**Linking worldwide demographic parameters of wolf (*Canis lupus*) populations to spatial socio-environmental variables**

Master thesis

by

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Abstract

To correctly assess and manage wildlife populations, in this case wolf (*Canis lupus*) populations, knowing if socio-environmental variables affect wolf parameters is essential for making appropriate management decisions. Here I analyse the relationship between accessibility, human footprint, forest loss and protected areas and the demographic parameters: pack size, litter size and survival rate, by conducting a spatial analysis. My hypotheses are the following: 1. Wolves located in areas with high human footprint should experience a lower survival rate. 2. Wolves in or close to protected areas are expected to have higher survival rates, than wolves outside of or further away from protected areas. 3. Forest loss and accessibility will have a negative impact on all three demographic parameters. Need to add in sentences about results, discussion and conclusion.

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**1. Introduction**

**1.0 General**

Ecologists have recognised the importance of researching population dynamics since the XXXXs (Reference). Demographic parameters, such as survival or mortality rate, birth rate, population growth rate, litter size, pack size and mechanisms such as dispersal, can be directly and indirectly linked to fluctuations observed in population sizes. Understanding how these may be affected by both internal and external factors is important for the maintenance of viable wildlife populations. Especially, as humans continue to expand their range into and impact on wild spaces, being able to explain how they influence wildlife populations is crucial.

A species, which has had a long ever-changing relationship with humans is the grey wolf (*Canis lupus*) (Ripple et al. 2014?). Their wide distribution across the globe and a long history of research on the species makes it the ideal model species to identify which spatial socio-environmental variables have an effect on their demographic parameters. Knowing how and if demographic parameters are influenced, allows us to make appropriate management choices and drafting of efficient legislation (Reference).

**1.1 Introduction to the species**

The grey wolf (*Canis lupus*) is a large carnivore which is present across most of the northern hemisphere (Ripple et al. 2014). Historically, it had a much larger contiguous range which due to hunting and persecution, resulted in the extirpation of wolves from many European countries and states in the US (Bangs & Fritts 1996; Fritts, Bangs & Gore; 1994; Wolf & Ripple 2017). Over the years wolves have started recolonising these areas, for example Germany and northwestern Montana (NWMT); or were reintroduced, such as in the case of Yellowstone National Park (YNP) (General= Chapron et al. 2014 & Ripple et al. 2014; YNP=Bangs & Fritts, 1996; NWMT=Fritts, Bangs & Gore, 1994). The most recent range of the wolf  is shown in Figure 1, a map published by the International Union for Conservation of Nature (IUCN) Red List in 2018 (Boitani et al. 2020).

*Current status of protection*

While the grey wolf is categorised as “Least Concern” on the IUCN Red List of Threatened Species with a stable population worldwide, it still faces threats at local scales (Boitani et al. 2020, 2022). In Europe the status ranges from “Least Concern” in Romania over “Vulnerable” in Germany, “Near Threatened” in Italy and Poland, “Endangered” in Portugal and Spain, and “Critically Endangered” in Norway to “Regionally Extinct” in Austria and Belgium (Boitani et al. 2022). This divergence calls for regional protection measures and conservation of wolves, taking into account the threats at a local scale.

Threats can have an impact on wolf populations in a variety of ways. In order to understand how exactly they affect populations we first need to define what a wolf population is and how it works. Accordingly, I will briefly explain wolf pack composition and behaviours such as breeding and dispersal and why they are important for population dynamics. Then I will more precisely link the three demographic parameters: litter size, pack size and survival rate to the threats of disease, forest loss, humans and roads.

Map

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**1.2 Wolf biology and behaviour**

*Pack composition and reproduction*

A complex social structure exists within wolf packs. The pack usually consists of a family of wolves led by the parents, priorly termed the alpha male and female, and several **juveniles** and pups (Reference). Occasionally, unrelated wolves will join an existing pack in a subordinate position (Reference). The constellation of a wolf pack varies by season. During pup season the pack is at its biggest, with all members of the pack contributing to pup rearing (Reference). The mother usually stays in the den the first X weeks to provide milk for the pups. Other pack members help feed the pups, by regurgitating food, especially the reproductive male (Reference). Once the pups reach the age of 6-8 weeks, they leave the den and start exploring their environment (Reference). By the age of 8 months, pups are largely independent and possess the ability to hunt by themselves, disperse and **(even)** breed (Mech & Boitani, 2003; Stahler et al., 2012). See Packard 2003 & Mech & Boitani 2003

*Feeding*

Wolves are large carnivores, which eat whichever prey they can come across, with slight variations across the globe. The diet of wolves is largely dependent on the availability of ungulates in the area, with their preferred type of ungulate varying by continent and season (Newsome et al. 2016; Janeiro-Otero et al. 2020; Latham et al. 2013). Prey switching has been observed in wolves in response to low prey availability (Gasaway et al. 1983; Sand et al. 2016). In areas with low numbers and diversity of wild prey, wolves will also depredate livestock and consume human rubbish, which has been observed in populations residing in Italy and Israel for example (Meriggi et al. 2011; Hefner & Geffen, 1999). However, if both wild and domestic prey are available wolves prefer wild prey (Meriggi et al. 2011; Newsome et al. 2016, Janeiro-Otero et al. 2020). Wolves have an intricate relationship with their prey and their dependency on certain prey species, has not only led to wolf population crashes, but even to local extinctions, as in the case of the “insert sample” wolf population (Reference). Therefore, a healthy prey base is important for the persistence of a viable wolf population and has been named as one of the two most important factors when determining suitable wolf habitat (Fritts, Bangs & Gore, 1994).

*Dispersal*

Dispersal takes place to and from all wolf packs, with both male and female wolves dispersing. It usually takes place around the age when wolves become sexually mature, although dispersers outside of this age range have been recorded. Morales-González et al. (2017) identified minimum and maximum ages of 8 months and 7.5 years in their review. Before wolves disperse and settle in a new territory permanently, they often precede this with exploratory forays (Fritts & Mech, 1981; van Ballenberghe 1983; Mancinelli & Ciucci 2018). During these forays, wolves seek out potential new territories and often stay away from their natal pack for extended periods of time, before returning again (Fritts & Mech, 1981; van Ballenberghe 1983; Mancinelli & Ciucci 2018). Wolves can either establish a new territory themselves and then find a mate, disperse together with a mate and establish a territory thereafter, or join an existing pack such as the case of: (give example) (Reference).

Dispersal is important to maintain genetic flow between different wolf packs and prevent inbreeding, which could lead to fitness loss, both on the individual and population level (Gilpin & Soulé, 1986). On the individual level, genetic mutations which lead to **morphological malformations/congenital anomalies** and lower body weight, among other things, have been observed in wolves in the Isle Royale and Scandinavian populations (Räikkönen et al. 2009, 2014; Robinson et al. 2019). On the population level it is expressed as decreased reproductive rate, litter size and overall survival (Hedrick et al. 2014; Liberg et al. 2005; Robinson et al. 2019).

**1.3 Wolf demographic parameters**

While the above behaviours have an integral role to play in wolf population dynamics, I chose to focus on three precise demographic parameters: 1. Pack size, 2. Litter size and 3. Survival rate. Wolf demographics are not clear cut in real life scenarios and it is difficult to determine the exact cause or effect of variables on demographic parameters independently of each other, as they are heavily intertwined. Some studies have managed to distinguish **some (environmental)** effects on life history traits such as litter size, pup survival and mortality, however these are often correlated and/or have **(inter-)related/subsequent effects/consequences** (Reference?).

The most recent reviews and meta-analyses of the three demographic parameters in question are compiled in Table 1. The most recent review on cause-specific mortality conducted on North American populations was performed by Creel and Rotella (2010), during which they identified the relationship between human offtake and total mortality in wolf populations. Several recent literature reviews exist on dispersal and this is a parameter which has been extensively researched. Mech (2020) highlighted the gaps in knowledge on natal wolf dispersal in 2020 and concluded that:.. . & Morales-González et al. (2021) reviewed dispersal distances and duration worldwide. Continue summarising. If possible, shorten everything. Übergang to the next part!

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Author(s) | Year | Parameter | Location | Type |
| Fernández-Gil et al. | 2020 | Pack size | Worldwide | Literature review |
| Morales-González et al. | 2017 | Dispersal | Worldwide | Literature review |
| Creel & Rotella | 2010 | Mortality | North America | Meta-analysis |
| (Janeiro-Otero et al. | 2020 | Diet |  | Literature review) |
| Mech | 2020 | Dispersal | Worldwide | Literature review |
| Chakrabarti et al. | 2022 | Survival | Worldwide | Original research with a table (Table 3, p.8) summarising survival rates |
| Table 1: Overview of the most recent literature reviews and meta-analyses on different wolf demographic parameters. | | | | |

*Pack size*

Pack size not only varies greatly in size within a single pack during a year, but also between different packs in a given area. Seasonal effects on pack size have been recorded in several wolf populations and in general, packs have the most members in late summer/beginning of autumn, when the pups of the year have been born, but winter mortality hasn’t set in yet (Reference; probably Mech some year). Adams et al. (2010) found that in autumn pack sizes in Alaska averaged 7.7 individuals, whereas in spring it averaged 5.4 wolves per pack. Some studies argue that pack size is determined by the ideal size to hunt prey, while others found that pup care and long-term investment in offspring also plays an important role (Mech & Boitani, 2003).

*Litter size*

The number of pups produced per litter varies, depending on the prey biomass available and the hunting status of a population (Boertje & Stephenson 1992; Fuller et al. 2003). Several studies found that in unexploited populations, litter sizes tended to be smaller than in exploited populations (Fuller et al. 2003). See Rausch 1967, Pimlott et al. 1969 for more. Another example of demographic parameters being **intrinsically** linked is presented by the study completed by Harrington et al. (1983). The study illuminated that litter size and survival of pups was linked to the number of **auxiliaries/helper**s in two study locations: Beltrami Island State Forest (BISF) and Superior National Forest (SNF) (Harrington et al. 1983).

*Survival/Mortality*

The most extensive prior research on the three present demographic variables has focused on wolf mortality, most likely due to the interest in the wolf as a game species. In general, when assessing threats to wolves, one can distinguish between anthropogenic, thus man-made; and natural causes. Anthropogenic causes encompass: hunting of wolves, both legally and illegally, and human built structures, such as roads (Murray et al. 2010). Natural mortality can be termed as any cause of death that would occur without human influence, such as age, disease, inbreeding and intra- and interspecific strife (Murray et al. 2010; Fuller et al. 2003). Finally, hybridisation with dogs *Canis lupus familiaris* is a threat to wolf populations and is widespread in Greece and Italy and sporadically occurs in many other European countries (Boitani et al. 2022).

Wolf mortality is largely dependent on human activity (Musiani & Paquet 2004; Mech some year). It can be distinguished between compensatory and additive mortality. In compensatory mortality, a certain threshold must be reached until an effect on the total mortality is seen.(Add in example of partially compensatory mortality: Stenglein et al. 2018) In additive mortality, this effect is immediately seen. Creel & Rotella (2010) found that human offtake, so **hunting/harvest** of wolves resulted in additive mortality in the Northern Rocky Mountains. In the absence of humans, wolves have high survival rates and have been documented in several populations, for example in Scandinavia (0.903), and Canada and the US (0.96) (Bull et al. 2009; Webb et al. 2011; Person & Russell, 2010).

In cases when natural mortality does occur, it is often in the form of diseases. Canine parvovirus (CPV) for example, reduced pup survival and therefore, also pack size and population size in wolf populations in northeastern Minnesota (Mech et al. 2008). Furthermore, as yearlings and young adults make up the majority of dispersersing individuals in wolf populations, dispersal rates may have been affected (Fuller 1989; Mech 1970; Mech et al. 2008). Similarly, Ballard et al. 1997 witnessed a decline in survival rate due to rabies in a wolf population in northern Alaska during the years of 1990-1992.

**1.4 Links to socio-environmental factors**

*Roads and accessibility*

Wolf mortality is affected by and can increase as the result of human infrastructure such as roads and the traffic associated with it. This has been recorded in populations in Croatia where a rise in mortality caused by collisions with vehicles was observed from 24.3% of all mortalities in 1996 to 50% for the years 2000 and 2001 (Huber et al. 2002). Moreover, in Spain mortalities caused by collisions in the Castilla y León region, which is the main area of wolf distribution, were partly associated with strong traffic and high speeds (Colino-Rabanal et al. 2011).

Roads provide easy access to areas for humans, which in turn can result in higher human-caused mortality in wolf populations (Mech 1977, 1989). This can be compensated by having areas with low road density or no roads at all in close proximity (Mech, 1989). Additionally, Fuller et al. (2003) identified that human tolerance of wolves in areas with high road density was an important factor, when determining the impact of roads on wolves.

*Forest loss*

Forest loss impacts wolves both directly and indirectly. It impacts wolves directly through habitat loss and degradation. This means wolves could be pushed into less favourable habitat, which in turn could lead to more conflict with humans. The indirect impact is through the way its prey is affected by the loss. This is especially apparent in populations of wolves present on islands, such as the Alexander Archipelago wolf, which is located on islands in Southeast Alaska. The Alexander Archipelago wolf (*Canis lupus ligoni*) relies on populations of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), the only ungulate available on some islands (Reference, Person some year?).

*Protected areas*

Smith et al. 2022

Borg et al. 2016

**1.5 Why do we need this research?**

Understanding the underlying patterns that drive wolf populations and identifying how these are affected by socio-environmental variables allows us to advise and establish appropriate wolf management and conservation strategies. Especially in light of ever changing legislation and public attitudes towards wolves, being able to accurately assess how wolf populations will respond to for example offtake from hunting is important.

The three chosen demographic parameters have been shown to be affected by a multitude of variables, as well as having multiple responses to these, as outlined above. To date, no worldwide spatial analysis has been conducted on how socio-environmental factors may impact litter size, pack size and survival rate of wolf populations. Therefore, I attempt to do so in this thesis.

**1.6 Hypotheses**

My hypotheses are the following. The socio-environmental factors accessibility, human footprint and forest loss should all have a negative impact on litter size, pack size and survival rate. Thus, higher accessibility, higher human footprint and high levels of forest loss, should result in small litter and pack sizes, as well as reduce survival rate. Wolves in protected areas should have higher survival rates than wolves outside of PAs.

**2. Materials and Methods**

**2.0 Literature review & data acquisition**

I conducted a review of the available literature on grey wolves and the four demographic parameters of pack size, litter size, dispersal and survival/mortality rate. I used the academic search engine GoogleScholar, as well as referring to the most recent literature reviews and meta-analyses (Table 1). I **formulated/phrased** the search strings in such a way that allowed me to find the most relevant results. All search strings included the words: “canis lupus”, “wolves”, “wolf” and a variation of search terms seeking demographic parameters, such as: “demography”, “mortality”, “survival”, “dispersal” “litter size” and “pack size”. The last search for all parameters was conducted in November 2022. I also searched the bibliographies of relevant papers for any additional studies.

When searching for relevant articles in GoogleScholar, I split the searches into two time periods, consisting of papers with a publication date before the year 2000 and after the year 2000. I prioritised papers published after 2000, as these contain the most recent information on wolf populations for this literature review. Furthermore, I limited my search to papers published in peer-reviewed journals or edited books by known wolf experts and in the English language.

To counteract a bias towards North America in the literature review, I conducted separate searches concentrating on Europe and Asia by adding specific countries with known wolf populations to the search string e.g. Greece, Israel and Pakistan. I did so by checking the current distribution of wolves on the most recent IUCN Red List available (Boitani et al. 2020).

Finally, I compiled a spreadsheet (**Appendix, Table X**) containing all demographic values contained in the papers, the location of the study area, the study area size and potential factors affecting the populations. These factors ranged from hunting status of a population to disease and prey availability.

**2.1 Data selection and preparation**

Next, I narrowed down the search on the three chosen parameters: litter size, pack size and survival rate. Dispersal was excluded from the analysis. Insert reason. I extracted the chosen demographic rates, along with information on the size of the study area and the location and years the study data was being collected and the year it was published. Maps showing the distribution of the studies were created in R. Countries were denoted according to ISO 3166 alpha-3 country codes and continents according to ISO 3166 alpha-2 codes, which can be found at: (Reference: https://www.iso.org/obp/ui/#search).

*Demographic data*

I chose to use the pack sizes given for winter, as at this point of the year the most **accurate/representative** estimates of pack size can be gained (WOLF BOOK,  Mech 19XX).

Litter sizes were recorded in various ways in the literature as well. They were estimated by the number of pups seen outside the den (at different times of the year), off of placental scars and corpora lutea/albicantia counts. I chose to use direct counts when available.

Wolf mortality was denoted in different ways in the literature. Some papers gave overall mortality, so a mortality rate which lasted the entire study period, others gave cause specific mortality rates and other papers yet, gave yearly rates of survival or mortality. To synthesise all values, I chose to use annual survival rates only. This meant that any studies which did not specify an overall annual survival rate were excluded from the analysis. I split the data in age categories when possible, adhering to age classification most often used in the literature (Reference, Mech?). Pups were determined as individuals up until the age of 12 months, yearlings from the age of 12-24 months and adults 24+ months (Reference, Mech?).

*Study area location and size*

For studies which gave precise coordinates of the study area, either a single set or ranges, these were used. When ranges were involved, the midpoint was taken. For studies with unknown coordinates the following methods were used. 1. Some papers referred to others for the study area description. If this was the case, I looked up the coordinates in those papers. 2. If the studies did not refer to another study, the name of the area was researched, for example: “Superior National Park” or “Yellowstone National Park”. I first looked up coordinates on the official websites of the locations, if they existed, such as the national parks service websites. If no official websites detailing the coordinates existed, I used the geographic database “insert name” to find the coordinates. Table X (Appendix) shows all studies and details the method which was used to obtain the coordinates used in the analysis. Studies which had no easily identifiable locations or were purely theoretical were excluded from the analyses. Similarly, not all studies provided information on the exact study area size. Thus, studies which didn’t specify an area size were excluded from the analyses.

*Classification of European populations*

In North America wolf populations are more easily distinguishable via distance or barriers than ones in Europe. In Europe there are considered to be nine main wolf sub-populations, which consist as part of a large meta-population (Boitani et al. 2022). Table 2 displays the most recent classification of the populations according to the IUCN Red List of 2022, as well as their conservation status (Boitani et al. 2022). When sorting the populations in Europe into separate populations this classification was used.

|  |  |  |
| --- | --- | --- |
| Population | Countries | IUCN Red List Status |
| Iberian | Portugal, Spain | Near Threatened |
| Western Central Alps | Austria, France, Italy, Switzerland | Near Threatened |
| Italian Peninsula | Italy | Near Threatened |
| Dinaric- Balkan | Albania, Bosnia & Herzegovina, Bulgaria, Croatia, Greece, Kosovo Montenegro, North Macedonia, Serbia, Slovenia, Turkey (European part) | Least Concern |
| Carpathian | Czech Republic, Hungary, Poland, Romania, Slovak Republic, Ukraine | Least Concern |
| Baltic | Estonia, Latvia, Lithuania, Poland | Least Concern |
| Central European | Austria, Belgium, Czech Republic, Denmark, Germany, Luxembourg, Netherlands, Poland | Near Threatened |
| Karelian (excluding Russia) | Finland | Near Threatened |
| Scandinavian | Norway, Sweden | Vulnerable |
| Table 2: The nine wolf sub-populations in Europe and their IUCN Red List Status in 2022. Adapted from Boitani et al. 2022. | | |

*Socio-economic data*

Spatial layers for the chosen socio-environmental variables: accessibility, forest loss, human footprint and protected areas were compiled from multiple databases, as detailed in Table 3 The most recent data available for each parameter was used.

|  |  |  |  |
| --- | --- | --- | --- |
| Variable | Unit | Year | Source |
| Accessibility | Land based travel time in minutes | 2015 | Weiss et al. 2018 |
| Forest loss | Tree cover (loss) | 2000-2019 | Hansen et al. 2013 |
| Human Footprint 2009 | 8 stressors (low-high) | 2009 (2018 release) | Venter et al. 2016, 2018 |
| (Human Modification | 13 stressors | 2016 | Kennedy et al. 2019, 2020) |
| Protected Areas | Protected areas coverage | 2022 | IUCN world database for protected areas available at: Insert link |
| Table 3: Different spatial socio-environmental variables used in the analyses with their units, year of publication and sources. | | | |

**2.2 Data analysis**