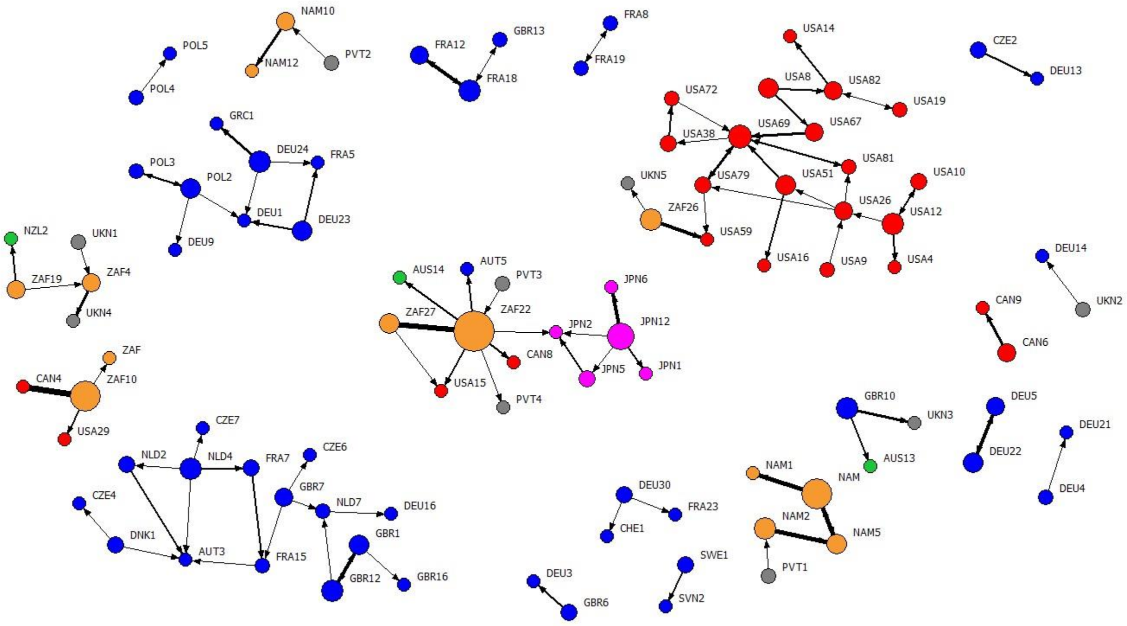


Figure 29. Graph representing the cheetah transfer network for the year 2013.

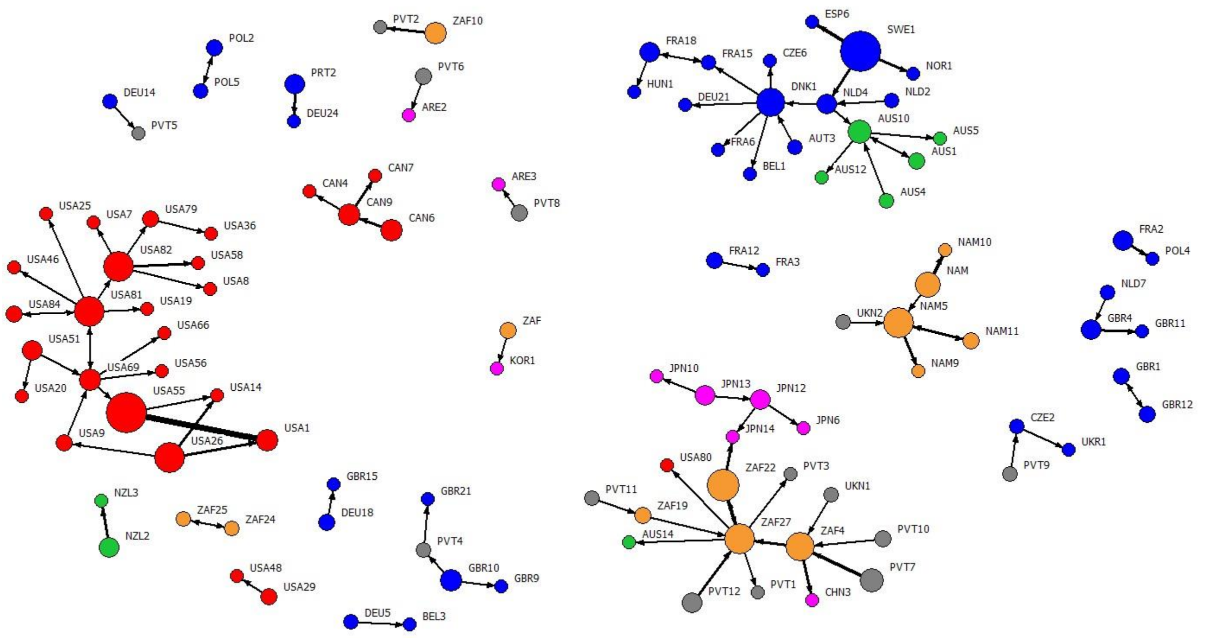


Figure 30. Graph representing the cheetah transfer network for the year 2014.

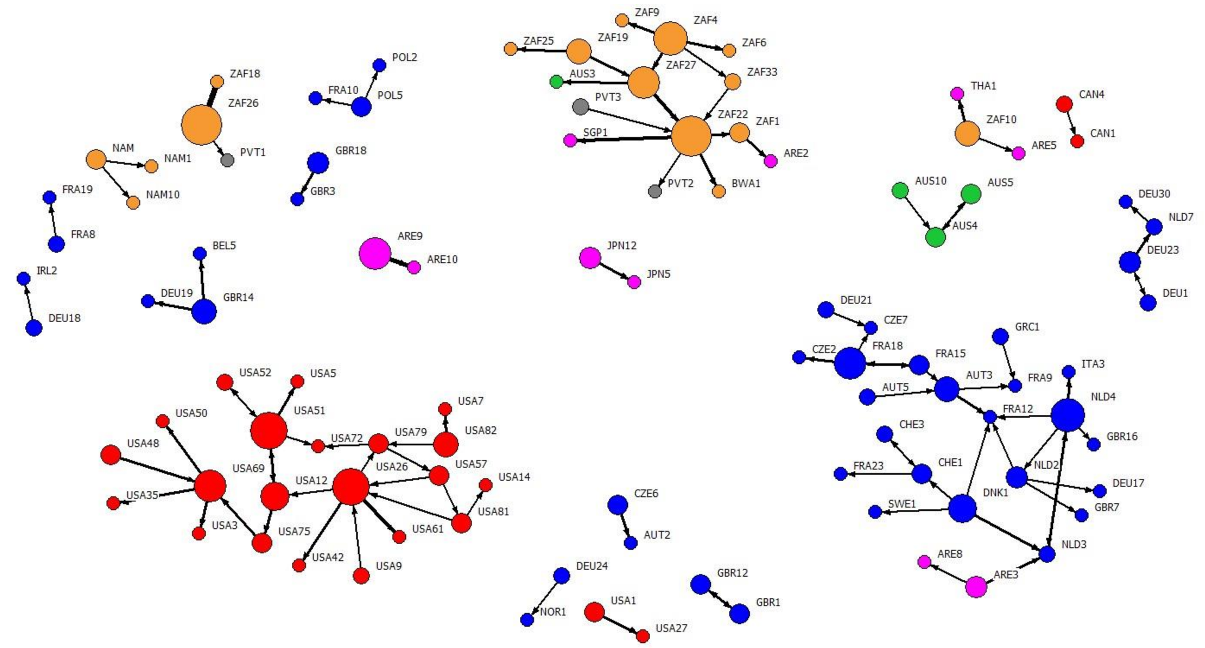


Figure 31. Graph representing the cheetah transfer network for the year 2015.

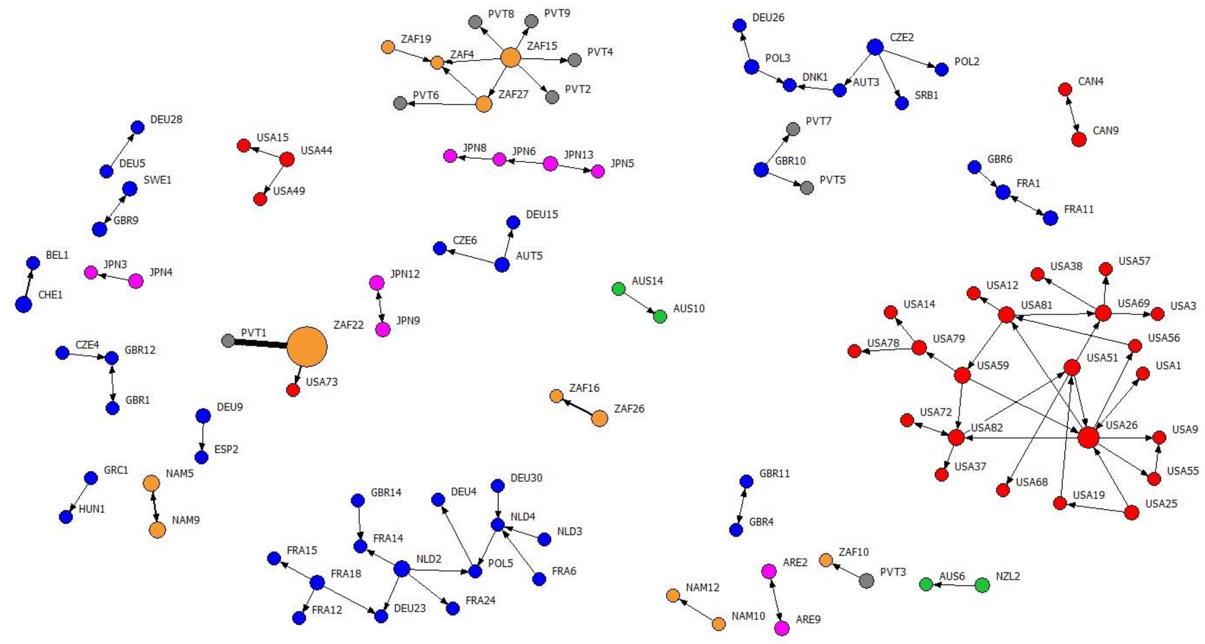


Figure 32. Graph representing the cheetah transfer network for the year 2016.

The networks' graphs obtained show that groups of facilities or components (set delimited by the researcher to be of 5 nodes or more that are interconnected) are formed together with smaller subgroups (less than 5 nodes interconnected). The fragmented structure of the graphs changes accordingly to the differences on the number of transfers, animals and facilities for every year analysed. The table below (Table 8) shows the summary of basic information about the structures of the social network graphs (number of nodes, number of ties and number of animals) besides the number of groups and subgroups formed for every year studied, the number of different countries and the states in the USA that participated in the network for that year. The number of USA states were chosen to be included separately due the intense activity of this country in the network.

Table 8. Basic information about the structure and graph design of cheetahs' transfers networks graphs from 1999-2016.

Year	Number of nodes (facilities)	Number of transfers	Number of cheetahs transferred	Number of countries	Number of USA states	Number of groups	Number of subgroups
1999	68	126	118	18	10	4	14
2000	86	157	139	21	18	3	16
2001	82	165	149	22	13	5	13
2002	78	110	108	20	11	6	10
2003	102	189	160	23	12	6	11
2004	88	186	155	20	18	6	13
2005	75	88	84	22	8	6	15
2006	111	198	183	29	13	7	18
2007	85	121	121	22	13	6	18
2008	89	150	138	23	10	4	8
2009	108	187	180	24	11	4	22
2010	102	172	166	22	14	4	14
2011	103	172	155	28	9	3	19
2012	115	189	168	27	14	5	23
2013	100	191	181	19	11	6	14
2014	109	207	189	25	13	4	19
2015	102	165	165	25	17	3	17
2016	106	193	192	23	14	4	23

Looking at Table 8, the number of nodes (participant facilities) varied from 68 (1999) to 115 (2012) in a non-specific order, giving us a mean of 94.94 (SD=13.79) institutions per year. The number of transfers and cheetahs transferred also varied randomly across the years, having a mean of 164.78 (SD=33.60) for transfers and a mean of 152.83 (SD=30.00) for cheetahs transferred. The complexity of the graphs varied, but generally increased with time since both number of nodes and ties increased with variations as is visible in Figure 33. The number of countries that participated into the cheetah transfer networks ranged from 18 (1999) to 29 (2006) each year and the yearly mean was 22.94 (SD=2.99). Moreover, the number of USA states ranged from 8 (2005) to 18 (2000, 2004), and the mean was 12.72 (SD=2.86).

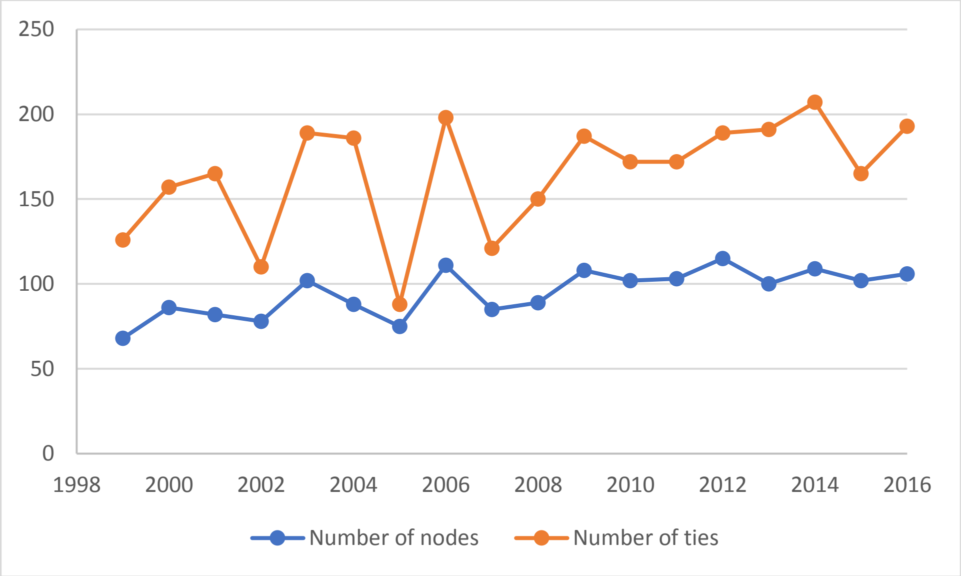


Figure 33. Number of nodes (zoos) and ties (number of cheetahs' transfers done between zoos) contained in each network per year of study (1999-2016). Both frequencies varied along time, but, in general, had increased in the last ten years.

In total, 53 countries participated on the cheetah transfers' network (either sending and/or receiving animals) from 1999-2016: Argentina, Australia, Austria, Belgium, Botswana, Canada, China, Croatia, Czech Republic, Denmark, Ethiopia, France, Germany, Greece, Hungary, India, Indonesia, Ireland, Israel, Italy, Japan, Jordan, Kazakhstan, Malaysia, Mexico, Morocco, Namibia, Netherlands, New Zealand, North Korea, Norway, Poland, Portugal, Qatar, Russia, Serbia, Singapore, Slovenia, Somalia, South Africa, South Korea, Spain, Sri Lanka, Sweden, Switzerland, Thailand, Tunisia, Ukraine, United Arab Emirates, United Kingdom, United States, Zambia, and Zimbabwe. In addition, 36 out of 50 states from United States participated transferring or receiving cheetahs during this period of 18 years: AL, AR, AZ, CA, CO, CT, DC, FL, GA, HI, IL, IN, KS, LA, MD, MI, MO, NE, NJ, NM, NV, NY, OH, OK, OR, PA, RI, SC, SD, TN, TX, UT, VA, WA, WI, and WV.

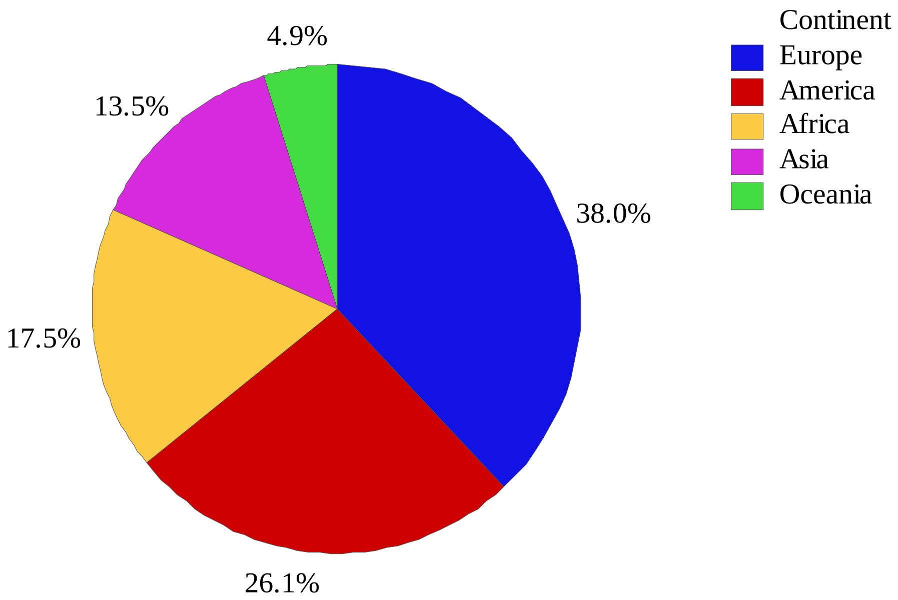


Figure 34. Percentage of different facilities in cheetahs' transfers networks by continent from 1999-2016. Percentages were calculated from the total number of different facilities (N=371) excluding privates, unknowns and facilities not specified. America (N=97), Africa (N=65), Asia (N=50), Oceania (N=18) and Europe (N=141).

In general, considering the 18 years of study, United States dominated in total number of facilities participating either sending or receiving animals for every year if analysed separately, but when analysed all the years together, summing the total number of different facilities for the whole period (1999-2016), Europe had the most different facilities participating in the networks (Figure 34). When only the number of facilities that sent animals out are considered for each year, United States still had the highest values for 17 years out of 18 years, losing in only one year (2005) to South Africa and Germany, which had the same number of facilities. Nevertheless, when considering only the number of facilities that received animals into their institutions, United States continues to lead the ranking for the 18 years of study. The second place for number of facilities included in the networks for both sending or receiving animals usually alternated between Germany, France, Japan, South Africa, and United Kingdom. In third place, occasionally, Czech Republic, Namibia and Australia appeared in the rank. Tables 9, 10 and 11 show the rank of countries by number of different facilities participating in the network sending animals out of their facilities, receiving animals into their facilities and total, respectively.

Table 9. Rank of countries with most facilities sending cheetahs out to another institution per year of study. The numbers in parenthesis represent the number of facilities from the country that participated sending animals to another institution on the year specified.

Year	1st	2nd	3rd
1999	United States (7)	United Kingdom (6)	France (4) Germany (4) South Africa (4)
2000	United States (17)	Germany (5)	Netherlands (4) South Africa (4) United Kingdom (4)
2001	United States (9)	South Africa (6)	Germany (5)
2002	United States (12)	France (7)	Australia (3) Namibia (3) South Africa (3)
2003	United States (10)	France (8) South Africa (8)	Germany (7)
2004	United States (12)	Germany (7)	South Africa (6)
2005	Germany (7) South Africa (7)	United States (6)	United Kingdom (4)
2006	United States (12)	South Africa (8)	Germany (6) United Kingdom (6)
2007	South Africa (8) United States (8)	Germany (5)	Czech Republic (4)
2008	United States (9)	South Africa (8)	Germany (6)
2009	United States (10)	South Africa (8) United Kingdom (8)	France (7)
2010	United States (13)	France (6)	South Africa (5)
2011	United States (10)	United Kingdom (8)	South Africa (6)
2012	United States (14)	South Africa (11)	France (6)
2013	United States (14)	France (6) Germany (6) South Africa (6) United Kingdom (6)	Namibia (4)
2014	United States (11)	South Africa (8)	France (4) United Kingdom (4)
2015	United States (14)	South Africa (8)	Germany (5)
2016	United States (14)	United Kingdom (8)	Japan (5) South Africa (5)

Table 10. Rank of countries with most facilities receiving cheetahs into their institution per year of study. The numbers in parenthesis represent the number of facilities from the country that participated receiving animals into their institution on the year specified.

Year	**1st**	**2nd**	**3rd**
1999	United States (10)	United Kingdom (6)	France (5) South Africa (5)
2000	United States (21)	United Kingdom (6)	France (4) Germany (4) South Africa (4)
2001	United States (15)	Germany (9)	South Africa (7)
2002	United States (17)	France (5) South Africa (5)	Germany (4) Namibia (4)
2003	United States (17)	France (10)	Germany (7)
2004	United States (19)	Germany (11)	South Africa (5) Australia (5)
2005	United States (9)	Germany (7)	United Kingdom (6)
2006	United States (15)	Germany (9)	South Africa (8)
2007	United States (15)	United Kingdom (6)	Czech Republic (5) South Africa (5)
2008	United States (12)	Germany (10)	South Africa (7)
2009	United States (14)	France (10)	South Africa (9)
2010	United States (22)	France (10)	Germany (5) United Kingdom (5)
2011	United States (13)	France (10)	United Kingdom (7)
2012	United States (21)	France (11)	South Africa (8)
2013	United States (18)	Germany (9)	France (8)
2014	United States (21)	United Kingdom (7)	South Africa (6)
2015	United States (19)	South Africa (8)	France (7)
2016	United States (24)	France (6) Japan (6)	Germany (5) United Kingdom (5)

Table 11. Rank of countries by total number of different facilities either sending or receiving cheetahs per year of study. The numbers in parenthesis represent the number of facilities from the country that participated either sending or receiving animals into their institution on the year specified.

Year	1st	2nd	3rd
1999	United States (15)	United Kingdom (8)	Germany (7) South Africa (7)
2000	United States (25)	Germany (9)	United Kingdom (8)
2001	United States (20)	Germany (10)	South Africa (9)
2002	United States (20)	France (10)	South Africa (7)
2003	United States (20)	France (13)	Germany (10)
2004	United States (24)	Germany (11)	South Africa (6) Australia (6)
2005	United States (13)	Germany (10)	South Africa (9)
2006	United States (20)	Germany (11) South Africa (11)	United Kingdom (9)
2007	United States (20)	South Africa (12)	Germany (6) United Kingdom (6)
2008	United States (15)	Germany (12)	South Africa (11)
2009	United States (19)	France (11) United Kingdom (11)	South Africa (10)
2010	United States (27)	France (11)	Japan (7) South Africa (7)
2011	United States (18)	France (10)	Germany (8) South Africa (8) United Kingdom (8)
2012	United States (24)	South Africa (13)	France (12)
2013	United States (20)	Germany (13)	France (8)
2014	United States (24)	South Africa (8) United Kingdom (8)	France (6) Australia (6)
2015	United States (24)	South Africa (12)	France (8) Germany (8)
2016	United States (26)	France (8) Germany (8) Japan (8) South Africa (8) United Kingdom (8)	Namibia (4)

Figure 35 shows the variations on mean outdegree of cheetahs transfers networks by year from 1999-2016. No pattern is seen along the years, but the values seems to alternate high and low peaks yearly for most of the years.

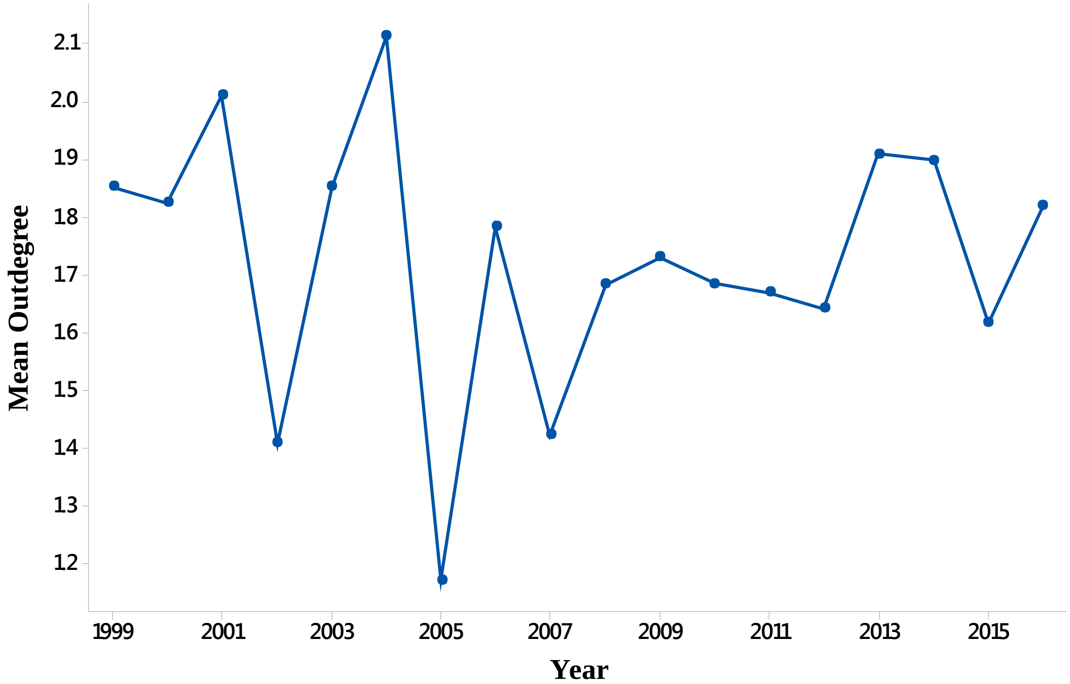


Figure 35. Mean outdegree centrality (described as number of transfers or weight of the tie) by year from 1999-2016.

The density and reciprocity values are shown in Tables 12 and 13. Figure 36 also shows the variation in percentage of reciprocated ties from years 1999-2016.

Table 12. Density Overall Procedure results from UCINET for cheetah transfers' networks from 1999-2016.

Year	Number of possible ties	Average Value	Total	Standard deviation	Average weighted degree
1999	4556	0.028	126	0.335	1.853
2000	7310	0.021	157	0.277	1.826
2001	6642	0.025	165	0.297	2.012
2002	6006	0.018	110	0.240	1.410
2003	10302	0.018	189	0.243	1.853
2004	7656	0.024	186	0.328	2.114
2005	5550	0.016	88	0.175	1.173
2006	12210	0.016	198	0.213	1.784
2007	7140	0.017	121	0.212	1.424
2008	7832	0.019	150	0.231	1.685
2009	11556	0.016	187	0.222	1.731
2010	10302	0.017	172	0.231	1.686
2011	10506	0.016	172	0.217	1.670
2012	13110	0.014	189	0.204	1.643
2013	9900	0.019	191	0.228	1.910
2014	11772	0.018	207	0.233	1.899
2015	10302	0.016	165	0.197	1.618
2016	11130	0.017	193	0.381	1.821

The number of possible ties was calculated using the formula n(n-1), where n=number of nodes present in the network; "Average value" equals the weight in average each node would have if all the nodes had the same weight; "Total" equals the sum of tie strengths.

Table 13. Reciprocity procedure run in UCINET for cheetah transfers' networks from 1999-2016.

Year	Symmetric Dyads	Asymmetric Dyads	Total dyads	Reciprocity	Percentage
1999	7	45	52	0.1346	13.46
2000	7	65	72	0.0972	9.72
2001	9	57	66	0.1364	13.64
2002	5	58	63	0.0794	7.94
2003	10	84	94	0.1064	10.64
2004	14	58	72	0.1944	19.44
2005	5	51	56	0.0893	8.93
2006	10	83	93	0.1075	10.75
2007	5	56	61	0.0820	8.20
2008	8	74	82	0.0976	9.76
2009	16	66	82	0.1951	19.51
2010	8	81	89	0.0899	8.99
2011	13	72	85	0.1529	15.29
2012	10	80	90	0.1111	11.11
2013	12	76	88	0.1364	13.64
2014	10	78	88	0.1136	11.36
2015	8	80	88	0.0909	9.09
2016	10	77	87	0.1149	11.49

*Dyad consists of a pair of nodes and its relational tie. Symmetric and asymmetric dyads, therefore, consists of a pair of nodes in which its relational ties are symmetric or not, respectively. Total dyads represent the total number of ties the network contains. Reciprocity are values calculated from the division of symmetric ties by the number of total possible ties. However, this method ignores the weight strengths of every tie.

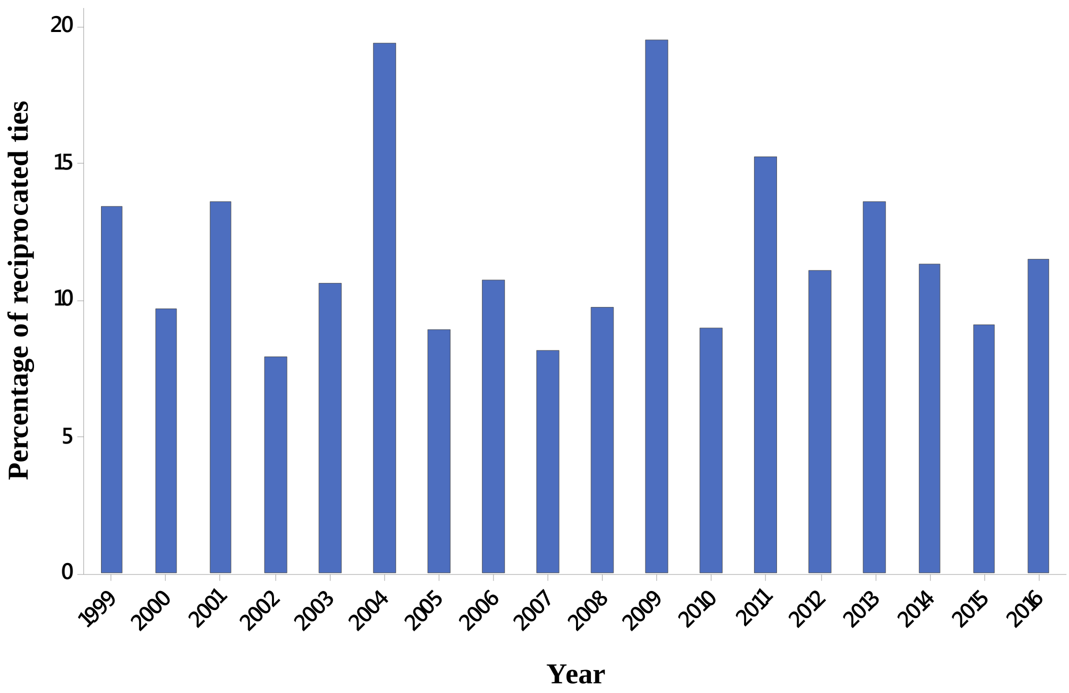


Figure 36. Percentage of reciprocated ties in cheetah transfers' networks from 1999-2016.

4.3.2 Growing network

The network metrics indicated that the biggest values of outdegree centrality were displayed by "PretDW" (Ann Van Dyk Cheetah Centre, N=232), "Namibia" (N=275) and "Yulee" (White Oak Conservation Centre, N=84), while for indegree "CheetahC" (Cheetah Conservation Fund, N=111), "Stellenbo" (Cheetah Outreach, N=75) and "Africat" (AfriCat Foundation , N=66) were the main facilities receiving cheetahs.

The density and reciprocity measures for the final network is shown in Table 14 and Table 15.

Table 14. Density for final growing network of cheetahs' transfers (1999-2016).

Year	Number of possible ties	Average Value	Total	Standard deviation	Average weighted degree
1999-2016	130,682	0.021	2728	0.448	7.536

Table 15. Reciprocity for final growing network of cheetahs' transfers (1999-2016).

Year	Symmetric Dyads	Asymmetric Dyads	Total dyads	Reciprocity	Percentage
1999-2016	186	710	896	0.208	20.8

4.4 Discussion

Observing cheetah social networks from 1999 to 2016 (Figures 14-31) it was possible to notice that a pattern of transference was being followed across the years. Some similarities were found, for example, a geographic group formed by American institutions, which exchanged individuals mostly inside America and rarely sent a cheetah abroad. In fact, according to the networks, the only time an American institution made an out-transference was in 2011 to a private institution, which since there is no information about its location, could also be located inside America. Furthermore, most of the times that an American institution interacted with a foreign institution were to receive an animal, especially from South African or European institutions. This could be related to the American Zoos only wishing to interact with zoos considered to be of the same standard in terms of conservation and animal welfare. In the US, the best zoos are usually members of the AZA and must meet accreditation criteria to be accepted as members (AZA, 2018). Alternatively, it could be that exchanges within the US are less logistically complicated (i.e. no quarantine regulations applying between some states) and potentially better for animal welfare (i.e. shorter transport time, especially as transportation is known to be very stressful to animals; Woodford, 2000).

Wild-caught animals are extremely important individuals for the maintenance of the genetic pool of the species, but the capture of individuals from the wild is believed to be almost zero in the last few years for conservation purposes (according to studbook data). The importation of individuals from African institutions could be due to the demand for displaying cheetahs by zoos due its charisma or because South Africa is recognized by CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) as the only cheetah-range country allowed to export for commercial captive breeding operations (CITES, 2014; Nowell & Rosen, 2018), and therefore, their animals could maximise the genetic pool of cheetahs located abroad. This intense exportation could also support the fact that South Africa is the country with the most interactions with private facilities. Since the animals' IDs were not taken into account in this study, the possibility of South Africa being only a transition place is not discarded. However, the majority of animals have left the country along the years and not a significant amount entered to balance, inducing the idea of the reproduction of those animals for exportation.

A similar situation to the American zoos is seen with Namibian institutions, which are grouped and interact only a few times outside Namibia. This fact is interesting because Namibia is the country that currently has the largest population of cheetahs in the wild (Marker, 1998; Marker & Dickman, 2010). Even though the number of cheetahs is high in Namibia very few individuals are sent abroad, emphasizing the importance of conservation of those animals in their natural habitat. In contrast, European institutions have a dynamic flow of transfers between many countries and are constantly exchanging cheetahs within and between countries. One possible reason for the European network transferring animals among different countries instead of only transferring inside each country is the geographical proximity and size of countries involved.

A comparison can be made with the American states, in which each could be considered equal to a small country, for example, and that, together with the number of institutions available for captive breeding, would explain the rare transfers of cheetahs from America to overseas countries. An important factor should be considered: transferring animals is a high cost task and impacts on the behaviour and health of individuals (Cunningham, 1996; Snyder et al., 1996; Williams & Hoffman, 2009; Dickens et al., 2010). The dilemma is completed when the genetics is taken into consideration: it is necessary to diversify the genetic pool of zoo populations to increase the chance of a successful breeding, but to do this it would be the best to exchange individuals from a different population and that would probably be the most distant population.

Most Asian countries had almost passive interactions, mainly receiving animals from outside their countries and not exchanging many animals, except for Japan and United Arab Emirates. Although the first is active in transferring animals only within its own country, the second also transfers to other countries, including outside Asia. Oceania countries were the minority, appearing occasionally and exchanging only within their continent. Again, like American institutions, Oceania institutions only received animals into their countries, especially from South Africa and sporadically from European institutions. This pattern reinforces the importance of South Africa in influencing the distribution of animals worldwide.

The low rate of exchange between countries, in general, motivates a discussion about the genetic value of some individuals. Cheetahs with the best genes (i.e. with a more diverse pool of genes) are more important or ranked higher than others due their breeding value. Keeping the best cheetahs inside the country is a “temptation” because it could increase the chance of a successful breeding in future generations. However, management mechanisms such as finding a suitable partner to mate would probably be given with less importance. The recommended network for transfers could therefore be affected by powerful countries, which could control the genetic pool, making a "selfish" network instead of sharing the animals to optimise the captive breeding programme in terms of its genetic goals. Nevertheless, if we then start to move many animals across continents, the risk of losing key animals would increase significantly, generating a possible cost-benefit imbalance for the pair of institutions willing to participate in the breeding process.

It is important to remember that captive breeding is supposed to be for the benefit of the species, but it is controlled by institutions whose goals could be different. For example, cheetahs are notoriously difficult to breed, therefore, if an institution had females that regularly breed, keeping her would be a "temptation" as her cubs could be a significant attraction for the zoo visitors (Carr, 2016; Withworth, 2012). It is known that institutions, which successfully breed giant pandas make significant financial gains from this situation (Vidal, 2014).

The influence of each institution in the network can be calculated using the social network analysis measures, mainly using measures of centrality. Thinking about captive breeding programmes, the main centrality measure of importance is probably the outdegree, once it is extremely important to reach the objectives that the animals keep moving between institutions to create a genetic flow. The birth of animals, while in accord with the regulations for breeding, should therefore be done with the main intention of serving as insurance individuals and must follow the recommendations stipulated by studbook keepers, including being transferred out to other institutions for the pairing of dissimilar individuals.

The values of outdegree for these data, represented by the proportional size of nodes on the graph, are the same as the strength of the ties, therefore they are the number of transfers done between two facilities. This was due to the nature of the network being weighted instead of binary, preventing the simple calculation of outdegree from being only the number of arrows leaving the node. The biggest outdegree values for most networks were from South African institutions, followed by Namibia, America and Netherlands. Comparing these data with the number of facilities that sent animals out, however, it is possible to see that America has a significant participation and other countries such as Germany and France, for example, also have many facilities sending animals out. Namibia, which was one of the countries with most transfers, does not appear high in the ranking very often, leading us to the conclusion that few Namibian institutions manage/control the flow of cheetahs.

In contrast, when focusing on indegree centrality, Namibia is the country with biggest values, indicating a large number of transfers received, mostly from facilities inside the country. The mean degree graph shows a variation across the years, with a high peak in 2004 followed by a low in 2005. The reason for this is uncertain, but it is necessary to consider the costs of transferring animals (Snyder, 1996; Weise et al., 2014). Therefore, the low could be a consequence of the high amount of money spent by facilities in 2004 and 2005.

Regarding the overall density of the graphs, it is possible to see that all of them are fragmented, usually with many components containing only few nodes and most of them are not very interconnected. The division of the sum of tie weights by the number of possible ties for all the years resulted in a very low average number that, when compared with the actual average weight, shows a "lack" of links between institutions. In reality, when we analyse only one specific year, we do not expect it to have extremely high density, since the zoos could not all be connected in a short period of time; that is, they are not capable of transferring many times in only one year because of money, time, quantity of animals available etc.

The reciprocity in cheetahs' transfers networks could be interpreted as animals that are exchanged between two "partner" facilities. This approach could reflect political agreements between the parties, possibly working around of favouring the relationship between the facilities, but not necessarily the best for the breeding of animals. The results calculated for each year showed that for none of the years the percentage of reciprocated ties were extremely high. The highest values appeared in 2004 and 2009, when about 20% of the total ties were reciprocated. Therefore, the relationships between the pairs of facilities have probably been respecting the necessities of moves according to breeding plans stipulated in benefit of the species. The political nature of animal exchanges in breeding programmes is normally difficult to investigate, however, the methods here presented show potential for research into this phenomenon (Conway, 1995).

Finally, the growing network showed a high number of nodes interconnected, expressing the emergence of new relationships between different partner organizations. Collaborations are extremely necessary for the success of captive breeding programmes, because inbreeding and genetic drift can be potentially avoided through matchings with animals from different institutions. Despite the high number of nodes, the network density showed that only about 21% of zoos had connections to one another along the 18 years of study. This limitation, as mentioned before, is perhaps related to availability of money or possible animals able to be transferred in the amount of time studied. However, the existent connections showed that almost every zoo is interconnected by another facility indirectly, except by two locations which were isolated in the analysis and exchanged only between themselves ("Bulawayo" and "Zimbabwe") during the period studied. The growing network reciprocity value maintain a similar percentage to the year by year networks, about 20%, even though the number of nodes is much bigger, which keeps the suggestion that most relationships are not made by political alliances, but by recommendations from the studbook keeper.

4.5 Conclusion

In general, the results express an apparent preference for cheetah transfers inside the countries or to countries geographically located close to each other apart from few institutions, especially from South Africa, which interacts with even intercontinental institutions. European institutions also exchange individuals externally of their countries, but still preferring to maintain the flow inside their continent. Since the costs and risks of death are important variables in the animals' transfers, the transfers of individuals inside continents, respecting the maximum genetic diversity recommended by breeding plans, would probably be the best option for conservation of the species.

It is important to keep increasing the density of connections along the years while avoiding exchanges only for partnerships to make sure the facilities work not only as entertainment, educational and research venues, but truly as institutions with conservation purposes. The results also show that there has been an effort in increasing collaborations of cheetah transfers between the facilities along the years, even though this has not been done for every single institution that participates in their captive breeding programme.

Social network analysis has been shown to help quantifying and visualizing the relationships of institutions for captive breeding purposes and has the potential of being a tool for constantly managing, tracking real transfer networks and comparing them with the expected model of breeding, which optimises the conservation of selected species. This study aims to propose and stimulate other professionals from captive breeding to better develop the idea and, perhaps, put the theoretical concepts in practice through the implementation of this method on management software such as ZIMs for Studbooks, for example.

Chapter 5 General discussion

The research project presented has confirmed studbooks to be of high importance for understanding breeding programmes due to the amount of data contained from years of husbandry of the determined species. Studbooks allow zoos to achieve their conservation goals. However, a neglected side of studbooks is the human dimension, studbooks are managed by people who have complex decision to make based on the animal data they possess but such decisions can be influenced by other data such as geographical, political and economic.

Given the ongoing extinction crisis, contributions from both communities (zoos and academics) are more essential than never before, so that the recovery of species could be done faster, and the prevention of new species being added to the list. The focus should be directed to threatened species, since they are in a risk status of disappearing from Earth and their self-sustainability is concerned (Mace et al., 2008). Thus, the zoo community could create a priority list of studbooks for analysis in terms of the conservation needs of a species. Furthermore, the multiple analysis of the same studbook data should be encouraged to increase confidence in conclusions derived from data analyses (i.e. proof of replicability; Goodman et al., 2016). Replication of analysis using same data can help to remove the biases that might exist within a researcher (Smith & Noble, 2014). Interest in Data Science has increased in universities around the world, where new courses are starting to operate and these courses train students to analyse big data and to look for factors that explain observed patterns (Baumer, 2015).

The information provided by studbooks could be more deeply explored and also include parallel research to enrich the outcome obtained from an analysis of those data. As was showed through the effects of studbook variables on the longevity and the effects of external variables on the reproductive success of cheetahs in chapter two. Longevity, unexpectedly, showed some positive influence from number of transfers done during life. This result generated several hypotheses to explain why captive cheetahs that experience more transfers during their life are living longer. There is no certain explanation for this cause so far, but this indicates some possible fields for investigation in the future.

Climate and GDP per capita had showed no significant influence on reproductive success, suggesting that husbandry practices from facilities, for example, might be more important than the country where the animal is located. However, studies considering enclosures characteristics and animal daily routine would demand a lot of time and will from the facilities to send this information via questionnaires. A possible way for solving this problem would be, again, through ZIMS using a standardized spreadsheet or similar, for example. That would require the facilities to make their data open access and mandatory input, otherwise a bias could happen from only leading zoological institutions inputting their information.

Social network analysis demonstrated to be very useful to find patterns of animal transfers along the time, including the quantity of facilities' participation sending or receiving individuals around the globe. Its most novel benefit for the management of captive animals, if applied, is its use for planning and monitoring breeding recommendations by studbook keepers and its capacity of simulations in favour of studbook keeper strategical decisions. This is extremely important not only for the perspective of the animals, but also for the zoos, once the costs of transferring an animal are very high, especially for large species. Careful analyses would help the institutions to have more control over the expenditures with animal transfers without ignoring the necessity of following biological "rules" related to breeding and animal welfare (Linhart et al., 2008).

5.1 Limitations

Although this project has generated interesting outcomes, some limitations were found along the development of the research which restrained its full achievement and need to be pointed for the best comprehension of results.

The accessibility of data was very limited, since full access to studbook information is currently only available to zoo members. Most of analysis were done based on online studbooks found on the Cheetah Conservation Fund (international studbooks from 1999 – 2016). Recommendations for breeding and inbreeding coefficients from cheetahs were not included in the analyses performed on this thesis using international studbooks, since this information is contained in separate documents which were not made available to the researcher.

For this reason, it was not possible to guarantee that all the transfers considered in this study were performed for captive breeding purposes. However, since the cheetah population is extremely affected by low genetic diversity and reproductive success, it is very likely that this was the case. Therefore, the results obtained from the thesis analysis are estimations, but are still valid considering the current fragile situation of cheetahs.

Zoo annual reports would also facilitate analysis that involves money income, expenditure and visiting numbers, for example, but again this type of information has restricted access and individual contact would not be viable since there are hundreds of zoos spread around the world and the response rate would probably be very low. Even when research requests are endorsed by zoo associations such as BIAZA, EAZA or WAZA, response rates are often hard to obtain in full, especially if it involves money expenditures, as is seen in a study from Gusset & Dick (2011).

The addresses encountered on the international studbooks were in fact postal addresses and made the analysis more time-consuming, since I had to look after all the institutions' physical addresses online to proceed with the following steps such as calculating the geographical coordinates of the locations or identifying climate categories. This process became even more complicated because some facilities denominations changed their names along the years, making the process more confusing even though the studbooks cited this change of names in a separate section of the report for the specific year. One way of making this information more easily available would be to put all this information in one unique table in the studbook containing postal/physical addresses and previous/current denominations. The information should also be updated regularly according to the release of studbooks and reported in all years of publication to make sure it is accessible independently of year of publication. Another difficulty found along the project was the lack of information regarding private facilities. Even though it is justified to not publish this information, country of location and at least some kind of identification (as numbers or acronyms for example) should be present to differentiate private facilities among them.

5.2 Recommendations from this research

1. The bibliometric review performed in chapter two showed that most studies developed with studbook data have focused on few specific scientific areas such as population management and genetics. The exploration of studbook data should be emphasized in multidisciplinary studies to fully extract and use temporal information stored in these books. Zoo management software such as ZIMS (Species 360) could also have a specific section for undergraduate or postgraduate researches using studbook data. Therefore, when someone had access to a studbook from a specific species, they could also find research based on data from those studbooks. Furthermore, this could offer an online space that allows experts to make constructive comments or discuss research topics in a forum style format.
2. Most research conducted with studbooks were done by universities and came, in general, from wealthy countries, as shown in chapter two. This inequality can decrease if more partnerships are established between universities and zoos from different areas of the world, where countries have less stable economies. This would enhance their animal collection, which many times cannot be found in other countries, or have a threat great extinction threat. International sponsors should prioritize financial grants to countries in need, so the research could also be developed locally with the help of NGOs and governmental organisations.
3. Cheetah transfers did not affect negatively longevity from our chapter three analyses. Therefore, the results suggest that zoos can do transfers without concerns about longevity for this species, if all the other recommended practices for welfare during transportations are followed. However, for zoos to act sustainable and make best use of their financial resources, animals should be exchanged over the smallest possible distances. Studbook keepers could use the “greedy algorithm” to optimise the

geographic location of zoo animals. Computational techniques such as that would facilitate the job of studbook keepers when considering locations for transportation of animals, since this task demands intense evaluation of information.

4. Investigations associating liver diseases in cheetahs with transfer's patterns would be useful to confirm the results obtained from chapter three. It could also include some hormonal analysis from before, during and after transportation to evaluate stress of animals in this process. If confirmed, environmental enrichment directed for exercising and expenditure of energy may help on the treatment/prevention of such diseases.
5. From our analysis, birth institution was one of the most important factors affecting cheetah survival. Therefore, more detailed studies of best practices are needed and should be disseminated to encourage improvements from facilities. Some studies had already proved the influence of husbandry practices, enclosure characteristics and public exposure on cheetahs' personality (Baker & Pullen, 2013), behaviour (Quirke et al., 2012), sperm output (Koester et al. 2015), and reproduction function (Koester et al., 2015), for example. All those factors and many others vary among zoos and deserve deeper exploration for the definition of patterns that minimise the negative effects of captivity.
6. Neither a zoo's climate nor country economic richness affected strongly cheetah reproductive success, thus zoos do not need to consider these factors when exchanging animals for captive breeding according to the GLM results from chapter three. Excellent performing zoos can be found in countries with low GDP per capita and in most climate types studied. Cheetah survival, however, was not analysed using Köppen-Geiger climate categories as was reproductive success, because the models developed in this study had already considered another categorical variable (birth institution). The

inclusion of climate in the model would make the analysis too complex for the extraction of conclusions.

7. The monitoring of animal transfers through social network analysis can help to avoid possible manipulations of animals against recommendations from the studbook keeper. For example, it can identify institutions behaving in "selfish networks"; that is, keeping a high ranked animal due to their high genetic value to increase successful reproductions in the future.
8. The analysis developed in chapter four demonstrated the existence of a small percentage of reciprocated ties both in the networks year by year and for the growing network. This leads us to infer that most transfers of cheetahs have been following the recommendations for breeding instead of political agreements between facilities. Exchanges between facilities without breeding purpose can still happen if the studbook keeper agrees, but they should not be the priority for transfers when the animals involved are part of the selected fertile group, which maintains the genetic pool of the population healthy and dynamic.
9. Anonymization of facilities' names could be used in some cases, especially in network analysis studies, to avoid exposition of them to external people (where an institution was reluctant to be identified), but still allow research to be developed. At the same time, some kind of identification such as country location would yet be very useful for some analyses. Changes in facilities' names should be reported every year of a studbook's release with postal/physical addresses to avoid confusion from readers.
10. Zoos are already organised to exchange animals in a geographical area, as showed by the network graphs in chapter four, but this would be enhanced by having the most genetically different animals closest together. Although the distance travelled during life was a factor affecting positively the longevity of animals in this study, its influence

was not very relevant (affecting less than 1%). Thus, reducing the distances from the animals for the best genetic proximity would not have a relevant negative impact on their longevity but would reduce the costs of transportations, allowing facilities to invest more money in other areas of need.

11. More collaborations between data scientists and zoological institutions could be performed since most of the time data scientists have the expertise but are limited regarding information available to them, while zoos have the data but generally do not have time or specialized personnel to deal with large and complex datasets in a more productive way. The bibliometric review revealed potential areas for developing research but there are still many possible applications from other areas, which could contribute, enrich research and advance science. The analyses of studbooks are still a very specialized topic but if treated with attention and given value they could bring great advances to zoo animal management and conservation science.

5.3 Future research

We hope this project helps to inspire other researchers to develop the ideas exposed in this thesis and look after other ways to improve zoo management and conservation science.

The procedure of building and comparing networks through time using studbook data could be applied to other species, which also deserve attention and conservation efforts, with emphasis on threatened species. Other species could show different patterns of connections among facilities and inter-species comparisons would also be useful to identify similarities and differences on the transfers of animals, including the degree centrality, reciprocity and density, for example. Depending on the pattern of connections expressed by the species, other measures of centralities could be used to explain the zoo collaborations for breeding.

The statistical analysis from this study considered only a few external variables that could be influencing captive breeding programmes' success, such as GDP per capita and climate. However, there are innumerable other variables outside the scope of studbooks which could be used to evaluate the behaviour of studbook variables. It is a decision for each researcher to identify possible associations that could be interfering on many steps of captive breeding, from management to reintroductions, and apply the best analysis to increase the percentage of variation explained the variable such as longevity or reproductive success. For instance, main factors that have proven to influence the success of carnivore reintroductions so far, according to Jule et al. (2008) are "habitat suitability, long-term food availability, the season of release, type of release (soft or hard), the source (wild-caught or captive-born) of released animals". In addition, as mentioned before, enclosure size and group size are also useful variables to be included when possible because of their effect on longevity and reproductive success.

The networks presented in this study and from other future studies could be used for the development of simulations such as the most convenient institution to transfer an animal based on distance of facilities, biological data (i.e. genetic suitability) and costs of transfers as suggested by the use of a "greedy algorithm". Also, it would help to make predictions about the behaviour of some nodes (facilities) when some of them leaves the network (i.e. when a zoo is closed down or is not breeding animals anymore or there was a disease outbreak as happened recently in the UK (foot and mouth disease); Rorres et al., 2018; Ortiz-Pelaez et al., 2006). Different kinds of node attributes instead of facility country could be included in the networks for the best visualization of connections such as previous experience in reproducing cheetahs in captivity. Collaborations between facilities could be deeply analysed using social network metrics (e.g. to measure reciprocity; Hanneman & Riddle, 2005) and the results used for the best management of the species.

Final Conclusion

This thesis has shown the growth of research being conducted using studbook data along years and their potential areas of exploration. It also showed some possible directions for making them more easily accessible to a broader community including academics from different areas of expertise, enriching research and making them more multidisciplinary. From 1988 to 2016, the main areas of study with studbook data from published papers focused on areas regarding animal management and genetic diversity, especially of mammals, even though this is not the taxon with most threatened species as indicated by IUCN Red List of Threatened Species reports. Furthermore, an association between the wealth of a country and the number of papers using studbooks were found.

Studbook variables were used to model longevity, and the number of transfers done during life by cheetahs (*Acinonyx jubatus*) surprisingly appeared to be the most relevant explanatory variable of those considered in the model, affecting about 6% of total longevity of cheetahs. Reproductive success was also modelled for the same species but, in general, did not showed significant effect from climate referred to the location of facilities or GDP per capita from their countries.

Social network analysis performed using cheetah international studbooks from 1999-2016 as a model indicated geographical patterns of connections made by the facilities concerning transfers of animals and indicated the most prominent facilities according to variations in degree centrality, proving to be a useful tool for management of transfers and recommendations for breeding to studbook keepers or to scientists interested in the area of zoo management and conservation.

It is my sincere belief that if zoos facilitate the analysis of studbook data by academics they will create a win-win situation, where species survival is enhanced through the generation of knowledge.

Appendices

Appendix 1 - Calculation of the Vincenty Ellipsoid distances in R using a “.txt” file containing geographic coordinates (Longitude, Latitude) from the sender facility (Lon1,Lat1) and the receiver facility (Lon2, Lat2) in parallel columns

```
>library("geosphere")
>library("xlsx”)
>DATAFRAME <- read.delim(“C:/PATH/FILENAME.txt”)
>Lon1 = DATAFRAME$Lon1
>Lon2 = DATAFRAME$Lon2
>Lat1 = DATAFRAME$Lat1
>Lat2 = DATAFRAME$Lat2
>p1=cbind(Lon1,Lat1)
>p2=cbind(Lon2,Lat2)
>DISTANCE=distVincentyEllipsoid(p1,p2,a=6378137,b=6356752.3142,
f=1/298.257223563)
>write.xlsx(DISTANCE,”C:/PATH/FILENAME1.xlsx”)
```

Appendix 2 – Longevity Analysis via GLM in R

```
>library(“MASS”)
>DATAFRAME<-read.table("C:/PATH/FILENAME.txt",sep="\t", header=TRUE)
>attach(DATAFRAME)
>names(DATAFRAME)
>dim(DATAFRAME)
>str(DATAFRAME)
>plot(DATAFRAME)
>shapiro.test(DATAFRAME$VARIABLE)
>cor.test(DATAFRAME$VARIABLE1,DATAFRAME$VARIABLE2,method="spearman")
>options(max.print=999999)
>m1 <- glm(deathage~gender+ntransfers+birthplace+agefirsttransfer+distancetrav ,
family="poisson")
>summary(m1)
>m2 <- glm(deathage~gender+ntransfers+birthplace+agefirsttransfer+distancetrav ,
family="quasipoisson")
>summary(m2)
>m3 <- glm.nb(deathage~gender+ntransfers+birthplace+agefirsttransfer+distancetrav)
summary(m3)
>anova(m3, test="Chisq")
>drop1(m3, test="Chisq")
>m4 <- glm.nb(deathage~ntransfers+birthplace+agefirsttransfer+distancetrav)
>summary(m4)
>birthplace <- relevel(birthplace, ref = "PRETDW")
>m4 <- glm.nb(deathage~ntransfers+birthplace+agefirsttransfer+distancetrav)
>summary(m4)
>anova(m4, test="Chisq")
```

```
>m4.null <- glm.nb(deathage~1)
>summary(m4.null)
>anova(m4, m4.null, test="Chisq")
>VIF(m4)
>exp(m4$coef)
>BIC(m4)
```

Appendix 3 – Reproductive success analysis via GLM in R

```
>library("MASS")
>OBJECT<-read.table("C:/PATH/FILENAME.txt",sep="\t", header=TRUE)
>attach(DATAFRAME)
>names(DATAFRAME)
>dim(DATAFRAME)
>str(DATAFRAME)
>plot(DATAFRAME)
>shapiro.test(DATAFRAME$VARIABLE)
>cor.test(DATAFRAME$VARIABLE1,DATAFRAME$VARIABLE1,method="spearman")
>options(max.print=999999)
>m.rep1=glm(repsuccess~averagegdp+climate, family="poisson")
>summary(m.rep1)
>m.rep2=glm(repsuccess~averagegdp+climate, family="quasipoisson")
>summary(m.rep2)
>m.rep3=glm.nb(repsuccess~averagegdp+climate)
>summary(m.rep3)
>anova(m.rep3, test="Chisq")
>m.null <- glm.nb(repsuccess~1)
>summary(m.null)
>anova(m.rep3, m.null, test="Chisq")
>AIC(m.rep1,m.rep2, m.rep3, m.null)
>BIC(m.rep1,m.rep2, m.rep3, m.null)
>VIF(m.rep3)
>exp(m.rep3$coef)
```

Scatterplot of reproductive success by GDP per capita

```
>library("ggplot2")
>graph <- ggplot(DATAFRAME, aes(x = VARIABLE1, y = VARIABLE2, color=VARIABLE3)) + geom_point(shape = 16, size = 5) + geom_hline(yintercept = AVERAGE_Y,linetype="dashed") + geom_vline(xintercept = AVERAGE_X, linetype="dashed")
>graph + scale_color_manual(values=c("black", "deepskyblue2", "darkorchid1", "blue2", "yellow2", "green2", "darkorange", "aquamarine1", "deeppink1", "red", "olivedrab")) + labs(x="LABEL_X",y="LABEL_Y", colour="LEGEND_TITLE") + theme_classic() + opts(axis.title.x = theme_text(vjust=-0.5))
```

Appendix 4 - Summaries from models m1, m2, m3 created during longevity analysis

summary(m1)

```
Deviance Residuals:

    Min       1Q   Median       3Q      Max
-72.389  -11.824    0.207   12.024   45.859

Coefficients:
                      Estimate Std. Error  z value Pr(>|z|)
(Intercept)          8.211e+00  6.265e-03 1310.663  < 2e-16 ***
genderM             -5.577e-03  1.271e-03   -4.387 1.15e-05 ***
ntransfers           5.166e-02  4.066e-04  127.072  < 2e-16 ***
birthplaceARNHEM    -5.913e-01  1.204e-02  -49.113  < 2e-16 ***
birthplaceBANHAM    -2.785e+00  6.457e-02  -43.129  < 2e-16 ***
birthplaceBASEL     -2.625e-01  1.049e-02  -25.012  < 2e-16 ***
birthplaceBATTLECR   1.681e-01  1.486e-02   11.311  < 2e-16 ***
birthplaceBELFAST   -7.669e-02  9.197e-03   -8.339  < 2e-16 ***
birthplaceBROXBOURN -3.957e-01  1.039e-02  -38.075  < 2e-16 ***
birthplaceCALDWELL   2.128e-01  9.240e-03   23.033  < 2e-16 ***
birthplaceCHICAGOLP  1.570e-01  8.503e-03   18.459  < 2e-16 ***
birthplaceCHTAHEXP  -1.994e+00  4.366e-02  -45.658  < 2e-16 ***
birthplaceCINCINNAT -3.953e-01  8.912e-03  -44.356  < 2e-16 ***
birthplaceCLEVELAND  2.394e-02  8.402e-03    2.850  0.00438 **
birthplaceCOLCHESTR -9.449e-01  1.871e-02  -50.514  < 2e-16 ***
birthplaceCOLUMBUS   1.042e-01  8.662e-03   12.028  < 2e-16 ***
birthplaceDANIEL     1.411e-01  1.510e-02    9.343  < 2e-16 ***
birthplaceDICKERSON -8.394e-02  7.480e-03  -11.221  < 2e-16 ***
birthplaceDUBBO      1.033e-01  8.179e-03   12.625  < 2e-16 ***
birthplaceDVURKRALV -1.970e-01  7.003e-03  -28.131  < 2e-16 ***
birthplaceEBELTOFT  -6.556e-01  9.558e-03  -68.589  < 2e-16 ***
birthplaceEDINBURGH -2.209e-01  1.847e-02  -11.956  < 2e-16 ***
birthplaceFONTAINE  -5.626e-01  1.591e-02  -35.355  < 2e-16 ***
birthplaceFORTWORTH -4.785e-01  1.291e-02  -37.070  < 2e-16 ***
birthplaceFOSSILRIM -1.013e-01  6.499e-03  -15.595  < 2e-16 ***
birthplaceFOTA      -2.571e-01  6.892e-03  -37.296  < 2e-16 ***
birthplaceGLASGOW    2.179e-01  1.490e-02   14.628  < 2e-16 ***
birthplaceHANNOVER  -1.236e-01  1.139e-02  -10.848  < 2e-16 ***
birthplaceHERNEBC   -1.087e+00  2.878e-02  -37.750  < 2e-16 ***
birthplaceHILVARENB -1.190e-02  6.870e-03   -1.733  0.08317 .
birthplaceHIMEJISH  -2.824e-02  1.088e-02   -2.596  0.00944 **
birthplaceHOEDSPRUI -1.847e-01  6.864e-03  -26.905  < 2e-16 ***
birthplaceHUIZENFD  -2.162e-01  8.247e-03  -26.210  < 2e-16 ***
birthplaceJACKSON   -1.193e-01  1.087e-02  -10.973  < 2e-16 ***
birthplaceJADERBERG  1.259e-01  1.116e-02   11.277  < 2e-16 ***
birthplaceKATOWICE  -1.487e+00  3.327e-02  -44.686  < 2e-16 ***
birthplaceKESSINGLA -1.287e+00  3.003e-02  -42.873  < 2e-16 ***
birthplaceKREFELD   -1.330e-01  1.042e-02  -12.766  < 2e-16 ***
birthplaceLAFLECHE  -6.026e-01  2.163e-02  -27.853  < 2e-16 ***
birthplaceLAPALMYR  -1.168e-01  7.760e-03  -15.048  < 2e-16 ***
birthplaceLETSATSI  -6.783e-01  9.032e-03  -75.094  < 2e-16 ***
birthplaceMAKTOUM   -1.128e-01  1.309e-02   -8.617  < 2e-16 ***
birthplaceMARWELL   -3.314e-01  8.630e-03  -38.402  < 2e-16 ***
birthplaceMEMPHIS   -1.844e-03  1.059e-02   -0.174  0.86175
birthplaceMONARTO   -1.715e-01  1.144e-02  -14.987  < 2e-16 ***
birthplaceMONTGOMRY -8.973e-02  1.012e-02   -8.864  < 2e-16 ***
birthplaceMOSCOW     2.348e-01  8.993e-03   26.109  < 2e-16 ***
```

```
birthplaceMUNSTER   -4.526e-02  7.214e-03   -6.275 3.50e-10 ***
birthplaceNADERMANN -6.611e-01  1.253e-02  -52.755  < 2e-16 ***
birthplaceNEUWIED    2.350e-01  8.634e-03   27.219  < 2e-16 ***
birthplaceNISHIMURO -8.648e-02  1.308e-02   -6.610 3.85e-11 ***
birthplaceNISHINODA -5.902e-01  2.227e-02  -26.505  < 2e-16 ***
birthplaceNURNBERG  -3.418e-01  9.644e-03  -35.445  < 2e-16 ***
birthplaceNZP-CRC   -3.069e+00  7.418e-02  -41.369  < 2e-16 ***
birthplaceNZP-WASH  -3.660e-01  1.102e-02  -33.226  < 2e-16 ***
birthplaceOAKHILL    1.889e-01  7.669e-03   24.635  < 2e-16 ***
birthplaceOLMENSE   -3.082e-01  1.171e-02  -26.321  < 2e-16 ***
birthplaceOLOMOUC   -4.892e-01  1.047e-02  -46.740  < 2e-16 ***
birthplaceORANA     -3.672e-01  1.395e-02  -26.331  < 2e-16 ***
birthplaceOUDTSHORN -2.772e-01  7.192e-03  -38.545  < 2e-16 ***
birthplacePARYS     -4.853e-01  9.429e-03  -51.467  < 2e-16 ***
birthplacePEAUGRES  -2.463e-01  7.184e-03  -34.283  < 2e-16 ***
birthplacePHOENIX    7.863e-02  9.371e-03    8.391  < 2e-16 ***
birthplacePRAHA     -3.845e-01  1.096e-02  -35.088  < 2e-16 ***
birthplacePRETDW    -2.380e-01  6.473e-03  -36.769  < 2e-16 ***
birthplaceRHINOLION -2.839e+00  6.406e-02  -44.317  < 2e-16 ***
birthplaceROCKTON   -1.172e-02  1.580e-02   -0.742  0.45797    
birthplaceROSTOCK   -2.203e-01  1.355e-02  -16.260  < 2e-16 ***
birthplaceSAFAWILD   7.601e-03  1.580e-02    0.481  0.63035    
birthplaceSAFRICA   -3.730e-01  9.229e-03  -40.419  < 2e-16 ***
birthplaceSALZBURG  -4.720e-01  8.398e-03  -56.204  < 2e-16 ***
birthplaceSD-WAP    -2.931e-02  6.838e-03   -4.286 1.82e-05 ***
birthplaceSHANGHAI  -3.277e-01  1.421e-02  -23.063  < 2e-16 ***
birthplaceSHARJAHBR -2.758e-01  1.383e-02  -19.940  < 2e-16 ***
birthplaceSINGAPORE -9.324e-01  2.467e-02  -37.796  < 2e-16 ***
birthplaceSTELLENBO -9.520e-02  1.685e-02   -5.648 1.62e-08 ***
birthplaceSTLOUIS   -1.982e-01  1.262e-02  -15.713  < 2e-16 ***
birthplaceSUSONO    -3.377e-01  1.385e-02  -24.392  < 2e-16 ***
birthplaceTOKYOTAMA -1.288e+00  3.033e-02  -42.470  < 2e-16 ***
birthplaceTOLEDO     4.974e-02  8.442e-03    5.893 3.80e-09 ***
birthplaceTORONTO   -3.245e-01  9.010e-03  -36.012  < 2e-16 ***
birthplaceTSAOBIS   -2.945e-01  1.400e-02  -21.036  < 2e-16 ***
birthplaceVARADAY    2.463e-01  1.437e-02   17.142  < 2e-16 ***
birthplaceVIENNA    -6.004e-01  1.619e-02  -37.075  < 2e-16 ***
birthplaceWARSAW    -3.484e-01  9.132e-03  -38.155  < 2e-16 ***
birthplaceWASSBRC   -9.878e-02  6.397e-03  -15.442  < 2e-16 ***
birthplaceWHIPSNADE -8.664e-03  8.211e-03   -1.055  0.29133    
birthplaceWILDS     -7.743e-01  2.196e-02  -35.262  < 2e-16 ***
birthplaceWINSTON   -2.467e-01  7.915e-03  -31.167  < 2e-16 ***
birthplaceWUPPERTAL -3.740e-01  1.481e-02  -25.252  < 2e-16 ***
birthplaceYULEE     -1.275e-01  6.710e-03  -18.995  < 2e-16 ***
agefirsttransfer     8.412e-05  8.293e-07  101.432  < 2e-16 ***
distancetrav         1.055e-05  1.855e-07   56.875  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 411956  on 738  degrees of freedom
Residual deviance: 264305  on 646  degrees of freedom
  (361 observations deleted due to missingness)
AIC: 271877

Number of Fisher Scoring iterations: 5
```

summary(m2)

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-72.389  -11.824    0.207   12.024   45.859

Coefficients:
                      Estimate Std. Error t value Pr(>|t|)
(Intercept)          8.211e+00  1.218e-01  67.443  < 2e-16 ***
genderM             -5.577e-03  2.471e-02  -0.226 0.821488
ntransfers           5.166e-02  7.901e-03   6.539 1.26e-10 ***
birthplaceARNHEM    -5.913e-01  2.340e-01  -2.527 0.011735 *
birthplaceBANHAM    -2.785e+00  1.255e+00  -2.219 0.026815 *
birthplaceBASEL     -2.625e-01  2.039e-01  -1.287 0.198550
birthplaceBATTLECR   1.681e-01  2.888e-01   0.582 0.560738
birthplaceBELFAST   -7.669e-02  1.787e-01  -0.429 0.667985
birthplaceBROXBOURN -3.957e-01  2.020e-01  -1.959 0.050515 .
birthplaceCALDWELL   2.128e-01  1.796e-01   1.185 0.236365
birthplaceCHICAGOLP  1.570e-01  1.652e-01   0.950 0.342546
birthplaceCHTAHEXP  -1.994e+00  8.486e-01  -2.349 0.019103 *
birthplaceCINCINNAT -3.953e-01  1.732e-01  -2.282 0.022788 *
birthplaceCLEVELAND  2.394e-02  1.633e-01   0.147 0.883470
birthplaceCOLCHESTR -9.449e-01  3.635e-01  -2.599 0.009555 **
birthplaceCOLUMBUS   1.042e-01  1.683e-01   0.619 0.536182
birthplaceDANIEL     1.411e-01  2.934e-01   0.481 0.630854
birthplaceDICKERSON -8.394e-02  1.454e-01  -0.577 0.563879
birthplaceDUBBO      1.033e-01  1.590e-01   0.650 0.516149
birthplaceDVURKRALV -1.970e-01  1.361e-01  -1.448 0.148230
birthplaceEBELTOFT  -6.556e-01  1.858e-01  -3.529 0.000446 ***
birthplaceEDINBURGH -2.209e-01  3.590e-01  -0.615 0.538613
birthplaceFONTAINE  -5.626e-01  3.093e-01  -1.819 0.069334 .
birthplaceFORTWORTH -4.785e-01  2.508e-01  -1.907 0.056900 .
birthplaceFOSSILRIM -1.013e-01  1.263e-01  -0.802 0.422578
birthplaceFOTA      -2.571e-01  1.339e-01  -1.919 0.055408 .
birthplaceGLASGOW    2.179e-01  2.895e-01   0.753 0.451914
birthplaceHANNOVER  -1.236e-01  2.214e-01  -0.558 0.576890
birthplaceHERNEBC   -1.087e+00  5.593e-01  -1.943 0.052509 .
birthplaceHILVARENB -1.190e-02  1.335e-01  -0.089 0.928987
birthplaceHIMEJISH  -2.824e-02  2.114e-01  -0.134 0.893792
birthplaceHOEDSPRUI -1.847e-01  1.334e-01  -1.384 0.166694
birthplaceHUIZENFD  -2.162e-01  1.603e-01  -1.349 0.177909
birthplaceJACKSON   -1.193e-01  2.112e-01  -0.565 0.572500
birthplaceJADERBERG  1.259e-01  2.169e-01   0.580 0.561924
birthplaceKATOWICE  -1.487e+00  6.466e-01  -2.299 0.021801 *
birthplaceKESSINGLA -1.287e+00  5.836e-01  -2.206 0.027728 *
birthplaceKREFELD   -1.330e-01  2.025e-01  -0.657 0.511467
birthplaceLAFLECHE  -6.026e-01  4.204e-01  -1.433 0.152272
birthplaceLAPALMYR  -1.168e-01  1.508e-01  -0.774 0.439014
birthplaceLETSATSI  -6.783e-01  1.755e-01  -3.864 0.000123 ***
birthplaceMAKTOUM   -1.128e-01  2.543e-01  -0.443 0.657628
birthplaceMARWELL   -3.314e-01  1.677e-01  -1.976 0.048575 *
birthplaceMEMPHIS   -1.844e-03  2.058e-01  -0.009 0.992853
birthplaceMONARTO   -1.715e-01  2.224e-01  -0.771 0.440877
birthplaceMONTGOMRY -8.973e-02  1.967e-01  -0.456 0.648466
birthplaceMOSCOW     2.348e-01  1.748e-01   1.343 0.179582
birthplaceMUNSTER   -4.526e-02  1.402e-01  -0.323 0.746896
birthplaceNADERMANN -6.611e-01  2.435e-01  -2.715 0.006813 **
birthplaceNEUWIED    2.350e-01  1.678e-01   1.401 0.161806
birthplaceNISHIMURO -8.648e-02  2.543e-01  -0.340 0.733884
birthplaceNISHINODA -5.902e-01  4.328e-01  -1.364 0.173093
```

```
birthplaceNURNBERG  -3.418e-01  1.874e-01  -1.824 0.068631 .
birthplaceNZP-CRC   -3.069e+00  1.442e+00  -2.129 0.033656 *
birthplaceNZP-WASH  -3.660e-01  2.141e-01  -1.710 0.087797 .
birthplaceOAKHILL    1.889e-01  1.490e-01   1.268 0.205386
birthplaceOLMENSE   -3.082e-01  2.276e-01  -1.354 0.176082
birthplaceOLOMOUC   -4.892e-01  2.034e-01  -2.405 0.016449 *
birthplaceORANA     -3.672e-01  2.710e-01  -1.355 0.175926
birthplaceOUDTSHORN -2.772e-01  1.398e-01  -1.983 0.047746 *
birthplacePARYS     -4.853e-01  1.832e-01  -2.648 0.008287 **
birthplacePEAUGRES  -2.463e-01  1.396e-01  -1.764 0.078193 .
birthplacePHOENIX    7.863e-02  1.821e-01   0.432 0.666037
birthplacePRAHA     -3.845e-01  2.130e-01  -1.806 0.071459 .
birthplacePRETDW    -2.380e-01  1.258e-01  -1.892 0.058938 .
birthplaceRHINOLION -2.839e+00  1.245e+00  -2.280 0.022909 *
birthplaceROCKTON   -1.172e-02  3.070e-01  -0.038 0.969547
birthplaceROSTOCK   -2.203e-01  2.634e-01  -0.837 0.403072
birthplaceSAFAWILD   7.601e-03  3.070e-01   0.025 0.980252
birthplaceSAFRICA   -3.730e-01  1.794e-01  -2.080 0.037932 *
birthplaceSALZBURG  -4.720e-01  1.632e-01  -2.892 0.003956 **
birthplaceSD-WAP    -2.931e-02  1.329e-01  -0.221 0.825516
birthplaceSHANGHAI  -3.277e-01  2.761e-01  -1.187 0.235772
birthplaceSHARJAHBR -2.758e-01  2.688e-01  -1.026 0.305250
birthplaceSINGAPORE -9.324e-01  4.794e-01  -1.945 0.052225 .
birthplaceSTELLENBO -9.520e-02  3.275e-01  -0.291 0.771410
birthplaceSTLOUIS   -1.982e-01  2.452e-01  -0.809 0.419080
birthplaceSUSONO    -3.377e-01  2.691e-01  -1.255 0.209893
birthplaceTOKYOTAMA -1.288e+00  5.894e-01  -2.185 0.029222 *
birthplaceTOLEDO     4.974e-02  1.641e-01   0.303 0.761827
birthplaceTORONTO   -3.245e-01  1.751e-01  -1.853 0.064325 .
birthplaceTSAOBIS   -2.945e-01  2.721e-01  -1.082 0.279465
birthplaceVARADAY    2.463e-01  2.792e-01   0.882 0.378071
birthplaceVIENNA    -6.004e-01  3.147e-01  -1.908 0.056863 .
birthplaceWARSAW    -3.484e-01  1.775e-01  -1.963 0.050037 .
birthplaceWASSBRC   -9.878e-02  1.243e-01  -0.795 0.427154
birthplaceWHIPSNADE -8.664e-03  1.596e-01  -0.054 0.956715
birthplaceWILDS     -7.743e-01  4.267e-01  -1.814 0.070067 .
birthplaceWINSTON   -2.467e-01  1.538e-01  -1.604 0.109262
birthplaceWUPPERTAL -3.740e-01  2.878e-01  -1.299 0.194275
birthplaceYULEE     -1.275e-01  1.304e-01  -0.977 0.328714
agefirsttransfer     8.412e-05  1.612e-05   5.219 2.42e-07 ***
distancetrav         1.055e-05  3.605e-06   2.927 0.003547 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasipoisson family taken to be 377.6714)

    Null deviance: 411956  on 738  degrees of freedom
Residual deviance: 264305  on 646  degrees of freedom
  (361 observations deleted due to missingness)
AIC: NA

Number of Fisher Scoring iterations: 5
```

Summary(m3)

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-5.6056  -0.5670   0.0209   0.5395   2.3142

Coefficients:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)          8.171e+00  1.473e-01  55.483  < 2e-16 ***
genderM             -6.293e-03  2.729e-02  -0.231 0.817606
ntransfers           6.031e-02  9.703e-03   6.216 5.10e-10 ***
birthplaceARNHEM    -5.683e-01  2.254e-01  -2.522 0.011682 *
birthplaceBANHAM    -2.753e+00  3.795e-01  -7.255 4.01e-13 ***
birthplaceBASEL     -2.746e-01  2.240e-01  -1.226 0.220363
birthplaceBATTLECR   1.777e-01  3.738e-01   0.476 0.634425
birthplaceBELFAST   -4.999e-02  2.102e-01  -0.238 0.812045
birthplaceBROXBOURN -3.832e-01  2.104e-01  -1.821 0.068574 .
birthplaceCALDWELL   2.452e-01  2.249e-01   1.090 0.275739
birthplaceCHICAGOLP  1.864e-01  2.010e-01   0.927 0.353883
birthplaceCHTAHEXP  -1.961e+00  3.765e-01  -5.209 1.90e-07 ***
birthplaceCINCINNAT -3.896e-01  1.875e-01  -2.078 0.037715 *
birthplaceCLEVELAND  5.315e-02  1.944e-01   0.273 0.784519
birthplaceCOLCHESTR -9.178e-01  2.839e-01  -3.233 0.001226 **
birthplaceCOLUMBUS   1.143e-01  2.098e-01   0.545 0.585893
birthplaceDANIEL     1.635e-01  3.758e-01   0.435 0.663612
birthplaceDICKERSON -6.132e-02  1.717e-01  -0.357 0.721063
birthplaceDUBBO      1.250e-01  1.943e-01   0.643 0.519933
birthplaceDVURKRALV -1.932e-01  1.610e-01  -1.200 0.230118
birthplaceEBELTOFT  -6.356e-01  1.883e-01  -3.375 0.000737 ***
birthplaceEDINBURGH -1.935e-01  3.748e-01  -0.516 0.605780
birthplaceFONTAINE  -5.385e-01  2.837e-01  -1.898 0.057657 .
birthplaceFORTWORTH -4.398e-01  2.466e-01  -1.783 0.074566 .
birthplaceFOSSILRIM -7.832e-02  1.518e-01  -0.516 0.605870
birthplaceFOTA      -2.460e-01  1.585e-01  -1.552 0.120729
birthplaceGLASGOW    2.373e-01  3.741e-01   0.634 0.525815
birthplaceHANNOVER  -9.404e-02  2.459e-01  -0.382 0.702120
birthplaceHERNEBC   -1.046e+00  3.759e-01  -2.784 0.005374 **
birthplaceHILVARENB  1.228e-02  1.608e-01   0.076 0.939124
birthplaceHIMEJISH  -4.078e-03  2.458e-01  -0.017 0.986766
birthplaceHOEDSPRUI -1.791e-01  1.598e-01  -1.121 0.262351
birthplaceHUIZENFD  -2.035e-01  1.840e-01  -1.106 0.268582
birthplaceJACKSON   -7.895e-02  2.466e-01  -0.320 0.748803
birthplaceJADERBERG  1.238e-01  2.825e-01   0.438 0.661332
birthplaceKATOWICE  -1.459e+00  3.755e-01  -3.886 0.000102 ***
birthplaceKESSINGLA -1.262e+00  3.757e-01  -3.358 0.000784 ***
birthplaceKREFELD   -1.036e-01  2.248e-01  -0.461 0.644970
birthplaceLAFLECHE  -5.783e-01  3.752e-01  -1.541 0.123205
birthplaceLAPALMYR  -9.941e-02  1.768e-01  -0.562 0.573885
birthplaceLETSATSI  -6.730e-01  1.830e-01  -3.678 0.000235 ***
birthplaceMAKTOUM   -8.163e-02  2.837e-01  -0.288 0.773530
birthplaceMARWELL   -3.268e-01  1.869e-01  -1.748 0.080392 .
birthplaceMEMPHIS   -2.738e-03  2.451e-01  -0.011 0.991088
birthplaceMONARTO   -1.467e-01  2.459e-01  -0.597 0.550697
birthplaceMONTGOMRY -5.955e-02  2.243e-01  -0.266 0.790577
birthplaceMOSCOW     2.589e-01  2.237e-01   1.157 0.247149
birthplaceMUNSTER   -3.134e-02  1.681e-01  -0.186 0.852075
birthplaceNADERMANN -6.205e-01  2.247e-01  -2.762 0.005751 **
birthplaceNEUWIED    2.558e-01  2.110e-01   1.213 0.225286
birthplaceNISHIMURO -5.888e-02  2.836e-01  -0.208 0.835531
birthplaceNISHINODA -5.588e-01  3.750e-01  -1.490 0.136251
```

```
birthplaceNURNBERG  -3.294e-01  2.009e-01  -1.640 0.101043    
birthplaceNZP-CRC   -3.036e+00  3.814e-01  -7.960 1.72e-15 ***
birthplaceNZP-WASH  -3.378e-01  2.244e-01  -1.505 0.132249    
birthplaceOAKHILL    2.154e-01  1.835e-01   1.174 0.240501    
birthplaceOLMENSE   -3.436e-01  2.447e-01  -1.404 0.160240    
birthplaceOLOMOUC   -4.729e-01  2.107e-01  -2.244 0.024813 *  
birthplaceORANA     -3.940e-01  2.842e-01  -1.387 0.165589    
birthplaceOUDTSHORN -2.555e-01  1.643e-01  -1.555 0.119986    
birthplacePARYS     -4.781e-01  1.994e-01  -2.398 0.016494 *  
birthplacePEAUGRES  -2.300e-01  1.634e-01  -1.407 0.159380    
birthplacePHOENIX    1.182e-01  2.244e-01   0.527 0.598378    
birthplacePRAHA     -3.801e-01  2.243e-01  -1.695 0.090129 .  
birthplacePRETDW    -2.206e-01  1.509e-01  -1.462 0.143789    
birthplaceRHINOLION -2.808e+00  3.803e-01  -7.384 1.54e-13 ***
birthplaceROCKTON   -1.908e-03  3.748e-01  -0.005 0.995939    
birthplaceROSTOCK   -2.034e-01  2.839e-01  -0.716 0.473747    
birthplaceSAFAWILD   2.088e-02  3.740e-01   0.056 0.955468    
birthplaceSAFRICA   -3.497e-01  1.979e-01  -1.767 0.077185 .  
birthplaceSALZBURG  -4.492e-01  1.770e-01  -2.538 0.011153 *  
birthplaceSD-WAP    -1.364e-02  1.600e-01  -0.085 0.932041    
birthplaceSHANGHAI  -3.034e-01  2.844e-01  -1.067 0.286023    
birthplaceSHARJAHBR -2.355e-01  2.839e-01  -0.830 0.406692    
birthplaceSINGAPORE -9.098e-01  3.754e-01  -2.424 0.015356 *  
birthplaceSTELLENBO -6.495e-02  3.782e-01  -0.172 0.863634    
birthplaceSTLOUIS   -1.867e-01  2.878e-01  -0.649 0.516446    
birthplaceSUSONO    -3.305e-01  2.857e-01  -1.157 0.247384    
birthplaceTOKYOTAMA -1.261e+00  3.756e-01  -3.356 0.000790 ***
birthplaceTOLEDO     6.157e-02  2.014e-01   0.306 0.759809    
birthplaceTORONTO   -3.112e-01  1.936e-01  -1.608 0.107931    
birthplaceTSAOBIS   -2.693e-01  2.838e-01  -0.949 0.342737    
birthplaceVARADAY    2.614e-01  3.764e-01   0.695 0.487356    
birthplaceVIENNA    -5.733e-01  2.837e-01  -2.021 0.043275 *  
birthplaceWARSAW    -3.465e-01  1.931e-01  -1.794 0.072784 .  
birthplaceWASSBRC   -8.061e-02  1.500e-01  -0.537 0.590949    
birthplaceWHIPSNADE  4.621e-02  1.945e-01   0.238 0.812189    
birthplaceWILDS     -7.661e-01  3.742e-01  -2.047 0.040658 *  
birthplaceWINSTON   -2.238e-01  1.771e-01  -1.264 0.206373    
birthplaceWUPPERTAL -3.434e-01  2.837e-01  -1.211 0.226031    
birthplaceYULEE     -1.146e-01  1.560e-01  -0.735 0.462623    
agefirsttransfer     9.164e-05  1.913e-05   4.792 1.65e-06 ***
distancetrav         1.056e-05  4.084e-06   2.587 0.009682 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(8.3913) family taken to be 1)

    Null deviance: 1170.67  on 738  degrees of freedom
Residual deviance:  754.34  on 646  degrees of freedom
  (361 observations deleted due to missingness)
AIC: 12800

Number of Fisher Scoring iterations: 1


              Theta:  8.391 
          Std. Err.:  0.430 

 2 x log-likelihood:  -12612.317 
```

Appendix 5 - Summary from m.rep1 and m.rep2 created during reproductive success analysis

Summary(m.rep1)

```
Deviance Residuals:
     Min        1Q    Median        3Q       Max
-12.7935   -3.3340   -1.5400    0.9502   25.9809

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.311e+00  4.727e-01   2.773  0.00555 **
averagegdp   4.587e-06  2.351e-06   1.951  0.05101 .
climateBSh   3.117e+00  4.679e-01   6.660 2.73e-11 ***
climateBSk   1.821e+00  4.642e-01   3.923 8.75e-05 ***
climateBWh   1.003e+00  4.610e-01   2.176  0.02957 *
climateCfa   1.422e+00  4.530e-01   3.139  0.00170 **
climateCfb   9.932e-01  4.539e-01   2.188  0.02868 *
climateCsa   6.897e-01  4.736e-01   1.456  0.14533
climateCsb   2.220e+00  4.738e-01   4.686 2.78e-06 ***
climateCwb   1.559e+00  4.829e-01   3.228  0.00125 **
climateDfa  -2.805e-01  5.224e-01  -0.537  0.59129
climateDfb   1.228e+00  4.686e-01   2.621  0.00877 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 4355.8  on 115  degrees of freedom
Residual deviance: 3097.1  on 104  degrees of freedom
AIC: 3565.8
```

Summary(m.rep2)

```
Deviance Residuals:
     Min        1Q    Median        3Q       Max
-12.7935   -3.3340   -1.5400    0.9502   25.9809

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.311e+00  2.937e+00   0.446    0.656
averagegdp   4.587e-06  1.460e-05   0.314    0.754
climateBSh   3.117e+00  2.907e+00   1.072    0.286
climateBSk   1.821e+00  2.884e+00   0.631    0.529
climateBWh   1.003e+00  2.864e+00   0.350    0.727
climateCfa   1.422e+00  2.815e+00   0.505    0.614
climateCfb   9.932e-01  2.820e+00   0.352    0.725
climateCsa   6.897e-01  2.943e+00   0.234    0.815
climateCsb   2.220e+00  2.944e+00   0.754    0.452
climateCwb   1.559e+00  3.000e+00   0.520    0.604
climateDfa  -2.805e-01  3.246e+00  -0.086    0.931
climateDfb   1.228e+00  2.912e+00   0.422    0.674

(Dispersion parameter for quasipoisson family taken to be 38.60511)

    Null deviance: 4355.8  on 115  degrees of freedom
Residual deviance: 3097.1  on 104  degrees of freedom
AIC: NA
```

Appendix 6 – Matrix development of social network analysis from years 1999-2016

```
>library("reshape")
>DATAFRAME <- read.delim("C:/PATH/FILENAME.txt")
>OBJECT1 <-cast (DATAFRAME, ZooSour ~ ZooRec, sum)
>OBJECT2 <-as.matrix(OBJECT1)
>write.table(OBJECT2, "FILENAME1.xls")
```

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