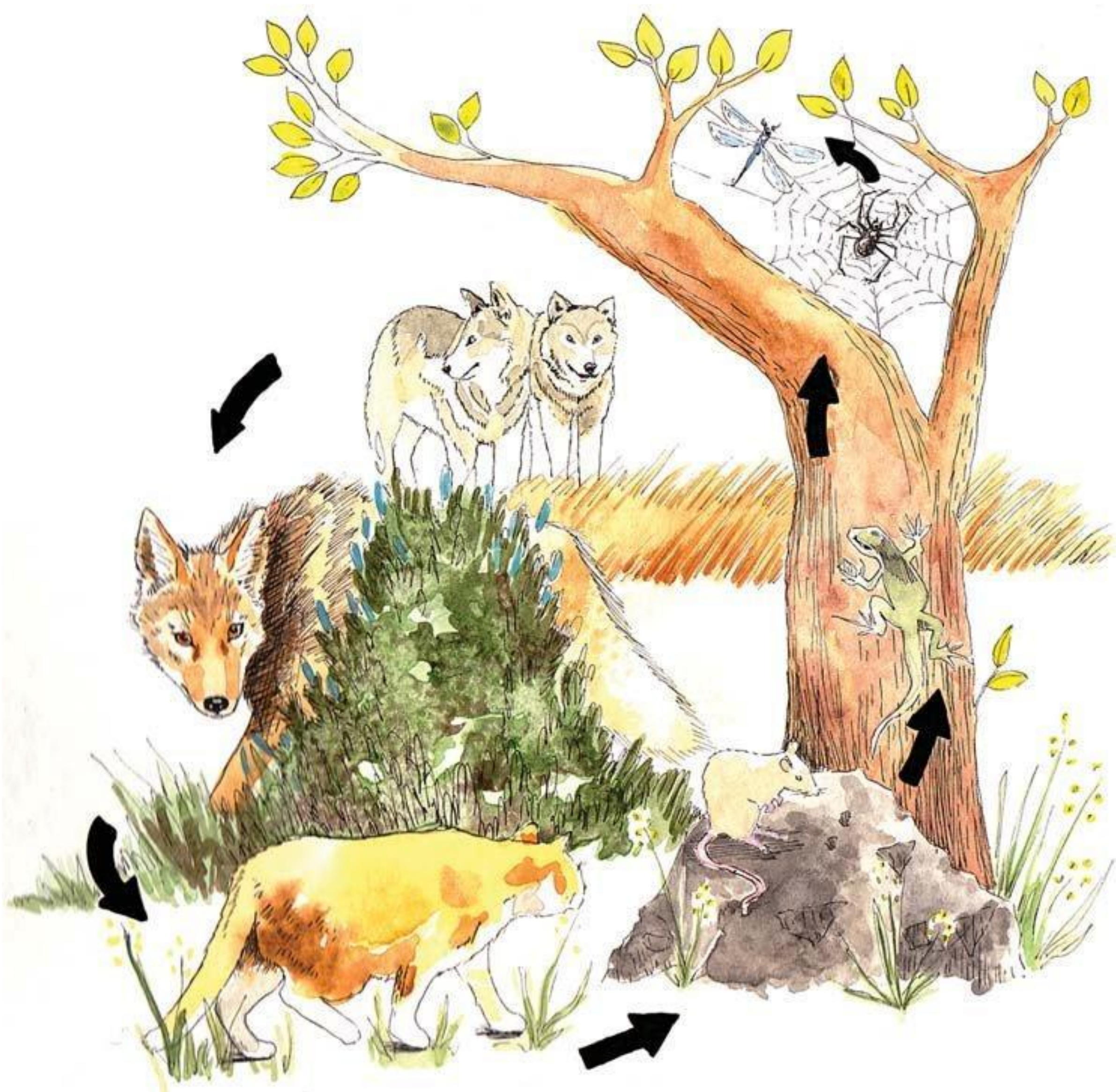
# The effects of wolves on mesopredators in Western-Europe




Jarco Drent S4101669

j.j.drent.1@student.rug.nl


Bachelors Thesis Life Sciences
WBBY901-05

Supervisor: Chris Smit

# Contents

# Abstract

The wolf is returning to Western Europe as an apex predator, which can have large consequences for mesopredators. All mesopredators are part of a food web together with other organisms. Changes in these food webs can cause trophic cascades, which could bring down an ecosystem. Here we provide a review of multiple studies looking at trophic cascades and interactions between apex predators and mesopredators. Apex predators can suppress mesopredators through lethal interactions and behavioural change, which can limit their abundance and distribution. With apex predators increasing in numbers, they could potentially outcompete smaller mesopredators. This depends on the complexity of the ecosystem, from productivity to habitat complexity. With this review, better insights are given into the possible effects of the wolf on multiple mesopredators present in Western Europe.

Keywords: Mesopredator release, Mesopredator, Apexpredator, Wolves, trophic cascades, food webs, Lethal interactions, Behavioural change

# Introduction

Worldwide there is a big decline in large terrestrial carnivores (Ritchie & Johnson, 2009). This happens through hunting and habitat loss of these large terrestrial carnivores(Ripple et al., 2014). Larger apex predators often need a large area to hunt in, because they can consume a lot of prey and therefore need the number of prey to be large in a large hunting area. With habitat loss it becomes more difficult for apex predators to find enough prey and to be able to migrate to other areas and mate with other non-relevant others (Ripple et al., 2014). This decline in apex predators often shows drastic consequences.

As a result of the loss in apex predators there has been a clear impact on the food webs. Because many of these large terrestrial carnivores are apex predators, they suppress mesopredators and keep different herbivores in check (Finke & Denno, 2004). The decline and sometimes even disappearance of apex predators can cause mesopredator release, where mesopredators take over, grow in population, and can make a mesopredator become the new apex predator (Conner & Morris, 2015). Larger herbivores sometimes have no natural enemies anymore, and smaller herbivores or rodents will be hunted even more, which can cause the extinction of some animals. With the rapid growth of the populations of larger herbivores like deer, plants, bushes, and trees can struggle to take root, and whole ecosystems get hurt because of this.

Clear benefits can be seen in the occurrence of apex predators. They can be able to suppress meso predators and also larger herbivores. This can be done through lethal interactions in which the apex predator kills either the mesopredator or herbivore, but also through behavioural interactions in which the presence of an apex predator can change behaviours found in mesopredators and herbivores. This, in turn, can limit the abundance and distribution of mesopredators (Ritchie & Johnson, 2009).

Western European countries pay more attention to these apex predators. Different countries have a return in forests and protect certain predators by law (Trouwborst, 2010). This provides a better and safer area for these predators to roam free. This change in how we view apex predators and how we handle our nature areas has resulted in an increase in overall predators in Western Europe and a return of the wolf (Trouwborst, 2010). It seems that our efforts in getting back our larger carnivores work, but the consequences are not yet fully known.

In this paper, an overview is given of the literature. Then the return of the wolf is discussed, and what the effects of these could be in an ecosystem. Next, lethal and behaviour changes seen in mesopredators will be shown. Multiple apex predators and mesopredators have been taken into account to observe the already known relationships between apex predators and mesopredators. A lot of research has been done on the effects of wolves on herbivores and vegetation. Also, the effects of wolves on mesopredators in the USA are known. However, the relationships between wolves and mesopredators are still unclear in Europe. This is why we focus on the relationships between apex predators and mesopredators in this paper. First, the trophic cascades will be explained by which apex predators can influence ecosystems. The vulnerability of ecosystems will be discussed, and why they are important. Then, literature on the apex predators: dingoes, lynx, jackals, coyotes, and wolves, was used to determine the overall possible effects of apex predators on mesopredators. By doing this, a better visualisation can be made of the possible effects wolves can have on mesopredators. In the end, the research question that will be answered is: what are the effects of the return of the wolf on mesopredators in Western Europe?

# Results

There have been many different studies on the interactions between apex and mesopredators. Most of the studies used in this paper are summarized in the table below. For every paper, the interaction between apex and mesopredator is given, and whether this effect was positive or negative. Then the region is given to see how similar this is to Western Europe. At last, the area size and the study length are given. These two factors can be a good indicator of how much each study matters. References used in this paper which were primarily theoretical and without any research, were taken out of the table.

**Table 1**. Apex predator mesopredator relationship together with the region, area size, and study length of the references used.

| Apex | Meso | Evidence release (0=suppression of mesopredator, 1=positive effect on mesopredator, 2=mixed effect 3=no effect | Country | Area size in km: S (0-100) M(100-10.000) L(10.000->) | Study length and size in (years), with the size of the studies between brackets | Reference |
|---|---|---|---|---|---|---|
| Wolf | Coyote | 0 | North America/ Canada | L | 1982-2011 (29) 1996-2010 (14) | Newsome et al. (2015) |
| | | | USA, Minnesota | S | 1975-2005(30) | Levi et al. (2012) |
| | | | United States | L | 1916-1944 (28) | Ripple et al. (2013) |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | North America | L | 1982-2011 (29) | Newsome et al. (2017) |
| | | | | M | 1960-2000 (40) | Smith et al. (2003) |
| | | | | S | 2001-2004 (3) | Berger et al. (2008) |
| | | | | S<br>M | 1991-2005(3) | Berger et al. (2007) * |
| | Golden Jackal | 0 | Bulgaria<br>Serbia | L<br>L | 2000-2009 (9) | Newsome et al. (2017) |
| | | | Bulgaria and Serbia, Greece | M | 2008-2015 (2-3 | Krofel et al. (2017) |
| | Fox | 1 | Italy | S | 2017-2018 (1) | Ferretti et al. (2021) |
| | | | North America | L | 1982-2011(29)<br>1996-2010(14) | Newsome et al. (2015) |
| | | | USA, Minnesota | S | 1975-2005(30) | Levi et al. (2012) |
| | | 2 | Sweden | L | 1827-1860 (33), 1866-1917 (51) | Elmhagen et al. (2007) |
| Lynx | Fox | 0 | Finland | L | 1989-2005 (17) | Elmhagen et al. (2010) |
| | | 2 | Sweden | L | 1827-1860 (33), 1866-1917 (51) | Elmhagen et al. (2007) |
| | | 0 | Spain | S | 2014-2016 (2) | Jiménez et al. (2019) |
| | | 0 | Europe, Northern Asia | M | 1952-2010 (*) | Pasanen-Mortensen et al. (2013) |
| | | 2 | Poland | M | 2012 (1) | Camilla et al. (2017) |
| | Egyptian mongoose | 0 | Spain | S | 2014-2016 (2) | Jiménez et al. (2019) |
| | European Badger | 1 | Spain | S | 2014-2016 (2) | Jiménez et al. (2019) |
| Coyote | Kit Foxes | 0 | USA, California | S/M | 1989-1991 (2) | Ralls et al. (1995) |
| | Fox | 0 | USA, California | S | 1985-1987 (2) | Soule et al. (1988) |
| | | | | | 1995-1997 (2) | Crooks et al. (1999) |
| | Cats | 0 | USA, California | S | 1985-1987 (2) | Soule et al. (1988) |
| | | | | | 1995-1997 (2) | Crooks et al. (1999) |

| | | | | | | |
|---|---|---|---|---|---|---|
| | Raccoon | 2 | USA, Illinois, Texas, Mississippi, Iowa | - | 1989-1997 (4) | Gehrt et al. (2003) |
| | | 0 | USA, California | S | 1995-1997 (2) | Crooks et al. (1999) |
| | Skunk | 0 | USA, California | S | 1995-1997 (2) | Crooks et al. (1999) |
| | Opossum | 0 | USA, California | S | 1995-1997 (2) | Crooks et al. (1999) |
| Dingo | Feral cat | 0 | USA, California | M | 2012 (1) | Cordon et al. (2015) |
| | Red Fox | 0 | Australia | M | 2012 (1) | Cordon et al. (2015) |
| | | | | S | 1951-1952 (1) 1947-1952 (5) | Letnic et al. (2011) |
| | | | | L | 1951-1952 (1) | Newsome et al. (2017) |
| | foxes/cats/goannas | 3 | Australia | M | 1994-2011 (3) | Allen et al. (2013) |
| Jackal | Bat-eared fox | 3 | South Africa | S/M | 2006-2007 (1) | Kamler et al. (2013) |
| | Cape fox | 0 | South Africa | S/M | 2006-2007 (1) | Kamler et al. (2013) |

*When the study was conducted in the United States, it is specified more where the study took place since the USA is so big. For the study length and size, when more than two studies have been used, this is averaged. *A study by Berger et al. (2007) had study sites of smaller and larger sizes and was thus placed in both groups. * Pasanen-Mortensen et al. (2013) used multiple studies within that period, but unclear how long each study was.*

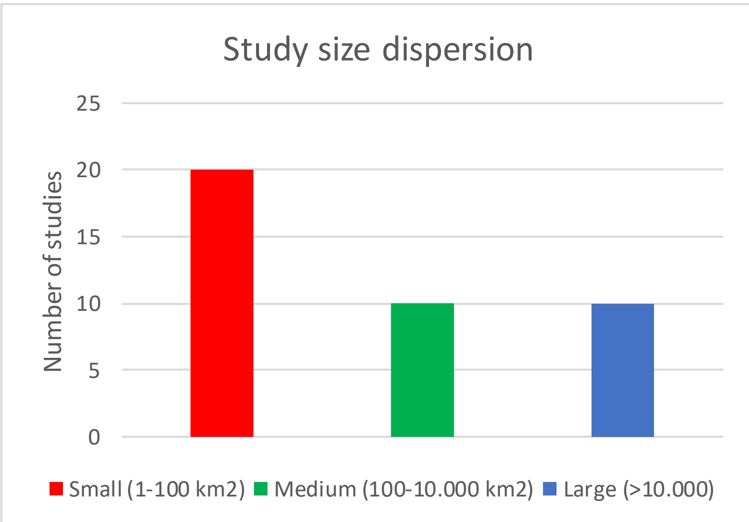



***Figure 1**. Showing the amount of studies per area size used in table one.*

Most apex predator mesopredator relationships were negative. Meaning that the presence of an apex predator resulted in a decline of mesopredators. Sometimes there was no effect found, and sometimes a mixed effect, but in two cases, the presence of an apex predator positively impacted the mesopredator. The wolf had a positive effect on the fox, and the lynx had a positive effect on the badger.

When looking at the references in table 1, approximately 50% of all references were from data in the

USA. This is probably because Yellowstone is one of the largest and most studied wolf areas. However, this landscape is very different from Western Europe, as is the species composition. Only 23% of the studies were conducted in Europe, and the other studies were from Australia, Asia, and Africa.
Most studies were done on a small-scale study area, as shown in figure 1. Small study areas were used in 50% of the studies, and medium and large study areas were used 25% of the time. Almost all of the small study areas had a short study time as well, approximately two years per study, with only two exceptions. Larger study areas tended to use a longer study period, with only one study being shorter than nine years.
The table includes seven studies on wolves and coyotes and only four on wolves and foxes, of which two also included coyotes in the ecosystem. Since only three mesopredators were used with wolves, other apex predator mesopredator relationships are useful to look at. Examples of these relationships are lynx with mongooses and badgers, coyotes with cats, raccoons, skunks, opossums, and dingoes with cats and goannas. Some of these smaller mesopredators will also be found in Western Europe, like mongooses, badgers, cats, raccoons, skunks, and opossums.

# Trophic cascades

In nature, there are food webs, which consist of multiple interdependent food chains in which animals can eat other animals or plants. Animals sometimes hunt the same animal or eat the same plants. Once these feeding habits are similar between animals, they can occupy the same trophic level. This results in food chains having a linear hierarchy in which food gets transferred when an organism eats another organism (Terborgh & Estes, 2010). Apex predators occupy the highest trophic level in a food chain. They are not being hunted by other animals and hunt the animals at lower trophic levels. Once these apex predators get eliminated from the environment they live in, this destabilizes ecosystems. This, in turn, can set off a chain reaction that can hurt the entire food chain at all trophic levels. Interactions between trophic levels are thus shown to be very important in causing these trophic cascades (Terborgh & Estes, 2010).

In these trophic levels, apex predators are only influenced by bottom-up processes, where they are dependent on the food available. Mesopredators and herbivores are influenced by bottom-up and top-down processes since they are also being hunted/scared away by predators. Both processes are important since bottom-up processes determine how many resources are available and top-down processes determine how these resources are distributed. The strength of which top-down control can play a role in an ecosystem depends on the productivity of an ecosystem(Elmhagen et al., 2010; Elmhagen & Rushton, 2007). When the productivity of an ecosystem is very high, this means that a lot of organic matter is being produced, profiting the lowest trophic levels and thus working its way up through all trophic levels. High productivity often equals high biodiversity and a more stable ecosystem. Extirpation or reintroduction of apex predators in a highly productive ecosystem will have less effect than in low productive ecosystems.

Without reintroduction, when an ecosystem is left alone for a while, the ecosystem can eventually reach a balance in which biotic and abiotic factors keep battling, and organisms can take a certain amount of change which is considered balance (Verma, 2018). Humans, however, are able to completely change this balance that nature strives for, as seen in the extirpation of wolves in Europe (Pasanen-Mortensen et al., 2013; Ripple et al., 2013). The ecological balance hypothesis says that ecosystem balance is very important for all organisms on the planet. Hence, we need to be extremely careful not to disturb this balance too much; one small human action can have huge consequences on an ecosystem and the balance in this ecosystem.

Once an apex predator like the wolf gets extirpated, the top-down process changes, and with it, the trophic levels. Bigger mesopredators like coyotes, lynx, or foxes will take over the top of the food chain (Conner & Morris, 2015). This process, which is called mesopredator release, will cause the mesopredator populations to significantly increase since the top-down process is gone. However, apex predator extinction does not always cause mesopredator release (Jachowski et al., 2020). The exploitation ecosystems hypothesis (EEH) proposes that predators suppress herbivore populations, and therefore plants can escape herbivore browsing (Elmhagen et al., 2010). So once the wolf disappears, the EEH predicts an eruption of plants. Besides the effects on herbivores and plants, the disappearance of wolves can have more consequences. Not all of these consequences are bad, for example when wolves got extirpated, the increase in coyotes caused an increase in songbirds and rodents because they suppressed the smaller carnivores like cats and foxes (Levi & Wilmers, 2012). However, deer populations were not suppressed anymore. This shows how important apex predators can be in an environment as they can suppress mesopredators. They are known to do this through behavioural change and lethal interaction. Again, showing that ecosystems are very complex, and all factors should be taken into account before determining the full effects of the loss or return of an apex predator.

# Lethal interaction

One of the main interactions thought of is the lethal interaction between apex predator and mesopredator. Lethal interactions can be classified as consumptive interactions since it involves the killing of prey and competitors (Haswell et al., 2017). These lethal interactions can be seen worldwide in many apex predator mesopredator environments (Dingo, Wolve, Lynx). Lethal interactions can have different forms. The first one is intraguild predation, which happens when the mesopredator is killed and eaten by a competitive predator. When an apex predator kills a mesopredator, this is called superpredation (Lourenço et al., 2014). Thirdly, interspecific killing, where the mesopredator is killed but not eaten. The last one, which is often not considered, is interspecific competition killing, where a predator kills the prey of the competitor and thus excludes them from the resources (Newsome & Ripple, 2015; Ritchie & Johnson, 2009).

There can be different reasons for lethal interactions. One can imagine it being for food or to kill competitors to have more resources for yourself. It can also be to show dominance over weaker predators or to eliminate a threat in your environment (Lourenço et al., 2014). Lethal interaction will decrease if the mesopredator and apex predator have less chance of meeting. The enemy constraint hypothesis proposes that mesopredators will lower their top-down influence on the ecosystem the closer they get to the predator of a higher trophic level. This was shown to be true in Europe and North America for wolves vs. coyotes and in Australia for Dingoes vs. the red fox in research by Newsome et al. (2017). Superpredation or interspecific killing is more likely to occur once the prey of both predators is of similar size because competition between both predators is higher (Pasanen-Mortensen et al., 2013).

# Behavioural change

Even though most of the early research was done on lethal interactions using the lethal effect models, it can also be thought that the behaviour of mesopredators changes in the presence of an apex predator (Gordon et al., 2015). As a result of this, one can imagine that the presence of apex predators can provide a safer environment for rodents or birds. Indeed, a lot of research shows that apex predators can change the behaviour of animals at lower trophic levels. Non-lethal interactions between predators can also be called non-consumptive responses because no one dies in this process (Haswell et al., 2017). Behavioural changes can happen through two processes, direct and indirect effects of apex predators. Direct effects of apex predators are risks imposed by the presence of apex predators in an ecosystem. Indirect effects of apex predators include the attraction of mesopredators by leaving prey behind, but can also be through, for example, the suppression of wolves on coyotes offering foxes a safer area. Mesopredators will always have to weigh the risks against the rewards. This will determine if a mesopredator will change its behaviour in the presence of an apex predator.

# Casussus

Dingoes, Lynx, Jackal, Coyotes, and Wolves are considered apex predators in different ecosystems. I will give examples of these apex predators in their ecosystems and the roles they play in relation to mesopredators in their environment. This will be used to derive possible consequences that the Wolf can have on mesopredators in West-Europe.

## 1. Dingoes

Dingoes in Australia, which are considered an apex predator, seem to suppress the invasive red fox and feral cat populations (Gordon et al., 2015; Letnic et al., 2012). The GUD is an experiment to test the food availability in a patch once a forager has exploited it. This can be used to test for perceived risks in these patches (Welch et al., 2017). This can be important to test whether the risks of mesopredator predation in an area are worth the risks of predation by apex predators (Gordon et al., 2015). The giving-up density (GUD) was calculated for rodents when dingoes were present. Rodents had a higher abundance and better foraging efficiency when dingoes were present (Gordon et al., 2015). It was also shown that where dingoes are present red fox abundances are lower (Letnic et al., 2011). This supports the hypothesis that apex predators suppress mesopredator abundances and behaviour.

Next to this, research has been done on the removal of dingoes in an ecosystem. This shows that the temporal removal of dingoes does not result in predictable changes in the overall abundance of dingoes in that area. Removal of dingoes does, however, result in fractured social stability. As a result, abundances can either increase or decrease (Wallach et al., 2009). Social status within apex predators should be considered when looking at control or reintroduction to predict the direction of abundance better. Also, the temporal removal of dingoes has been plotted against mesopredator abundances. This shows no clear results, suggesting that temporal control of apex predators does not immediately result in mesopredator release (Allen et al., 2013). Temporal removal of apex predators in an ecosystem will thus not result in fast and predictable results.

## 2. Lynx

The lynx in many ecosystems can be considered an apex predator. In Spain, the lynx was reintroduced, which in turn caused a decline in multiple meso predators. The red fox, feral cat, Egyptian mongoose, and stone marten populations declined, whereas the European badger was the only exception. Its population did not decrease but even slightly increased. (Jiménez et al., 2019). Lynx are also known to kill golden jackals, which might also cause a decline in jackal populations once lynx are present (Pasanen-Mortensen et al., 2013). In Spain, the recapture rate of red foxes and Egyptian mongoose was lower in the lynx territory(Jiménez et al., 2019). This suggests that they change their behaviour in these areas through either avoidance or by becoming more vigilant. In another research, foxes show attraction to the smell of lynx (Wikenros et al., 2017). The age of the lynx also had an influence on how the foxes reacted. Lynx can leave leftovers behind, which is something foxes can utilize since they are scavenger hunters as well. Lynx do kill foxes and often as interspecific killing since fox bodies are left behind and not eaten (Pasanen-Mortensen et al., 2013). This could explain why foxes did become more vigilant near those sites as a result of the risks of lynx in the area (Wikenros et al., 2017).

There is always a trade-off for smaller predators since apex predators can leave food behind on which they can scavenge. However, apex predators are also known to kill mesopredators, which makes foxes become more vigilant. In a study on lynx and foxes, foxes were attracted by the smell of lynx since this can be a sign of higher food abundance in the region. But the foxes also become more vigilant (Wikenros et al., 2017). This shows that Lynx can suppress foxes but might also offer benefits in the form of food in other situations.

## 3. Jackal

Jackals are apex predators in some areas, like the desert. However, in Europe, it is often not an apex predator since wolves are the apex predators, but where wolves are absent, jackals can be the apex predator. Jackals are known to interact with red foxes. Foxes can flee their kills and leave them behind if a golden jackal is present; only the scent does not scare the foxes away (Ritchie & Johnson, 2009). This can be explained by the fact that golden jackals are known to kill bat-eared foxes and, thus, probably also red foxes (Pasanen-Mortensen et al., 2013; Welch et al., 2017). Black-backed jackals are also known to suppress cape foxes but not bat-eared foxes (Kamler et al., 2013). Even though the suppression was not visible of bat-eared foxes, the behaviour of both species was affected by the presence or absence of black-backed jackals. Once jackal populations started to decrease and started to disappear, the fox population increased by 64%. When the jackals were present, the foxes showed more activity during the night and had larger group sizes, showing behavioural changes in the foxes (Kamler et al., 2013). This supports the mesopredator release because the foxes are suppressed by jackals and also change their behaviour when they are present.

## 4. Coyotes

Coyotes are known to kill many different mesopredator species. The abundance of coyotes was negatively correlated with the overall mesopredator abundance (Crooks & Soulé, 1999). Coyotes can suppress the fox, raccoon, skunk, domestic cats/feral cats, and opossum populations, for example (Jachowski et al., 2020; Levi & Wilmers, 2012; Soule et al., 1988). Evidence for this was that when coyote abundance decreased, the overall mesopredator abundance increased. An earlier research by Gehrt et al. (2003) actually did not show a negative relationship between coyotes and raccoons. With raccoons not showing avoidance behaviour and not a high predation rate by coyotes.

Coyotes are larger predators and are impacted more by a loss of habitat than smaller mesopredators. This was also shown by Crooks et al. (1999). As said before, coyotes are known to kill foxes. Ralls & White (Ralls & White, 1995) show that 78% of kit foxes were killed by larger canids. Coyotes only ate half of the kit fox kills they made (Ralls & White, 1995). Suggesting that not only intraguild predation plays a role but also interspecific killing. Swift foxes, in turn, were seen to avoid areas with high bush abundance, which could prevent a clear line of sight (Crooks & Soulé, 1999). This could be because the risk of getting eaten by coyotes was higher in these areas. Suggesting that there are many interactions between predators, whether it is through competition for resources or through killing fellow predators. In research done by Crooks and Soulé (1999), coyotes were shown to be a high source of mortality in cats (Prugh et al., 2009). And even though coyotes are considered apex predators in some ecosystems, they can also be a mesopredator in others (Levi & Wilmers, 2012). In these other ecosystems, coyotes are suppressed by wolves and are even at the risk of being killed by wolves (Berger et al., 2008; Levi & Wilmers, 2012; Smith et al., 2003). In the end, coyotes are able to suppress different mesopredators when they are present, also supporting the mesopredator release.

## 5. Wolves

As said before, a lot of research has been done on the effects of wolves on herbivores and plants. However, little is known about the effects of wolves on smaller mesopredators worldwide. Only the jackal, coyote, and fox have been used to see what the effects of wolves were on them.

Wolves are thought to have a suppressing effect on the jackal populations in Europe. Where wolves were present, established jackal populations were lower. Also, the decline in wolves was matched by an increase in jackal populations over time (Krofel et al., 2017). When wolves were recolonized, jackals even left or went to areas with less dense wolf populations. Even though this shows top-down control of wolves on jackals, coexistence is also observed. This could be because the diets do not match completely, and jackals can feed off the leftovers of wolves. However, this has not been proven yet (Krofel et al., 2017).

Also, on coyote populations, wolves have a negative effect (Levi & Wilmers, 2012; Newsome & Ripple, 2015). Wolves do not kill coyotes often, but they are responsible for half of the quick coyote deaths. The coyotes also dispersed more when wolves were very abundant (Berger & Gese, 2007). Coyotes were also seen to change their foraging behaviour from hunting to a more scavenging foraging strategy (Ferretti et al., 2021). Also, between coyotes and wolves, there is coexistence observed. This is mainly shown through the tolerance of wolves on coyotes, which is higher when their shared prey abundances are higher (Ritchie & Johnson, 2009). When prey species are not abundant, wolves will outcompete coyotes and drive them to extinction if immigration is not possible for coyotes (Ripple et al., 2013). Wolves are shown to decrease coyote populations, which in turn causes fox populations to increase. If wolves start to decline, the coyote population, in turn, increases, and the fox population decreases(Newsome & Ripple, 2015).

Even though wolves can kill foxes, they often do not do this. A probable explanation would be that foxes pose no threat to wolves and have no overlap in prey species, which makes wolves and foxes very uncompetitive. Foxes are even attracted to wolves in general since they provide some form of protection against, for example, coyotes, and they can also leave food behind. Since foxes are also scavenger hunters, wolves can provide an increase in food availability for foxes (Ferretti et al., 2021).

# Discussion

Western Europe consists of a varying landscape. There are industrialized areas, cities, mountains, flatlands, rivers, agriculture, and nature areas with forests. This variation in landscape could dictate where the wolf will go and thus which mesopredators and prey it will encounter. Consequently, the wolf might react differently to mesopredators in certain areas within Western Europe and vice versa. Research by Newsome et al.(2016) shows that wolves in Asia seem to eat quite some domestic animals, whereas, in the US, they eat almost only wild animals. In Europe, it differs; in Greece and Spain, wolves eat a lot of domestic animals, but in the Alps or Central Europe, they eat more wild animals. Western Europe has a lot of urban areas and fewer nature reserves, which makes competition for wild ungulates much higher in Western Europe, where prey is less abundant. In Western Europe, wolves might go for more domestic animals reducing competition between the wolf and other mesopredators. However, because the area is quite small, mesopredators might have less space to avoid wolves which makes encounters inevitable. This makes smaller, more populated areas difficult since it has pros and cons for apex predator and mesopredator relationships.

Wolves have been shown to alter the behaviour of mesopredators by their presence, but also the behaviour and abundance of herbivore species can be influenced by the presence of an apex predator like the wolf. This can be important once an apex predator and mesopredator have overlapping diets. Herbivores can reduce predation risks by becoming more vigilant and increasing their group size (Kuijper et al., 2013)(**5**). In Yellowstone, wolves have been shown to impact elk behaviour, and predation risks differed between habitat types (Proffitt et al., 2009). With Western Europe having mainly smaller areas, risks of predation might be higher, making larger herbivores more vigilant in the presence of wolves. This can positively impact plant species and biomass (Ripple et al., 2013). With a better functioning ecosystem, we expect all species to benefit, including smaller mesopredators.

One apex predator which lives partly in the same area in Europe as the wolf is the lynx. The red fox, feral cat, Egyptian mongoose, and stone marten all hunt smaller birds and small rodents, which overlaps more with the food consumption of the lynx. European badgers, however, are more omnivorous, having a diet of mainly worms and fruit. Because this diet overlaps less with the lynx, they even increased in abundance a bit. This last part might be the same for wolves since badgers can scavenge the leftover food from wolves and will not have a lot of competition for food. Wolves, however, do not eat a lot of smaller birds and rodents; they will try to hunt mainly larger herbivores when available. This makes competition with other smaller mesopredators less, but not insignificant.

As shown in the results, almost all mesopredators declined in the presence of an apex predator. In Australia, foxes declined with an increase in dingoes. Dingoes are more similar to wolves in size than the lynx, and they can also prey on larger herbivores when they are present. However, in the desert, they mainly hunt smaller prey like rabbits and small rodents because these prey are more abundant. This could have the same effect in Western Europe when larger herbivore species are less abundant in some areas. Here competition between the wolf and smaller mesopredators might be higher. Even the fox, which was shown to benefit from wolves being present, might show a decline.

Even when food does not overlap between the apex predator and mesopredator, the behaviour of the mesopredator will change nonetheless. Behavioural changes of mesopredators can be partly determined by the GUD value. You would expect that mesopredators that can get killed by wolves foraging in a wolf-dense environment will have a higher GUD value, which means that there might be a high density of food remaining after foraging. The European badger, for example, might probably show a lower GUD value since they face less danger from being around wolves. We propose that this GUD value is calculated for every mesopredator inside and outside wolf territory. This way, we can have a predictor for risks in mesopredator species, and thus how much a mesopredator is changing their behaviour because of the wolf.

From the results, we can see that a lot of the research has been done in smaller areas. A study by Newsome et al. (2015) found that smaller areas might not be the best indicator for the effects of apex predators on mesopredators. For Western Europe, however, it might be good to also value these smaller area size studies since Western Europe also consists of many fragmented areas. When the areas are much smaller, the productivity might not be lower. Once the productivity is lower, coexistence between apex predators and mesopredators might increase since apex predators cannot reach big enough numbers to suppress mesopredators (Ritchie & Johnson, 2009).

To conclude, it is probable that the return of the wolf will cause some lethal interactions and behavioural changes. The effects on foxes and wild cats can be positive since they can both scavenge, and wolves can leave prey behind. Wolves have less competition with foxes and feral cats since they are much smaller predators, and their prey does not overlap a lot. Wolves can also provide a safer area because they scare away jackals, and jackals can be a bigger danger to foxes and cats than wolves. Since wolves can still kill foxes and cats, they will have to increase their vigilance near wolf areas. Badgers have been shown to not be affected by lynx. Wolves, however, are much larger and might pose a greater risk to them, so we expect badgers to decrease slightly with wolves being present. The effects on raccoons, mongoose, and martens will probably also be negative since they do not benefit from prey that are left behind, so they only face the risks of predation by wolves. These three species will then probably disperse more and try to avoid contact with wolves as much as possible, which will limit their abundance and distribution. These mesopredators could possibly be moving more towards cities and human settlements since wolves try to avoid these places as much as possible. Higher mesopredator abundance near human settlements can become a problem once they start to hunt livestock like chickens. Jackals can benefit from left behind prey but are a larger mesopredator of which the diet overlaps with that of the wolf. Since this competition can be high between both species, we expect a negative effect between wolf abundance and jackal abundance. Jackals will avoid wolves and migrate to areas with lower wolf densities. However, since coyotes are also observed to change their hunting style from hunting to scavenging, it can be expected that some jackals will turn to scavenging the left-behind prey. The individuals that will do this might increase their vigilance. With all mesopredators changing their behaviours, new dynamics will establish in the ecosystem. To be able to fully understand the effects Wolves have on all mesopredators, more research has to be done on all mesopredator and wolf interactions.

# References


Allen, B. L., Allen, L. R., Engeman, R. M., & Leung, L. K.-P. (2013). Intraguild relationships between sympatric predators exposed to lethal control: Predator manipulation experiments. *Frontiers in Zoology*, *10*(1), 39. https://doi.org/10.1186/1742-9994-10-39

Berger, K. M., & Gese, E. M. (2007). Does interference in competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, *76*(6), 1075–1085. https://doi.org/10.1111/j.1365-2656.2007.01287.x

Berger, K. M., Gese, E. M., & Berger, J. (2008). Indirect Effects and Traditional Trophic Cascades: A Test Involving Wolves, Coyotes, and Pronghorn. *Ecology*, *89*(3), 818–828. https://doi.org/10.1890/07-0193.1

Conner, L. M., & Morris, G. (2015). Impacts of Mesopredator Control on Conservation of Mesopredators and Their Prey. *PLOS ONE*, *10*(9), e0137169. https://doi.org/10.1371/journal.pone.0137169

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, *400*(6744), Article 6744. https://doi.org/10.1038/23028

Elmhagen, B., Ludwig, G., Rushton, S. P., Helle, P., & Lindén, H. (2010). Top predators, mesopredators and their prey: Interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology*, *79*(4), 785–794. https://doi.org/10.1111/j.1365-2656.2010.01678.x

Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecology Letters*, *10*(3), 197–206. https://doi.org/10.1111/j.1461-0248.2006.01010.x

Ferretti, F., Pacini, G., Belardi, I., ten Cate, B., Sensi, M., Oliveira, R., Rossa, M., Burrini, L., & Lovari, S. (2021). Recolonizing wolves and opportunistic foxes: Interference or facilitation? *Biological Journal of the Linnean Society*, *132*(1), 196–210. https://doi.org/10.1093/biolinnean/blaa139

Finke, D. L., & Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature*, *429*(6990), 407–410. https://doi.org/10.1038/nature02554

Gehrt, S. D., & Clark, W. R. (2003). Raccoons, Coyotes, and Reflections on the Mesopredator Release Hypothesis. *Wildlife Society Bulletin (1973-2006)*, *31*(3), 836–842.

Gordon, C. E., Feit, A., Grüber, J., & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings: Biological Sciences*, *282*(1802), 1–8.

Haswell, P. M., Kusak, J., & Hayward, M. W. (2017). Large carnivore impacts are context-dependent. *Food Webs*, *12*, 3–13. https://doi.org/10.1016/j.fooweb.2016.02.005

Jachowski, D. S., Butler, A., Eng, R. Y. Y., Gigliotti, L., Harris, S., & Williams, A. (2020). Identifying mesopredator release in multi-predator systems: A review of evidence from North America. *Mammal Review*, *50*(4), 367–381. https://doi.org/10.1111/mam.12207

Jiménez, J., Nuñez-Arjona, J. C., Mougeot, F., Ferreras, P., González, L. M., García-Domínguez, F., Muñoz-Igualada, J., Palacios, M. J., Pla, S., Rueda, C., Villaespesa, F., Nájera, F., Palomares, F., & López-Bao, J. V. (2019). Restoring apex predators can reduce mesopredator abundances. *Biological Conservation*, *238*, 108234. https://doi.org/10.1016/j.biocon.2019.108234

Kamler, J. F., Stenkewitz, U., & Macdonald, D. W. (2013). Lethal and sublethal effects of black-backed jackals on cape foxes and bat-eared foxes. *Journal of Mammalogy*, *94*(2), 295–306. https://doi.org/10.1644/12-MAMM-A-122.1

Krofel, M., Giannatos, G., Ćirović, D., Stoyanov, S., & Newsome, T. (2017). Golden jackal expansion in Europe: A case of mesopredator release triggered by continent-wide wolf persecution? *Hystrix*, *28*, 9–15. https://doi.org/10.4404/hystrix-28.1-11819

Kuijper, D. P. J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., & Jędrzejewska, B. (2013). Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography*, *36*(12), 1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x

Letnic, M., Greenville, A., Denny, E., Dickman, C. R., Tischler, M., Gordon, C., & Koch, F. (2011). Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography*, *20*(2), 343–353. https://doi.org/10.1111/j.1466-8238.2010.00600.x

Letnic, M., Ritchie, E. G., & Dickman, C. R. (2012). Top predators as biodiversity regulators: The dingo Canis lupus dingo as a case study. *Biological Reviews*, *87*(2), 390–413. https://doi.org/10.1111/j.1469-185X.2011.00203.x

Levi, T., & Wilmers, C. C. (2012). Wolves–coyotes–foxes: A cascade among carnivores. *Ecology*, *93*(4), 921–929. https://doi.org/10.1890/11-0165.1

Lourenço, R., Penteriani, V., Rabaça, J. E., & Korpimäki, E. (2014). Lethal interactions among vertebrate top predators: A review of concepts, assumptions and terminology. *Biological Reviews*, *89*(2), 270–283. https://doi.org/10.1111/brv.12054

Newsome, T. M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C. R., Dellinger, J. A., López-Bao, J. V., Peterson, R. O., Shores, C. R., Wirsing, A. J., & Ripple, W. J. (2016). Food habits of the world's grey wolves. *Mammal Review*, *46*(4), 255–269. https://doi.org/10.1111/mam.12067

Newsome, T. M., Greenville, A. C., Ćirović, D., Dickman, C. R., Johnson, C. N., Krofel, M., Letnic, M., Ripple, W. J., Ritchie, E. G., Stoyanov, S., & Wirsing, A. J. (2017). Top predators constrain mesopredator distributions. *Nature Communications*, *8*(1), Article 1. https://doi.org/10.1038/ncomms15469

Newsome, T. M., & Ripple, W. J. (2015). A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology*, *84*(1), 49–59. https://doi.org/10.1111/1365-2656.12258

Pasanen-Mortensen, M., Pyykönen, M., & Elmhagen, B. (2013). Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, *22*(7), 868–877. https://doi.org/10.1111/geb.12051

Proffitt, K. M., Grigg, J. L., Hamlin, K. L., & Garrott, R. A. (2009). Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. *The Journal of Wildlife Management*, *73*(3), 345–356. https://doi.org/10.2193/2008-210

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The Rise of the Mesopredator. *BioScience*, *59*(9), 779–791. https://doi.org/10.1525/bio.2009.59.9.9

Ralls, K., & White, P. J. (1995). Predation on San Joaquin Kit Foxes by Larger Canids. *Journal of Mammalogy*, *76*(3), 723–729. https://doi.org/10.2307/1382743

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Ripple, W. J., Wirsing, A. J., Wilmers, C. C., & Letnic, M. (2013). Widespread mesopredator effects after wolf extirpation. *Biological Conservation*, *160*, 70–79. https://doi.org/10.1016/j.biocon.2012.12.033

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Smith, D. W., Peterson, R. O., & Houston, D. B. (2003). Yellowstone after Wolves. *BioScience*, *53*(4), 330. https://doi.org/10.1641/0006-3568(2003)053[0330:YAW]2.0.CO;2

Soule, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M., & Hill, S. (1988). Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. *Conservation Biology*, *2*(1), 75–92.

Terborgh, J., & Estes, J. A. (Eds.). (2013). *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island press.

Trouwborst, A. (2010). Managing the Carnivore Comeback: International and EU Species Protection Law and the Return of Lynx, Wolf and Bear to Western Europe. *Journal of Environmental Law*, *22*(3), 347–372. https://doi.org/10.1093/jel/eqq013

Verma, A. K. (n.d.). *ECOLOGICAL BALANCE : AN INDISPENSABLE NEED FOR HUMAN SURVIVAL*.

Wallach, A. D., Ritchie, E. G., Read, J., & O'Neill, A. J. (2009). More than Mere Numbers: The Impact of Lethal Control on the Social Stability of a Top-Order Predator. *PLOS ONE*, *4*(9), e6861. https://doi.org/10.1371/journal.pone.0006861

Welch, R. J., Périquet, S., Petelle, M. B., & le Roux, A. (2017). Hunter or hunted? Perceptions of risk and reward in a small mesopredator. *Journal of Mammalogy*, *98*(6), 1531–1537. https://doi.org/10.1093/jmammal/gyx100

Wikenros, C., Jarnemo, A., Frisén, M., Kuijper, D. P. J., & Schmidt, K. (2017). Mesopredator behavioral response to olfactory signals of an apex predator. *Journal of Ethology*, *35*(2), 161–168. https://doi.org/10.1007/s10164-016-0504-6