When the predator becomes prey

How are mammalian mesocarnivore distribution and behaviour influenced by mammalian apex carnivores?

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Abstract

Mammalian carnivores can have a big influence on ecosystems through direct killing effects, the fear they impose on their prey and cascading effects down to lower trophic levels. Although most research focuses on apex carnivores, the ecological role of mesocarnivores receives increasingly more attention as well. However, mesocarnivores are influenced by apex carnivores themselves as well, whereby apex carnivores are known to kill mesocarnivores, a process called “intraguild predation” (IGP), exerting a form of population control. Recent research, suggests that the ecological effects of IGP are much greater than only population suppression. In this thesis I will review the influence that apex carnivores have on the distribution and behaviour of mesocarnivores. I found that the main motive for IGP seems to be competition for resources. As a result, to survive in an area with apex carnivores, mesocarnivores have to specialize on certain food sources and outcompete the apex carnivores. Furthermore, the safety match hypothesis suggests that mesocarnivores try to avoid apex carnivores both spatially and temporally. This seems to result in mesocarnivores choosing habitats and foraging times regardless of their prey, which can make it look as if the mesocarnivores are avoiding their prey. The presence of apex carnivores also appears to influence feeding behaviour and group behaviour. However, because it is difficult to perform an experimental study on this subject, it is difficult to rule out other hypotheses that could explain the observed patterns. Finally, I will discuss the possibility of humans playing a similar role as apex carnivores, which seems to be possible for some, but not for all mesocarnivore species. All in all, it looks like apex carnivores influence many aspects of mesocarnivore ecology , but since most studies on this subject are observational, it is difficult to draw hard conclusions about the extent of these influences.

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Introduction

Mammalian carnivores have been recognised as important drivers of ecological communities. They exert a top-down influence on the community through the direct killing of their prey, the fear they impose on their prey and the cascading effects down to the lower trophic levels (Roemer, Gompper, and Van Valkenburgh 2009; Donadio and Buskirk 2006). A famous example of such a fear-driven cascading effect on the ecosystem is found in Yellowstone Park, where wolves (*Canis lupus*) had been absent from the 1920's until the 1990's. In this period, elk (*Cervus elaphus*) had no risk of predation and could browse freely. When the wolves returned, the elk started to avoid areas with high risk of predation by wolves. This drastically changed the vegetation in these areas. Thus, the fear wolves imposed on the elk affected the ecosystem down to the lowest trophic levels (Beschta and Ripple 2010). Carnivores themselves, however, are also influenced by the rest of the community through bottom-up processes. Prey availability (Thompson and Gese 2010) and abiotic factors such as for example snow conditions (Pozzanghera et al. 2016) are important factors in determining the potential for carnivores to survive in a particular habitat.

Most research about mammalian carnivores has focused on the large, or apex, carnivores. However, mammalian mesocarnivores are also increasingly recognised as having an important ecological role (Roemer, Gompper, and Van Valkenburgh 2009; Pozzanghera et al. 2016; Kamler, Stenkewitz, and Macdonald 2013), a role that has only become bigger in recent years due to the human-induced decline in large carnivore populations (Prugh et al. 2009). Due to this decline in large carnivore populations, the ecological role of the mesocarnivore changed significantly in at least two important aspects. Firstly the decline in large carnivores has been accompanied by a steep rise in mesocarnivore populations, which has been named "mesopredator release" (Prugh et al. 2009; Clinchy et al. 2016; Suraci et al. 2016; Suraci, Clinchy, and Zanette 2017). Secondly, because in many areas the large carnivores have gone extinct, the mesocarnivores in those areas have become the top of the food chain (Roemer, Gompper, and Van Valkenburgh 2009; Prugh et al. 2009). As a result of these two changes, the impact of mesocarnivore populations on the rest of the community has increased significantly. In order to fully understand the consequences of these changes in mesocarnivore communities and their effects on the rest of the community it is important to understand the dynamics of mesocarnivore communities in the "original" communities, where large carnivores are still present.

Just like large carnivores, mesocarnivores exert a top-down influence on lower trophic levels, by direct killing of their prey and the trophic cascades accompanying this (Suraci et al. 2016; Roemer, Gompper, and Van Valkenburgh 2009; Kamler, Stenkewitz, and Macdonald 2013). Unlike large carnivores, that are at the top of the food chain in their habitat and therefore cannot cause any bottom-up influences, mesocarnivores can exert bottom-up influences on the large carnivores. However, just like all other animals, mesocarnivores are influenced by the rest of the community too. Similarly to large carnivores, mesocarnivores are influenced by bottom-up factors such as prey abundance and vegetation structure (Pozzanghera et al. 2016; Roemer, Gompper, and Van Valkenburgh 2009). Mesocarnivores are also under the influence of top-down control by the large carnivores (Thompson and Gese 2010; Heithaus and Heithaus 2001; Prugh et al. 2009). Thus, mesocarnivore communities are influenced by a combination of bottom-up and top-down factors that, together, are important in shaping mesocarnivore communities.

The most extreme form of top-down control of mesocarnivores by large carnivores is intraguild predation (IGP), which involves the direct killing of mesocarnivores by large carnivores (Roemer, Gompper, and Van Valkenburgh 2009; Donadio and Buskirk 2006). The most obvious effect of killing mesocarnivores in IGP-interactions is population suppression. However, research suggests that there are more effects of IGP on the mesocarnivore community that could be even more important. There are strong indications that not just the abundance, but also the distribution and behaviour of mesocarnivores are influenced by IGP (Heithaus and Heithaus 2001; Thompson and Gese 2010; Prugh et al. 2009; Suraci et al. 2016; Allen et al. 2015).

In this thesis I will discuss how the distribution and behaviour of mammalian mesocarnivores are influenced by mammalian apex carnivores. To try to answer this question I have conducted a literature study starting with two review studies on the ecology of mesocarnivores by Roemer et al. (2009) and Prugh et al. (2009), complemented with a couple of recent case studies on IGP-interactions between mesocarnivores and apex carnivores. From here on I read numerous case-studies cited in these articles and two theoretical studies about the effects of IGP by Heithaus and Heithaus (2001) and Holt and Polis (1997).
To delimit the subject, I will first discuss the definitions of mesocarnivores and apex carnivores. Secondly, I will discuss under which conditions IGP can occur. Subsequently, I will discuss the general effects of IGP on mesocarnivores and the effects on the spatial and temporal distribution of mescarnivores. Then, I will address other possible behavioural changes of mesocarnivores caused by IGP, concerning feeding behaviour and group behaviour. Finally, since there are no apex carnivores left in many antropogenic landscapes, I will discuss whether humans can play a similar role as an apex carnivore for mesocarnivores.

What is a mesocarnivore?

Mesocarnivores are generally described as midsized carnivores, or carnivores that are not the apex predator in their system, but there is no clear definition of what a mesocarnivore is and what a large or apex carnivore is. It greatly depends on the complete food web and the other carnivores that are present in a certain area. Still, there are several factors that enable us to classify certain carnivores as mesocarnivores and others as apex carnivores (Prugh et al. 2009).

The easiest categorization is by bodyweight. Most literature cites a weight range of about 1 to 15 kg to define mesocarnivores (Prugh et al. 2009). Every carnivore heavier than 15 kg would then be an apex predator. This definition indirectly also takes into account the role of the carnivore in the ecosystem, since large carnivores generally feed on larger prey too. For example in Kruger National Park, lions (*Panthera leo*) are the apex predator and wild dogs (*Lycaon pictus*) are a mesocarnivore according to their weight class. The main food sources for lions in this area are wildebeest (*Connochaetes taurinus*), buffalos (*Syncerus caffer*) and zebras (*Equus burchelli*) whereas wild dogs mostly feed on the much smaller impala (*Aepyceros melampus*) (Mills and Gorman 1997).

This definition is quite arbitrary, however because it is also very important what other carnivores are present in an area (Roemer, Gompper, and Van Valkenburgh 2009; Prugh et al. 2009). Coyotes (*Canis latrans*) can for example be the apex predator in areas where wolves have gone extinct, but a mesocarnivore in Yellowstone Park, where wolves do live (Prugh et al. 2009). In the same way, the above mentioned wild dogs are mesocarnivores in Kruger National Park, but the similarly sized domestic dogs (*Canis familiaris*) are effectively apex carnivores in the Great Indian Bustard Sanctuary (Vanak and Gompper 2010). Therefore it is also important to look at the position a carnivore has in the food web. Carnivores that are on the top of the food chain are then considered as apex carnivores and the carnivores below them are mesocarnivores.

If the only criterion would be the place in the ecosystem, this would mean that every carnivore could be an apex carnivore if no other carnivores are present. But, as stated above, large carnivores tend to have different diets than mesocarnivores (Prugh et al. 2009; Roemer, Gompper, and Van Valkenburgh 2009). Because of their smaller body sizes mesocarnivores are able to get enough nutrients from smaller prey, whereas larger carnivores should feed on larger prey to survive. Therefore, large prey benefit from the absence of large carnivores, whereas small prey benefit from the absence of mesocarnivores. This difference ensures that many mesocarnivores are not able to fully take over the role of apex carnivore if the real apex carnivore goes extinct (Roemer, Gompper, and Van Valkenburgh 2009). Another dietary difference is the amount of carnivory. Large carnivores are often hypercarnivorous, which means they feed almost solely on meat (Roemer, Gompper, and Van Valkenburgh 2009). Mesocarnivores however are often more diverse in feeding habits. Different fox species for example, can, among other things, feed on meat, fruit and insects (Kamler, Stenkewitz, and Macdonald 2013; Roemer, Gompper, and Van Valkenburgh 2009). However, black bears (*Ursus americanus)* are clearly apex carnivores although they are not hypercarnivorous either (Allen et al. 2015; Suraci, Clinchy, and Zanette 2017).

All in all, to define mesocarnivores and apex carnivores, body size, diet and the position in the food web should all be taken into account. A rule of thumb can be that apex carnivores are heavier than 15 kg, at the top of the food chain and hypercarnivorous, whereas mesocarnivores are 1-15 kg, not at the top of the food chain and more omnivorous. But, as stated before, there are many exceptions. For very large carnivores such as wolves, bears and lions and quite small carnivores such as fishers (*Martes pennanti*) and raccoons (*Procyon lotor*) it is quite clear, but for intermediate carnivores such as badgers (*Meles meles*), coyotes and dogs it depends on the rest of the ecosystem whether they are apex carnivores or mesocarnivores. Finally, it is important to note that there can be several different species of mesocarnivores and apex carnivores in one ecosystem.

When does intraguild predation occur?

Intraguild predation (i.e. apex carnivores killing mesocarnivores) is very common in ecosystems where apex carnivores and mesocarnivores live together (Heithaus and Heithaus 2001). Donadio and Buskirk (2006) propose three main motives for apex carnivores to engage in IGP: to reduce competition, to protect themselves or their young from a potential aggressor or just for the nutritional benefits.

The first hypothesis that IGP mainly takes place to reduce competition is the one most used in the literature (Donadio and Buskirk 2006). This can only be a motive if there is a dietary overlap between apex carnivores and mesocarnivores. When two carnivores compete for the same basal resource and one of them, the apex carnivore, is dominant in the IGP-interactions this is called “asymmetrical intraguild predation” (Heithaus and Heithaus 2001). This is for example the case in the Pinon Canyon Maneuver Site, Colorado, where the main cause of mortality for the population of swift foxes (*Vulpes velox*) is predation by coyotes, one of the apex predators. Furthermore, they, among other things, both feed on northern grasshopper mice (*Onychomys leucogaster*), Ord’s kangaroo rat (*Dipodomys ordii*) and deer mice (*Peromyscus maniculatus*) (Thompson and Gese 2010). This is a clear example of asymmetrical IGP. Most examples of IGP are asymmetrical, since competition for food is the most common motive for IGP and the apex carnivore is generally always able to kill the mesocarnivore (Donadio and Buskirk 2006).

The second hypothesis states that the nutritional benefits can be a motive to engage in IGP. But it appears that mesocarnivores that are killed in IGP-interactions are usually not eaten (Donadio and Buskirk 2006). Therfore this does not seem to be a very important motive. However, there is some evidence that apex carnivores do eat mesocarnivores. Firstly, there is some anecdotal evidence of apex carnivores killing mesocarnivores, seemingly with the purpose of eating them (White et al. 2002). They observed a pack of wolves killing a couple of young wolverines (*Gulo gulo*). The researchers thought the wolves ate them, but they did not see the actual eating process (White et al.

2002). Secondly, there is some evidence from dietary analysis. Analysis of wolf faeces in British Columbia showed traces of, among other things, martens (*Martes americana*) and minks (*Mustela vison*) (Darimont et al. 2004). These observations indicate that there are situations in which apex carnivores kill mesocarnivores with the purpose of eating them.

Finally, carnivores could kill each other to protect themselves or their young. Since most IGP-interactions are asymmetrical however, it is unlikely that apex carnivores want to protect themselves from mesocarnivores. Therefore, it can only be a motive to protect their young or when there is mutual killing. An example of a carnivore killing a similar sized or even bigger carnivore is found in north-eastern Minnesota. There are reports of wolves killing adult black bears in that area, so an apex carnivore killing another apex carnivore (Rogers and Mech 1981). There are also observations of IGP when the most likely motive was protection of their young. White et al. observed wolves killing a wolverine in Alaska, which was probably to protect their den (White et al. 2002).

Although resource overlap seems to be the main reason to engage in IGP, this does not mean that there will always be IGP when two carnivores live in the same area and have a partly overlapping diet. There are costs involved with IGP: it costs energy to kill other animals and there is always the risk that you will be injured or killed yourself. Donadio and Buskirk (2006) analysed approximately 100 cases of IGP to try to find which factors may increase or decrease the chance that two carnivores will get into a lethal fight. A very important factor seems to be the body size. If the body size difference is too small, the risk is too big and if the body size difference is too big the benefits of killing the competitor are too small. Therefore most IGP-events took place when the larger carnivore was 2-5.4 times bigger than the small one. The predatory habits of the carnivores also seemed to play a role. Hypercarnivorous animals have better developed weaponry to kill animals and are also more likely to use that weaponry to kill other carnivores (Donadio and Buskirk 2006). Finally, the relatedness seems to play a role. If two species are phylogenetically more related, they are more likely to attack each other than when they are not very related (Donadio and Buskirk 2006). A possible explanation for this is that the more related animals are, the more likely they occupy a comparable ecological niche. Not only dietary overlap will be bigger in related species but also for example habitat preferences (Donadio and Buskirk 2006).

Although it is not always very clear why IGP occurs, most of the IGP-confrontations seem to result from dietary overlap and therefore competition for the same resources. Other possible motives can be protection or the nutritional benefits of killing and eating mesocarnivores. Additional factors that can increase the chance of lethal encounters are an intermediate body size difference, the predatory habits and the amount of relatedness.

Possible effects of intraguild predation on mesocarnivores

Specialize and outcompete

As stated above, IGP mostly takes place to eliminate possible competitors that have partly the same diet. This means it’s in fact a mechanism of competition. There are two kinds of competition, namely exploitative competition and interference competition (Krebs 2014). In exploitative competition different animals compete for resources that are short in supply, for example two different carnivores that try to be a more efficient hunter for a shared prey species. The competitor that is competitively superior will be able to obtain relatively more resources. In interference competition one competitor tries to harm another competitor regardless the abundance of the prey. IGP is an extreme example of interference competition where the apex carnivore kills the mesocarnivore, its competitor (Donadio and Buskirk 2006).

Because of their smaller size, mesocarnivores will (almost) always lose interference competition when they have to compete with an apex carnivore (Donadio and Buskirk 2006). If they nonetheless want to survive in these regions they have two options, namely to outcompete the apex carnivores or to reduce dietary overlap.

The first possible strategy is to outcompete the apex carnivores in the exploitative competition, or in other words, become more efficient hunters than the apex carnivores (Heithaus and Heithaus 2001; Holt and Polis 1997; Suraci, Clinchy, and Zanette 2017). Theoretical models suggest that if the mesocarnivores would not be able to outcompete the apex predators, they will not be able to survive in a habitat where there is a relatively high risk of being killed in an IGP-interaction (Heithaus and Heithaus 2001).

This intrinsic and necessary difference in effectiveness of hunting between mesocarnivores and apex carnivores, in combination with their difference in body size, has some important implications. In low productive environments with relatively few resources, mesocarnivores will be able to outcompete the apex carnivores due to their smaller size and higher effectiveness. However, in high productive habitats, there are enough resources available for the apex carnivores to be able to suppress and partly exclude mesocarnivores from the habitat (Holt and Polis 1997).

The higher efficiency of mesocarnivores has another major implication. When apex predators disappear from an ecosystem, which happened a lot in the past centuries due to human influences, the mesocarnivores are released from the top-down control exerted by the apex carnivores. This often results in a very big increase of mesocarnivore population size, a process called “mesopredator release”. Because of the higher hunting efficiency of these mesocarnivores, this population growth of the mesocarnivores means the hunting pressure on the prey population increases even more, causing direct prey populations to collapse, which has cascading effects to lower trophic levels (Heithaus and Heithaus 2001; Roemer, Gompper, and Van Valkenburgh 2009; Suraci, Clinchy, and Zanette 2017; Prugh et al. 2009). An example of this process is found in the Strzelecki desert in Australia. The dingo (*Canis dingo*) is the main apex carnivore in this region. A dingo barrier fence creates one dingo-free and one dingo-rich area. In the dingo-free area the abundance of the red fox (*Vulpes vulpes*), a mesocarnivore, is much higher than in the dingo-rich area where the foxes are almost completely absent. The population of the little button-quail (*Turnex velox*), an important prey species of the red fox and to a lesser extent the dingo, shows the exact opposite pattern, namely a high abundance in the dingo-rich area and a low abundance in the dingo-free area (Gordon, Moore, and Letnic 2017). This is an example where the absence of an apex carnivore facilitates population growth of a mesocarnivore, which in turn causes prey abundance to decline.

Thus far I have only discussed the possibility of outcompeting the apex carnivores. Mesocarnivores can also survive however, by reducing dietary overlap. Mesocarnivores can achieve this by specializing on another food resource than the apex carnivore, or if they live in an area where another prey species preferred by the apex carnivore (Heithaus and Heithaus 2001). After all, if there is little dietary overlap, the chance of IGP-interactions decreases too (Donadio and Buskirk 2006).

Summarizing, to survive in an area with high IGP, mesocarnivores have to be more effective hunters than the apex carnivores or choose other main food sources. Because they are often more effective hunters than apex carnivores, mesocarnivores are able to survive in lower quality habitats. Their effectiveness can also cause them to have devastating effects on prey populations when the apex carnivore goes extinct.

Safety match hypothesis

When mesocarnivores are not able to outcompete the apex carnivore, they have to try to increase their fitness in another way. A strategy they can use to achieve this, is reducing the risk of encountering an apex predator. This is called safety matching (Heithaus and Heithaus 2001; Thompson and Gese 2010). Safety matching can be done both spatially and temporally (Suraci, Clinchy, and Zanette 2017).

Spatial

The most common method of safety matching is to avoid areas with many apex predators. Many case-studies showed mesocarnivores avoiding areas that included possibly dangerous apex carnivores (Allen et al. 2015; Kamler, Stenkewitz, and Macdonald 2013; Mills and Gorman 1997; Suraci, Clinchy, and Zanette 2017).

One of the most striking examples was described by Mills and Gorman (1997). They investigated the distribution of wild dogs in the Kruger National Park in South Africa. In this park, wild dogs are mesocarnivores and lions, and to a lesser extent spotted hyenas (*Crocuta crocuta*), are the main apex carnivores, of which the lions are known to be an important source of dog mortality (accounting for around 40% of dog mortality) (Mills and Gorman 1997). The dogs live in packs of approximately 8-10 individuals that inhabit territories of 400-900 square kilometres. The main prey species of the dogs are the impala (80% of eaten biomass) and the kudu (*Tragelaphus strepsiceros*) (8% of eaten biomass). The lions mostly feed on other species, like zebra, buffalo and wildebeest.

When they compared the average dog abundancy with the average prey biomass in the same area, they found the counterintuitive result that a low average prey biomass was correlated with a high dog abundancy and vice versa (Figure 1). When they compared the different types of habitat, Mills and Gorman (1997) found that some habitats that were preferred by impala were avoided by the dogs. There was however a strong preference of lions for the same regions that were preferred by the impala and avoided by the dogs. Thus, the counterintuitive negative correlation between dogs and prey biomass seemed to be explained by an avoidance of lion-rich areas by the dogs, while the impala were higher in abundance in the lion-rich areas.

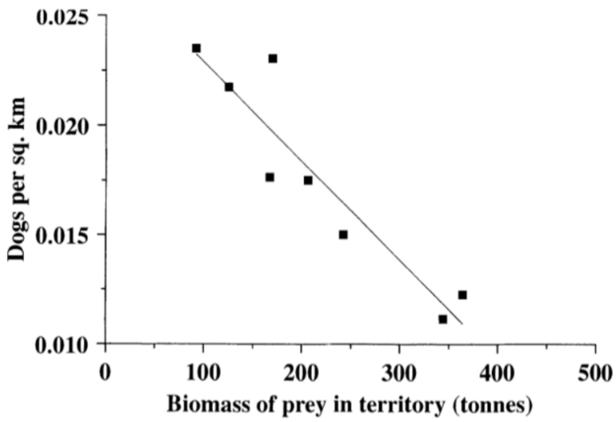

Figure 1. Relationship between wild dog density per territory and prey biomass (impala + kudu) in that territory. Figure and text adapted from Mills and Gorman (1997). A high prey biomass is correlated with a low dog density.

It is not clear however if the impala prefer the lion-rich habitats because the dogs avoid them or if they prefer them because they like the resources in the habitat better. It very well could be that the impala choose to go to the lion-rich habitats because they are safety-matching themselves. As far as I know, there are no real experimental designs on this subject, so real cause and effect conclusions cannot be drawn, but numerous case-studies suggest that mesocarnivores avoid apex carnivore-rich habitats which can lead them to also avoid prey-rich habitats (Allen et al. 2015; Kamler, Stenkewitz, and Macdonald 2013; Mills and Gorman 1997; Suraci, Clinchy, and Zanette 2017).

For the spotted hyenas a comparable trend was observed, however this trend was not nearly as strong. This can be explained by the fact that hyenas are not an important cause of mortality for the dogs, but are probably just perceived as annoying by the dogs. So it seems necessary to have real IGP to get such strong effects (Mills and Gorman 1997).

Another method to safety match spatially is by choosing habitats where possible carnivores can be detected at large distances. Thompson and Gese (2010) did observations on swift foxes and coyotes in the Pinon Canyon Maneuver Site in Colorado where different land uses led to different habitats that form a “natural experimental design”. The foxes, that are the mesocarnivores, and the coyotes, the apex carnivores, mostly use the same basal resources.
They came to similar conclusions as Mills and Gorman (1997) concerning a positive correlation of coyote abundance with prey abundance and a negative correlation of fox abundance with coyote abundance, and therefore a negative correlation of fox abundance with prey abundance as well. Additionally, they found that swift fox abundance showed a negative correlation with habitat complexity. In areas where the grass was higher on average, the swift fox abundance was lower. Since swift foxes rely mainly on eyesight to spot possible dangers, they probably avoid these areas with dense vegetation to decrease the chance of getting surprised by an attacking coyote.

Generally, the common theory is that predators follow the resource match hypothesis, which states that predator abundance should be highest where prey abundance is highest. The apex predators in the examples above seem to follow this theory quite well (Mills and Gorman 1997; Thompson and Gese 2010). The safety matching behaviour however can result in the counterintuitive result that mesocarnivores are least abundant where their prey is most abundant. This can be explained by mesocarnivores escaping IGP by choosing habitats where apex carnivores are less abundant or where they are more easily detectable.

Temporal

A decreased chance of IGP can also be achieved by temporal safety matching. Since many carnivores are either mostly diurnal or mostly nocturnal, being active at moments when apex carnivores are not active can greatly decrease the chance of being killed in IGP-interactions.

Suraci et al. (2017) found an example of this temporally safety matching behaviour in raccoons at Vancouver island in Canada, where black bears are one of the apex carnivores. The two carnivore species had big dietary overlap in the intertidal. They found similar results as the studies mentioned above regarding spatial safety matching. When they compared the temporal activity of the raccoons with that of raccoons in apex carnivore-free habitats, they found that raccoons were more nocturnal in the presence of the largely diurnal bears. This seems to indicate that raccoons try to avoid bear predation by being active at moments the bears are not active (Suraci, Clinchy, and Zanette 2017).

A side note to this result is that bears also were an important exploitative competitor of raccoons, which was shown by the fact that higher mesocarnivore abundances in regions where bears were absent did not lead to a lower prey abundance. In other words, bears seemed to be just as effective a hunter as raccoons. Suraci et al.’s (2017) results can therefore also be caused by the strong exploitative competition of the bears, rather than by interference competition in the form of IGP.

To conclude, mesocarnivores can escape IGP and the corresponding negative fitness effects by decreasing the chance of encountering an apex carnivore. In order to achieve this, they can choose habitats with few apex carnivores, habitats where they can easily detect and escape the apex carnivores or by being active at moments when apex carnivores are not.

Other behavioural changes

Apart from their choice of habitat, mesocarnivores are known to change their behaviour in several other ways in the presence of aggressive apex carnivores. They have been observed to change their feeding behaviour (Allen et al. 2015; Suraci et al. 2016; Prugh et al. 2009), their social behaviour (Kamler, Stenkewitz, and Macdonald 2013; Prugh et al. 2009) and their territory sizes (Kamler, Stenkewitz, and Macdonald 2013).

Feeding behaviour

The effects of the presence of apex carnivores on feeding and foraging behaviour of mesocarnivores are relatively well described. Allen et al. (2015) studied the effects of pumas (*Puma concolor*) and black bears, both apex carnivores, on the scavenging behaviour of an array of mesocarnivore species, including fishers, coyotes and bobcats (*Lynx rufus*). Their experimental design included observations of several scavengers on freshly killed deer carcasses, and observations on the carcasses of deer that were hit by a car and subsequently prepared and placed on certain locations within a day. The conclusions were that the presence of pumas near a carcass did not affect the mesocarnivore presence, but did lower the total time mesocarnivores fed on a carcass. The average duration of a single feeding-bout also decreased in the presence of pumas. For black bears the results were even more convincing. Mesocarnivore presence was 3 times lower when black bears were present and the total feeding time diminished from 270 minutes with bears absent to 6 minutes with bears present. This study indicates that mesocarnivores spend less time eating in the presence of apex carnivores, probably because they are more vigilant and do not want to stay in the same spot for too long. An alternative explanation for the decreased feeding time in the presence of bears could be that the bears spot the carcasses faster and they eat everything before the mesocarnivores even have a chance to feed on the carcass (Allen et al. 2015).

More studies show a comparable influence of apex carnivores on mesocarnivore behaviour. Suraci et al. (2016) have performed one of the few truly experimental studies on this subject, in the Gulf islands. They used playbacks of the sound of domestic dogs, which are the only apex predators left in that area, to test if raccoons would change their foraging behaviour in the intertidal when they thought dogs were present. As a control they used playbacks of non-predatory animals namely harbour seal (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*). The results of these experiments are shown in figure 2. The figure shows that when the dog sounds were played back, more than half of the racoons left the intertidal immediately and if they did stay, their foraging time decreased dramatically compared to the control group. When the playbacks were repeated for a whole month, both the average time spent in the intertidal and the proportion of time in the intertidal spent foraging decreased significantly compared to the control group. Because only playbacks were used, this study shows that just the fear of an apex carnivore can have a significant effect on mesocarnivores, that is to say, no direct killing is needed to achieve this effect.

The effects on the raccoons' prey were also remarkable. Within a month prey abundance in the intertidal was similar to the abundance on islands that were not inhabited by raccoons at all (Suraci et al. 2016). In other words, the fear of the apex carnivores can completely diminish the effect mesocarnivores have on their prey.

These studies show that the presence of large carnivores, or even just the perceived presence of large carnivores can alter the feeding and foraging behaviour of mesocarnivores drastically, which can largely restore the prey populations, even if the mesocarnivore abundance is not altered.

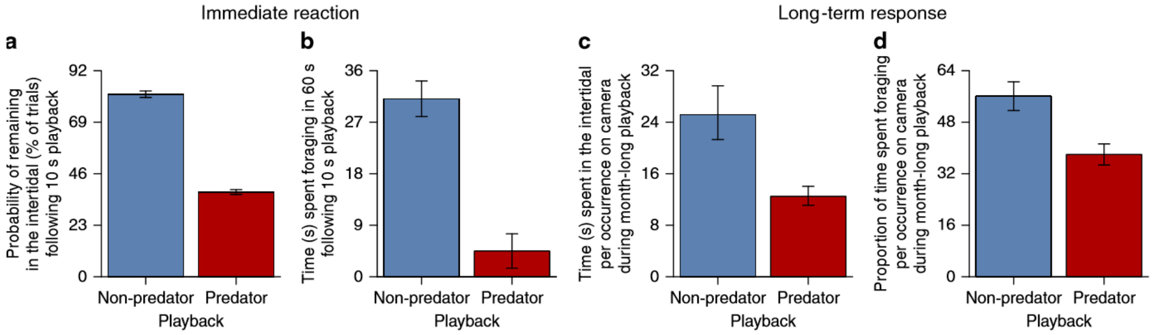

Figure 2. The effects of playbacks of predatory and non-predatory animals on mesocarnivore foraging. **a)** Probability of remaining in the intertidal, immediately after hearing the playback. **b)** Time spent foraging, immediately after the playback. **c)** Time spent in the intertidal per occurrence, during month-long playback. **d)** Proportion of time in the intertidal spent foraging, during month-long playback. Figure and text adapted from Suraci et al. (2016). Predatory playbacks reduce both time spent in the intertidal and proportion of time in the intertidal spent foraging. The effects are both short-term and long-term.

Group Behaviour

Group behaviour of mesocarnivores can also be influenced by the presence of apex carnivores. Group sizes and home ranges can differ between populations that live in the presence and absence of apex carnivores respectively (Kamler, Stenkewitz, and Macdonald 2013; Prugh et al. 2009). Kamler et al. (2013) compared these traits in cape foxes (*Vulpes chama*) and bat-eared foxes (*Otocyon megalotis*) that live in the presence of black-backed jackals (*Canis mesomelas*) with foxes that live in the absence of jackals. They describe the foxes as small carnivores and the jackals as mesocarnivores, but since the IGP-relationship is approximately the same I think it is safe to assume that the results can also apply to an apex carnivore–mesocarnivore relationship.

Bat-eared foxes live in groups and showed an increase in group size in the presence of jackals. Previous research suggests that bat-eared foxes in larger groups have got a lower predation risk so the researchers conclude that the larger groups are an adaptive response to increase their fitness (Kamler, Stenkewitz, and Macdonald 2013). However, there was a big difference in food source (termites) availability in the two different regions, which caused the bat-eared fox density to be higher in the jackal-rich habitat. This could have influenced the group size as well and therefore these conclusions should be handled with care.

For the cape foxes the home ranges were bigger in the area containing jackals than in the area where jackals were absent. This could be explained by the foxes avoiding jackal-rich regions and therefore needing bigger home ranges to be able to gather enough food. An alternative explanation could be that the higher cape fox density in the jackal-poor area causes the home ranges to be smaller, a relationship that has been shown before (Kamler, Stenkewitz, and Macdonald 2013).
Finally, because both fox species seemed to avoid the jackal-rich regions their mutual spatial relationship changed. Because they both were driven away from some regions they tended to inhabit the same regions together. So because of the fear of the larger carnivores they lived in much closer proximity to each other.

So, it seems like the group sizes of smaller carnivores can increase to protect themselves from predation of larger carnivores and home ranges can increase to lower the chance of running into larger carnivores. However, more experimental studies should be performed to rule out alternative explanations, such as the relationship between population size and home range size.

Can humans replace the role of apex carnivores?

The effect of apex carnivores on mesocarnivores seems to be very diverse and involving various aspects of the mesocarnivore ecology. Nowadays, due to urbanisation, habitat loss and hunting, many carnivores have gone (regionally) extinct (Prugh et al. 2009; Roemer, Gompper, and Van Valkenburgh 2009). As mentioned before, this loss of top-down control on mesocarnivore populations can lead to mesopredator release, which can have deleterious effects on the prey population (Prugh et al. 2009). On the other hand, humans are far more lethal for many animals than most apex carnivores and can have a very large impact on ecosystems (Clinchy et al. 2016). This brings up the question whether humans can, at least partially, take over the role of apex carnivores in exerting top-down control of mesocarnivores.

There are numerous factors that cause the influence of humans to be fundamentally different than that of apex carnivores. For example, it seems like some mesocarnivores, like raccoons and foxes, thrive in urbanised regions (Prugh et al. 2009; Recio et al. 2015). Possible explanations for this positive effect of urbanisation can be that apex carnivores are often absent in those areas or that humans add a lot of resources to the ecosystem through, for example, trash, pet food and crops (Prugh et al. 2009). Furthermore, humans are usually not competitors for the same basal resources. Suraci et al. (2016) predict that numerical suppression of mesocarnivores through removal programs or hunting will not restore ecosystem stability. Because the individuals that were not removed can keep on foraging and feeding unhindered where and when they want, the researchers do not think this will have the same ecosystem-level impact as true apex carnivore top-down control. They state that the presence of apex carnivores and the so called “landscape of fear” they create are vital to suppress deleterious mesocarnivore effects (Suraci et al. 2016).

Other research suggests that humans can certainly have similar effects as apex carnivores. Clinchy et al. (2016) performed a comparable playback experiment as Suraci et al. (2016) in the UK. They placed plastic pails that contained food hidden in sand, near the burrows of badgers. They subsequently used playback experiments with sounds of harmless animals (sheep), apex carnivores (brown bears (*Ursus arctos*) and wolves), and humans. Dogs were used as a positive control that badgers should almost certainly fear. Bears and wolves have been extinct in Britain since 900 AD and 1700 AD respectively. They found that human sounds had by far the greatest impact on the badgers’ foraging behaviour compared to the sheep sounds. Among the effects were a delay of foraging until the human sounds had stopped completely, increased vigilance, fewer badgers visiting the food patches and fewer visits per badger (Clinchy et al. 2016).

Clinchy et al. (2016) conclude that the return to Britain of apex carnivores and the fear they initiate would not restore the ecosystem to the original stable state because the mesocarnivores are already in fear of humans. They also conclude that humans are capable of inducing much more fear than natural apex carnivores. However, I do not agree with them that that conclusion can be drawn on the basis of their experiment, since they only tested the amount of fear in a region where apex carnivores have been absent for centuries. To be able to draw such a conclusion, an experiment is needed that compares mesocarnivore fear of humans with mesocarnivore fear of apex carnivores in a region where both humans and apex carnivores are a threat to mesocarnivores.

Another, indirect way in which humans can induce fear in mesocarnivores is in rural areas with many, relatively free ranging, domestic dogs (Vanak and Gompper 2010). Domestic dogs in the Great Indian Bustard Sanctuary are an important cause of mortality for Indian foxes (*Vulpes bengalensis*). When Vanak and Gompper investigated the factors that determine Indian fox distribution, they found that the foxes live in different habitats than the dogs. This seems to be partly due to a difference in habitat preferences, but also partly because the foxes avoid the dogs. Thus, the foxes seem to safety-match to reduce the risk of encountering an apex carnivore, namely domestic dogs, just like with natural apex carnivores. A side note to this conclusion is that it is difficult to distinguish the effects of dogs from the effects of humans since dogs generally live together with humans. Therefore, this result could also be caused by human-induced fear instead of, or in addition to, dog-induced fear.

Humans influence mesocarnivore communities in a direct way by hunting and killing. Besides that, the indirect role of humans with respect to shaping mesocarnivore communities can go two ways. For some mesocarnivores that are comfortable in urban environments, humans can have a positive influence on their population by removing apex carnivores and adding food resources to the ecosystem. For other, more timid mesocarnivores, humans can exert comparable and maybe even larger influences on the mesocarnivore community than apex carnivores, by inducing fear. Furthermore, domestic animals like dogs can also act as an apex carnivore and thereby influence mesocarnivore distribution and behaviour.

Synthesis

Interactions between apex carnivores and mesocarnivores are important factors in shaping the mesocarnivore community and, through cascading effects, the rest of the community. Apex carnivores probably perceive mesocarnivores as an opponent or a threat and therefore engage in intraguild predation. Intraguild predation has far reaching consequences on the mesocarnivore community. The most obvious one is the population suppressing effect, but there seem to be other effects as well. One of these effects is that mesocarnivores are forced to specialize themselves, to outcompete the apex carnivores to sustain a viable population. Secondly, the distribution of mesocarnivores is altered in such a manner that the chance of encountering an apex carnivore is minimised. This can be done by avoiding areas that are inhabited by many apex carnivores, by avoiding habitats in which it is difficult to spot apex carnivores or by being active on moments that apex carnivores are not active. Furthermore, mesocarnivores seem to be more vigilant in the presence of apex carnivores and therefore spend less time feeding or foraging. Finally, group size and territory size can increase, respectively to protect against apex carnivores and to have more chance of avoiding apex carnivores. The above mentioned effects of apex carnivores are not only achieved due to direct killing, but also for a large part by the fear apex carnivores inspire in mesocarnivores.

A major side note to the conclusions is that these are mostly drawn on the basis of observational studies in natural, and therefore uncontrollable, habitats. The conclusions are mostly drawn on the basis of correlations between the presence or absence of apex carnivores and specific types of behaviour. Many other factors can play a role as well, such as abiotic factors, vegetation properties and prey species. The “natural experiments” were designed in a way that these factors were ruled out as much as possible. Together with these empirical studies, theoretical models predict similar results. Therefore it seems legitimate to conclude that apex carnivores are at least part of the explanation for the observed patterns. To better understand the effects of apex carnivores and IGP on the mesocarnivore community, more experimental studies should be set up to test causality. Possible experimental studies on this subject could involve inspiring fear by making mesocarnivores think there are apex carnivores present, in a similar way as Suraci et al. (2016) and Clinchy et al (2016). Another possibility for research on this subject is provided by the recent resurgence of wolves in Germany, Denmark and the Netherlands (Kuijper et al. 2016). This could be used as a good natural experiment to observe the effects of apex carnivores, by comparing areas where the wolves have returned recently with areas where they are still absent or areas where they have been present for a long time.

With the decline of apex carnivore populations over the last centuries, mesocarnivores have benefited from the release of this top-down control. This has led to mesopredator release and the subsequent cascading effects on the rest of the ecosystem. For some mesocarnivores it seems that humans or their domestic animals can take over some of the fear driven effects, but for other mesocarnivores humans may even be accelerating the mesopredator release. Therefore, it seems likely that, with the continued decline of apex carnivores and increased urbanisation in many regions, certain mesocarnivore populations will continue to grow even further, posing an increasing pressure on the rest of the ecosystem.

To conclude, mesocarnivore communities are influenced by apex carnivores in several different ways. With the decline of worldwide apex carnivore populations, mesopredator release is an increasing problem. Population suppression alone does not seem to be a viable solution to maintain stable ecosystems. In many ecosystems, restoration of apex carnivore populations may be the only way to maintain the complicated and versatile effects apex carnivores can exert on mesocarnivore communities. In order to fully understand the complex effects of the apex carnivore-mesocarnivore interaction, more experimentally designed studies should be conducted on this subject.

References

Allen, Maximilian L., L. Mark Elbroch, Christopher C. Wilmers, and Heiko U. Wittmer. 2015. "The Comparative Effects of Large Carnivores on the Acquisition of Carrion by Scavengers." *The American Naturalist* 185 (6): 822–33.

Beschta, Robert L, and William J Ripple. 2010. "Recovering Riparian Plant Communities with Wolves in Northern Yellowstone , U . S . A ." *Restoration Ecology* 18 (380): 380–89.

Clinchy, Michael, Liana Y. Zanette, Devin Roberts, Justin P. Suraci, Christina D. Buesching, Chris Newman, and David W. Macdonald. 2016. "Fear of the Human 'super Predator' Far Exceeds the Fear of Large Carnivores in a Model Mesocarnivore." *Behavioral Ecology* 27: arw117.

Darimont, Author C T, M H H Price, N N Winchester, Source Journal, and No Nov. 2004. "Predators in Natural Fragments : Foraging Ecology of Wolves in British Columbia's Central and North Coast Archipelago." *Journal of Biogeography* 31 (11): 1867–77.

Donadio, Emiliano, and Steven W Buskirk. 2006. "Diet, Morphology, and Interspecific Killing in Carnivora." *The American Naturalist* 167 (4): 524–36.

Gordon, Christopher E, Ben D Moore, and Mike Letnic. 2017. "Temporal and Spatial Trends in the Abundances of an Apex Predator, Introduced Mesopredator and Ground-Nesting Bird Are Consistent with the Mesopredator Release Hypothesis." *Biodiversity and Conservation* 26 (6). Springer Netherlands: 1445–62.

Heithaus, Michael R, and Michael R Heithaus. 2001. "Habitat Selection by Predators and Prey in Communities with Asymmetrical Intraguild Predation." *Oikos* 92 (3): 542–54.

Holt, R.D., and G.A. Polis. 1997. "A Theoretical Framework for Intraguild Predation." *American Naturalist*, 745–64.

Kamler, Jan F., Ute Stenkewitz, and David W. Macdonald. 2013. "Lethal and Sublethal Effects of Black-Backed Jackals on Cape Foxes and Bat-Eared Foxes." *Journal of Mammalogy* 94 (2): 295–306.

Krebs, C. 2014. "Species Interactions 1: Competition." In *Ecology: The Experimental Analysis of Distribution and Abundance.*, Sixth Edit, 173–97. Harlow: Pearson.

Kuijper, D.P.J, B Elmhagen, S Chamaille, H Sand, K Lone, and J P G M Cromsigt. 2016. "Paws without Claws ? Ecological Effects of Large Carnivores in Anthropogenic Landscapes." *Proceedings of the Royal Society B* 283: 20161625.

Mills, Michael G L, and Martyn L Gorman. 1997. "Society for Conservation Biology Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park." *Conservation Biology* 11

(6): 1397–1406.
Pozzanghera, C.B., K.J. Sivy, M.S. Lindberg, and L.R. Prugh. 2016. “Variable Effects of Snow Conditions across Boreal Mesocarnivore Species.” *Canadian Journal of Zoology* 94 (10): 697–705.
Prugh, Laura R., Chantal J. Stoner, Clinton W. Epps, William T. Bean, William J. Ripple, Andrea S. Laliberte, and Justin S. Brashares. 2009. “The Rise of the Mesopredator.” *BioScience* 59 (9): 779–91.
Recio, Mariano R., Carmen M. Arija, Sara Cabezas-Díaz, and Emilio Virgós. 2015. “Changes in Mediterranean Mesocarnivore Communities along Urban and Ex-Urban Gradients.” *Current Zoology* 61 (5): 793–801.
Roemer, Gary W., Matthew E. Gompper, and Blaire Van Valkenburgh. 2009. “The Ecological Role of the Mammalian Mesocarnivore.” *BioScience* 59 (2): 165–73.
Rogers, Lynn L, and L David Mech. 1981. “Interactions of Wolves and Black Bears in Northeastern Minnesota.” *Journal of Mammalogy* 62 (2): 434–36.
Suraci, Justin P., Michael Clinchy, Lawrence M. Dill, Devin Roberts, and Liana Y. Zanette. 2016. “Fear of Large Carnivores Causes a Trophic Cascade.” *Nature Communications* 7. Nature Publishing Group: 10698.
Suraci, Justin P., Michael Clinchy, and Liana Y. Zanette. 2017. “Do Large Carnivores and Mesocarnivores Have Redundant Impacts on Intertidal Prey?” *PLoS ONE* 12 (1): 1–19.
Thompson, Craig M, and Eric M Gese. 2010. “Food Webs and Intraguild Predation : Community Interactions of a Native Mesocarnivore.” *Ecology* 88 (2): 334–46.
Vanak, Abi Tamim, and Matthew E. Gompper. 2010. “Interference Competition at the Landscape Level: The Effect of Free-Ranging Dogs on a Native Mesocarnivore.” *Journal of Applied Ecology* 47 (6): 1225–32.
White, Kevin S., Howard N. Golden, Kris J. Hundertmark, and Gerlad R. Lee. 2002. “Predation by Wolves, *Canis lupus*, on Wolverines, *Gulo gulo*, and an American Marten, *Martes americana*, in Alaska.” *Canadian Field-Naturalist* 116 (1): 132–34.