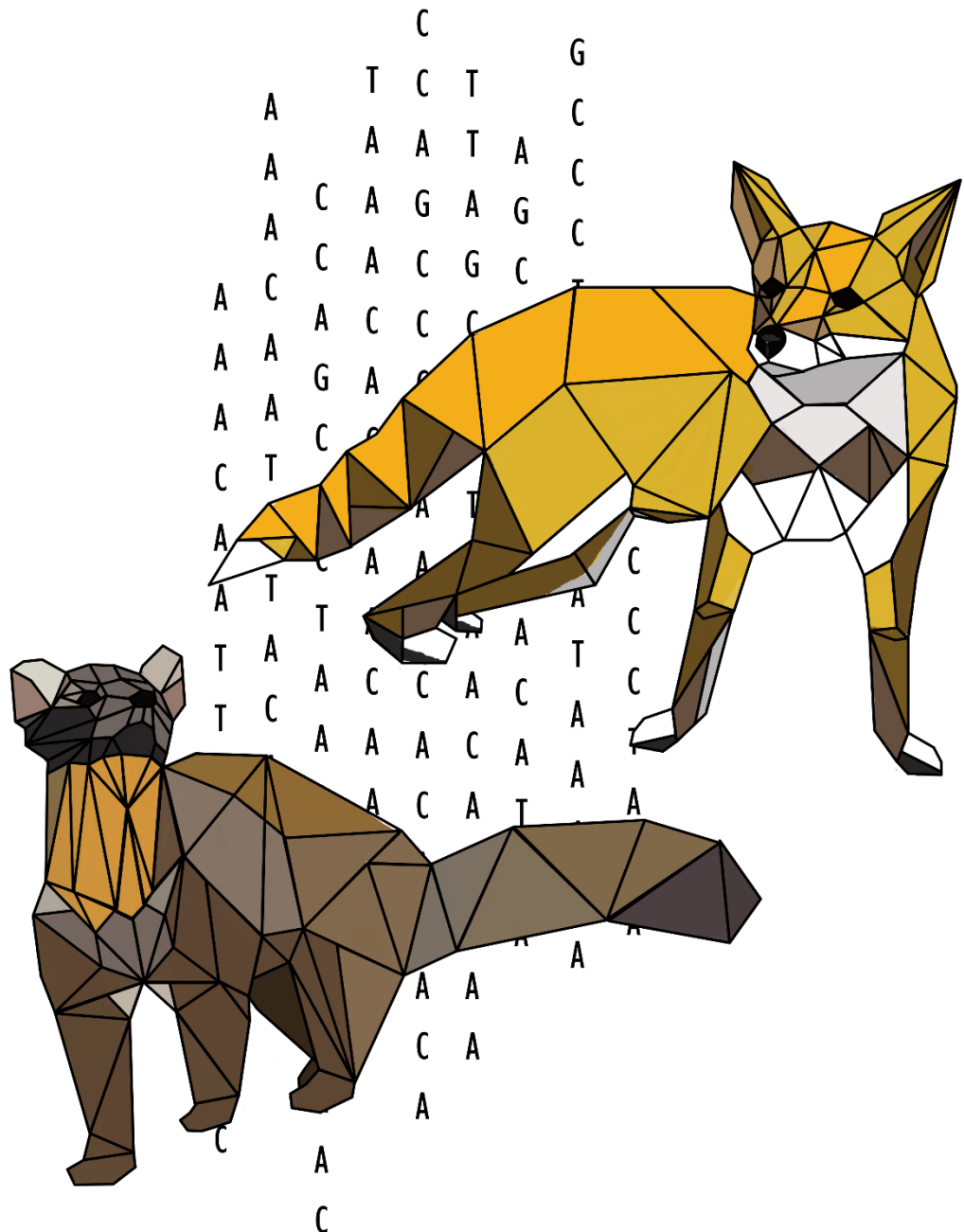


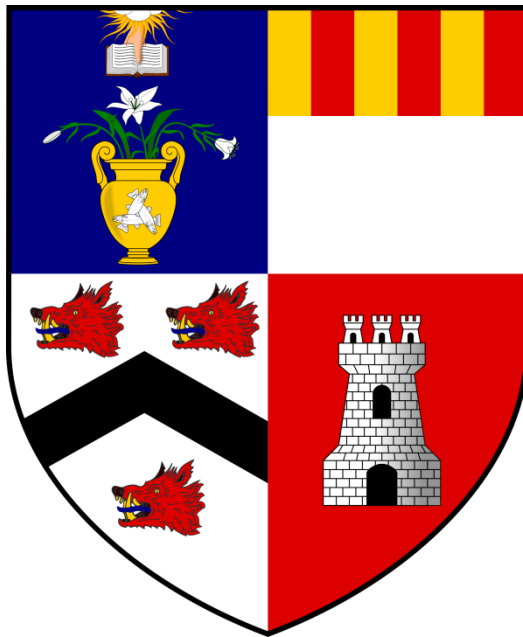
# LETHAL AND NON-LETHAL INTERACTIONS AND COMPETITION IN GUILDS OF BOREAL FOREST PREDATORS

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*LETHAL AND NON-LETHAL INTERACTIONS  
AND COMPETITION IN GUILDS OF BOREAL  
FOREST PREDATORS*



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## GENERAL SUMMARY

Species interactions are a central issue to ecology. Alongside abiotic factors, species interactions, have shaped life on earth and continue to determine the distribution, dynamics, and composition of species assemblages. However, in the study of species interactions, those among vertebrate predators and their ecological implications have been overlooked. They have been increasingly recognised and studied as relevant drivers of species coexistence, yet their prevalence, drivers and magnitude in most natural systems remains largely uncertain. This thesis is centred on the interactions among predators in European systems and on their implications for prey of conservation concern. In Chapter 1, the evidence of lethal interactions among forest grouse predators in Europe is reviewed. It addresses the questions of how common lethal interactions are, how likely, and under what circumstances, do they lead to demographic suppression of the victim. Lethal interactions among predators are numerous. However, most remain untested for demographic effects, which are rare and should not be presumed without robust evidence. A simple framework drawing from demographic theory is proposed to evaluate whether interactions meet the requirements to cause suppression: (i) frequent killings, most often motivated by food and (ii) the ability to kill demographically valuable individuals such as breeding females. In Chapter 2, non-lethal interactions among three mammalian carnivores in Scotland are explored over multiple scales through a camera trapping study. Different life-history traits among the three carnivores are used to test whether known drivers of lethal interactions such as size-ratios or trophic overlap also determine the intensity of non-lethal interactions. These were found not to be good predictors of non-lethal interactions. In Chapter 3, the results of a large-scale metabarcoding study of the vertebrate component of the diet of red fox and pine marten are presented. Diet diversity, trophic overlap, prey switching, potential instances of intraguild predation and predation of prey of conservation concern were considered. Additionally, the existence and direction of the functional response of these predators to spatial changes of several groups of prey were approximated through regression analysis and compared between years and seasons of contrasting food availability. The diets of foxes and martens were highly diverse, and largely overlapping, especially in their use of short-tailed field voles. As their main prey crashed in the system, foxes increasingly relied on deer carrion and dog faeces for food while martens increased their predation of forest birds and other seasonally available prey such as amphibians or reptiles. However, martens

continued to exploit mostly field voles throughout the study. There were multiple possible instances of intraguild predation. However, it is not possible to conclusively determine whether they originate from true predation, scavenging, or interspecific coprophagia. Similarly, events of predation of prey of conservation were identified, but cannot be extrapolated to a population impact. Foxes and martens had generally positive functional responses to their prey. The strengths of these relationships were often constant throughout the study area or varied seasonally. The direction of the functional response only varied significantly between the two predators in one instance (moorland prey). Chapter 4 explores the possibility of widespread interspecific coprophagia of domestic dog faeces by red foxes. Different explanations for the occurrence of dog DNA in the diet of red foxes were considered and consumption of faeces was considered the most plausible. This finding hints at interesting avenues of future work, where interspecific coprophagia may be a relatively widespread form of facilitation among animals. This work has attempted to further our understanding of predator interactions by addressing the prevalence and importance of predator interactions among a considerable proportion of European predators and mapping red fox and pine marten interactions in Scotland. Many aspects remain unexplored, such as the potential synergies among the interactions of multiple sympatric predators or the demographic implications of non-lethal interactions. Two major lines of future work in the field are the integration of positive and negative interactions among vertebrate predators and the integration of scale-dependent interactions. This thesis also highlights the need of an integrated approach to wildlife management conservation, by considering the direct and indirect influences of different interventions and uses of the landscape, paired with a better understanding predator-prey and predator-predator interactions.

## **ABSTRACT**

Species interactions shape life on earth determine the functioning of ecological communities. Although increasingly studied and recognised, interactions among vertebrate predators, and their implications, have been largely neglected in ecology. Through a literature review, this thesis explores the prevalence and strength of lethal interactions among predators across Boreal and Temperate Europe, as well as the likelihood of such interactions to cause demographic impacts on their victims. Then, lethal, and non-lethal (avoidance) interactions are mapped using red foxes, pine martens and Eurasian badgers in Scotland as a case study and a combination of camera trapping and metabarcoding diet analysis. Lethal interactions among predators in Europe are numerous. However, most pairwise interactions remain untested for demographic impacts. How likely they are to inflict such impacts depends on the frequency of killings and the victim's demographic value. The strength of non-lethal interactions between martens and foxes and badgers was not related to the intensity of the threat posed by the two larger predators. Trophic overlap between martens and foxes was generally high but varied seasonally and annually. As their shared main prey became scarcer martens relied more on forest prey and foxes on anthropogenic foods. Potential instances of intraguild predation of martens by foxes were detected. However, these cannot be conclusively discerned from scavenging or interspecific coprophagia. The latter has been found to be a common occurrence with foxes frequently feeding on dog faeces. Future work should consider synergies of predator interactions among multiple sympatric predators. The integration of positive and negative interactions and of scale-dependent interactions offers fertile grounds for future research. The findings of this thesis stress the need for an integral approach to wildlife management and conservation and a need to better understand complex systems of predator-prey and predator-predator interactions.

# CHAPTER 1

Lethal interactions among forest-grouse predators are numerous, motivated by hunger and carcasses, and their impacts determined by the demographic value of the victims

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## ABSTRACT

New vertebrate communities are emerging in Europe following the recovery of multiple native predators to highly anthropized landscapes where predator control is still prevalent. While the lack of reference points for these communities creates novel challenges for conservationists and wildlife managers, they also provide opportunities to further our understanding of species interactions. Despite a growing body of evidence, many aspects of interactions among predators remain poorly understood, impairing our ability to anticipate the effects of such changes in predator communities. Through a systematic literature review, we gathered all the available evidence concerning the existence, strength, and demographic impacts of lethal predator interactions among forest grouse predators in Europe. We found a highly interconnected predator community, with 44 pairwise lethal interactions among 12 taxa. Three of these resulted in some degree of population suppression of the victim, while another three did not. However, most interactions (38) have not been evaluated for population suppression. Additionally, we highlight how predators interact simultaneously with a large range of other predators and identified at least two further species likely suppressed through the combined impacts of multiple predators. We propose that interactions causing demographic suppression are characterized by impacts on individuals with high survival elasticity, and that they are motivated by food limitation and additionally, in mammals, by competition for carcasses. Predator interactions, and our still poor understanding of them, introduce large uncertainties to conservation actions based on the management of predator abundances, which should be carefully evaluated.

## Chapter 2

# The best defence is not being there: avoidance of larger carnivores is not driven by risk intensity

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### ABSTRACT

Species interactions are key factors determining the distribution and structure of species assemblages. Owing to their central positions, mid-ranking mammalian carnivores are involved in interactions with numerous species, including competition for resources and instances of killing by higher ranking predators. Lethal interactions can directly influence species' demography. However, the fear of lethal interactions, competition, or both, may also affect when and where individuals are active (i.e., non-lethal interactions). Although differences in body size and trophic overlap are known predictors of the frequency of lethal interactions, their influence on non-lethal interactions is uncertain. Through camera trapping, we studied non-lethal interactions between a small mesocarnivore (pine marten), a potential killer and intense competitor (red fox) and a moderate competitor and unlikely killer (Eurasian badger). We determined overlap and differences in their diel activity patterns and the degree of spatial overlap in two seasons with contrasting resource availability. Additionally, we estimated the effect of larger carnivore detection rates on pine marten detection rates and compared time intervals between pine marten visits to baited stations in the absence and presence of either or both larger carnivores. Our results are consistent with pine martens distributing their daily activity to maximise overlap with prey and to minimise competition and risk of aggression over the spatial scale. Pine martens also responded to the immediate threat of larger carnivores irrespective of the threat they pose by taking 4 to 7 days longer to return to a station. Small-scale non-lethal interactions such as these may enable pine martens to coexist closely with two larger carnivores, yet it remains uncertain whether their population incurs a demographic cost through restricted access to resources. Carnivore's risk-avoidance strategies could be harnessed to protect prey species of interest. However, our results suggest avoidance is short-lived and recurrent stimuli would be necessary.

## CHAPTER 3

# From metabarcoding to ecology: functional response, prey switching, competition, intraguild predation and prey conservation.

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### ABSTRACT

Understanding how wild carnivores change their ingestion rates as the availability of their prey varies in a landscape (i.e., functional response) is seldom feasible. Diet analysis through metabarcoding can overcome many of the limitations of traditional methods, allowing us to cost-efficiently resolve the diets of carnivores with high-resolution, which may enable the determination of the existence and direction of functional responses ( $\pm$ ). Red foxes and pine martens are two widely sympatric carnivores. Foxes are known and able to kill martens, and are well adapted to hunt small rodents in open habitats, yet in Scotland, both have highly overlapping diets based on open habitat rodents with no apparent signs of competitive exclusion. Additionally, it is feared that predation by foxes and martens may jeopardise vulnerable populations of prey. In this study, we have analysed the vertebrate component of the diet of red foxes and pine martens using metabarcoding to determine potential instances of intraguild predation and identify predation of vulnerable prey. We describe the diversity and breadth of the diet of both predators. We also consider how the overlap between the two, and changes over two seasons and years with contrasting availabilities of prey to explore patterns of possible competition. Furthermore, we study the existence of functional responses to various prey groups by determining how the probabilities of occurrence of these groups in the diet of both predators vary according to spatial changes in their availability as proxied by habitat measures. As expected, we found highly diverse but narrow diets. The diet of both predators largely overlapped but had marked seasonal and annual variation. We also identified several possible instances of intraguild predation, and predation of vulnerable prey. The occurrence in



the diet of the predator's main prey increased with its availability in the landscape. This effect weakened during the seasons with higher prey availability. Martens, and not foxes, exploited their shared main prey at higher rates when food was most limiting. The strength of the response to changing availabilities of prey only differed among the two predators for moorland prey, where foxes but not martens exploited such prey when their main prey was scarce. Relationships between occurrence in the diet and landscape availabilities for other alternative prey did not differ among the two species, varying only seasonally or remaining constant throughout the study. Alternative prey accessible at ground-level was generally more important in the diet of foxes, while arboreal prey was virtually absent in the diet of fox, but seasonally important in the diet of marten. Through a metabarcoding analysis, this study offers a highly resolved description of the vertebrate diet of these two carnivores that enables a crude approximation to their functional responses to prey. Competition for prey between the two carnivores may be strong during transition periods in their shared prey's abundance. However, trophic overlap indices may not reflect this accurately. Adaptive prey switching during periods of food scarcity offers a mechanism of coexistence between red foxes and pine martens, yet the latter may still be subject to locally important mortalities through intraguild predation by foxes. This work highlights the need to clarify the underlying processes that determine predation of prey of conservation interest to evaluate the effectiveness of possible management interventions.

## CHAPTER 4

# Interspecific coprophagia by wild red foxes: DNA metabarcoding reveals a potentially widespread form of commensalism among animals

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### ABSTRACT

Species interactions shape the dynamics of ecological communities. While the significance of antagonistic interactions such as predation is well documented, facilitative interactions among vertebrates remain poorly understood. Specifically, vertebrates are known to consume other species' faeces yet the role of coprophagy in species dynamics is unknown, not least due to the methodological challenges of documenting it. In this study, we document a high and variable occurrence of domestic dog DNA in red fox scats and investigate whether it can be attributed to interspecific coprophagia and to dog faeces acting as an alternative food source when wild prey is scarce. Through a large-scale metabarcoding study of red fox and pine marten scats, we tested whether experimental artifacts or other sources of DNA could account for dog DNA, and regressed the occurrence of dog in the diet of fox against that of short-tailed field voles. Additionally, we determined the calorific value of dog faeces through calorimetric explosion. We found, for the first time, that red foxes, but not pine martens, regularly exploit domestic dog faeces, which are highly calorific. The timing of the increase of dog occurrence and a negative relationship with the occurrence of the fox's main prey point to dog faeces as an alternative resource to fluctuating prey. We argue the benefits of interspecific coprophagia outweigh its potential impacts and should be considered a form of commensalism. Thus, through interspecific coprophagia, foxes accessed an exogenous resource of human origin that could partly buffer them from fluctuations of their main prey to the potential detriment of their prey and competitors. Metabarcoding has revealed a hitherto unsuspected facilitative interaction that could contribute to stabilising ecological communities owing to the facultative

and indirect nature of the interaction and its potential to offset destabilising effects of antagonistic interactions. Furthermore, if widespread, interspecific coprophagia could boost the connectivity, modularity, or both, of ecological networks with consequences to robustness against species loss. The prevalence of interspecific coprophagia should be quantified in other systems and the implications of considering this and other facilitative interactions in vertebrate systems assessed. Tools such as metabarcoding offer a way forward.