Understanding large mammalian metapopulation trends in Sub-Saharan Africa: a meta-analysis and supporting conceptual model.

Bachelor thesis, Utrecht University

Name: Lizzy Peerenboom

Student number: 6253067

Supervisor: Prof. dr. Martin Wassen

Second reader: Prof. dr. Gert Jan Kramer

Submission date: 29-01-2020

Number of words: 8203

Image retrieved from: https://www.earthtouchnews.com/conservation/human-impact/is-it-time-for-conservation-to-move-beyond-the-fence/

Table of contents

1. Abstract

Populations of many mammalian species are under pressure due to fragmentation and isolation of their habitat. They are often confined to designated protected areas and are surrounded by unsuitable habitats, such as human settlements. Nevertheless, for populations to persist without active human involvement, they depend on individuals' exchange, thus needing to venture out into this unsuitable habitat. Different parameters of population dynamics influence these fragmented populations. However, research is often specified to one population or species only. A general understanding can help to uncover the most pressing problems for these populations.

This thesis investigates the impacts of different population dynamics parameters on large mammalian species' metapopulation trends in Sub-Saharan Africa by synthesizing results from several studies. This was done using a meta-analysis, yielding a total of 35 papers. Next to a meta-analysis, a conceptual model was used to perform several thought experiments on the influence of two parameters. The meta-analysis showed that several parameters were more researched and impacting than others, and several in(consistencies) were found regarding impacts and the implications that authors mentioned. In conclusion, the mortality rate and individuals' ability to disperse from their habitat were most impacting on metapopulation trends. The results have some implications for both future research as the course of conservation, indicating that a shift in conservation might be in order to secure the viability of metapopulations.

2. Introduction

Sub-Saharan Africa is a major region that embraces an extensive range of habitats and ecosystems with varying degrees of species diversity and is specifically well known for its mammals. A region where indigenous people lived for many centuries and used natural-resources sustainably, putting little demand on other organisms and the ecosystem. In modern-day society, the consequences of an ever-growing human-population looking for short-term gains instead of sustainable use induce serious threats to the future persistence of many species and ecosystems, with over 99% of modern extinctions attributed to human activity (Stuart et al., 1990; Wilson & Primack, 2019).

Species that undergo the consequences from these threats generally have declining populations, leading to a cascade of other impacts. If a certain species population declines to critical numbers, it is at risk of becoming locally extinct in the area where the population persists. When a species is locally extinct, it can no longer maintain critical interactions and ensure the functionality and stability of ecological communities. Species extinction can also indirectly negatively influence ecosystem services contributing to human-wellbeing. Conservation biologists consider the decline of populations on the African continent and worldwide of great concern, and conserving threatened species has been made one of the goals for ensuring sustainable development to protect the future of the planet (Wilson & Primack, 2019; United Nations Development Programme, 2020).

African nations have established an extensive network of protected areas to conserve species and ecosystems. There are currently 8448 protected areas in Africa, encompassing more than 6 million km^2 of terrestrial and marine habitats (UNEP-WCMC, 2020). A protected area is a clearly defined geographical space dedicated to achieving the long-term conservation of nature with associated ecosystem services. One of its specific objectives is to maintain viable and ecologically functional populations (IUCN, 2008; IUCN, n.d.). Research indicates that protected areas can deliver positive outcomes, but evidence has remained largely inconclusive of the actual overall effectiveness of protected areas in maintaining species populations (Geldmann et al., 2013). Due to drivers such as human population growth, habitat loss, fences, roads, and other human constructs, protected areas are at risk of becoming increasingly fragmented, smaller, and isolated. This so-called anthropogenic fragmentation poses a severe threat to the long-term viability of many wildlife populations. Anthropogenic fragmentation is particularly important in an African context because most protected areas cannot be considered sufficiently large enough to truly fulfill biodiversity needs. Additionally, the human-dominated areas bordering reserves restrict animal movements and dispersal going inside and outside (Cheptou et al., 2017; Newmark, 2008; Wilson & Primack, 2019).

The roles of fragmentation, isolation, and dispersal in driving population dynamics can be brought together in the concept of metapopulations. Due to the processes mentioned above, widespread wildlife populations are divided into several increasingly smaller subpopulations. When individuals move between subpopulations and interact to some degree, the ensemble of subpopulations forms a metapopulation (Begon et al., 2014, p. 255; Gilpin, 2012; Wilson & Primack, 2019). Understanding the dynamics that influence metapopulation trends in increasingly fragmented areas can be considered of great importance within conservation biology and the field of sustainability as a whole, as it is essential for uncovering the best efforts to preserve species (Bonebrake et al., 2010). This thesis will focus on the dynamics and trends of large mammalian metapopulations in order to generate new insights and add to this understanding.

2.1 Problem definition, aim, and research questions.

Scientific knowledge on animal-population decline is fragmentary at best. Individual studies often present small-sized samples because the research is expensive and involves challenging fieldwork (Bonebrake et al., 2010; Harrison, 2011). This is also applicable to scientific research concentrating on metapopulation trends in Africa, which often focuses on a specific species and area or country, such as the African leopard in Tanzania or the Swaynes Hartebeest in Ethiopia (Havmøller et al., 2019; Mamo et al., 2012).

To support decision-making in conservation practice and guide future research, there is a need for a general understanding. Any standalone study's usability can be diminished if not compared and related to other similar studies. Questions of broader interest, such as the most pressing problems threatening populations, are not unheard of in ecology. Summarizing the findings of a group of studies can help reach this general understanding (Pullin & Knight, 2003; Arnqvist & Wooster, 1995; Gurevitch et al., 2001).

This thesis intends to mechanically research the parameters of population dynamics and their relation to metapopulation trends to reduce the fragmentation within research and create a better general understanding. The research will be done via a meta-analysis approach, which synthesizes results from separate studies, and a supplementary conceptual model. This thesis specifically focuses on research done in Sub-Saharan Africa on large mammalian species, as large ungulates and carnivores often occur at low densities, increasing their vulnerability to extinction. This, combined with the fact that they also frequently play critical roles in ecosystem functioning and the many challenges this region faces, calls for new insights (Wilson & Primack, 2019; Estes et al., 2011; Ripple et al., 2014).

The following research question will be answered: *Which parameters of population dynamics are significantly impacting on metapopulation trends of mammalian species in Sub-Saharan Africa?* In order to answer this question, four sub-questions are constructed:

1. Which metapopulation parameters can be successfully extracted from literature in order to quantify population dynamics?
2. Are the results consistent across studies and, if not, what are the underlying reasons for inconsistencies?
3. Can population dynamics be simulated via a simplified metapopulation model?
4. Can decisive factors for extinction risk be defined based on the metapopulation model?

3. Population dynamics: theory and concepts

In the 1960s, Robert MacArthur and Edward O. Wilson published their island biogeography theory after studying communities on islands to find explanations for the differences in species richness. According to this widely accepted scientific theory, two features of an island affect immigration and extinction rates of species and thus its species diversity. The first one is the island's *size*. Small islands should have a higher extinction rate than large islands because there are fewer resources and less diverse habitats. The second feature is the island's *distance from the mainland*. The island closest has more immigration, as the farther a potential new species has to travel, the less likely it is to reach the island (Miller & Spoolman, 2012, p. 93).

The reason for mentioning the theory of island biogeography in this thesis, is that it is used to study and make predictions about wildlife in areas of natural habitats, such as protected areas, surrounded by developed land (Miller & Spoolman, 2012, p. 195). Principles from the theory of island biogeography can be found in both landscape ecology and metapopulation ecology, which use different approaches to address similar questions about the effects of spatial structure on ecological processes (Howell et al., 2018). This research mostly implements concepts from the metapopulation discipline to conduct a meta-analysis, but some concepts also overlap with landscape ecology. Several key concepts play a central role in this research, wherefore a short definition of these concepts and their link to population dynamics will be disclosed in the sections below. The relations between these concepts are illustrated in an analytical framework (**Figure 2**).

3.1 Protected areas as patches

Inspired by the theory of island biography, metapopulation theory assumes that habitat occurs in patches surrounded by an unsuitable matrix. The matrix is the dominant background patch type, which in modified landscapes is often not native vegetation. A patch then refers to a distinct habitat unit within which a subpopulation occurs. Subpopulations live in patches with variable sizes and exchange individuals to a greater or lesser extent. Thus, metapopulation theory adopts the view that subpopulations, which the metapopulation exists of, are separated in space and interact to a certain degree (Hanski & Ovaskainen, 2003; Fischer & Lindenmayer, 2007; Hanski & Gaggiotti, 2004).

Patches are not directly connected, but there are several ways individuals can migrate between them. Individuals can travel through the matrix's unsuitable habitat or use the spatial elements corridors and stepping stones when these are present in the landscape. Corridors connect otherwise isolated patches via linear strips of habitat, and stepping stones are series of small, non-connected patches that allow for movement (Hanski & Gaggiotti, 2004; Fischer & Lindenmayer, 2007; Baum et al., 2004).

This thesis regards the protected areas in Sub-Saharan Africa as patches or habitat islands where subpopulations of large African mammals live. The areas surrounding the protected areas can be seen as the matrix composed of, for instance, industrial activities, human settlements, and mining operations. These areas are unsuitable for animals to live in, as the highly altered landscape and anthropogenic threats potentially decrease their feeding opportunities, breeding activities and increase the mortality rate (Moilanen & Hanski, 2001; Miller & Spoolman, 2012, p. 195; Brudvig et al., 2017; Gilpin, 2012). However, it is important to note that not all areas outside protected areas are unsuitable habitat. They can function as corridors, stepping stones, or suitable patches that are not designated for protection. **Figure 1** systematically shows the Patch-Corridor-Matrix model.

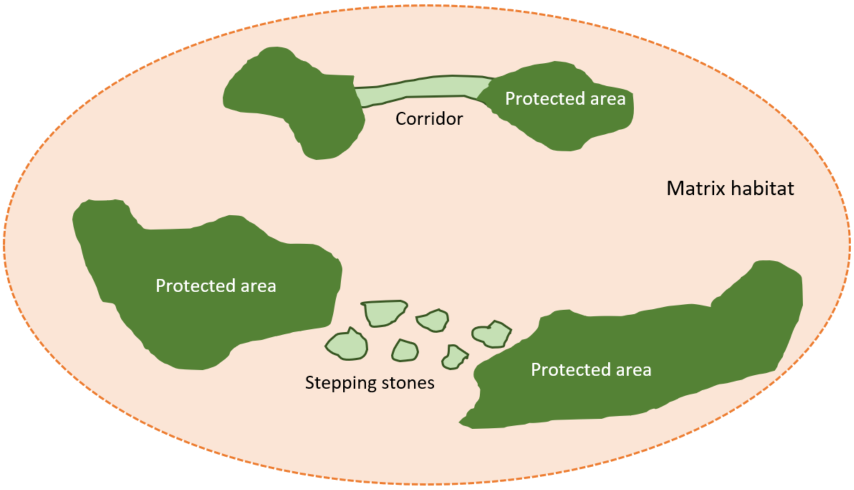

Figure 1*: Graphical representation of the Patch-Corridor-Matrix model. The protected areas function as patches, connected via either corridors or stepping stones of suitable habitat. The background matrix habitat is considered unsuitable. Representation adapted from Fischer and Lindenmayer (2007).*

3.2 Fragmentation and connectivity

Linking the Patch-Corridor-Matrix model to metapopulation theory, two other concepts are essential, namely fragmentation and connectivity. Fragmentation is the process by which habitats are transformed into smaller, more isolated patches. This can result in losses as individual patches become too small to support subpopulations. Subpopulations can also become more sensitive to stochastic events and genetic deficiencies due to inbreeding, increasing vulnerability to eventual local extinction, and decreasing the metapopulation's total size. Additionally, overall mortality may increase as individuals spend more time in migration, and the mortality rate in the matrix is likely to be higher than in the habitat patches (Cheptou et al., 2017; Moilanen & Hanski, 2001; Fischer & Lindenmayer, 2007; Wilson & Primack, 2019).

Furthermore, connectivity is critical for allowing movement between patches (Moilanen & Hanski, 2001). Moilanen & Hanski (2001) took a metapopulation perspective on connectivity and suggested that connectivity could best be defined at the patch scale. It is then the connectedness between patches of suitable habitat for a given species (Fischer & Lindenmayer, 2007). Dispersal and the colonization of different and new patches are vital for species as they need to locate food supplies and find new mates. With low connectivity, individuals are at substantial risk of failing to locate another suitable patch (Miller & Spoolman, 2012, p. 195; Gilpin, 2012). Especially Africa's large migratory herbivore species, which travel vast distances to find resources to stay alive, have population declines due to being restricted to small parts of their range and facing obstacles while dispersing. Now nearly all of Africa's once-migratory herbivores persist in small and scattered populations (Harris et al., 2009; Wilson & Primack, 2019). The same goes for large carnivore species, which are wide-ranging and therefore come into frequent contact with reserve borders and venture into the matrix (Woodroffe & Ginsberg, 1998).

3.3 The subpopulation

Finally, several factors that play a part on the subpopulation level also indirectly influence metapopulation dynamics, mainly by altering the size of the subpopulation. The size of the patch has already been mentioned. According to theory, smaller patches result in smaller subpopulations (Cheptou et al., 2017). Other factors influencing the subpopulation size are the rate at which a population increases or decreases (the population growth rate), the mortality rate in the patch, and the carrying capacity or minimum viable population size. If the carrying capacity in a patch is exceeded, this may lead to a decrease in population size as the area no longer supports the number of individuals. Likewise, when the number of individuals is below the minimum viable population size, the population has a substantial risk of extinction (Begon et al., 2014, p. 142, 390). Finally, the area size and the population size determine the average density. With a higher density, a more crowded patch will result in more dispersal due to increased competition (Begon et al., 2014, p. 141).

3.4 Analytical framework: the essential parameters

Now the key concepts have been identified, they need to be parameterized to be useful in searching the literature for the meta-analysis and later reporting on the parameters in the results. Integrating the Patch-Corridor-Matrix model, metapopulation dynamics, fragmentation, and connectivity has resulted in identifying several parameters deemed necessary for concluding on trends in metapopulations within this thesis. These parameters and their relations form the analytical framework of this thesis. They are schematically shown in **Figure 2** and are briefly summarized below.

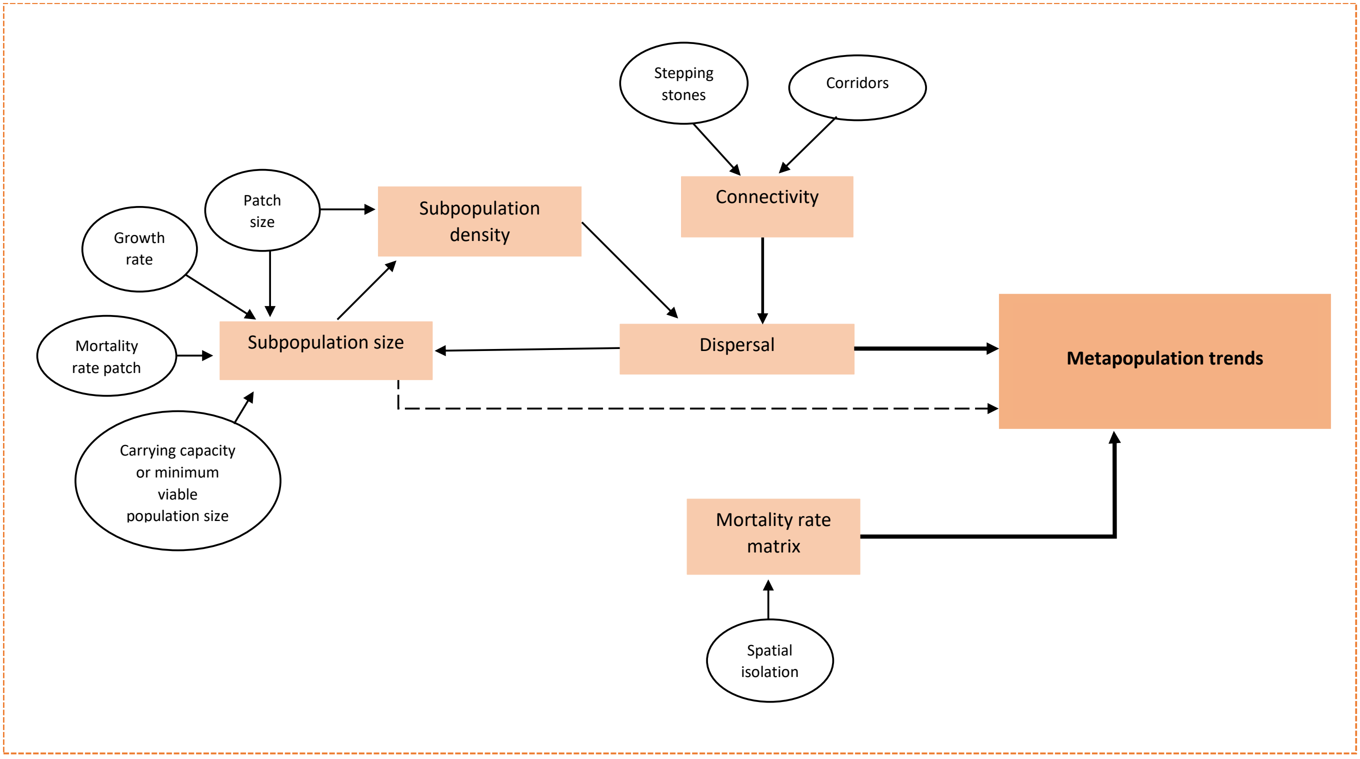

Figure 2*: Overview of the analytical framework displaying the different parameters identified from the theory and concepts.*

As derived from the concepts and theory, the availability and spatial elements of stepping stones and corridors in the matrix influence the connectivity between suitable habitat patches. In turn, connectivity influences the ease with which individuals can disperse. Dispersal keeps the subpopulations together in a metapopulation, and decreasing dispersal possibilities influence the subpopulation in a patch via, for example, increased vulnerability to stochastic events (Fischer & Lindenmayer, 2007; Gilpin, 2012).

Another influence on metapopulation trends is the mortality rate in the matrix. When an individual has a likelier chance of dying before reaching another patch, the metapopulation's stability will decrease. As adopted from the theory of island biography, the larger the distance between patches, the less likely it is an individual will reach the other patch during dispersal (Cheptou et al., 2017; Miller & Spoolman, 2012, p. 93). The term spatial isolation indicates the distance between patches.

At the patch scale, the size of the subpopulation is determined by several factors as mentioned in the concepts above. Consecutively, fluctuations in subpopulation sizes can result in different metapopulation trends.

4. Methods

Multiple research methodologies were applied to answer the research question and the supporting sub-questions of this thesis. As mentioned in the introduction, the primary research method is a meta-analysis to systematically review the literature and data on population dynamics of large mammalian species in Sub-Saharan Africa. Next to the meta-analysis, a simple conceptual metapopulation model was used to perform several thought experiments with the data. The section below describes how the meta-analysis process and the conceptual model were applied to this thesis in greater detail.

4.1 Data collection

4.1.1 Meta-analysis

Justification and description of literature sources.

The research question asked for information about parameters linked to population dynamics, which must be the results of scientific research. Therefore, the literature search was conducted with "Web of Science," an established search engine for scientific articles. As this research does not focus on policies and practices, there was no need to include grey literature.

Document selection and criteria for inclusion

For the selection of included papers, the four-phases of the PRISMA framework were followed. This framework was used to report the selection of papers. There are four phases: *identification*, *screening*, *eligibility*, and *included articles* (Moher et al., 2009).

The *identification* phase entails database searching for relevant articles. This was be done via search terms in "Web of Science," related to the theory, concepts, and research question. This approach yielded several possible combinations of keywords and search terms, which can be found in

Appendix A. For the primary selection criterion, the paper needed to be found under one of these search terms.

The *screening* phase entails excluding articles based on their quality and scope. This was done by screening the article for specific inclusion and exclusion criteria. Suitable papers were selected according to the following secondary selection criteria:

- Reading the title, abstract, and keywords must give the impression that the paper's research is focused on or connects to population dynamics and trends and is thus applicable to this meta-analysis.
- Reading the title, abstract, and keywords must give the impression that the research includes at least some quantitative data.
- The area of research must be in a region in Sub-Saharan Africa.
- The species subject must be mammalian and large, excluding large primates and sea mammals.
- The date of publication must be 2000 or later.

After screening, the selection of papers was further narrowed down in the section *eligibility* to align with the data necessary for the analysis. Hence, an additional filter was applied. The article must contain at least two of the parameters discussed in the section analytical framework and include useful, relevant information about these parameters and the impact on population dynamics. **Table 1** shows the parameters and the possible data to retrieve.

Parameters	Data	Specified parameters	Data
Population size	The size of the total population in the study area or the size of the researched population	**Carrying capacity or minimum viable population size**	The maximum or minimum population size for the study area
Population growth rate	The decrease or increase in population size		
Population density	The number of individuals per km^2		
Survival rate or mortality rate matrix	Percentage, number, or chance of either survival or mortality outside the patch		
Survival rate or mortality rate patch	Percentage, number, or chance of either survival or mortality outside the patch		
Dispersal	The dispersal ability and occurrence.	**Dispersal distance**	Distance in km
Study area	The total area of the study in km^2 (including patches and matrix)		
Patch area	The total area of the patch (e.g., reserve or national park) in km^2	**Minimum patch area requirement**	In km^2

Connectivity	The level of connectivity	**Stepping stones and corridors**	The availability of stepping stones and corridors and their spatial elements
Spatial isolation	The distance in km between patches		

Table 1*: The parameter table including the parameters identified from theory and concepts. Several parameters have been further specialized. The data that should be retrieved from the studies is defined.*

As can be seen in Appendix A, the combination of search terms is extensive. This was done to narrow the number of results, as some combinations yielded 500 papers or more, making the *screening* phase not feasible within this thesis. Thus, in order to supplement the final paper selection for the meta-analysis, forward citation was used. Forward citation is a method whereby articles are identified that cite an original article after publication (FAU, n.d.). All papers selected from the *identification* and *screening* phase were checked for other articles using the "times cited" option in "Web of Science." For these supplementing articles, the *screening* process was likewise followed to verify that all selected papers comply with primary and secondary selection criteria. The final *included articles* are summarized in **Table 2**, which can be found completed in Appendix B.

Author(s)	Species	Parameters	Data parameters	Impact on (meta)population trends	Country	(Grand) Species order

Table 2*: The meta-analysis table that was filled in for each included article. The seven columns display the data obtained from the papers.*

4.2 Data analysis

4.2.1 Meta-analysis

The analysis of the data has been divided into four sections. First, the distribution of data was visualized in percentages, figures, and tables. Second, the data on the parameters were evaluated on the type of data emerging from the studies. Third, the studies were checked on consistencies regarding population trends. These (in)consistencies were described in percentages of papers. Last, the potential impacts of the parameters were assessed by highlighting the author's findings.

4.2.2 The conceptual model

In this section of the results, a conceptual model and data from the meta-analysis were used to perform several simple thought experiments. The conceptual model was freely interpreted and altered to fit this research after one of the first metapopulation models, developed by MacArthur and Wilson (1967) and the additional equations of ecologist A. A. Sharov (n.d.). The model centers around the island-mainland theory. There is a single source population (the mainland) from which dispersal to the islands occur. The distance from the mainland and the island's size determine the number of species present (MacArthur & Wilson, 1967).

Regarding this conceptual model, the following assumptions were made:

- The number of species present will be viewed as the number of individuals present.
- There is one main unfenced patch from which individuals disperse.
- Due to the simplicity of the model, the exchange of individuals between patches does not occur.

It is possible to calculate the number of individuals in a given patch with the following formula:

$$ln\left(\frac{p*}{1-p*}\right) = \gamma + \alpha \cdot S - \beta \cdot D$$

P* is the proportion of individuals compared to the main patch, S the patch area's diameter, and D the patch area's distance to the mainland (Sharov, n.d.). **Table 3** was filled in with data from the meta-analysis (see Appendix D Table D1). To determine the parameter values γ, α, and β for the formula linear regression of Ln(p*/(1-p*)) against S and D was then performed using the statistical software SPSS. Parameters S and D were varied for four scenarios to see the difference in population sizes.

Patch No.	**Patch size, km^2**	**Diameter, km (S)**	**Distance from the main patch, km (D)**	**Number of individuals (N)**	**The proportion of individuals (p*)**	**Ln(p*/(1-p*))**
1						
2						
3						

***Table 3**: Table representation of the type of data used from the meta-analysis in order to determine the parameter values for γ, α and β. Adapted from the quantitative population ecology lectures by ecologist Sharov (n.d.).*

5. Results

A total of 35 papers that researched population dynamics of large mammalian species in Sub-Saharan Africa and complied with primary and secondary selection criteria were selected using Web Of Science. Of those 35 papers, 20 were found using combinations of the specific search terms, and 15 papers were found using forward citation.

The results of the meta-analysis are discussed below. First, the distribution of data is shown, specifically the different species, countries, and parameters addressed in the studies. In addition, the data on the parameters is analyzed. Third, population trends across studies are checked on consistency. After this, the potential impacts of the parameters that the authors mention in their research will be outlined. The final part of the results focuses on performing several small thought experiments with the data and the conceptual model.

5.1 Distribution of data

5.1.1 Species

The 35 papers researched a total of 10 different mammalian species (**Table 4**). The leopard (*Panthera pardus*) and African wild dog (*Lycaon pictus*) are researched the most, and the Grevy's zebra (*Equus grevyi*) and Brown hyena (*Parahyaena brunnea*) the least. Some researched sub-species, such as the Grevy's zebra, are mentioned as their species group in the distribution of data to maintain a clear overview.

Suppose the researched species are grouped in their species order. In that case, the carnivora are most researched, as shown in **Figure 4**. Carnivora were researched 25 times, whereas Proboscidea, Perissodactyla, and Artiodactyla, which can be grouped in the grand order ungulates, were researched 15 times.

Species	
Leopard	8
African wild dog	6
Cheetah	5
Lion	5
African elephant	5
Black rhinoceros	4
Giraffe	3
Wildebeest	2
Brown hyena	1
Zebra	1
Total	40

Table 4*: The different species that were researched in the 35 studies. The number of times the species occurred is also displayed, which totaled to 40 times.*

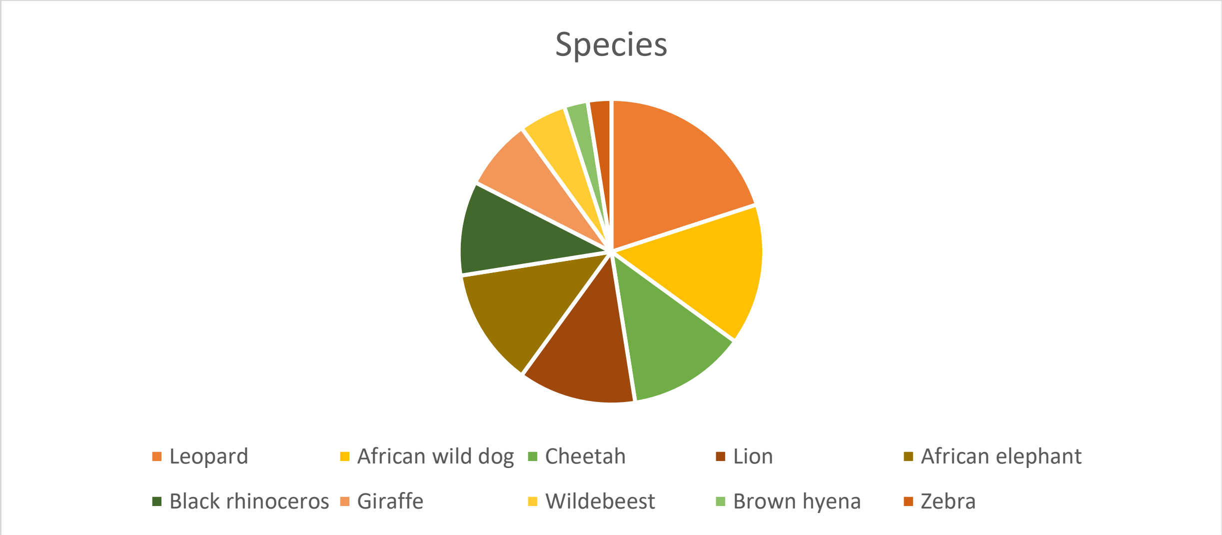

Figure 3*: Pie chart illustrating the proportion of species researched in the 35 included studies. The legend indicates the ten different species.*

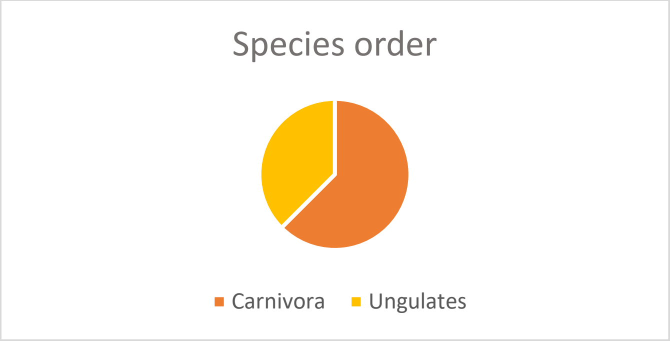

Figure 4*: Pie chart illustrating the proportion of species researched grouped in their (grand) order. The carnivora consist of the species Lion, Leopard, Cheetah, Brown hyena, and African wild dog. The ungulates consist of the species Black rhinoceros, Giraffe, Wildebeest, African elephant, and Zebra.*

5.1.2 Countries

The 35 papers have study areas in a total of 12 countries in Sub-Saharan Africa. Most papers studied population dynamics in protected and surrounding areas in South Africa. Papers also covered Tanzania, Namibia, and Kenya to a large extent. Several countries are researched only once. The focus is primarily on southern and east Africa, with only two countries studied in central Africa and one in western Africa.

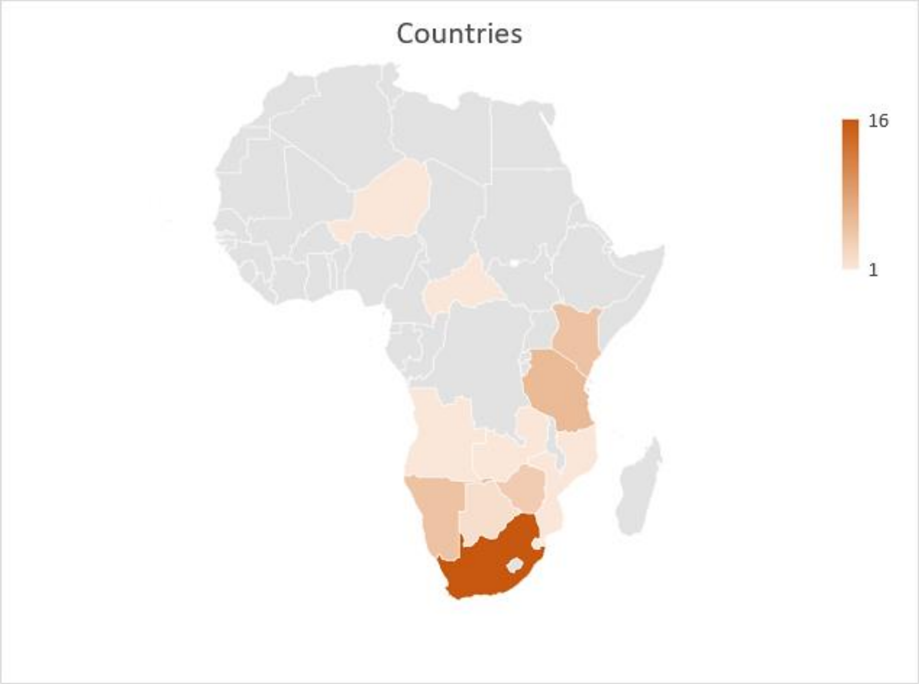

Figure 5*: Map showing the different countries researched. The legend runs from 1 to 16 and is indicated by a colour difference from light orange to dark orange.*

Countries	
South Africa	16
Tanzania	6
Kenya	5
Namibia	5
Zimbabwe	4
Botswana	2
Mozambique	1
Swaziland	1
Central African Republic	1
Niger	1
Angola	1
Zambia	1

Table 5*: The 12 different countries in which the research took place and the number of times the countries occurred.*

5.1.3 Parameters

Parameters	**Number of papers that have adequate data**
Population size	27 (77%)
Patch area size	20 (57%)
Population density	12 (34%)
Study area size	11 (31%)
Dispersal distance	10 (29%)
Survival or mortality rate patch	10 (29%)
Survival or mortality rate matrix	9 (26%)
Connectivity	9 (26%)
Dispersal	7 (20%)
Population growth rate	7 (20%)
Carrying capacity or minimum viable population size	6 (17%)
Stepping stones and corridors	3 (9%)
Minimum patch area size	2 (6%)
Spatial isolation	1 (3%)

***Table 6**: The different parameters and the number of times adequate data was found, including the percentages of papers.*

As shown in **Table 6**, the parameter most researched and covered in 77% of the papers is the population size. Patch area size, population density, and study area size are also covered to a large extent. The parameters stepping stones and corridors, minimum patch area size, and spatial isolation did not often appear in the studies.

5.2 Analysis of the data on the parameters

Study and patch area size, population size, population growth rate, and population density

The size range of the parameters area size is between 50 km^2 and 1.5 million km^2, making this the parameter with the most expansive range (Bisset & Bernard, 2011; Cushman et al., 2016). The second broadest range is the researched or estimated population sizes, ranging from a single leopard to 45000 African elephants (Fattebert et al., 2013; Tshipa et al., 2017). While the density was given for all species except the giraffe and the wildebeest, population growth rate occurred less and only for five species (see table C1 and C2 in Appendix C for statistical data). These parameters are always given in either numbers, km^2, percentages, or individuals per km^2 and, thus, quantitative data.

Carrying capacity, minimum population size, and minimum patch size

All three parameters are either given in numbers or km^2. Only for the African wild dog the minimum patch size and corresponding minimum population size is known. The carrying capacity was shown for five species, corresponding with either a given patch size or packed under the term "small reserve," for which no specific size was given but can be approximated and based on current small reserve sizes. These three parameters determine above or below which numbers the subpopulation is no longer viable.

Dispersal and dispersal distance

Of the seven papers with adequate dispersal data following the parameter-table, only one paper had adequate data on dispersal occurrence quantified. The paper by Lee and Bolger (2018) researching the Masai giraffe mentioned a movement or dispersal probability of 0.008 or 0.8%, which is very low. The rest of the papers only mentioned ability and occurrence in wording, such as the paper of Davies-Mostert et al. (2015), which mentioned that dispersal was impeded due to fencing, but there were still some confirmed cases. There was also no information on the percentage or amount of individuals that disperse within a population. Despite data on dispersal occurrence not being quantitative, the dispersal distances were given in km, as shown in **Table 7**.

Dispersal distance (in km)				
Wildebeest (migratory)	60-75	>130		
Elephant (migratory)	108-260			
Lion	110	52	200	11.7
Cheetah	16	57.1		
Leopard	194.5	11	2.7	
African wild dog	37			

Table 7*: The dispersal distances in km for six species.*

Connectivity, stepping stones, and corridors

In the studies included in this meta-analysis, connectivity was given as a qualitative value. It was given only in words such as "low" or "increased.” "Low,” "suboptimal," or "high" connectivity can potentially be placed on a scale, but it does not provide adequate data that can be used in quantitative models, experiments, and measurements. No spatial data was available regarding stepping stones and corridors as well.

Paper	**Connectivity**
Havmøller et al., 2019	**Low**
Dolrenry et al., 2020	⬆
Morrison et al., 2016	⬇
Fattebert et al., 2013	●
Lee & Bolger, 2017	**Low**
Morrison & Bolger, 2014	●
Williams et al., 2017	**Low**
Fattebert et al., 2015	⬆
Cushman et al., 2016	⬆ ⬇

Table 8*: The nine papers that have adequate data on connectivity. The green arrows pointing upwards indicate increased connectivity. The red arrows pointing downwards indicate decreased connectivity. The green dots indicate that the papers concluded that there was connectivity due to stepping stones and corridors.*

Mortality rate patch and matrix

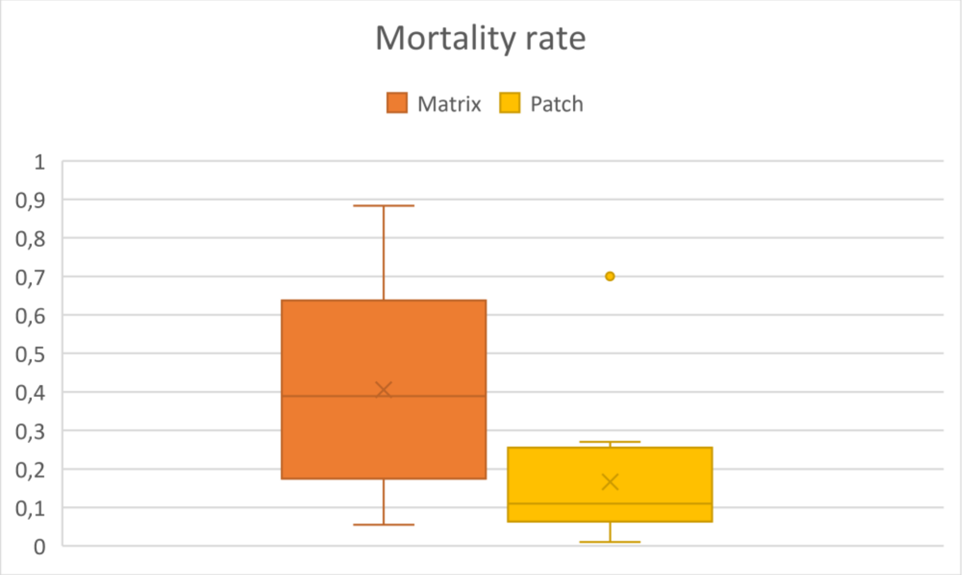

***Figure 6**: Boxplot displaying the mortality rate in the matrix and patch.*

The boxplot displays the mortality rates for the matrix and the patch. The survival rates mentioned in the studies have been converted to mortality rates (1-survival rate=mortality rate), and percentages have been converted to numbers (75% = 0.75). The cross represents the mean of data, which for the matrix is 0.057 and for the patch 0.1662.

5.3 Consistencies

Next to data on parameters, the studies made a connection to the dynamics of the population. Regarding all studies, there seem to be several (in)consistencies in the results and findings (see Appendix B for a description of the impact on population trends of each paper). The most significant (in)consistencies are listed below.

Of the studies that researched mortality outside the patch, 10 (29%) papers disclosed either a high(er) mortality rate in the matrix or increasing anthropogenic threats and disturbances in the matrix and along patch boundaries. However, two papers (6%) reported a low(er) mortality rate, indicating a small inconsistency.

8 (23%) papers reported on the stability of the subpopulation in the patches. Of these researched subpopulations, 2(6%) were considered stable, and 6 (14%) were considered unstable, unviable, or experienced a decline in performance and health. Furthermore, for 3 (9%) subpopulations, active management, such as mimicking dispersal, was necessary to secure long term persistence.

9 (26%) papers reported on the dynamics of the metapopulation. There were many inconsistencies in these findings. Only one paper reported an increase in the metapopulation's viability, opposite to 3 papers that indicated increasing risks for future persistence. The three papers that indicated the necessity of active management for the subpopulation also relate this to the metapopulation level, illustrating that the metapopulation dynamics only exist through management. The final two papers did not indicate an increase or decrease in the viability but indicated that there was most likely an exchange of individuals, thus discovering possible metapopulations.

5.4 Potential impacts of parameters.

From the literature found in the meta-analysis, it appeared that authors based on their study had an idea about the potential impact of the parameters they examined or included. The most substantial potential impacts are highlighted in this section.

Conform to metapopulation theory, several authors highlight the importance of area size and the impact it could have on the population. Lindsey et al. (2011) estimated large area requirements for achieving viability in a cheetah population. Linklater & Swaisgood (2010) reported that more extensive reserves and lower release densities should be favored for black rhinoceros populations. The findings of Havmøller et al. (2019) are related to the need for maintaining large areas of continuous, well-protected habitat to preserve viable populations of large carnivores.

However, not every author came to the same conclusion regarding the possible impact of area size. Edwards et al. (2019) reported the highest published estimate for brown hyena density within a small enclosed reserve, showing that small enclosed reserves can support relatively large numbers of individuals of certain species. Additionally, researchers Bisset & Bernard (2011) and Miller & Funston (2014) reported large population growth rates in small enclosed reserves for cheetahs and lions as well.

According to several studies, the mortality rate in the matrix and around reserve borders seems to have a substantial impact. Williams et al. 2017 documented that anthropogenic threats and associated mortality in the matrix appear to be the main threats to their researched leopard population. The research of Lee et al. (2016), Swanepoel et al. (2015), Jenkins et al. (2015), Van der Meer et al. (2014), Balme & Hunter (2010), and Balme et al. (2009) all documented the same urgency of the parameter mortality and elaborated on the potential negative consequences for the population.

The final parameter that emerged from the studies as having a considerable potential impact is dispersal or the dispersal ability. The reason for the reduction in performance for a black rhinoceros population research by Le Roex et al. (2018) was the inability to disperse, leaving the population completely isolated. Elliot et al. (2020) also report impeded dispersal ability and mention a very serious concern for negative consequences such as inbreeding.

Di Minin et al. (2013), which researched six of the ten species, summarized several of the potential impacts mentioned and concluded that having a network of larger protected areas connected through dispersal may represent the most effective way to maintain viable metapopulations of wide-ranging species.

5.5 Conceptual model

In the conceptual model interpretation of MacArthur and Wilson's theory (1967), data from the meta-analysis was used from three species; lion, cheetah, and leopard. The model species can therefore be viewed as a non-existent large cat or *Felidae* species. Udzungwa Mountains National Park (1990km^2) was selected as the "mainland" with 58 individuals from which dispersers can travel to other patches (Havmøller et al., 2019). Three different patches were selected with area sizes of 220, 188, and 125km^2, and this accounted for 42, 11, and 4 individuals, respectively (Balme et al., 2009; Elliot et al., 2020; Buk et al., 2018). For the distances between the patches and the main patch, the dispersal distances from the data were used as examples (See **Table 7**). The patches were distributed according to theory. That is, larger patches and patches closer to the main patch should have more individuals. Linear regression resulted in the following formula (see Appendix D for the table and the SPSS output):

$$ln\left(\frac{p*}{1-p*}\right) = -12{,}073 + 0{,}624 \cdot \mathrm{S} - 0{,}007 \cdot \mathrm{D}$$

5.5.1 Scenarios

Baseline scenario:

In the baseline scenario, two additional patches were added to bring the total patch number to 5 (Patch D and E). These two patches were not selected from the data but were fabricated, and their population size was calculated with the equation above. The metapopulation consisted of 159 individuals. **Table 9** shows the data on patch A to E in the baseline scenario, and **Figure 7** visually shows the baseline scenario.

Patch	Individuals (N)	Distance from the main patch (D)	Patch size (km^2)
Patch A	42	11	220
Patch B	4	52	125
Patch C	11	200	188
Patch D	0	80	60
Patch E	44	40	235

Table 9*: Table showing the data used for the baseline scenario of the conceptual model. Patch A, B, and C were selected from the meta-analysis. Patch D and E were fabricated.*

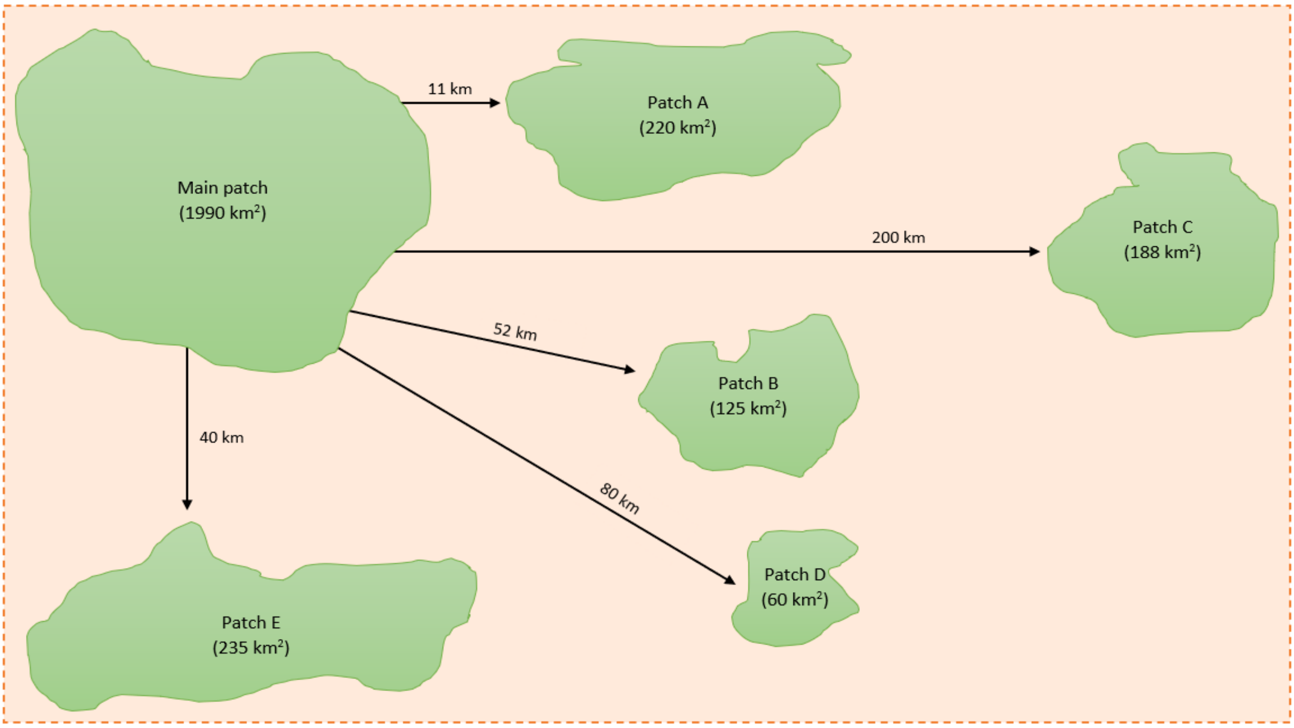

Figure 7*: Graphical representation of the baseline scenario of the conceptual model. For the distances to the main patch, the measured dispersal distances of 11 km (Fattebert et al., 2015), 52 km, and 200 km (Dolrenry et al., 2020) have been selected from the meta-analysis. The figure is not to scale.*

Scenario 1: larger, uninterrupted areas.

The first scenario looked at the change in population size when enlarging the patch area size by combining two patches. Patch B and E were merged to form one larger patch at the distance of patch E. The total area size remained the same as the baseline scenario. Under this scenario, the metapopulation's total size increased by 5,7% to 168 individuals (see Appendix D, Table D3 for the data corresponding to scenario 1).

Scenario 2: many small patches due to fragmentation.

In the second scenario, the effect of fragmentation was simulated. Patch A, C, and E were fragmented into smaller patches with similar distances to the main patch. There was a new total of 10 patches. Again, the area size remained the same as the baseline scenario. Fragmenting patches into smaller sizes lead to a substantial 57,9% decrease in metapopulation size. The population dropped to 67 individuals (see Appendix D, Table D4 for the data corresponding to scenario 2).

Scenario 3: same area size, different distance from the main patch.

In the third scenario, the same area size of 150km^2 was adopted with one patch at a distance of 15 km from the main patch and the second patch on a distance of 75 km, thus multiplied with factor 5. This resulted in a difference of 4 individuals (see **Table 10**).

Patch	**Individuals (N)**	**Distance from the main patch (D)**	**Patch size (km^2)**
Patch F	12	15	150
Patch G	8	75	150

Table 10: *The patches, number of individuals (N), distance from the main patch (D), and patch size corresponding with scenario 3: same area size, different distance from the main patch.*

Scenario 4: same distance from the main patch, different area size.

In the fourth and final scenario, the same distance from the patch of 50km was adopted. One patch size was 80 km^2, and one was 400 km^2, again multiplied with factor 5. This resulted in a difference of 57 individuals (see **Table 11**).

Patch	**Individuals (N)**	**Distance from the main patch (D)**	**Patch size (km^2)**
Patch H	1	50	80
Patch I	58	50	400

Table 11: *The patches, number of individuals (N), distance from the main patch (D), and patch size corresponding with scenario 4: same distance from the main patch, different area size.*

6. Discussion

6.1 Interpretation and implications of results

The meta-analysis of 35 studies that researched large mammalian species in Sub-Saharan Africa yielded several insights into the different impacts and mechanics of population dynamics parameters. Overall, the results suggest that the parameters' mortality rate in the matrix and dispersal ability are the most significantly impacting on population trends. Nevertheless, several inconsistencies in both the studies' results and the author's views on the impacts need to be addressed, conform with the ability to extract useful data on these parameters from literature and the ability to use them in simplified models.

The 35 studies researched only ten species, while there are many more large mammalian species. The reason for this may be that charismatic species, such as lions, generate global interest. Therefore, the need for reliable estimates of population trends is understood by a broad spectrum of society, motiving the application of research (Elliot et al., 2020). As for the different locations, East and Southern Africa have the most savannah-woodland ecosystems where these large mammals occur, which could logically explain the amount of research done in these areas (Wilson & Primack, 2019).

Regarding the successful extraction of parameters from literature to quantify dynamics, dispersal occurrence, connectivity, stepping stones, and corridors seem to be given in qualitative and descriptive data for all but one paper only. This might indicate that there is no standardized and easily applicable method to quantify these parameters. Contrary to theory, authors do not seem to prioritize stepping stones and corridors. Connectivity is mentioned in the research, but more given in combination with the parameters dispersal and mortality rate in the matrix, which cause an increase or decrease in connectivity (Fattebert, 2015; Cushman et al., 2016).

For the dispersal occurrence, quantitative data is also missing from the studies. The parameter is possible to quantify, as Lee and Bolger (2018) have shown. However, quantifying dispersal occurrence might not be that important if the distance and ability are known. Hampered dispersal seems to impact population dynamics significantly, as several authors elaborated (Buk et al., 2018; Le Roex et al., 2018; Elliot et al., 2020).

Within patches, the subpopulation appears to be unstable instead of stable more often. This is primarily attributed to a combination of the area being too small and the patch being fenced, thus interfering with the parameter dispersal. In these patches, active management is often needed to secure viability, combat overpopulation, and combat inbreeding (Buk et al., 2018; Davies-Mostert et al., 2015; Miller & Funston, 2014). According to these studies, fencing protected areas and diminishing dispersal ability seems to have several serious negative consequences. The use of fencing in Africa's protected areas has been a topic of debate for some time. On the one hand, it protects both humans and wildlife from potential conflicts, and separation can therefore be mutually beneficial (Woodroffe et al., 2014, Creel et al., 2013; Packer et al., 2013).

On the other hand, fencing makes subpopulations more vulnerable, interfering with dispersal (Woodroffe et al., 2014; Cushman et al., 2018). Additionally, fencing does not always seem to work. In the studies of Miller & Funston (2014) and Davies-Mostert et al. (2015), some individuals managed to break through the fences, diminishing their use.

When individuals can disperse, they are often faced with mortality in the matrix. The reports of higher mortality rates outside the patch seem to be very consistent. Many authors also stress the effects of this higher mortality in the matrix for population dynamics. This suggests that this parameter could therefore be considered significantly impacting. One of the two only papers that indicated a low(er) mortality rate in the matrix was the research by Suraud et al. (2012). They mentioned that their researched giraffe population was doing very well due to the absence of natural predators and hunting. At the same time, Lee et al. (2016) concluded for a different population that even giraffes are not entirely safe from the dangers of the matrix.

The significant impact of mortality rate outside the patch might indicate that a different approach towards conserving large mammalian species is in order to secure the future viability of metapopulations. Authors Durant et al. (2017) already pleaded for a paradigm shift in conservation towards declining mortality rates outside protected areas. A more holistic approach should be adopted that promotes human-wildlife coexistence in the matrix, instead of just focusing on protected areas. Supporting this plead, the study of Dolrenry et al. (2020) showed that this approach could have positive outcomes. In their research, increased human tolerance towards lions created better connectivity and increased the metapopulation's viability. This was likewise one of the two studies that reported a low(er) mortality rate outside the patch. The efforts to reduce human-carnivore conflict of Balme et al. (2019) also showed to be very successful at promoting the recovery of leopard populations.

Decreasing mortality via less conflict could also lead to the opportunity of defencing protected areas, thus allowing for more natural dynamics. Rather than enclosing wildlife, fences may be used to enclose small areas of intense conflicts, such as settlements (Woodroffe et al., 2014).

6.1.1 Interpreting the results of the conceptual model

When interpreting the results of the conceptual model, the parameter area size seems to have a substantially bigger influence on determining population size than the parameter distance from the main patch. The model also showed that combining areas had a beneficial effect, and fragmenting areas resulted in a large decline of the metapopulation, thus supporting theory and the claim of Havmøller et al. (2019) for large areas of continuous habitat to preserve viable populations of large carnivores.

In their theory of island biography, Mac Arthur and Wilson report that multiple regression analyses have shown that area alone accounts for most of the variation in species numbers on islands (MacArthur & Wilson, 1967). Subsequently, spatial isolation, or the distance between patches, was mentioned only once in the meta-analysis and did not have a significant impact (Buk et al., 2018). Distance might therefore be less critical than initially thought. However, the model used was extremely simplified, only incorporating two parameters that influence population dynamics. So the conceptual model should not be regarded as scientifically accurately displaying real-life dynamics per sé, as further elaborated in the next section limitations.

6.2 Limitations

Despite the insights obtained and the extensive information gathered from the studies, this research was limited in some aspects. Most evidently, not all parameters which could have significant impacts are included and analyzed. The most evident parameter is habitat quality, which may affect the probability of local extinction and influences the size of the subpopulation (Begon et al.,2014, p. 380; Moilanen & Hanski, 1998). However, habitat quality is a complicated parameter to assess and is weakly conceptualized, hampering the possibility to incorporate in a meta-analysis (Mortelliti et al., 2010). This parameter was therefore deliberately left out of the scope of this thesis.

Considering metapopulation dynamics, the parameters extinction and colonization rate were also not included in the parameter table. These determine the rate at which patches go either extinct or are recolonized. These parameters would have been very useful for modeling as many of the metapopulation models incorporate these factors, such as the popular Levins model. However, to determine these parameters, data is needed from the absence and presence of one species in patches over a large amount of time (Hanski & Gaggiotti, 2004). This would require very different research and would not result in the same selection of studies as the other parameters. Evidently, the impact of these parameters cannot be concluded from this thesis.

Next to excluded parameters, the methodology's selection criteria exclude a variety of possible studies and species subjects. The generalizability of the results is limited to large mammalian species in African ecosystems. However, this does not mean that the same parameter impacts do not apply for similar species and settings elsewhere, but the results cannot conclude on that.

Lastly, the conceptual model has many limitations, such as there being no dispersal between patches, and the mortality rate in the matrix has not been incorporated. However, the conceptual model was never intended to be highly accurate. It was a means to perform several thought experiments to see how the data can be used from the meta-analysis.

6.3 Recommendations for future research

Besides adding the non-included parameters in future research or expanding the inclusion criteria, quantifying connectivity seems to be a logical step forward. If more knowledge on the impact of connectivity is wished-for, more quantified data is required. There are several options for quantifying connectivity, and when researchers better understand these options, they can extract the maximum possible amount of connectivity information from their data. Connectivity can then also be better included in future meta-analyses (Arnqvist & Wooster 1995; Fagan, 2006).

Future research could also look more into the importance of quantitative data for dispersal and whether or not the data given in most studies as seen in this thesis on dispersal occurrence and ability is sufficient.

Lastly, as the world is rapidly changing, a new perspective could be added considering climate change. Where climate change increases the frequency and severity of extreme weather events and further degrades habitat, it affects ecosystem processes and animal abundances (Woodroffe et al., 2014; Chamaille-Jammes et al., 2008). Climate change could thus have substantial impacts on the parameters and populations that were addressed in this study. It is wise not to overlook these possible future impacts considering metapopulations.

7. Conclusion

In this thesis, the primary purpose was to research parameters of population dynamics to uncover which parameters significantly impact metapopulation trends and to create a better general understanding. Based on the results, it can be deduced that mortality rate in the matrix and dispersal ability are the two most impacting parameters, followed to a lesser extent by patch area size, which was met by some debate. In some aspects, the results aligned with the theory. On other aspects, such as the importance of distance between patches and connectivity, not.

Data found via meta-analyses can be used in a simplified metapopulation model, but its use was limited to only two parameters in this thesis. In order to fully model all dynamics, different parameters should have been assessed. Nevertheless, even the small thought experiments showed that area size was somewhat influencing and distance not, supporting claims by both authors and theory that large extensive areas could be beneficial. So, decisive factors for possible extinction could be determined using metapopulation models with data from meta-analyses, but it should only be interpreted as conceptual in this thesis.

Future research could focus on quantifying more parameters, such as connectivity. As this thesis has shown, synthesizing results from several studies might uncover trends that do not entirely align with current theory and conservation efforts. Even though the authors did not agree on the specific impacts on all parameters, the impacts of the two most consequential ones were consistent. The results add to the idea that in order to protect the vital mammalian species found in Sub-Saharan Africa, a shift in conservation practice might be necessary. The thought must be let go of conserving species in protected areas where they must often be actively managed, but instead, allow for more natural metapopulation dynamics.

8. Acknowledgements

I would like to begin by thanking my thesis supervisor Prof. dr. Martin Wassen for his advice, feedback, and support throughout the process of this thesis. Even during these difficult times of having to discuss everything online, I felt that communication was clear and helpful. Special thanks also to my feedback group.

I would also like to take this opportunity to thank my dad Henk, who, not only for this thesis but for the last three and a half years of my bachelor's, was always there for me, helping me a great deal when I got lost and needed advice.

9. References

Arnqvist, G., & Wooster, D. (1995). Meta-analysis: synthesizing research findings in ecology and evolution. *Trends in Ecology & Evolution*, *10*(6), 236-240.

Balme, G. A., Slotow, R., & Hunter, L. T. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (Panthera pardus) population. *Biological Conservation*, *142*(11), 2681-2690.

Balme, G. A., Slotow, R. O. B., & Hunter, L. T. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal conservation*, *13*(3), 315-323.

Baum, K. A., Haynes, K. J., Dillemuth, F. P., & Cronin, J. T. (2004). The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, *85*(10), 2671-2676.

Begon, M., Howarth, R. W., & Townsend, C. R. (2014). *Essentials of Ecology* (4th ed.). Hoboken, NJ, United States: Wiley.

Bissett, C., & Bernard, R. T. F. (2011). Demography of cheetahs in fenced reserves in South Africa: implications for conservation. *African Journal of Wildlife Research*, *41*(2), 181-191.

Brudvig, L. A., Leroux, S. J., Albert, C. H., Bruna, E. M., Davies, K. F., Ewers, R. M., ... & Resasco, J. (2017). Evaluating conceptual models of landscape change. *Ecography*, *40*(1), 74-84.

Buk, K. G., van der Merwe, V. C., Marnewick, K., & Funston, P. J. (2018). Conservation of severely fragmented populations: lessons from the transformation of uncoordinated reintroductions of cheetahs (Acinonyx jubatus) into a managed metapopulation with self-sustained growth. *Biodiversity and conservation*, *27*(13), 3393-3423.

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F., & Clobert, J. (2008). Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology*, *77*(1), 135-144.

Cheptou, P. O., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to fragmentation: evolutionary dynamics driven by human influences. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1712), 20160037.

Creel, S., Becker, M. S., Durant, S. M., M'soka, J., Matandiko, W., Dickman, A. J., ... & Zimmermann, A. (2013). Conserving large populations of lions–the argument for fences has holes. *Ecology letters*, *16*(11), 1413-e3.

Cushman, S. A., Elliot, N. B., Macdonald, D. W., & Loveridge, A. J. (2016). A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. *Landscape Ecology*, *31*(6), 1337-1353.

Davies-Mostert, H. T., Mills, M. G., & Macdonald, D. W. (2015). The demography and dynamics of an expanding, managed African wild dog metapopulation. *African Journal of Wildlife Research*, *45*(2), 258-273.

Di Minin, E., Hunter, L. T., Balme, G. A., Smith, R. J., Goodman, P. S., & Slotow, R. (2013). Creating larger and better connected protected areas enhances the persistence of big game species in the Maputaland-Pondoland-Albany biodiversity hotspot. *PloS one*, *8*(8), e71788.

Dolrenry, S., Hazzah, L., & Frank, L. (2020). Corridors of tolerance through human-dominated landscapes facilitate dispersal and connectivity between populations of African lions Panthera leo. *Oryx*, *54*(6), 847-850.

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R. S., & Frank, L. (2014). A metapopulation approach to African lion (Panthera leo) conservation. *PloS one*, *9*(2), e88081.

Durant, S. M., Mitchell, N., Groom, R., Pettorelli, N., Ipavec, A., Jacobson, A. P., ... & Young-Overton, K. (2017). The global decline of cheetah Acinonyx jubatus and what it means for conservation. *Proceedings of the National Academy of Sciences*, *114*(3), 528-533.

Edwards, S., Noack, J., Heyns, L., & Rodenwoldt, D. (2019). Evidence of a high-density brown hyena population within an enclosed reserve: the role of fenced systems in conservation. *Mammal Research*, *64*(4), 519-527.

Elliot, N. B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., ... & Gopalaswamy, A. M. (2020). The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*, *2*(7), e217.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Wardle, D. A. (2011). Trophic downgrading of planet Earth. *science*, *333*(6040), 301-306.

Fagan, W. F. (2006). Quantifying connectivity: balancing metric performance with data requirements. *Connectivity conservation*, 297-317.

Fattebert, J., Balme, G., Dickerson, T., Slotow, R., & Hunter, L. (2015). Density-dependent natal dispersal patterns in a leopard population recovering from over-harvest. *PloS one*, *10*(4), e0122355.

Fattebert, J., Hunter, L., Balme, G., Dickerson, T., & Slotow, R. (2013). Long-distance natal dispersal in leopard reveals potential for a three-country metapopulation. *South African Journal of Wildlife Research-24-month delayed open access*, *43*(1), 61-67.

FAU. (n.d.). *LibGuides: Guide to Science Information Resources: Backward & Forward Reference Searching*. Https://libguides.fau.edu/science_resources/reference_searching

Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global ecology and biogeography*, *16*(3), 265-280.

Foley, C. A., & Faust, L. J. (2010). Rapid population growth in an elephant Loxodonta africana population recovering from poaching in Tarangire National Park, Tanzania. *Oryx*, *44*(2), 205-212.

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., & Burgess, N. D. (2013). Effectiveness of terrestrial protected areas in maintaining biodiversity and reducing habitat loss. *Collaboration for Environmental Evidence, Bangor, United Kingdom*, 61.

Gilpin, M. (Ed.). (2012). *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press.

Githiru, M. (2017). The forgotten Grevy's zebra Equus grevyi population along the Kasigau Corridor ranches, SE Kenya: recent records and conservation issues. *African Journal of Ecology*, *55*(4), 554-563.

Gurevitch, J., Curtis, P. S., & Jones, M. H. (2001). Meta-analysis in ecology.

Hanski, I. A., & Gaggiotti, O. E. (Eds.). (2004). *Ecology, genetics and evolution of metapopulations*. Academic Press.

Hanski, I., & Ovaskainen, O. (2003). Metapopulation theory for fragmented landscapes. *Theoretical population biology*, *64*(1), 119-127.

Hanski, I., & Simberloff, D. (1997). The metapopulation approach, its history, conceptual domain, and application to conservation. In *Metapopulation biology* (pp. 5-26). Academic Press.

Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P., & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, *7*(1), 55-76.

Harrison, F. (2011). Getting started with meta-analysis. *Methods in Ecology and Evolution*, *2*(1), 1-10.

Havmøller, R. W., Tenan, S., Scharff, N., & Rovero, F. (2019). Reserve size and anthropogenic disturbance affect the density of an African leopard (Panthera pardus) meta-population. *PloS one*, *14*(6), e0209541.

Heinrichs, J. A., Bender, D. J., & Schumaker, N. H. (2016). Habitat degradation and loss as key drivers of regional population extinction. *Ecological Modelling*, *335*, 64-73.

Howell, P. E., Muths, E., Hossack, B. R., Sigafus, B. H., & Chandler, R. B. (2018). Increasing connectivity between metapopulation ecology and landscape ecology. *Ecology*, *99*(5), 1119-1128.

IUCN. (2008). *About*. https://www.iucn.org/theme/protected-areas/about

IUCN. (n.d.). *Category II: National Park*. https://www.iucn.org/theme/protected-areas/about/protected-areas-categories/category-ii-national-park

Jenkins, E., Silva-Opps, M., Opps, S. B., & Perrin, M. R. (2015). Home range and habitat selection of a reintroduced African wild dog (Lycaon pictus) pack in a small South African game reserve. *African Journal of Wildlife Research*, *45*(2), 233-246.

Koricheva, J., & Gurevitch, J. (2014). Uses and misuses of meta-analysis in plant ecology. *Journal of Ecology*, *102*(4), 828-844.

Lee, D. E., & Bolger, D. T. (2017). Movements and source–sink dynamics of a Masai giraffe metapopulation. *Population Ecology*, *59*(2), 157-168.

Lee, D. E., Bond, M. L., Kissui, B. M., Kiwango, Y. A., & Bolger, D. T. (2016). Spatial variation in giraffe demography: a test of 2 paradigms. *Journal of Mammalogy*, *97*(4), 1015-1025.

le Roex, N., Paxton, M., Adendorff, J., Ferreira, S., & O'Riain, M. J. (2018). Starting small: long-term consequences in a managed large-mammal population. *Journal of Zoology*, *306*(2), 95-100.

Lindsey, P. A., Du Toit, J. T., & Mills, M. G. L. (2004). Area and prey requirements of African wild dogs under varying habitat conditions: implications for reintroductions. *South African Journal of Wildlife Research-24-month delayed open access*, *34*(1), 77-86.

Lindsey, P., Tambling, C. J., Brummer, R., Davies-Mostert, H., Hayward, M., Marnewick, K., & Parker, D. (2011). Minimum prey and area requirements of the Vulnerable cheetah Acinonyx jubatus: implications for reintroduction and management of the species in South Africa. *Oryx*, *45*(4), 587-599.

Linklater, W. L., & Swaisgood, R. R. (2008). Reserve size, conspecific density, and translocation success for black rhinoceros. *The Journal of Wildlife Management*, *72*(5), 1059-1068.

MacArthur, R. H., & Wilson, E. O. (1969). *The theory of island biogeography* (Vol. 1). Princeton university press.

Mamo, Y., Mengesha, G., Fetene, A., Shale, K., & Girma, M. (2012). Status of the Swaynes Hartebeest, (Alcelaphus buselaphus swaynei) meta-population under land cover changes in Ethiopian protected areas. *International Journal of Biodiversity and Conservation*, *4*(12), 416-426.

Miller, G. T., & Spoolman, S. (2012). *Living in the Environment* (International Edition). Brooks/Cole Cengage Learning.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (Panthera leo) populations in small, fenced reserves in South Africa: a management dilemma. *African Journal of Wildlife Research*, *44*(1), 43-55.

Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). *Preferred Reporting Items for Systematic Reviews and MetaAnalyses: The PRISMA Statement*. PLoS Med 6(7): e1000097. doi:10.1371/journal.pmed1000097

Moilanen, A., & Hanski, I. (1998). Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology*, 79(7), 2503-2515.

Moilanen, A., & Hanski, I. (2001). On the use of connectivity measures in spatial ecology. *Oikos*, *95*(1), 147-151.

Morrison, T. A., & Bolger, D. T. (2014). Connectivity and bottlenecks in a migratory wildebeest Connochaetes taurinus population. *Oryx*, *48*(4), 613-621.

Morrison, T. A., Link, W. A., Newmark, W. D., Foley, C. A., & Bolger, D. T. (2016). Tarangire revisited: Consequences of declining connectivity in a tropical ungulate population. *Biological Conservation*, *197*, 53-60.

Mortelliti, A., Amori, G., & Boitani, L. (2010). The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia*, *163*(2), 535-547.

Newmark, W. D. (2008). Isolation of African protected areas. *Frontiers in Ecology and the Environment*, *6*(6), 321-328.

Oginah, S. A., Ang'ienda, P. O., & Onyango, P. O. (2020). Evaluation of habitat use and ecological carrying capacity for the reintroduced Eastern black rhinoceros (Diceros bicornis michaeli) in Ruma National Park, Kenya. *African Journal of Ecology*, *58*(1), 34-45.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., ... & Polasky, S. (2013). Conserving large carnivores: dollars and fence. *Ecology letters*, *16*(5), 635-641.

Pullin, A. S., & Knight, T. M. (2003). Support for decision making in conservation practice: an evidence-based approach. *Journal for Nature Conservation*, *11*(2), 83-90.

Ricketts, T. H. (2001). The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, *158*(1), 87-99.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167).

Sharov, A. A. (n.d.). *Metapopulation model. http://alexei.nfshost.com/PopEcol/lec12/metpop.html*

Stuart, S. N., Adams, R. J., & Jenkins, M. (1990). *Biodiversity in sub-Saharan Africa and its islands: conservation, management, and sustainable use* (Vol. 6). IUCN.

Suraud, J. P., Fennessy, J., Bonnaud, E., Issa, A. M., Fritz, H., & Gaillard, J. M. (2012). Higher than expected growth rate of the Endangered West African giraffe Giraffa camelopardalis peralta: a successful human–wildlife cohabitation. *Oryx*, *46*(4), 577-583.

Swanepoel, L. H., Somers, M. J., Van Hoven, W., Schiess-Meier, M., Owen, C., Snyman, A., ... & Dalerum, F. (2015). Survival rates and causes of mortality of leopards Panthera pardus in southern Africa. *Oryx*, *49*(4), 595-603.

Tshipa, A., Valls-Fox, H., Fritz, H., Collins, K., Sebele, L., Mundy, P., & Chamaillé-Jammes, S. (2017). Partial migration links local surface-water management to large-scale elephant conservation in the world's largest transfrontier conservation area. *Biological Conservation*, *215*, 46-50.

Turkalo, A. K., Wrege, P. H., & Wittemyer, G. (2018). Demography of a forest elephant population. *PloS one*, *13*(2), e0192777.

UNEP-WCMC. (2020). *Protected Planet | Africa*. Protected Planet. https://www.protectedplanet.net/region/AF

United Nations Development Programme. (2020). *Goal 15: Life on land*. UNDP. https://www.undp.org/content/undp/en/home/sustainable-development-goals/goal-15-life-on-land.html

van der Meer, E., Fritz, H., Blinston, P., & Rasmussen, G. S. (2014). Ecological trap in the buffer zone of a protected area: effects of indirect anthropogenic mortality on the African wild dog Lycaon pictus. *Oryx*, *48*(2), 285-293.

Weise, F. J., Lemeris Jr, J. R., Munro, S. J., Bowden, A., Venter, C., van Vuuren, M., & van Vuuren, R. J. (2015). Cheetahs (Acinonyx jubatus) running the gauntlet: An evaluation of translocations into free-range environments in Namibia. *PeerJ*, *3*, e1346.

Williams, S. T., Williams, K. S., Lewis, B. P., & Hill, R. A. (2017). Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. *Royal Society open science*, *4*(4), 161090.

Wilson, J. W., & Primack, R. B. (2019). *Conservation Biology in Sub-Saharan Africa*. Open Book Publishers.

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, *280*(5372), 2126-2128.

Woodroffe, R., Hedges, S., & Durant, S. M. (2014). To fence or not to fence. *Science*, *344*(6179), 46-48.

Woodroffe, R., Rabaiotti, D., Ngatia, D. K., Smallwood, T. R., Strebel, S., & O'Neill, H. M. (2020). Dispersal behaviour of African wild dogs in Kenya. *African Journal of Ecology*, *58*(1), 46-57.

10. Appendix A: Search terms

Patch Characteristics (size)

(meta-population OR metapopulation OR subpopulation)
AND
(habitat size OR patch size OR reserve size OR area size OR patch area)
AND Africa* AND (national park OR protected area OR reserve)

Results: 68
Primary criterion: 19
Secondary criterion: 15

Connectivity and fragmentation

(meta-population OR metapopulation OR subpopulation)
AND (fragment* OR connectivity OR isolation) AND (stepping stone OR corridor)
AND Africa* AND (Protected area OR reserve OR national park)

Results: 11
Primary criterion: 6
Secondary criterion: 3

Patch Characteristics (spatial isolation)

(meta-population OR metapopulation OR subpopulation)
AND
(spatial isolation OR distance between patches OR patch distance)
AND Africa* AND (national park OR protected area OR reserve)

Results: 3
Primary criterion: 2
Secondary criterion: 0

Patch requirements: maximum population size

(meta-population OR metapopulation OR subpopulation)
AND (carrying capacity OR maximum population size) AND Africa* AND (national park OR protected area OR reserve)

Results: 8
Primary criterion: 5
Secondary criterion: 5

Population structure

(meta-population OR metapopulation OR subpopulation)
AND (survival rate OR extinction rate OR extinction risk OR mortality rate OR growth rate OR decline rate)
AND Africa* AND (Protected area OR reserve OR national park)

Results: 27
Primary criterion: 9
Secondary criterion: 7

Dispersal

(meta-population OR metapopulation OR subpopulation)
AND (dispersal rate OR dispersal distance OR migration rate OR movement probability)
AND Africa* AND (Protected area OR reserve OR national park)

Results: 13
Primary criterion: 6
Secondary criterion: 4

Total papers Web of Science : 34
After removing duplicates: 20 (14 duplicates)

11. Appendix B: The meta-analysis table

Author(s)	Species	Parameters	Data parameters	Impact on (meta)population trends	Country	(Grand) Species order
Havmøller et al., 2019	Leopard (*Panthera pardus*)	Study area: Udzungwa Mountains	16.000 km^2	Near reserve boundaries increasing human disturbance and threats to survival, which negatively impacts density.	Tanzania	Carnivora
		Patches: Udzungwa Mountains National Park. Kilombero Nature Reserve.	1990 km^2 1345 km^2	Metapopulation could be at risk if they lose connectivity with the major adjacent ecosystems.		
		Population size	58			
		Density in reserve. Density in the matrix.	8/100 km^2 2/100 km^2			
		Connectivity	There is little connectivity, matrix is human-dominated, hence leopard movements between protected areas may be absent or only sporadic.	Large areas of continues protected habitat are a requirement for securing the viability of large carnivore populations.		
Buk et al., 2018	Cheetah (*Acinonyx jubatus*)	Patches: Median reserve size (50 reserves) (all fenced)	125 km^2	Functioning as a *managed* metapopulation.	South Africa	Carnivora
		Median population size	4	No persistence of the population without intervention.		
		Population density	2.7/100 km^2			
		Dispersal	Only a few unassisted dispersal accounts.	Removing fences not realistic as the matrix is highly developed and		

			Little ability due to fences.	mortality would be high.		
		Spatial isolation and dispersal distance	16 km			
Githiru, 2017	Grevy's zebra (*Equus grevyi*)	Study area: Kasigau Corridor REDD++ Project Area	2000 km^2	Most of the zebra are in the ranch lands (matrix).	Kenya	Ungulata
		Population size	36	Small and stable subpopulation, but disconnected. Connecting to neighbouring national park would result in genetic benefits.		
		Population density	9/100 km^2			
Jenkins et al., 2015	African wild dog (*Lycaon pictus*)	Patch: Mkhuze Game Reserve (fenced but permeable)	360 km^2	The size of the reserve results in an unviable and unstable population.	South Africa	Carnivora
		Population size	13			
		Dispersal	Dispersal outside reserve due to reserve being too small.	Threats and mortality along boundaries when individuals disperse.		
Lindsey et al., 2011	Cheetah (*Acinonyx jubatus*)	Patch: Mean reserve size	267 km^2	Large areas are required for cheetahs.	South Africa	Carnivora
		Mean population size	6.61	These area requirements are currently larger than 65-100% of reserves.		
		Population size required to preserve genetic diversity	10 (in absence of other predators) 15 (other predators)	If the area size is lower, population not supported.		
		Patch size required to preserve genetic diversity	203 km^2 (in absence of other predators) 2424 km^2 (other predators)			

Dolrenry et al., 2020	Lion (*Panthera leo*)	Study area: Amboseli-Tsavo ecosystem	3684 km^2	Increased viability of the metapopulation.	Kenya	Carnivora
		Researched population (dispersing individuals)	189	Higher survival rate of lions in the study area due to corridors of 'human tolerance'.		
		Dispersal distance	110, 52 and 200 km			
		Connectivity	Increased connectivity due to increased human tolerance in the matrix	Increased connectivity facilitates long-term persistence of lion populations both within and outside protected areas.		
		Mortality rate study area (matrix)	0.10			
		Mortality rate outside study area (matrix)	0.20			
Morrison et al., 2016	Wildebeest (*Connochaetes taurinus albojubotus*)	Study area: Tarangire-Manyara Ecosystem	25000 km^2	Extent of ecosystem has declined and simplified. Population more vulnerable to fluctuations. There is a reduction in the overall population size compared to historical numbers. But conservation efforts helped stabilize the population.	Tanzania	Ungulata
		Patches: Tarangire National park. Lake Manyara national park. Manyara Ranch.	2600 km^2 317 km^2 177 km^2			
		Population size	6500 - 13000			
		Dispersal distance (migration)	60-75 km			
		Connectivity	Gradual loss of connectivity			
Oginah et al., 2020	Eastern black rhinoceros (*Diceros bicornis michaeli*)	Patch: Ruma National Park	126 km^2	Park has potential to support other sub-populations and contribute to metapopulation.	Kenya	Ungulata

		Population size	21			
		Carrying capacity	65			
Le Roex et al., 2018	Black rhinoceros (*Diceros bicornis*)	Patch: Unnamed reserve (fenced)	145 km^2	Population performance and health reduced over time.	South Africa	Ungulata
		Population size	38	Low genetic diversity due to inbreeding.		
		Population growth rate	6%			
		Population density	27/ 100km^2	Results indicate effects of isolating small populations.		
		Survival rate patch	0.9345			
Davies-Mostert et al., 2015	African wild dog (*Lycaon pictus*)	Patches: (total: 9, all fenced)	437 km^2	*Managed* metapopulation.	South Africa	Carnivora
		Mean group size	11	High density due to small reserve sizes.		
		Population growth rate	8%			
		Population density	3.3/100 km^2			
		Dispersal	Impeded due to fencing, but still some confirmed cases of natural dispersal.	Metapopulation not viable due to natural dispersal but through management.		
		Survival rate patch	0.91			
Linklater & Swaisgood, 2010	Black rhinoceros (*Diceros bicornis michaeli*)	Study area: 12 patches (fenced)	No specific area size	Movements constrained due to fencing.	Namibia & South Africa	Ungulata
		Population size	34	Smaller reserves pose an increased risk to rhino survivorship.		
		Mortality /injury rate Reserve <115km^2 >180km^2	27% 6.3%			
Lindsey et al., 2004	African wild dog (*Lycaon pictus*)	Minimum population size	5	Below 5 population not viable.	South Africa	Carnivora

		Minimum patch area requirement (fenced)	Northern South Africa: 65 km^2 Eastern South Africa: 72 km^2 North-eastern South Africa: 147 km^2	Below area size population not viable.		
Fattebert et al., 2013	Leopard (*Panthera pardus*)	Population size	1	Individual successfully travelled through matrix.	South Africa Mozambique, Swaziland	Carnivora
		Dispersal distance	194.5 km	Long-distance dispersal indicates metapopulation dynamics.		
		Connectivity	There is connectivity due to stepping stones and corridors.			
		Stepping stones and corridors.	Protected Areas functioned as stepping stones and corridors			
Miller & Funston, 2014	African Lion (*Panthera leo*)	Patch: 14 small, fenced reserves	220 km^2	In small reserves populations need to be *managed* to combat overpopulation. High levels of inbreeding question viability.	South Africa	Carnivora
		Population size	15			
		Survival rate patch	0.745			
		Density	22/ 100 km^2			
		Dispersal	Natural dispersal almost non-existent due to little ability, but still some counts.			
Edwards et al., 2019	Brown Hyena (*Parahyaena brunnea*)	Reserve size Okonjima Nature Reserve (fenced)	200 km^2	Very high density. Area supports population. However, possible concern for inbreeding depression and loss of genetic diversity.	Namibia	Carnivora
		Population size	48			
		Population density	24.01/100 km^2			

Chamaille-Jammes et al., 2008	African Elephant (*Loxodonta Africana*)	Patch: Hwange National Park (unfenced)	15000 km^2	Population likely part of larger metapopulation. Local regulation due to dispersal and mortality.	Zimbabwe	Ungulata
		Carrying capacity	37136			
		Population density	200/100 km^2			
		Dispersal	There is dispersal which likely regulates population			
Balme et al., 2009	Leopard (*Panthera pardus L.*)	Patch: Phinda Private Game Reserve (not fenced)	220 km^2	Mortality mostly due to humans in surrounding matrix. Interventions to reduce anthropogenic mortality have positive outcomes on leopard populations.	South Africa	Carnivora
		Population size	42			
		Mortality rate matrix	0.241			
		Population growth rate	14%			
Di Minin et al., 2013	African wild dog, black rhino, cheetah, elephant, leopard and lion.	Study area: KwaZulu-Natal province	92.000 km^2	Current management strategies are unlikely to enhance metapopulation persistence should catastrophic events affect populations in the future. Large, wide-ranging, mammal species may experience lower extinction risks in better connected reserve networks.	South Africa	Carnivora & Ungulata
		Patches: Small reserves (current situation) (fenced)	No specific area size			
		Carrying capacity	Wild dog: 14 Black Rhino:44 Cheetah:10 Elephant: 115 Leopard: 37 Lion: 23			
Foley & Faust, 2010	African elephant (*Loxodon*	Patch: Tarangire National Park (not fenced?)	2600 km^2	Growing subpopulation due to favourable conditions.	Tanzania	Ungulata

	ta Africana)					
		Population size	668			
		Population growth rate	7.1%			
		Mortality rate patch	1%			
Elliot et al., 2020	African lion (*Panthera leo*)	Patch: Lake Nakuru National Park (fenced)	188 km^2	Low abundance and complete isolation is cause for concern (inbreeding and genetic integrity).	Kenya	Carnivora
		Population size	11			
		Population density	6.75 /100 km^2			
Woodroffe et al., 2020	African wild dog (*Lycaon pictus*)	Study area: Laikipia, Samburu and Isiolo county	No specific area size	Dispersal plays central role in wild dog population dynamics. High mortality of dispersers is likely to reduce effective connectivity between patches of suitable habitat.	Kenya	Carnivora
		Population size	74			
		Mortality rate dispersers (matrix)	88.3%			
		Dispersal distance	37 km			
Turkalo et al., 2018	African forest elephant (Loxodonta cyclotis)	Patch Dzanga-Ndoki National Park	1220 km^2	Safety in park and problems in surrounding areas. Likely more stable conditions, population growth.	Central African Republic	Ungulata
		Mortality rate patch	3.5%			
		Population growth	2.5%			
		Population size	1625			
Lee & Bolger., 2017	Masai giraffe (*Giraffa camelopardalis tippelskirchi*)	Study area: Tarangire Ecosystem (free-ranging)	1700 km^2	No subpopulation was completely isolated.	Tanzania	Ungulata
		Patches: 5 patches with subpopulations	No specific area sizes	Subpopulations with higher wildlife protection efforts and fewer		

				anthropogenic impacts made the greatest per capita contributions to the metapopulation. Metapopulation is most likely decreasing.		
		Metapopulation size	790			
		Growth rate metapopulation	0.941 or 1.015 (two estimates)			
		Dispersal	0.008 (movement probability)			
		Connectivity	low			
Tshipa et al., 2017	African elephant (Loxodonta Africana)	Patch: Hwange National Park (unfenced)	15000km^2	Migration outside protected area.	Zimbabwe	Ungulata
		Estimated population size	-45000	High density causes competition and dispersal.		
		Dispersal distance (migration)	108-260 km			
Morrison & Bolger, 2014	Wildebeest (*Connochaetes taurinus*)	Study area: Tarangire-Manyara ecosystem (include several patches)	20000km^2	Several bottlenecks which lack protection with matrix on each side threatening migration.	Tanzania	Ungulata
		Population size	5682	56% of movement outside PA's.		
		Dispersal distance (migratory)	>130km			
		Connectivity	There is connectivity due to available corridors			
		Corridors	Migratory route passes through corridor, but bottleneck (as narrow as 800m) surrounded by matrix			
Bissett & Bernard, 2011	Cheetah (*Acinonyx jubatus*)	Patches: Kwandwe Private Game Reserve.	220 km^2	Small conservation areas can play a role as sources for cheetahs and even	South Africa	Carnivora

		7 small fenced reserves.	50-300 km^2	in the presence of lions, cheetah populations will increase.		
		Mortality rate patch	0.70			
Suraud et al., 2012	West African giraffe (*Giraffa camelopardalis peralta*)	Study area: Fakara Plateau (Kouré, Fandou), the North Dallol Bosso, and the Intermediate Zone	No specific area size	Species living outside protected areas. Population doing very well due to absence of hunting and predators. However, increased habitat fragmentation will divide and decrease population.	Niger	Ungulata
		Survival rate matrix	0.945			
		Population growth rate	12-13%			
Balme et al., 2010	Leopard (*Panthera pardus*)	Patch: Phinda-Mkhuze Complex (permeable)	660 km^2	Mortality rate higher outside reserves.	South Africa	Carnivora
		Population density reserve	11.11/100 km^2			
		Population density matrix	2.49/100km^2			
		Dispersal	There is dispersal into non protected areas.			
		Mortality rate matrix	0.358			
Williams et al., 2017	Leopard (*Panthera pardus*)	Study area: Soutpansberg Mountains	6800 km^2	Rapid decline in population.	South Africa	Carnivora
		Population density	3.65/100km^2	Population relatively isolated.		
		Connectivity	The area has suboptimal connectivity			
		Mortality matrix	6/8 died during the study time (0.75)	Anthropogenic mortality biggest threat to leopards outside protected areas.		
Lee et al., 2016	Giraffe (*Giraffa camelopardalis*)	Study area: Tarangire ecosystem (free-ranging)	1700km^2	Adult female survival is highly spatially variable.	Tanzania	Ungulata

		(includes patches)		Increasing anthropogenic effects along reserve boundaries, decreasing adult survival.		
		Population size (females)	860			
		Survival rate patches	0.90			
Weise et al., 2015	Cheetah (*Acinonyx jubatus*)	Study area: Unfenced areas, private free-range conservation areas	No specific area size	Few reserves large enough for cheetahs, high mortality in the matrix	Namibia	Carnivora
		Population size	23			
		Survival rate matrix	0.40			
		Dispersal distance	57.1 km			
Fattebert et al.., 2015	Leopard (*Panthera pardus*)	Patch: Phinda Private Game Reserve (permeable)	234 km^2	Dispersal patterns changed over time, i.e. as the leopard population density increased. Only one leopard reached adulthood in a different patch. This may have long-term implications for the genetic diversity of these leopards.	South Africa	Carnivora
		Population size	35			
		Dispersal distance	11 km (males) & 2.7 km (females)			
		Carrying capacity (density)	11.2 / 100km^2			
		Connectivity	Indirectly improved through re-establishing dispersal patterns disrupted by anthropogenic pressures.			
Van der Meer et al., 2014	African wild dog (*Lycaon pictus*)	Patch: Hwange National Park (unfenced)	15,000 km^2	Mortality in the matrix way higher that in the patch, yet packs move closer to patch border or outside. Population reduced over time.	Zimbabwe	Carnivora
		Mortality rate matrix	(2.54/6) 0.42			

		Mortality rate patch	(0.50/4.50) 0.11			
Cushman et al., 2016	African lion (*Panthera leo*)	Study area: Kavango Zambezi Transfrontier Conservation Area	1.5 million km^2	Reductions in the extent of the protected area network and/or fencing protected areas will result in large declines in the extent of population connectivity.	Angola, Botswana, Namibia, Zambia and Zimbabwe	Carnivora
		Dispersal distance	11.7 km			
		Population size	11			
		Corridor	Creation of corridors to funnel dispersers between protected areas increased overall connectivity of the population.			
		Connectivity	The article links several scenarios to the level of connectivity which either increases or decreases.			
Swanepoel et al., 2015	Leopard (*Pathera pardus*)	Study area: Includes patches and matrix	No specific area size	Anthropogenic mortality higher in the matrix. Cause of concern as mortality rates > 30% for solitary carnivores could lead to population declines.	South Africa, Botswana, Namibia	Carnivora
		Population size	162			
		Survival rate matrix	0.55			
		Survival rate patch	0.88			

12. Appendix C: Quantitative data parameters

Population density per 100 km^2						
African elephant	200					
Black rhinoceros	27					
Brown hyena	24,01					
Lion	22	6,75				
Leopard	8	2	11,11	2,49	3,65	11,2
Zebra	9					
African wild dog	3,3					
Cheetah	2,7					

Table C1*: The population density for 9 species and 14 researched populations.*

Population growth rate			
Black rhinoceros	6%		
Leopard	14%		
African wild dog	8%		
African elephant	7,1%		
Giraffe	1,5%	-5,9%	12-13%

Table C2*: The population growth rates of 7 different researched populations given in percentages.*

	Patch size		**Carrying capacity**		**minimum viable population size**
Black rhinoceros	126 km^2	Small reserve	65	44	
African elephant	15000 km^2	Small reserve	37136	115	
Leopard	100 km^2	Small reserve	11.2	37	
African wild dog	65-147 km^2	Small reserve	14		5
Lion	Small reserve (no specific area size)		23		

***Table C3**: The data for the carrying capacity and minimum viable population size for 5 species with corresponding patch sizes.*

13. Appendix D: The conceptual model

Patch No.	**Patch size, km^2**	**Diameter, km (S)**	**Distance from main patch, km (D)**	**Number of individuals (N)**	**Proportion of individuals (p*)**	**Ln(p*/(1-p*))**
1	220	20,98	11	42	0,72	0,94
2	125	15,81	52	4	0,07	-2,59
3	188	19,39	200	11	0,19	-1.45

***Table D1**: data used from the meta-analysis in order to determine the parameter values for γ, α and β. Adapted from the quantitative population ecology lectures by ecologist Sharov (n.d.).*

Coefficients[a]

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	-12,073	,000		.	.
	S	,624	,000	,917	.	.
	D	-,007	,000	-,408	.	.

a. Dependent Variable: Ln(p*/(1-p*))

***Table D2**: the output of linear regression of Ln(p*/(1-p*)) in SPSS.*

Patch	Individuals (N)	Distance from the main patch (D)	Patch size (km^2)
Patch A	42	11	220
Patch C	11	200	188
Patch D	0	80	60
Patch BE	57	40	360

***Table D3**: The patches, number of individuals (N), distance from the main patch (D) , and patch size corresponding with scenario 1: Larger, uninterrupted areas.*

Patch	Individuals (N)	Distance from the main patch (D)	Patch size (km^2)
Patch A1	0	11	70
Patch A2	0	10	65
Patch A3	1	9	85
Patch B	4	52	125
Patch C1	0	200	80
Patch C2	0	205	108

Patch D	0	80	60
Patch E1	0	38	35
Patch E2	3	40	110
Patch E3	1	42	90

***Table D4**: The patches, number of individuals (N), distance from the main patch (D) , and patch size corresponding with scenario 2: Many small patches due to fragmentation.*