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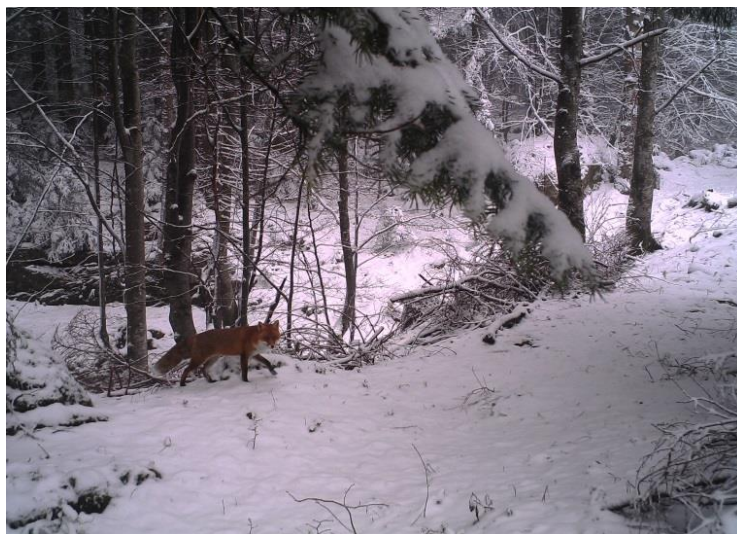COLLEGE OF ENVIRONMENTAL SCIENCES AND ENGINEERING
SCHOOL OF NATURAL SCIENCES

Behind enemy lines: investigating suppression & coexistence between sympatric carnivores in Plitvice Lakes, Croatia

Thesis for the degree of Doctor of Philosophy (PhD)

Peter Michael Haswell

2019

Long the path, | lofty the toil,

for seekers of Mimir's spring;

sacrifice for sight, | such is the trade,

to sip the mead of Suttung.

Purpose and strength, | possess you must,

feeder of ravens for the wild;

be willing to hang, | Nidhogg at your heals,

waiting for waters to clear.

After the spear-din, | on the ninth day,

is mastery truly manifest?;

small the sips, | sorely won,

from many days of drudgery.

Of kinsfolk of men, | one you are just,

each adds his logs to the pyre;

seeker of betterment, | whomever you be

mind's worth is yours to wear.

P. M. Haswell, 2019

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Abstract

This thesis fills knowledge gaps regarding spatio-temporal interactions between sympatric carnivores, mesopredator risk mitigation behaviour, and thus, the mechanisms that enable coexistence. In the Anthropocene biodiversity crisis, discerning how and when diversity is maintained is critical. Employing a robust multi-method approach, a model study system was used to examine the top-down effects of wolves, *Canis lupus* and Eurasian lynx, *Lynx lynx*, upon red fox, *Vulpes vulpes* in Plitvice Lakes National Park, Croatia.

Chapter Two utilises novel foraging experiments, combining camera traps with the giving-up density (GUD) framework. Foxes responded to wolf urine by taking less food, spending less time at patches, leaving at higher quitting harvest rates, and adjusting their behaviour when at patches, spending less time foraging and more time being vigilant and sniffing the ground. Chapter Three examines spatial relationships using occupancy modelling. Foxes were not spatially excluded by large carnivores, but were in fact attracted to them (or at least the same conditions) and more detectable in their presence. The positive association was most strongly related to lynx, however, conversely, foxes responded elusively towards human activity. Chapter Four examines temporal relationships using kernel density estimates, circular statistics and nocturnality risk ratios. Fox activity overlapped with other carnivores but avoided peak activity periods, having significantly different record distributions. Foxes were more nocturnal in higher intensity large carnivore presence, seemingly using the cover of darkness to remain safe. High human activity however mediated this interaction, decreasing its strength.

Subtle temporal avoidance and fine-scale spatio-temporal risk mitigation strategies can enable mesopredator access to resources and predator coexistence in the presence of intraguild aggression. Where food subsidies are absent, humans may increase mesopredator elusiveness but may also offer some level of temporal shielding from large carnivores. Protected area management should consider ecological baselines and the effects of human disturbance.

Acknowledgements

First and foremost tremendous gratitude goes to my partner Dr. Elizabeth. A. Shepherd for her support both in the hard years prior to my beginning the thesis, desperately searching for a way to fund my studies, and, of course, during all the years while conducting this work. For tolerating my time away on field work, my obsessive passion for wildlife and my general eccentricities, I am truly indebted. You have always been there to support and encourage me, picking me up when things got hard and spurring me ever forwards. You kept my belly full, my being from loneliness and my spirits high. I am so very grateful. For being there with ever affectionate intentions throughout the years, supporting me at home, and even assisting with field work, a huge but uncommunicable gratitude also goes to my loveable wonderdog, Alfred.

This thesis would not be what it is without the vast knowledge and advice of my lead supervisor Dr. Matt. W. Hayward. Matt's standards are high as I hope the thesis reflects and it is him who opened me up to many of the methodologies and concepts that have become key to the thesis. Matt has to be the quickest and most efficient editor I have come across, something which I have benefited from greatly. Matt leads by great example and his advice has been pivotal in creating and refining this thesis. For this, and for pushing me to develop as a scientist and as a person, I owe him tremendous thanks. My long-time mentor Prof. Josip Kusak is also deserving of tremendous gratitude and praise. For taking me on as a collaborator in the first place, showing me the ropes of large carnivore research, helping make any of the field work possible and for guiding me throughout. A huge thank you for helping me spend so much enjoyable time, and contribute to wildlife conservation, in such a unique and beautiful part of the world. I hope I have done Croatia proud. Plitvice will forever be a special and wondrous place for me. Last but not least, a huge thank you to my second supervisor, Dr. Katherine. A. Jones. Initially my internal examiner, Kat's advice was so useful that it was only just that she became part of my supervisory team. Offering great observations on animal behaviour, research methodologies, and always checking my work made sense, Kat was pivotal in helping to hone this work as well as keeping me going. Both Matt and Kat also helped guide me greatly and taught me much about being an educator during my time at Bangor. To Matt, Josip and Kat, I thank you so very much for your sound advice, pastoral care and brilliant mentorship. I could not have asked for more.

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Chapter 1.

Introduction

"*From the forest came the call*"

Jack London

Cultural arguments over what is natural and unnatural are somewhat irrelevant as all activities carried out by humans, *Homo sapiens*, can be deemed natural because they are within the realms of biological possibilities (Harari 2014). The biosphere has however been greatly modified by our actions with severe impacts to biodiversity and community structure, including the removal of megafauna and reduction of wild terrestrial mammal biomass (Bar-On, Phillips & Milo 2018). This has resulted in simplified trophic systems (Estes *et al.* 2011). Such reduction of biodiversity could be considered morally wrong if one perceives non-human entities to have intrinsic value regardless of human benefit (Callicott 2002). Leopold's (1949) "land ethic", for example, suggests extending moral consideration to nonhuman organisms and, in fact, all components of an ecosystem (soil, water, plants etc.).

From an anthropocentric standpoint, one might also consider the impoverishment imposed upon those who might otherwise take pleasure from the aesthetic value or intellectual stimulation provided by nature (Cafaro 2001). If we hurt nature then we hurt ourselves (Krishnamurti 1985). It is becoming clear that this simple concept may be true on more grounds than perhaps previously realised. Dramatic modification and declines in biodiversity are also of growing concern due to the realisation of the consequences this has for our own future prosperity (Ripple *et al.* 2017). Due to the vulnerability of large carnivores to anthropogenic pressure, their potential to provide ecosystem services, or perhaps simply due to the value people place upon their attributes, there is increasing interest in the conservation and ecological function of large carnivores (Mech 2012; Ripple *et al.* 2014). It is because of an intrigue in the mechanisms of the natural world and a desire to encourage appreciation for

the most vulnerable members of our global community (non-human species) that this work was conducted.

In order to further our understanding, wherever the body of knowledge is inconclusive and there is a need for greater accuracy, we must question traditional conclusions, employing what is useful and building upon it. To this end we have engaged in scientific dialogue questioning the methodologies, evidence base and generalisability of top-down ecological processes (Allen *et al.* 2017a;b; Haswell, Kusak & Hayward 2017). The concept of trophic cascades stemming from large carnivores through mesopredator and herbivore regulation has captured a great deal of research and public interest (Ripple *et al.* 2014). Exploration of the literature suggested a focus on cascading outcomes and demographic regulation of strongly competing predators, alongside questions over the quality of evidence on the trait mediated effects larger carnivores have on mesopredators.

Apex predators can limit mesopredator numbers and access to resources through direct killing or interference competition; restricting space, time and food use through harassment, but also by presenting risk (Linnell & Strand 2000). Top-down suppression may have cascading effects, consequently moderating the effects mesopredators have on their prey species (Ritchie & Johnson 2009). It is however important to investigate not only the cascading impacts of large carnivores but also the mechanisms that may cause cascades (Glen *et al.* 2007). As such, this thesis does not examine the consequences of trophic cascades stemming from mesopredator suppression, but focuses on providing a solid root to understanding the behavioural mechanisms that might begin cascading processes.

We used a model study system, examining the top-down effects of wolves, *Canis lupus* and Eurasian Lynx, *Lynx lynx*, upon red fox, *Vulpes vulpes* in Plitvice Lakes National Park, Croatia. The Dinaric Mountains, where this research was conducted, hold some of the richer carnivore communities in Europe (Jenkins 2013; Jenkins, Pimm & Joppa 2013; Pimm *et al.* 2014). The region has received little scientific attention with regards to predator-predator interactions; in fact we are aware of only one such study (Krofel & Jerina 2016). The study area is close to the Mediterranean Basin - an area highlighted as Europe's biodiversity hotspot (Myers *et al.* 2000). The thesis thus offers an important contextual contribution towards understanding species interaction patterns.

Spatial exclusion and the regulation of mesopredator abundance have received more solid attention since our investigations began (Newsome & Ripple 2014; Newsome *et al.* 2017b).

This thesis however quite deliberately set out to study sympatric species, examining finer scale behavioural interactions; contributing information on interspecific interactions where body size differences are larger (wolf-fox) and taxonomic relatedness more distant (lynx-fox) than those classic examples that have since formed the basis of the enemy constraint hypothesis (Johnson & VanDerWal 2009; Levi & Wilmers 2012; Newsome *et al.* 2017b). Alongside understanding the mechanisms that might lead to spatial exclusion or demographic suppression, it is also important to understand those that foster species coexistence and thus diverse predator communities. Such knowledge could be used to help prevent trophic simplification and ensure ecosystem robustness (Estes *et al.* 2011).

Conservationists and managers are faced with the conundrum of requiring generalities and simple concepts in order to be able to take action, but difficulty comes from the fact that systems are complex, so this approach might prove problematic (Haswell, Kusak & Hayward 2017). As such we require an understanding of how general rules are altered by circumstance. Consideration of the context dependency of interactions between species is paramount to avoiding inappropriate management action (Allen *et al.* 2017a). Evidence clearly supports the acknowledgement that top-down pressure exists in some form or other but the strength of impact may vary with other process drivers such as environmental productivity and human influence (Hollings *et al.* 2014; Wikenros *et al.* 2017a). Literature highlights the potential for humans to act as super predators, alter ecological interactions and create risk for carnivores (Frid & Dill 2002; Haswell, Kusak & Hayward 2017; Smith *et al.* 2017). Most national parks are not truly a pristine environment given the presence of humans within (and around) them so anthropogenic influence was examined alongside interspecific interactions between predators.

The following literature review provides the reader an introduction to food webs, interspecific interactions and the concepts relevant to the research conducted. It offers an overview of how large carnivores interact with other species and the contexts that shape these interactions, particularly human activity. The review also highlights knowledge gaps that the rest of the thesis attempts to fill.

Literature review: Large carnivore impacts are context dependent

Peter M. Haswell[12], Josip Kusak[3], Matt W. Hayward[1456]

Author contribution statement

P.M.H. conceived and wrote the manuscript. M.W.H contributed to the writing. J.K. and M.W.H provided editorial advice. All authors gave final approval for publication.

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Abstract

Interactions between large carnivores and other species may be responsible for impacts that are disproportionately large relative to their density. Context-dependent interactions between species are common but often poorly described. Caution must be expressed in seeing apex predators as ecological saviours because ecosystem services may not universally apply, particularly if inhibited by anthropogenic activity. This review examines how the impacts of large carnivores are affected by four major contexts (species assemblage, environmental productivity, landscape, predation risk) and the potential for human interference to affect these contexts. Humans are the most dominant landscape and resource user on the planet and our management intervention affects species composition, resource availability, demography, behaviour and interspecific trophic dynamics. Humans can impact large carnivores in much the same way these apex predators impact mesopredators and prey species - through density-mediated (consumptive) and trait/behaviourally-mediated (non-consumptive) pathways. Mesopredator and large herbivore suppression or release, intraguild competition and predation pressure may all be affected by human context. The aim of restoring 'natural' systems is somewhat problematic and not always pragmatic. Interspecific interactions are influenced by context, and humans are often the dominant driver in forming context. If management and conservation goals are to be achieved then it is pivotal to understand how humans influence trophic interactions and how trophic interactions are affected by context. Trade-offs and management interventions can only be implemented successfully if the intricacies of food webs are properly understood.

Introduction

When understanding and managing trophic dynamics, what is deemed a natural or unnatural interaction must first be considered (Rolston 2001). The aim of restoring 'natural' systems in the modern era becomes somewhat problematic. Wildlife conservation is still possible in human dominated landscapes but maintaining top-down ecological processes in such landscapes is challenging (Chapron *et al.* 2014; Linnell *et al.* 2015; López-Bao *et al.* 2015). The impacts of world-wide predator decline and the relative importance of direct and indirect species interactions have been highlighted as fundamental ecological questions (Sutherland *et al.* 2013). Yet caution has been expressed in seeing apex predators like the gray wolf *Carnivora Canidae Canis lupus* as ecological saviours because ecosystem services may not

universally apply, particularly if inhibited by anthropogenic activity (Mech 2012). Furthermore, there is only one intact terrestrial predator guild in the world (Africa), so all other guilds may reflect the impacts of the Pleistocene megafauna extinctions and shifting baselines to mesopredator-dominated systems (Fleming, Allen & Ballard 2012; Valkenburgh *et al.* 2015). The question arises as to what the conservation benchmark or baseline is, was or should be given a particular ecological context (Berger 2008; Hayward 2009; 2012).

Species at higher trophic levels are often lost more rapidly than those at lower trophic levels (Dobson *et al.* 2006). Apex predator decline and trophic simplification is something of great concern worldwide (Johnson 2010; Estes *et al.* 2011; Ripple *et al.* 2014). It is imperative to understand the interactions and potential impacts of apex predators because their absence or decline can have undesired effects (Jackson *et al.* 2001; Terborgh *et al.* 2001; Berger, Gese & Berger 2008). The consequences of upper trophic level decline and the loss of ecosystem services provided by large carnivores could lead to environmental degradation through the release of top-down control upon herbivores (Ripple & Larsen 2000; Hebblewhite *et al.* 2005; Beschta & Ripple 2012) and mesopredators (Prugh *et al.* 2009; Ritchie & Johnson 2009; Newsome & Ripple 2014). If healthy populations of top predators can be maintained within ecosystems, they should also contain healthy communities and populations of the many species that perform a diversity of ecosystem services at lower trophic levels (Dobson *et al.* 2006).

As the most dominant landscape user and primary resource consumer on the planet (Paquet & Darimont 2010), humans greatly modify the landscapes and communities that apex predators interact with through a myriad of disturbance types (Frid & Dill 2002; Blanc *et al.* 2006; Sibbald *et al.* 2011). The positive (Kilgo, Labisky & Fritzen 1998; Kloppers, St. Clair & Hurd 2005; Leighton, Horrocks & Kramer 2010) or negative (Hebblewhite *et al.* 2005; Pelletier 2006; Jayakody *et al.* 2008) nature of this disturbance however depends entirely on management perspective (Reimoser 2003). Humans can impact apex predators in much the same way as they impact smaller predators and prey species, through density-mediated (consumptive) and trait/behaviourally-mediated (non-consumptive) pathways (Ordiz, Bischof & Swenson 2013). Impacts can be direct (Virgos & Travaini 2005; Packer *et al.* 2009) or indirect through effects on other species or habitat (Sidorovich, Tikhomirova & Jedrzejewska 2003; Rogala *et al.* 2011).

Context-dependent interactions between species are common but often poorly described (Chamberlain, Bronstein & Rudgers 2014). This review examines the contextual impacts of large carnivores and the potential for human interference through effects on species assemblage, environmental productivity, landscape and predation risk (Fig. 1.1, Table. 1.1). If we are to predict the consequences of predator management, it is critical to understand the dynamics of interspecific relationships between organisms (Prugh *et al.* 2009; Elmhagen *et al.* 2010; Ripple *et al.* 2014) and to determine if this context can be manipulated to achieve management and ecosystem service goals (Kareiva *et al.* 2007).

A search of literature was conducted using Web of Science and Google Scholar with "OR" and "AND" search operators and a mixture of key words (apex predator*, large carnivore*, carnivore*, mesopredator release, mesopredator*, mesocarnivore*, large herbivore*, herbivore suppression, grazing, browsing, predation pressure*, interspecific, interspecific interaction*, interspecific killing, predation, intraguild predation, competition, competitor*, trophic cascade*, predation risk*, ecosystem service*). Reference trails, recommended papers or appropriate material already in the possession of the authors were also used to inform this review.

Predation risk

Predators consume prey but they also provide risk (Fortin *et al.* 2005; Brown & Kotler 2007). Harassment and the associated energetic losses of responding to predation risk can carry costs to overall fitness (Creel 2011). Predation risk is a powerful motivator that can affect behaviour and how an animal uses time and space as well as investment in other antipredator strategies (Brown, Laundré & Gurung 1999; Ripple & Beschta 2004; Willems & Hill 2009). Predation risk and disturbance create trade-offs between avoiding risk or perceived risk and other fitness enhancing activities (e.g. feeding and breeding), such that risk avoidance carries energetic costs in the form of missed opportunities (Brown 1992; Brown, Laundré & Gurung 1999; Eccard & Liesenjohann 2014). Human disturbance may incur similar responses to risk in wildlife (Frid & Dill 2002; Leighton, Horrocks & Kramer 2010; Erb, McShea & Guralnick 2012).

Risk-induced interactions between predators and other organisms can have cascading effects (Ritchie & Johnson 2009; Miller *et al.* 2012; Ripple *et al.* 2014). A forager's response to its landscape of fear (Laundré, Hernández & Ripple 2010; Laundré *et al.* 2014) may alter the species composition, behaviour, adaptive evolution or population dynamics of its prey and

perhaps its predators or competitors (Brown & Kotler 2007). Non-consumptive behavioural interactions can be significant ecological drivers and should not be overlooked (Peckarsky *et al.* 2008; Heithaus *et al.* 2009; Ritchie & Johnson 2009).
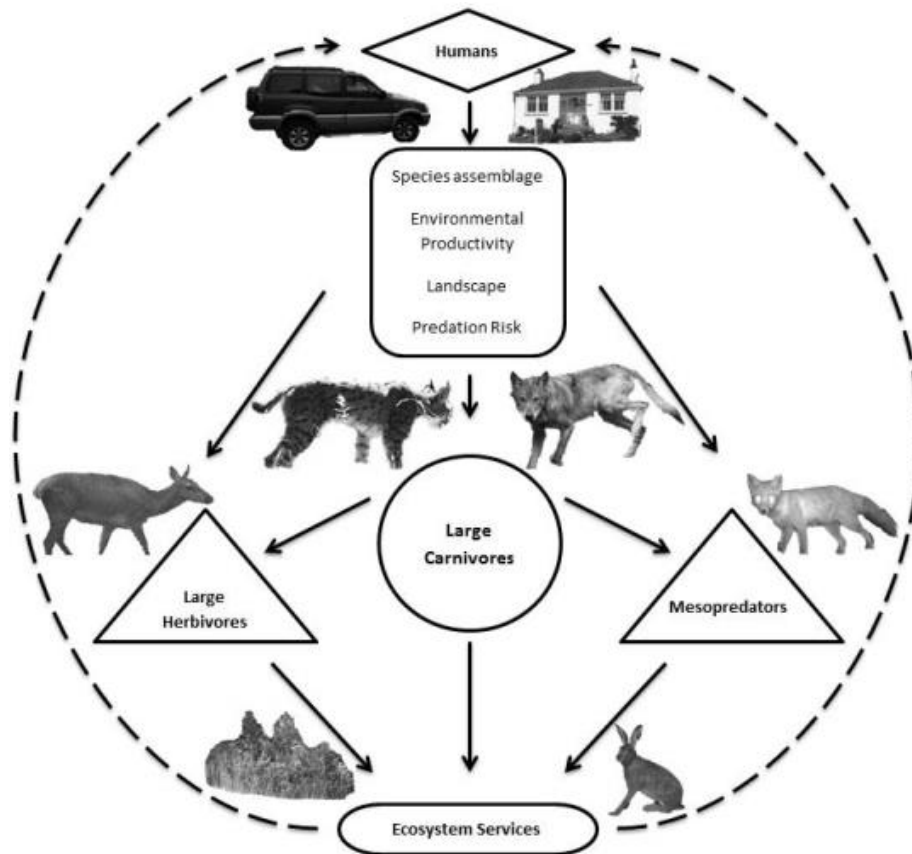
Figure. 1.1. How the human context affects food-webs. Benefits derived from large carnivores could be dependent on human context. As the most dominant landscape and resource user on the planet, humans have the potential to influence ecosystems and the organisms that inhabit them. The impacts of humans on other species in a given context could alter the direction or severity of consumptive and non–consumptive interactions between species. Humans can affect top-down control from large carnivores which can have trickle down effects through trophic interactions, affecting habitat use and foraging behaviour with consequences for ecosystem services (solid arrows). These services can in-turn feedback to affect humans (dashed arrows). This figure represents a simplified flow diagram of how context affects the impacts from large carnivores; additional mechanisms have been excluded for clarity.

Interactions with mesopredators

Larger predators can sometimes limit the impacts, range and densities of smaller predators (Henke & Bryant 1999; Prugh *et al.* 2009; Levi & Wilmers 2012). Soulé et al. (1988) observed that, in the absence of larger more dominant predators, smaller predators and omnivore populations increase markedly in abundance, by up to ten times that before release. The mesopredator release hypothesis predicts that a decrease in abundance of top-order predators results in an increase in the abundance of mesopredators due to a reduction in intra-guild predation and competitive suppression (Ritchie & Johnson 2009; Letnic & Dworjanyn 2011). Suppression of mesopredators can result in density reductions or even complete exclusion of these smaller predators from habitats or regions in both time and space (Linnell & Strand 2000; Berger & Gese 2007; Newsome & Ripple 2014).

Interspecific competitive killing, intraguild predation and interspecific interference competition are common in a whole range of mammalian carnivores (Lourenco *et al.* 2014), particularly between species with elements of niche overlap and species of the same family having not too dissimilar body mass (Palomares & Caro 1999; Linnell & Strand 2000; Ritchie & Johnson 2009). Two main mechanisms offer explanation for mesopredator suppression by apex predators: direct lethal encounters, and behavioural responses to risk (Ritchie & Johnson 2009).

There is great debate about the strength of impacts large carnivores have upon mesopredators (Letnic *et al.* 2009; 2011; Allen *et al.* 2013). There is some evidence that predation threat and impacts of mesocarnivores upon native rodents, such as *Rodentia Muridae Notomys fuscus*, are lower in the presence of dingoes (Letnic, Crowther & Koch 2009; Letnic & Dworjanyn 2011). However, some express caution in assigning causality to short-term observations of correlated, but unvalidated population indices which may falsely suggest mesopredator release (Fleming, Allen & Ballard 2012; Allen *et al.* 2013; Hayward & Marlow 2014). While there is little doubt in the value of stable ecosystems complete with top predators (Estes *et al.* 2011; Ripple *et al.* 2014), untangling the web of ecological interactions and clearly identifying ecosystem services from apex predators will require careful experimental design.

In an extensive review, Ritchie & Johnson (2009) discuss a number of trophic assemblages where mesopredators are suppressed by larger predators and found only two studies identifying scenarios where scent or vocal predator cues had little impact upon mesopredators (Gehrt & Prange 2007; Prange & Gehrt 2007). Interactions between species may vary

depending upon context. Larger predators may competitively suppress smaller predators but also provide scavenging opportunities (Khalil, Pasanen-Mortensen & Elmhagen 2014). Habitat complexity, resource availability and the density or complexity of predator communities may affect the outcomes of interactions between predators (Ritchie & Johnson 2009; Khalil, Pasanen-Mortensen & Elmhagen 2014). Mesopredator prey species comprise a vast array of herbivores, detritivores, seed dispersers and seed predators (Catling 1988; Russell & Storch 2004; Panzacchi *et al.* 2008). Such species have variable interactions with vegetation communities (Zamora & Matias 2014; Wang & Yang 2015; Yi & Wang 2015). Any consequential cascades resulting from mesopredator release are also likely to be context-dependent.

Contexts affecting mesopredator interactions

Species assemblage

Vulnerability and interactions between predators may be influenced by niche overlap and relatedness (Berger & Gese 2007; Gehrt & Prange 2007; Ritchie & Johnson 2009), but also by species specific factors such as defence or grouping behaviour (Cooper 1991; Palomares & Caro 1999; Prange & Gehrt 2007). Mesopredators, such as the bobcat *Carnivora Felidae Lynx rufus* (5-15kg), can coexist with larger predators of similar size but different families, like the coyote *Carnivora Canidae Canis latrans* (8-20kg), even when a smaller mesopredator the gray fox *Carnivora Canidae Urocyon cinereoargenteus* (3-5kg) did not (Fedriani *et al.* 2000).

In many North American trophic systems lacking larger carnivores, coyotes can interact competitively and suppress mesocarnivores (Henke & Bryant 1999; Linnell & Strand 2000; Kamler *et al.* 2003). The extent of this suppression may be somewhat dependent on the presence of other predators. Red foxes *Carnivora Canidae Vulpes vulpes* for example pose more of a threat to kit fox *Carnivora Canidae Vulpes macrotis* populations because they can access dens (Ralls & White 1995; Cypher *et al.* 2001). Coyotes could have an additive negative impact (through predation) or benefit kit foxes through interference competition and suppression of red foxes (Cypher *et al.* 2001).

In the presence of a larger canid, coyotes were supressed by wolves and red foxes became more abundant (Levi & Wilmers 2012). North American wolves impact coyote distribution, abundance (33% lower in wolf abundant sites) and dispersal survival rates (Berger & Gese

2007; Newsome & Ripple 2014). In the presence of a feline apex predator however, coyotes were only killed by mountain lions *Carnivora Felidae Puma concolor* defending or usurping food caches during winter when diets overlapped significantly more (Koehler & Hornocker 1991). The overall impacts of predator communities and the outcomes of mesopredator suppression might depend directly on the number, density and composition of predator dominance levels (Chakarov & Krueger 2010).

At its most extreme scale, human influence can result in mesopredator range expansion and population growth, through the removal of apex predators (Kamler *et al.* 2003; Selås & Vik 2006; Ripple *et al.* 2013) or competing mesopredators (Courchamp, Langlais & Sugihara 1999; Rayner *et al.* 2007; Trewby *et al.* 2008). In some circumstances, release can result in the increase of a prey source shared by apex and mesopredators (Henke & Bryant 1999). Decline in prey species of mesopredators is however more common (Sargeant, Allen & Eberhardt 1984; Sovada, Sargeant & Grier 1995; Elmhagen *et al.* 2010). Caution must be expressed when interfering with ecological interactions as mesopredator release can carry economic and social costs (Prugh *et al.* 2009).

The introduction of alien predators may also alter trophic dynamics, complicating intraguild competition and affecting food webs (Crooks & Soulé 1999; Rayner *et al.* 2007; Krauze-Gryz *et al.* 2012). Wolf-dog interactions in particular stand out as an anthropogenic introduction to species assemblages with variable context-dependent outcomes (Lescureux & Linnell 2014). Levels of co-existence between native and alien species may be dependent on niche flexibility, landscape and resource abundance (Bonesi, Chanin & Macdonald 2004; Bonesi & Macdonald 2004; Brzezinski, Swiecicka-Mazan & Romanowski 2008). The maintenance and recovery of native or naturalised predators may in some contexts help to mitigate the impacts of invasive mesopredators (Glen *et al.* 2007; McDonald, O'Hara & Morrish 2007; Ritchie *et al.* 2012). Introduced predators, although posing their own threat to native prey species may also suppress the impacts of smaller alien predators in certain contexts (Hanna & Cardillo 2014). Predator eradication can have unforeseen consequences even with conservation in mind. Invasive species removal may have undesired effects through mesopredator release, rather than alleviating predation pressure upon native species as intended (Rayner *et al.* 2007).

Environmental productivity

Apex predators can affect food availability to smaller predators through the provision of carrion (Wilmers & Getz 2005), exploitative competition (Selås & Vik 2006), kleptoparasitism (Gorman *et al.* 1998), landscapes of fear (Laundré, Hernández & Ripple 2010; Kuijper *et al.* 2013), and possibly through indirect impacts on habitat structure and provisioning of refuge for mesopredator prey (Letnic & Dworjanyn 2011). Bottom-up factors however influence population densities of herbivores and consequently their predators (East 1984; Hayward, O'Brien & Kerley 2007).

The strength of top-down mesopredator control and consequently the strength of cascades from large carnivores can be determined by ecosystem productivity (Elmhagen & Rushton 2007; Elmhagen *et al.* 2010; Hollings *et al.* 2014). In contexts where bottom up effects are strongly influential the mesopredator release response to apex predator control may be limited. Coyote predation upon kit foxes can account for 75-90% of mortality (Eliason & Berry 1994; Ralls & White 1995; Linnell & Strand 2000). Such predation may be most significant when food availability is low or when kit fox populations are small (Cypher *et al.* 2001). During a coyote control programme where kit fox release did not occur as expected, food availability (lagomorph abundance) was observed to be the primary factor driving population dynamics of both species (Cypher & Scrivner 1992).

Humans can influence the type and severity of interspecific competition amongst carnivores by artificially boosting food availability, and consequently mesopredator populations (Crooks & Soulé 1999; Linnell & Strand 2000; Bateman & Fleming 2012). Maintaining mesopredators far above their carrying capacity with nutritional subsidies may particularly unbalance natural regulation if accompanied by habitat fragmentation (Crooks & Soulé 1999; Dickman 2008). Large carnivores can also adapt to capitalize on anthropogenic food sources (Ciucci *et al.* 1997; Kusak, Skrbinšek & Huber 2005; Newsome *et al.* 2014). However, humans often inhibit large carnivore use of space and time (Whittington, St Clair & Mercer 2005). Both direct and indirect human influence on prey numbers, accessibility and hunting opportunities may cause prey switching and impact activity patterns with consequences for competitive interactions and the resultant impacts of large carnivores (Theuerkauf *et al.* 2003; Allen & Leung 2012).

Landscape

The interplay between predation risk and habitat features can shape foraging decisions and habitat use (Camacho 2014). Predation risk is not homogenous across landscapes or species; habitat features can interact with escape tactics to shape interspecific interactions (Wirsing, Cameron & Heithaus 2010). Predation risk is not always driven by predator density alone and mesopredator landscape use can sometimes be more dominantly driven by habitat features (Heithaus *et al.* 2009).

In many cases humans have drastically reduced available habitat for native fauna (Paquet & Darimont 2010). The impacts large carnivores have on other species and ecosystems may be relative to their interactions with anthropogenic landscapes. Human landscape modification may alter species interactions and occupancy by benefitting those species more resilient to anthropogenic disturbance (Cove *et al.* 2012; Erb, McShea & Guralnick 2012; Ruiz-Capillas, Mata & Malo 2013). Urban predators can provide ecosystem services as well as conflicts but human conflict often dominates management decisions (Dodge & Kashian 2013).

Human presence does not always necessitate extreme avoidance by large carnivores (Theuerkauf *et al.* 2007) and not all human landscapes will inhibit ecological interactions between predators (Berry *et al.* 1992; Standley *et al.* 1992). Landscape modification and the management of larger predators in fenced reserves for example can also have conservation benefits for mesopredators (Van Dyk & Slotow 2003). In other contexts, human landscape use may have negligible impact on mesopredator occupancy (Schuette *et al.* 2013) or negative effects through elevated populations of domestic competitors (Krauze-Gryz *et al.* 2012).

Predation risk

As well as direct killing, large carnivores impact habitat use and foraging effort of smaller mesopredators (Thurber *et al.* 1992; Palomares & Caro 1999; Ritchie & Johnson 2009). Interference competition between carnivores through harassment (Linnell & Strand 2000; Berger & Gese 2007; Mukherjee, Zelcer & Kotler 2009), prey competition (Cypher *et al.* 2001) and kleptoparasitism (Cooper 1991; Gorman *et al.* 1998) can generate avoidance of larger carnivores through spatio-temporal partitioning (Crooks & Soulé 1999; Durant 2000; Hayward & Slotow 2009).

Rarity and inconsistency of agonistic interactions and/or behavioural avoidance of encounters may permit co-existence between some predators (Durant 2000; Fedriani *et al.* 2000). Distribution of predators over large spatial scales can however be driven by competitive interactions (Elmhagen *et al.* 2010; Newsome & Ripple 2014). Mesopredators sometimes use peripheries of larger predator territories (Thurber *et al.* 1992; Berger & Gese 2007; Miller *et al.* 2012), presumably reducing encounter rates and increasing fitness. Fearful interactions between predators may permit the co-existence of multiple prey species, with certain species existing where dominant predators limit the spatio-temporal presence of subordinate predators (Berger, Gese & Berger 2008; Miller *et al.* 2012).

As a consequence of interspecific aggression between carnivores (Thurber *et al.* 1992; Palomares & Caro 1999; Berger & Gese 2007), foraging decisions by mesopredators are also influenced by risk from their own predators (Mukherjee, Zelcer & Kotler 2009; Ritchie & Johnson 2009; Roemer, Gompper & Valkengurgh 2009). The extent to which mesopredators are impacted by larger predators and the degree to which they have to adjust their foraging efforts, activity patterns, vigilance and risk taking is likely to vary depending on predator assemblage, habitat and food availability (Ritchie & Johnson 2009).

Humans can also influence interspecific interactions (Crooks & Soulé 1999). Additional anthropogenic landscapes of fear (Frid & Dill 2002) could further limit foraging opportunities for mesopredators. Alternatively anthropogenic interference with larger predators (Theuerkauf *et al.* 2003; George & Crooks 2006; Erb, McShea & Guralnick 2012) could potentially reduce suppression.

Interactions with large herbivores

Large carnivores can be important mortality drivers of ungulate populations (Jędrzejewski *et al.* 2002; Melis *et al.* 2009), maintaining herd health through the removal of unhealthy individuals (Kusak *et al.* 2012). Although not universal, density-driven terrestrial cascades are common (Schmitz, Hamback & Beckerman 2000). On Isle Royale, USA for example, wolves have been found to regulate moose *Cetartiodactyla Cervidae Alces alces* population dynamics and in doing so dampen the effects of climactic change upon herbivore and scavenger communities (Wilmers *et al.* 2006).

Both herbivore density and behaviour can be altered by the presence and actions of predators (Beckerman, Uriarte & Schmitz 1997; Montgomery *et al.* 2013). In many circumstances the

role of "landscapes of fear" (Laundré, Hernández & Ripple 2010), predation risk and the avoidance of predators are also believed to be closely linked to how ungulates use time and space (Brown, Laundré & Gurung 1999; Kronfeld-Schor & Dayan 2003; Harmsen *et al.* 2011) as well as how they forage (Kotler, Gross & Mitchell 1994; Altendorf *et al.* 2001; Laundré, Hernández & Altendorf 2001). There is an increasing amount of literature investigating the impacts that ungulate foraging patterns may have upon ecosystems and vegetation community structure (Reimoser, Armstrongb & Suchantc 1999; Gill 2000; Tschöpe *et al.* 2011). Large carnivores may hold influence over patterns of ungulate grazing pressure and its consequent impacts (Ripple & Beschta 2004; Creel *et al.* 2005; Estes *et al.* 2011).

There is a great deal of flexibility in how large carnivores such as wolves use time and space (Kusak & Haswell 2013). The causal factors behind activity patterns are highly variable (Kolenosky & Johnston 1967; Ballard *et al.* 1997; Theuerkauf 2009). Anthropogenic influences are often strong drivers (Ciucci *et al.* 1997; Theuerkauf *et al.* 2003; Kusak, Skrbinšek & Huber 2005). How large carnivores interact with herbivores is likely to be dependent on this context. Foraging and space-time use patterns of herbivores and the role of behaviourally-mediated carnivore impacts may ultimately dictate potential ecosystem services that could benefit local communities (Hebblewhite *et al.* 2005; Ripple *et al.* 2014). However trophic cascades from large carnivores are not guaranteed in every ecological context (Ford *et al.* 2015).

Context's affecting interactions with large herbivores

Species assemblage

In Europe, the limiting effects of lynx *Carnivora Felidae Lynx lynx* and wolf upon roe deer *Cetartiodactyla Cervidae Capreolus capreolus* density were stronger when both species were present than by one species alone (Melis *et al.* 2009). Where one species was present alone (most commonly the wolf) mean roe deer density was 917 per 100km^2 but only 167 in the presence of both predators (Melis *et al.* 2009). This suggests that predators can have additive effects on shared prey and that generally lynx are a more dominant predator of roe deer in Europe. The composition of large carnivores in a given scenario is clearly consequential to the effects upon herbivore communities.

In south-eastern Norway, roe deer fawns were consumed by red foxes (8.6% spring-summer diet, (Panzacchi *et al.* 2008). Red foxes had a highly varied diet so fawns were not considered important to the population dynamics of red foxes, implying that there was unlikely to be any stabilising feedback mechanism between the species (Panzacchi *et al.* 2008). Where mesopredators are released from apex predator suppression, mesopredators could have more pronounced impacts on herbivore recruitment (Berger, Gese & Berger 2008). This may offer some compensation for a lack of adult ungulate predation by large carnivores. However, even if density-driven effects could be compensated by mesopredators, smaller carnivores are unlikely to replace the behavioural dynamics between larger carnivores and adult ungulates.

Harvesting of larger trophy individuals or the removal of larger predators in general due to human conflicts could have catastrophic effects (Packer *et al.* 2009). Larger wolves >39kg (usually older and/or male animals) have been observed to have higher attack and kill rates in Yellowstone National Park where improvements in handling success are not counteracted by a reduction in pursuit ability (MacNulty *et al.* 2009). The association between increased body weight and prey size in carnivores could be driven by size-related energetic costs (Carbone *et al.* 1999; 2007) and size-related predator performance (MacNulty *et al.* 2009). Local conditions may affect composition and characteristics (gender, size or age) of predator social groups (Van Orsdol, Hanby & Bygott 1985). Food loss rates from kleptoparasites like ravens are relative to wolf pack size and can consequently further affect kill rates (Hayes *et al.* 2000; Kaczensky, Hayes & Promberger 2005). Temporal success, preferences and social structure can influence predation rates and consumption of different prey species (Jędrzejewski *et al.* 2002). Social dynamics and population demography could also influence the direction or strength of cascades due to predation patterns.

Interspecific relationships may also have a variable temporal context that is not constant (Koehler & Hornocker 1991). Herbivores can have seasonal habitat preferences and dietary requirements (Degmečić *et al.* 2011). Large carnivores can also exhibit seasonal or context driven dietary shifts (Odden, Linnell & Andersen 2006; Garrott *et al.* 2007; Latham *et al.* 2013) and habitat use (Alexander, Logan & Paquet 2006). Population structure, body condition, parasite load, climate, predator density and predation risk may all interact to drive herbivore landscape use (Montgomery *et al.* 2013).

Herbivore response to risk may in itself be subject to competitive partitioning between herbivores, particularly around key habitat sites such as water sources (Hayward & Hayward

2012). Resource competition between herbivores may alter landscape use patterns (Dolman & Waber 2008; Hibert *et al.* 2010). While displacement is context specific and likely to be dependent on levels of niche overlap (Iranzo *et al.* 2013), the potential for domestic herbivores to outcompete wild herbivores is probably high (Latham 1999).

Wild and domestic herbivores forage and interact with vegetation communities in different ways, with domestic stock often causing greater degradation (Hill *et al.* 1991; Hester & Baillie 1998; Fuller 2001). Domestic livestock often aggregate more, and their limited ranging behaviour is exacerbated through herding and human directed foraging at convenient locations (Albon *et al.* 2007). This type of herbivory will likely result in limited impacts from large carnivores upon domestic grazing/browsing pressure, with consequences being predominantly human driven. When livestock are free-ranging their response to predation risk is still different to that of wild herbivores, as well as being somewhat attenuated (Muhly *et al.* 2010).

The introduction of competitive alien herbivores (e.g. domestic stock) can also lead to apparent competition and increased predation of native species by predators (Dolman & Waber 2008). Poor husbandry practices and high livestock predation rates could potentially either exacerbate or reduce large carnivore impacts on native species depending on context. Furthermore, livestock guarding dogs that accompany livestock interact with predators (Lescureux & Linnell 2014). Livestock guarding dogs, along with human presence may add to landscapes of fear for large carnivores but may also serve to maintain interactions between predators and native prey.

The traditional role of humans as part of the predator guild in communities is often overlooked. Aboriginal hunters were important apex predators in Australia following their arrival and the extinction of the megafauna (Fleming, Allen & Ballard 2012). In the absence of its human hunting partners, the dingo may not truly fulfil the role of an apex predator and its modern ecological function may differ given vast anthropogenic habitat modification (Fleming, Allen & Ballard 2012). In a similar fashion, our understanding of how indigenous North American's impacted the landscape is still developing (Lightfoot *et al.* 2013). The sustainability of such impacts are debateable, but it is clear that the removal of human regimes from wilderness designations in the USA will not replicate the ecological conditions present since its colonisation by European settlers (Kay 1994).

The role of humans in the modern food web and the very different nature of our interactions and impacts is something worth considering. Modern hunting practices and regulations vary dramatically across the globe and the impacts will no doubt vary too. The attractive re-wilding concept of re-establishing self-sustaining ecosystems with minimal human disruption may help to maintain large carnivore-herbivore interactions, but requires careful consideration of desired outcomes (Brown, McMorran & Price 2011). Such management intervention may not always be pragmatic or necessarily a true reflection of the historic *status quo*. An understanding of how humans influence trophic dynamics could help to better predict and steer landscape management to desired outcomes.

Ecosystem productivity

Resource driven landscape use (Owen-Smith 2014) and bottom-up effects of environmental productivity are often a major driving force influencing large herbivore distribution and abundance (Coe, Cumming & Phillipson 1976; East 1984; Karanth *et al.* 2004). For example, roe deer abundance in Europe was positively correlated with environmental productivity (Melis *et al.* 2009). The impacts of large predators were however weak in productive environments and regions with mild climate but noticeably greater in regions with harsher winters and lower productivity (Melis *et al.* 2009). Climatic features such as temperature or snow depth can also interact with local complexities, impacting the strength of predation pressure and trophic cascades (Post *et al.* 1999; Sanford 1999). The strength of impacts from large carnivores may be dependent on productivity and climatic context.

A forager in a low energy state has less to lose from predation and a higher marginal value of energy to be gained so is more likely to forage in riskier habitats, change their forage selection decisions and reduce food patches to a greater extent (Brown, Morgan & Dow 1992; Brown & Kotler 2007; Hayward, Ortmann & Kowalczyk 2015). Competition for game animals between humans and large carnivores (Virgos & Travaini 2005) may affect predator energy states and consequently predation patterns. Conversely, anthropogenic food provisioning, such as at refuse (Ciucci *et al.* 1997), urban (Rodewald, Kearns & Shustack 2011) or hunting sites (Selva, Berezowska-Cnota & Elguero-Claramunt 2014) may alter predation risk trade-offs and interactions between species, potentially decoupling interspecific relationships (Rodewald, Kearns & Shustack 2011). Where anthropogenic foods dominate predator diet, impacts of large carnivores upon wild herbivores could become

minimal or alternatively could increase due to inflated predator numbers, energy or time resources.

Landscape

Landscape-scale or micro-habitat predation patterns of large carnivores can impact upon local vegetation communities. Wolf predation of deer can impact habitat heterogeneity through the creation of nutrient pulses at kill sites (Bump, Peterson & Vucetich 2009). Wolf predation success and prey vulnerability may be dependent on the amount of open grassland adjacent to streams (Kauffman *et al.* 2007). If large herbivores are predated more successfully and forage less in high risk areas (Ripple & Beschta 2004; Fortin *et al.* 2005; Crosmary *et al.* 2012), one might expect woody plant regeneration and vegetation succession (Berger 1999; Berger *et al.* 2001; Hebblewhite *et al.* 2005).

In Yellowstone National Park's northern winter range, elk *Cetartiodactyla Cervidae Cervus canadensis* movement preference for vegetative cover types was influenced by the spatial distribution of wolves (Fortin *et al.* 2005). Risk driven habitat preferences may be responsible for observed reductions in aspen *Malpighiales Salicaceae Populus tremuloides* browsing pressure by elk in the presence of wolves (Ripple & Larsen 2000; Ripple *et al.* 2001; Fortin *et al.* 2005). The extent of the impacts behaviourally-mediated trophic cascades have on aspen recruitment in Yellowstone has however been debated (Kauffman, Brodie & Jules 2010; Winnie 2012; Beschta *et al.* 2014; Winnie 2014). Trophic cascades may be more complicated than the three tiered systems proposed; in complicated food webs interactions can go up, across and down the trophic web (Strong 1992; Polis *et al.* 2000). In Yellowstone, interactions between environmental productivity, habitat features, human activities outside the park, predators and herbivores, as well as contributing impacts of engineers, such as beavers *Rodentia Castoridae Castor canadensis*, are likely to contribute and interact to affect vegetation communities through both behaviourally- and density-mediated mechanisms (Marshall, Hobbs & Cooper 2013; Painter *et al.* 2015).

Anthropogenic landscape alterations such as higher road densities, fire regimes and housing developments can have negative impacts on the presence and activity of large carnivores (Theuerkauf *et al.* 2003; Hebblewhite, Munro & Merrill 2009; Haskell *et al.* 2013). Anthropogenic disturbance may span further than expected, with activities outside protected areas having strong effects on species within reserves (Parks & Harcourt 2002). Even human landscape modification intended to conserve (e.g. fenced reserves) may alter natural predator-

prey dynamics through consequent changes in prey vulnerability and predator behaviour (Davies-Mostert, Mills & Macdonald 2013). Human landscape alteration can also create new landscapes of fear for large herbivores (Semeniuk *et al.* 2014). Such interferences could inhibit desirable ecological interactions.

Predation risk

Through behavioural mechanisms predators can influence prey species landscape use (Laundré, Hernández & Altendorf 2001; Willems & Hill 2009; Laundré *et al.* 2014), and consequently, the impacts of herbivores upon habitat structure (Fortin *et al.* 2005; Kuijper *et al.* 2013). How populations and individuals respond to predation risk is unlikely to be consistent across contexts. Behavioural responses to environmental cues of predation risk may be sensitive to fluctuations in predation pressure (Berger 1999) but can also remain stable in its absence (Chamaille-Jammes *et al.* 2014). The strength of response to risk and the relative influence of predation risk to a predator's overall limiting effect is likely to be affected by the environment as well as predator and prey characteristics (Creel 2011). It is suggested that prey species respond to overall risk rather than predator abundance alone (Heithaus *et al.* 2009). In some circumstances, prey species escape probability, habitat use and consequently resource exploitation can be higher where predators are more abundant (Heithaus *et al.* 2009). Individual factors such as gender (Laundré, Hernández & Altendorf 2001) and the presence of offspring (Wolff & Horn 2003) can also influence investment in anti-predatory responses like vigilance.

Risk of predation can cause prey to be more cautious in how they forage, becoming more vigilant (Altendorf *et al.* 2001; Wolff & Horn 2003; Halofsky & Ripple 2008), more mobile, thereby reducing predictability (Fortin *et al.* 2009), alter habitat use (Laundré, Hernández & Altendorf 2001; Creel *et al.* 2005; Fortin *et al.* 2005), respond to risk cues (Berger 1999; Mella, Banks & McArthur 2014), forage less in risky patches (Brown 1988; Koivisto & Pusenius 2006; Andruskiw *et al.* 2008) or at restricted times (Brown & Kotler 2007), forage in larger groups, diluting risk (Hebblewhite, Pletscher & Paquet 2002; Isvaran 2007; Fortin *et al.* 2009), or in smaller groups reducing detection (Hebblewhite, Pletscher & Paquet 2002; Fortin *et al.* 2009). In any one circumstance a myriad and combination of these antipredator tactics may be implemented.

Behavioural responses by prey also encourage countermeasures in predators such as stealth, boldness and space-time use selection (Hopcraft, Sinclair & Packer 2005; Brown & Kotler

2007). Fear and predation risk create somewhat of a tactical predator-prey foraging game. "Prey face different risks from predators with different tactics, and their antipredator responses vary accordingly" (Creel 2011). Predator specific strategies in prey may also promote coexistence among predator species, if employing vigilance or avoidance strategies against one sort of predator causes the forager to be more vulnerable to another (Sih, Englund & Wooster 1998).

Variation in response to predators may be driven by local selective pressures. Predator hunting strategies, foraging behaviour and social organisation of herbivores alongside environmental variables will lead to context-dependent herbivore response to predation risk (Samelius *et al.* 2013). Prey species response to predation risk in turn impacts lower trophic levels in what is ambiguously known as a trophic cascade (Polis *et al.* 2000).

Human activities can also impact patch predation risk, landscapes of fear and habitat use by both predators and large herbivores (Hebblewhite, Munro & Merrill 2009; Rogala *et al.* 2011; Sibbald *et al.* 2011). Non-consumptive (Frid & Dill 2002; Blanc *et al.* 2006; Leighton, Horrocks & Kramer 2010) and consumptive (Sand *et al.* 2006; Ciuti *et al.* 2012; Proffitt *et al.* 2013) human interactions with large herbivores can affect predation risk responses. Whether an elk was harvested by humans or not in North America was found to be a consequence of individual response to a human mediated landscape of fear (Ciuti *et al.* 2012). Older female elk generally adopted habitat preferences and the use of a running or hiding strategy that lead to their survival (Ciuti *et al.* 2012).

In the absence of human hunting pressures large herbivores may adjust their behaviour in response to large carnivores (Berger, Swenson & Persson 2001). Human interactions with ungulates may sometimes benefit large carnivores (Kilgo, Labisky & Fritzen 1998). However, anthropogenic selection can also impact behavioural evolution and herbivore learning in a different and opposing manner to that of large carnivores, potentially negating their impacts (Sand *et al.* 2006; Ciuti *et al.* 2012).

Individual behaviour, learning and the selective pressures of large carnivores and humans over time may be important drivers of large herbivore behaviour and its potential cascading effects. It is essential to know whether human interactions yield desired outcomes or interfere with the impacts of large carnivores through intensified or competing selection pressures.

Conclusions

Interactions between species are complicated. Suppression of one species by another can be driven by a varying intensity of both density- and behaviourally-mediated mechanisms. Impacts from large carnivores will not be homogenous across contexts. Factors intrinsic to prey, predators and the given system (species composition, environmental productivity, landscape, and predation risk) will culminate to produce the resultant dynamics in a given context. The mixture of variables yielding interspecific relationships with large carnivores in a given context will in turn interact with additional features at lower trophic levels, dictating further interspecific interactions, ecosystem services and the presence of trophic cascades from large carnivores.

Human-induced changes could have cascading effects for the entire carnivore community, on prey communities of both apex and mesopredators and consequently habitat structure and biodiversity (Fig. 1.1). The impacts of humans on other species, the types and intensity of human activity in a given context could alter the direction or severity of other interspecific interactions (Table. 1.1). Humans can remove large carnivores from systems altogether, undesirably influence large carnivore activity, disrupt foraging, reduce survival success or breeding capability, suppress habitat use and ultimately interfere with trophic interactions.

An understanding of whole ecosystems and the processes that maintain them is key to ensuring sustainability. If we are to understand ecological systems, it is important for basic monitoring of common as well as rare species to be undertaken alongside novel experimental approaches. Whilst managers, politicians and the public might desire standardised answers, blanket assumptions of the role of large carnivores across contexts and inflexible or misinformed approaches to their management are damaging. In order to take appropriate management and conservation action in any given context, interspecific interactions, the outcome of human interference and the trade-off between ecosystem services and anthropogenic land uses must be informed by robust experimentation and analysis. It is imperative that the consequences of intervention, particularly predator control are understood.

Table. 1.1. Human impacts and their potential consequences to trophic systems.

Both direct influences and consequent alterations to interspecific interactions can affect ecological processes. The positive (+), negative (-) or neutral (=) impacts of human interventions on a guild of organisms are likely to vary dramatically and will be dependent on context. Human interactions with apex predators can alter mesopredator release (MR), large herbivore release (LHR), predation (P), competition (C), food availability (F), seed predation (SP) and seed dispersal (SD). Negative human influences on large carnivores can release those species they suppress. This could in turn have cascading effects, potentially increasing (↑) or decreasing (↓) pressure on other species further down the food chain.

Human-wildlife interaction	Large Carnivores	Large herbivores	Mesopredators	Small herbivores	Vegetation
Hunting Large Carnivores	- (↑ P)	- (↑ P of young, MR) + (adults ↓ P)	+ (↓ C) - (↓ consistency of F, scavenging)	- (↑ P, MR)	- (↑ P, LHR) - (↓ SD, MR) + (↓ SP)
Hunting large herbivores	- (↓ F)	- (↑ P)	- (↓ F, scavenging & young herbivores) + (↓ C)	- (↑ P, MR) + (↓ P, ↓ C)	- (↓ SD, MR) - (↑ SP, MR) + (↓ P) + (↑ SD) + (↓ SP)
Alien predators	- (↑ C) =	- (↑ P) = + (↓ P)	- (↑ C) = + (↓ C)	- (↑ P, MR) = + (↓ P, ↓ C)	- (↑ P, LHR) - (↓ SD, MR) - (↑ SP, MR) = + (↓ P) + (↑ SD) + (↓ SP)
Alien herbivores	- (↓ F) = + (↑ F)	- (↑ C) = + (↓ P)	- (↑ C) = +(↓ C) + (↑ F)	- (↑ C) = + (↓ P)	- (↑ P) - (↓ SD, MR) - (↑ SP, MR) = + (↓ P) + (↑ SD) + (↓ SP)
Food provisioning (predators)	+ (↑ F)	- (↑ P) = + (↓ P)	- (↑ C) + (↑ F) + (↓ C)	- (↑ P, MR) + (↑ F) + (↓ P)	- (↓ SD, MR) - (↑ SP, MR) + (↓ P) + (↑ SD) + (↓ SP)
Food Provisioning (herbivores)	+ (↑ F)	+ (↑ F)	- (↑ C) + (↑ F)	- (↑ P) + (↓ P) + (↑ F)	- (↑ P) - (↓ SD) - (↑ SP) = + (↓ P) + (↑ SD) + (↓ SP)
Habitat loss	-	-	-	-	-
Habitat fragmentation	-	- + (↓ P)	- + (↓ C)	- - (↑ P, MR) + (↓ P)	- - (↑ P) - (↓ SD) - (↑ SP) + (↑ SD) + (↓ SP)
Disturbance (risk)	- + (↑ F)	- - (↑ P) + (↓ P)	- - (↑ C) + (↓ C)	- - (↑ P) + (↓ P)	- (↑ P) - (↓ SD) - (↑ SP) = + (↓ P) + (↑ SD) + (↓ SP)

Acknowledgements

Thesis structure

In order to make worthwhile inferences, ecologists must use the most robust approaches available (Hayward *et al.* 2015). This thesis examines interspecific interactions at multiple scales within one relatively unmodified study location. It utilises experimental and observational approaches alongside multiple analytical methodologies. Such an approach offers a more robust perspective than singular studies or methodological approaches, while also addressing the practicalities of real-world research (Allen *et al.* 2017b; Bruskotter *et al.* 2017).

Chapter One begins by concisely reviewing our understanding of top-down suppression of mesopredators by larger carnivores and the contexts which shape the outcomes of these interspecific relationships (Haswell, Kusak & Hayward 2017). This review provided the broad base from which to identify knowledge gaps. Simple goals emerged from this review; to understand if risk and suppressive effects exist when predators occur in sympatry, to explore the behavioural strategies employed by mesopredators that permit sympatric coexistence and to understand the impact of human disturbance.

Chapter Two establishes whether risk is perceived by foxes that occur in sympatry with larger carnivores. The investigation also explores the costs, and strategic mechanisms that occur where mesopredators respond to an olfactory risk cue (urine). Chapters Three and Four evaluate the consequences of risk along spatial and temporal niche axes while also examining human influence on these broader processes. Chapter Three expands to see whether the fine-scale risk mitigation employed by foxes in Chapter Two translates to a landscape of fear, whereby animals perceive spatial heterogeneity in predation risk (Laundré, Hernández & Altendorf 2001; 2010; Bleicher 2017). This chapter asks if foxes avoid broad spaces used by large carnivores or act elusively in their presence. Chapter Four examines whether foxes avoid larger carnivores in time. A strategy which may mitigate against complete spatial avoidance (Kohl *et al.* 2018).

The thesis concludes in Chapter Five by evaluating the contribution of the works to the current knowledge base, exploring recent progressions in the field and acknowledging pathways for further advancement. While not directly part of the thesis research project, the published paper provided in Appendix F (Haswell *et al.* 2019) was inspired by Chapter Two. This complimentary paper attempts to bridge the gap between theory and real world practice, highlighting the application of the giving-up density framework to livestock predation management.

This thesis is composed of introduction and conclusions chapters with the main body as a series of publications and scripts prepared ready for publication. This approach offers readers the opportunity to engage with sections independently or with the thesis as a whole.

Study site

Plitvice Lakes National Park (Plitvice), is situated between 44° 44' 34" and 44° 57' 48" N and 15° 27' 32" and 15° 42' 23" E, in the Dinaric Mountains, Croatia (Šikić 2007). The mountainous karst (limestone and dolomite) landscape ranges from 367 to 1279 m and, excepting the iconic lakes and waterfalls, is characterised by scarce surface water (~1%), underground drainage systems, sink holes and caves (Šikić 2007; Romanić *et al.* 2016). Annual precipitation is 1,550 mm with temperatures fluctuating between winter lows of -3°C and summer highs of 36°C (Šikić 2007). Forest cover is predominantly Dinaric beech and fir trees (*Fagus sylvatica* and *Abies alba*). Data collection sites, roads and water bodies alongside the boundaries and location of the national park are shown in Fig. 1.2.

Tourism and recreation are permissible within the 297 km^2 park where approximately 1770 people live within 19 settlements (Firšt *et al.* 2005; Romanić *et al.* 2016). The number of people visiting Plitvice has grown from 928,000 visitors in 2007 to over 1.72 million in 2017 (Smith 2018). Tourist activity is predominantly centred on the lakes, although some visitors also hike and cycle throughout the park. Dog, *Canis lupus familiaris,* walking is relatively rare. Driving by most visitors is restricted to the tarmacked roads in the south, east and northern edges of the park. A few small livestock herds (Sheep, *Ovis aries*, and cattle, *Bos taurus*) operate with guardian and herding dogs, near the southern highway. Direct interactions between humans and large carnivores are relatively rare in Plitvice, although livestock predation, predation of pet dogs and highway mortality have been observed for wolves.

The park protects the drainage basin for the lakes but also houses a great diversity of wildlife. Plitvice is home to a diverse guild of large carnivores and mesocarnivores. This includes the

gray wolf, *Canis lupus*, Eurasian lynx, *Lynx lynx*, brown bear, *Ursus arctos*, red fox, *Vulpes vulpes*, European wildcat, *Felis silvestris,* European badger, *Meles meles*, stone marten, *Martes foina*, pine marten, *Martes martes*, European polecat, *Mustela putorius*, stoat, *Mustela erminea*, weasel, *Mustela nivalis* and Eurasian otter, *Lutra lutra*. Golden jackal, *Canis aureas* were not recorded within Plitvice during the study. One record is however known from nearby an adjacent town (Saborsko) in winter 2013; a pup was also later captured within the park during wolf collaring efforts in 2017 (*Josip Kusak unpubl. data*). European roe deer, *Capreolus capreolus*, red deer, *Cervus elaphus*, and wild boar, *Sus scrofa*, constitute the parks large wild ungulate community.

Red foxes are found throughout the park; however density and home range size are yet to be estimated. At least three different gray wolf packs are known to make use of the park as part of their territories, potentially numbering at least 18 individuals (including known pups) with a density of 1.4-1.6 wolves per 100 km^2 (JK *unpubl. data,* estimates based on 100% MCP polygons and snow tracking of two packs utilising PLNP during 2015). Spot pattern analysis of camera trap photos suggested a minimum of 6 lynx were using the park in 2015, although the actual number is likely higher than survey efforts or availability of identifiable photos suggests (JK *unpubl. data*). The only available home range estimate for lynx (male) using Plitvice in 2017-2018 was 354 km^2; only part of this territory was within the park and overlapped completely with a limited dataset of tracking points from a female lynx (JK *unpubl. data*).

Figure. 1.2. Map of study sites.

Plitvice Lakes National Park

Legend:
- ● GUD Experiments
- ▲ Camera traps
- — Streams & rivers
- — Roads
- ■ Lakes
- ▨ Plitvice Lakes National Park

Left; map of Plitvice lakes National Park, Croatia. Black dots detail the giving-up density (GUD) study site locations conducted in the summer of 2015 which provided data for chapter two of this thesis. Red triangles detail the locations of camera trap sites (Oct 2015 - Oct 2016), which provided data utilised in chapters three and four. The hatched green area details the boundaries of the national park. Roads are in grey and water in blue.

Below; map detailing the geographic location of the study site.

Chapter 2.

Although predator communities have been widely studied, intact European communities have however received comparatively little attention. Additionally, relatively limited attention has been given to how smaller predators adjust their foraging behaviour in response to the potential threat posed by sympatric large carnivores. Chapter Two examines the response of foxes to a risk cue (wolf urine) using the methodological approach of giving-up densities (GUDs). Particular attention was given to recommendations from leading practitioners (Brown 1988; Bedoya-Perez *et al.* 2013). Many of these intricacies, alongside biologically relevant elements that were absent from previous studies, were incorporated into the final experimental approach (Appendix A). One of the major improvements to traditional approaches was the addition of wildlife cameras instead of sand to gather tracks (see Appendix C: *Camera traps & giving-up densities*). This more accurately identified foragers and enabled the study of the behaviour behind the GUDs. Rather than just understanding if foxes perceive urine as a risk cue, the application of cameras permitted the study of how foxes responded to this risk cue.

Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators

Peter M. Haswell[12], Katherine A. Jones[1], Josip Kusak[3], Matt W. Hayward[1456]

A highlighted student paper, communicated by Christopher Whelan:

Having noteworthy implications for wildlife conservation and management; this paper provides significant insight in the study of giving-up densities, foraging ecology and intraguild interactions.

Author contribution statement

The study was conceived, designed and executed by P.M.H who also wrote the manuscript. M.W.H contributed to the design, analysis and writing of the manuscript. K.A.J contributed to the design and analysis. J.K. assisted with permits, logistics and execution of the study. M.W.H, K.A.J and J.K. provided editorial advice.

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Abstract

Where direct killing is rare and niche overlap low, sympatric carnivores may appear to coexist without conflict. Interference interactions, harassment and injury from larger carnivores may still pose a risk to smaller mesopredators. Foraging theory suggests that animals should adjust their behaviour accordingly to optimise foraging efficiency and overall fitness, trading off harvest rate with costs to fitness. The foraging behaviour of red foxes, *Vulpes vulpes*, was studied with automated cameras and a repeated measures giving-up density (GUD) experiment where olfactory risk cues were manipulated. In Plitvice Lakes National Park, Croatia, red foxes increased GUDs by 34% and quitting harvest rates by 29% in response to wolf urine. In addition to leaving more food behind, foxes also responded to wolf, *Canis lupus*, urine by spending less time visiting food patches each day and altering their behaviour in order to compensate for the increased risk when foraging from patches. Thus, red foxes utilised olfaction to assess risk and experienced foraging costs due to the presence of a cue from gray wolves. This study identifies behavioural mechanisms which may enable competing predators to coexist, and highlights the potential for additional ecosystem service pathways arising from the behaviour of large carnivores. Given the vulnerability of large carnivores to anthropogenic disturbance, a growing human population and intensifying resource consumption, it becomes increasingly important to understand ecological processes so that land can be managed appropriately.

Introduction

Direct interactions between predators and other species can lead to indirect consequences further down the food web via trophic cascades (Ripple *et al.* 2016). Direct predation as well as behavioural/trait-mediated mechanisms can be important drivers of such processes (Beckerman, Uriarte & Schmitz 1997; Schmitz, Krivan & Ovadia 2004; Trussell, Ewanchuk & Matassa 2006). Evidence for trophic cascades stemming from large carnivores is growing (Ripple *et al.* 2014); however influence strength and study validity are hotly debated (Kauffman, Brodie & Jules 2010; Newsome *et al.* 2015; Allen *et al.* 2017a). Understanding the importance of trophic interactions is a fundamental ecological question (Sutherland *et al.* 2013). Understanding mechanisms, consequences and behavioural responses to predation pressure are crucial first steps in understanding the importance of trophic interactions.

Mesopredator release (MR) describes the increase of mesopredator populations after a decline in larger, apex predators (Soulé *et al.* 1988; Crooks & Soulé 1999). Intraguild predation, competitive killing and interference competition are common where niches overlap (Palomares & Caro 1999; Ritchie & Johnson 2009; Lourenco *et al.* 2014). Interference interactions from larger carnivores pose a risk to smaller mesopredators and may ultimately affect population demography (Linnell & Strand 2000). Apex predators do not always suppress spatial occupancy and mesopredator abundance (Lesmeister *et al.* 2015; Lyly *et al.* 2015). However, continent-wide patterns of mesopredator release have been identified (Letnic *et al.* 2011; Newsome & Ripple 2014; Pasanen-Mortensen & Elmhagen 2015). Suppressive interactions between carnivores combined with bottom-up effects of environmental productivity can ultimately drive predator and prey species abundance (Elmhagen & Rushton 2007; Elmhagen *et al.* 2010).

Gray wolves, *Canis lupus* have been observed to kill and chase foxes (Mech & Boitani 2005, p. 269). Some evidence also suggests wolves may contribute to the control of red fox, *Vulpes vulpes* populations (Elmhagen & Rushton 2007). In much of eastern and southern Europe, red foxes co-occur with wolves (Mech & Boitani 2010; Hoffmann & Sillero-Zubiri 2016). A negligible presence of fox hair in wolf diet suggests foxes are not regularly eaten by wolves in Europe (Štrbenac *et al.* 2005; Krofel & Kos 2010; Stahlberg *et al.* 2017). Low mortality could reflect effective avoidance of larger predators (Durant 2000). However, interspecific killing may of course occur without consumption (Murdoch *et al.* 2010). Even in the absence of direct killing, it is plausible that wolves may still behaviourally suppress red foxes through harassment, injury and fear of encounters. Literature suggests minimal dietary overlap between the two carnivores (Patalano & Lovari 1993; Bassi *et al.* 2012). Competition for landscape features such as den sites, scavenging opportunities and kleptoparasitism however, could still give rise to negative interactions. Conversely, foxes scavenge from wolf kills in Europe (Selva *et al.* 2005; Wikenros, Stahlberg & Sand 2014), suggesting they may exhibit positive behavioural responses toward the species presence even where kleptoparasitism might be risky.

Foxes alter their behaviour in response to the presence of larger carnivores, habitat features and hazardous objects (Berger-Tal *et al.* 2009; Vanak, Thaker & Gompper 2009; Hall *et al.* 2013). This suggests they are capable of assessing and responding to environmental risk cues. Red foxes have well-developed sensory systems and are known for their flexible behaviour, diet and ability to thrive in anthropogenic landscapes (Randa *et al.* 2009; Bateman & Fleming

2012; Lesmeister *et al.* 2015). Olfaction plays an important role in detecting scavengeable food sources (Ruzicka & Conover 2012) and logic suggests it would also play an important role in risk evaluation. A wealth of research exists supporting the recognition and behavioural response of prey species towards odours of their predators (Apfelbach *et al.* 2005). However we know of only two studies examining the influence of olfactory predation risk cues on food harvest by red foxes under the giving-up density (GUD) framework (Mukherjee, Zelcer & Kotler 2009; Leo, Reading & Letnic 2015). We expanded upon this knowledge by investigating the role of urine in risk analysis and studying behavioural responses in order to explain changes in food harvest.

When responding to predation risk, foragers must trade-off the fitness benefits of avoiding predators with the costs of avoidance in any given context (Brown, Laundré & Gurung 1999; Brown & Kotler 2007; Haswell, Kusak & Hayward 2017). The better an individual animal is at assessing risk, the more effectively it can forage, balance its energetic cost-benefits and the greater its overall fitness. Methodologies developed by Brown (1988; 1992) and Mukherjee et al. (2009) were adapted to investigate fox giving-up densities (GUDs) and foraging behaviour (methodological considerations, Appendix A). A GUD is the amount of food left behind in a given food patch after the forager quits the patch (Brown 1988). As a forager devotes time to harvesting a food patch (assuming it is depletable), the available resources decline as does the harvest rate (Brown 1988). Foragers should leave a given patch once the harvest rate (H) is equal to the sum of the metabolic costs (C), predation costs (P) and missed opportunity costs (MOC) i.e. $H = C + P + MOC$ (Brown 1988; Shrader *et al.* 2012). By holding other parameters constant between food patches, it is possible to investigate species or habitat specific differences in predation cost (Brown 1988). Increases in predation risk should increase the GUD with animals foraging less in risky patches (Brown 1988). GUDs can help measure the response of organisms to olfactory cues and their perception of the predation costs (P) associated with foraging, thus illuminating ecological processes.

Understanding the contribution of different biodiversity components to ecosystem functioning is vital (Sutherland *et al.* 2013). Suitable scientific information becomes especially essential if wildlife is to be properly managed in public trust (Treves *et al.* 2017). The existence of mesopredator release has become more widely supported (Ritchie & Johnson 2009; Newsome *et al.* 2017b), yet understanding of the mechanisms and processes are still needed if the consequences of anthropogenic intervention are to be fully understood. Furthermore, cross-context assumptions should be avoided and there is still great need to

understand the impacts of large carnivores for any given system (Kuijper *et al.* 2016; Haswell, Kusak & Hayward 2017). This paper examined red fox foraging behaviour in response to an olfactory risk cue (wolf urine) in order to test the importance of olfaction in risk analysis, identify any resultant suppression and the foraging strategies employed where apex predators pose risk.

Methods

Study site

Plitvice Lakes National Park (PLNP) is in the Dinaric Alps, Croatia between 44° 44' 34" and 44° 57' 48" N and 15° 27' 32" and 15° 42' 23" E (Šikić 2007). The park (297 km^2) is a mosaic of mountains and valleys with altitude ranging from 367 to 1279 m above sea level (Romanić *et al.* 2016). The karst (limestone and dolomite) landscape of the park is characterised by underground drainage systems, sink holes and caves, and contains ~1% surface water with a series of streams, rivers, lakes and waterfalls (Šikić 2007). Topography can influence microclimates within the park but, in general, summers tend to be mild and sunny and winters long with heavy snowfall; temperatures range between winter lows of -3°C and summer maximums of 36°C and annual precipitation is 1,550 mm (Šikić 2007).

Romanić et al. (2016) estimate approximately 1770 people occupy 19 settlements within the park's boundaries. Being a national park, the only economic uses permitted within the boundaries are tourism and recreation (Firšt *et al.* 2005).

Between July and September 2015, foraging experiments were conducted within the mixed beech (*Fagus sylvatica*) and fir (*Abies alba*) forests of PLNP. Forest roads were surveyed for carnivore signs with the assistance of a detection dog ≥ 1 week prior to the experiments - maximising data yield by selecting sites with fox presence. During surveys the dog did not leave the road. Population density of red fox in Croatia is estimated at 0.7 animals per km^2, with a territory size of 1.43 km^2 per fox (Slavica *et al.* 2010; Galov *et al.* 2014). Home ranges between fox group members can often overlap (30-100%) (Poulle, Artois & Roeder 1994). Fox individuals could not be identified by pelage markings but distance between sites (≥ 1.5 km) ensured site independence and was greater than distances previously used (Mukherjee, Zelcer & Kotler 2009; e.g., Leo, Reading & Letnic 2015). Twelve sites were attempted. In early July, foxes foraged from three of those sites in the north-west of the park; a less accessible area, partly open to hiking and local traffic but receiving far fewer tourists than the

lakes. These sites were then repeated in late August to give a better temporal representation of response consistency.

GUD Methodology

Feeding stations were positioned similarly to those used by Altendorf et al. (2001) with each site consisting of a 2 x 3 grid with six food patches spaced 60 m apart. Patches were placed in woodlands, with three patches on either side of an unpaved forest road to maximise detection likelihood and keep road related risk consistent. Each food patch contained twenty 4 g dog food pieces (80 g per patch, Bakers Complete Meaty Meals Chicken), systematically mixed in 8 L of local substrate put through a 5 mm sieve and placed inside a 14 L bucket half submerged in the ground. To increase detection of the food patches by foragers, 5 ml of liquid leached from raw meat was applied to the surface of the soil within the bucket each day. We measured GUDs and replenished food pieces daily. Sites were visited in the hottest parts of the day (afternoon) to ensure foragers were not disturbed.

To standardise harvest rate (H), the structure of artificial patches was kept consistent (substrate and food). The substrate to food ratio was chosen after trials with less soil were harvested completely and trials with more soil were harvested minimally (PMH *unpubl. data*). A decline in harvest rate over time was thus ensured through the use of a depletable food source in a suitable volume of inedible soil matrix (Brown 1988; Bedoya-Perez *et al.* 2013). Six food patches were available to the same forager to ensure consistent missed opportunity costs (MOC). Patch consistency kept energetic costs (C) consistent and data collection occurred during typical summer weather conditions. Habitat-associated risks were kept somewhat consistent by using just mixed beech and fir woodlands. Although not explicitly mentioned in earlier studies (Mukherjee, Zelcer & Kotler 2009; Leo, Reading & Letnic 2015), the influence of human scent contamination was minimised during data collection by wearing thick gloves, a mouth mask and long sleeved clothes kept in the presence of the liquid leached from meat rather than smelling of detergent. Predation costs (P) were manipulated using scent treatments.

Foxes foraged from feeding stations within a day during pilot studies (PMH *unpubl. data*). The first day of the eleven day experimental cycle was untreated to provide an opportunity for detection and acclimatisation. A control scent consisting of 25 g of sand scented with 3 ml of mint extract (Asda Extra Special Peppermint Extract) was spread across a piece of locally sourced moss (15 x 15 cm) placed on the ground 15 cm to the north of the bucket on day two

and left during the remaining control-treatment days. On day seven, the control treatment was removed from all patches and 25 g of granules scented with wolf urine (PredatorPee®, Wolf Urine Yard Cover Granules) were placed on fresh moss in the same location as the procedural control. Throughout the five day treatment periods, both odours and volumes used were detectable by researchers.

Daily replenishment of GUDs should result in higher predictability and exploitation of patches by foragers in what has been termed the "magic pudding" effect (Bedoya-Perez *et al.* 2013). An eleven day window was used for each experiment to reduce the likelihood of foragers becoming over-reliant upon predictable food patches. We deemed that there was less expectation of a response to wolf urine given its application later in the test procedure when foxes would be more familiar and reliant upon food patches. Thus, the experimental approach was considered conservative.

During the experiment, automated cameras were set to record 30-second videos with 30-second intervals. Cameras were positioned 0.4 m high on trees 2 m from feed stations and angled to ensure buckets were in central view. Camera-traps permitted accurate species identification of those responsible for the GUDs as well as the collection of additional behavioural data.

Additional variables

Soil penetration could affect GUDs if some substrates were harder to dig through than others. This was measured by dropping a wooden 1 m ruler into the bucket from shoulder height and measuring the depth that the ruler penetrated the soil.

A photograph was taken from each GUD patch towards the road, 30 m away. Photos were taken consistently with a 3 megapixel camera always fully zoomed out. A systematic grid sample of 100 pixels (10 x 10) was analysed from each photograph (0.003% of pixels). Pixels were assigned to categories of open (no material blocking view to the road) or other (biotic or abiotic material) to calculate the percentage visibility to the road (number of open pixels) at each location. Pictures were analysed using SamplePoint V1.58 - a method that provides accuracy comparable with field methods for ground cover measurements (Booth, Cox & Berryman 2006).

Data for the fraction of moonlight illuminated at midnight was obtained from the US naval observatory (http://aa.usno.navy.mil/data/index.php). Due to each experiment day beginning

one afternoon and running overnight until the next afternoon, an experimental day beginning on the afternoon of June 26th and finishing the afternoon of June 27th for example was ascribed moonlight data from midnight on June 27th.

GUD Analysis

Camera-trap videos were used to identify the last known forager and assign GUD data for each experiment day. On rare occasions where cameras failed to trigger but the patch had been visited (N = 8 from 195 total GUDs), field signs were used to confirm fox visits. GUD scores were assigned to foxes when they were the last species identified foraging at the patch (every occasion foxes visited) with the exception that once a patch was discovered by foxes, all following days where a visit was not recorded were assigned the maximum GUD of 20 to ensure data reflecting patch avoidance was also included. Foxes were captured on video during both scent treatments for all sites, so death of subjects could be ruled out.

Following Leo et al. (2015), we treated GUDs as count data. The counts were commonly occurring (food pieces were often left behind resulting in higher GUDs) and, as such, a negative binomial regression (negative binomial distribution with a log link) generalized linear mixed model (GLMM) was used to examine the influence of independent variables upon GUDs (Heck, Thomas & Tabata 2012). All analysis was conducted in IBM SPSS Statistics 22. The fixed effect was scent treatment. Covariates were percentage visibility to the road, soil penetration (cm) and fraction of the moon illuminated. The repeated measures aspect of data points from the same patch and a random effect for patch location were also included. Robust standard error estimation was used to handle any violations of model assumptions and the Satterthwaite approximation was applied to denominator degrees of freedom (few level 2 units, unbalanced data and more complex covariance matrices).

Behavioural analysis

The number of visits and total visit duration per experiment day was extracted from the videos. New visits were considered to begin if the period between two videos was greater than 15 minutes. Visit duration was recorded as the amount of time in seconds from the beginning of the first video and the exact time the fox (any body part) was no longer visible on the last video for that visit. The influence of scent treatment, percentage visibility to the road, soil penetration and fraction of the moon illuminated upon total visit duration was analysed with a negative binomial regression GLMM. Visit frequency per experiment day

was analysed with a loglinear (Poisson distribution & log link) GLMM. All other model parameters were the same as for the GUD analysis.

Where foxes visited patches, behavioural data were extracted from videos taken by automated cameras using Solomon Coder Beta 15.11.19. Strict definitions of behaviours were described in an ethogram (Appendix B). Given that identification of most behaviour required the orientation of the head or neck to be identifiable, the length of videos was recorded as only the duration during which the animals head orientation was identifiable i.e. once the head and neck had left the visible field, video timing stopped. Videos where animals were not present throughout the entirety of the thirty second video did not then skew the data. Duration of time spent engaging in major and minor vigilance, foraging from the bucket and sniffing the ground were extracted from each video. Percentage of time spent enacting behaviours ((total behaviour duration / total video length)*100) was calculated for each patch and experiment day. Percentage of time spent enacting behaviours were analysed with negative binomial regression GLMMs. All other model parameters were the same as for the GUD analysis.

Quitting harvest rate curves

Following the protocol of Kotler at al. (2010) quitting harvest rates (QHR) were calculated for each treatment. Overall handling time (h) was estimated with Kotler and Brown's (1990) multiple regression equation derived from Holling's (1959) disc equation: $t = (1/a)[\ln(N_0/N_f)] + h(N_0\text{-}N_f)$. t = the total time spent at patches (visit durations obtained from camera trap footage), a = attack rate, N_0 = Initial amount of dog food pieces in the patch (20) and N_f = the GUD. Two variables, $\ln(N_0/N_f)$ and $(N_0 - N_f)$ were created, these variables were then regressed against values for t, the coefficients of which yielded estimates for $1/a$ and h, respectively.

We then used h, in this case 16.79 s/food piece to create a new variable t_{new} [$t_{new} = t - h(N_0\text{-}N_f)$]. Using the regression $t_{new} = (1/a)[\ln(N_0/N_f)]$, subsets of values for t_{new} and $[\ln(N_0/N_f)]$ were then used to obtain coefficients giving estimates for $1/a$ and thus a (1/coefficient value = a) for each scent treatment. Estimates of h and treatment specific a were then used in Hollings disc equation to calculate QHR for each resource density (1-20 food pieces): QHR = (a*GUD)/(1+a*h*GUD). Mean GUDs were also used to obtain a characteristic QHR for each treatment. In order to fully characterize risk management strategy, the treatment specific harvest rate curves and QHR for mean GUDs were then plotted.

Results

GUDs

A total of 195 fox GUD measures were obtained. Even with a conservative experimental approach (less expectation of a response to wolf urine given its application later in the test procedure when foxes would be more familiar and reliant upon food patches), there was a significant effect of scent treatment upon GUDs ($F_{1, 93} = 17.243$, $P < 0.001$). GUDs were significantly higher (less food harvested from patches) during wolf urine treatment (14.98 ±6.94 SD, N=127) than under the control treatment (mint, 11.16 ±7.10 SD, N= 68). Soil penetration ($F_{1, 45} = 0.376$, $P = 0.54$), percentage visibility to road ($F_{1, 5} = 2.629$, $P = 0.17$) and fraction of the moon illuminated ($F_{1, 38} = 0.747$, $P = 0.39$) did not have a significant effect on GUDs.
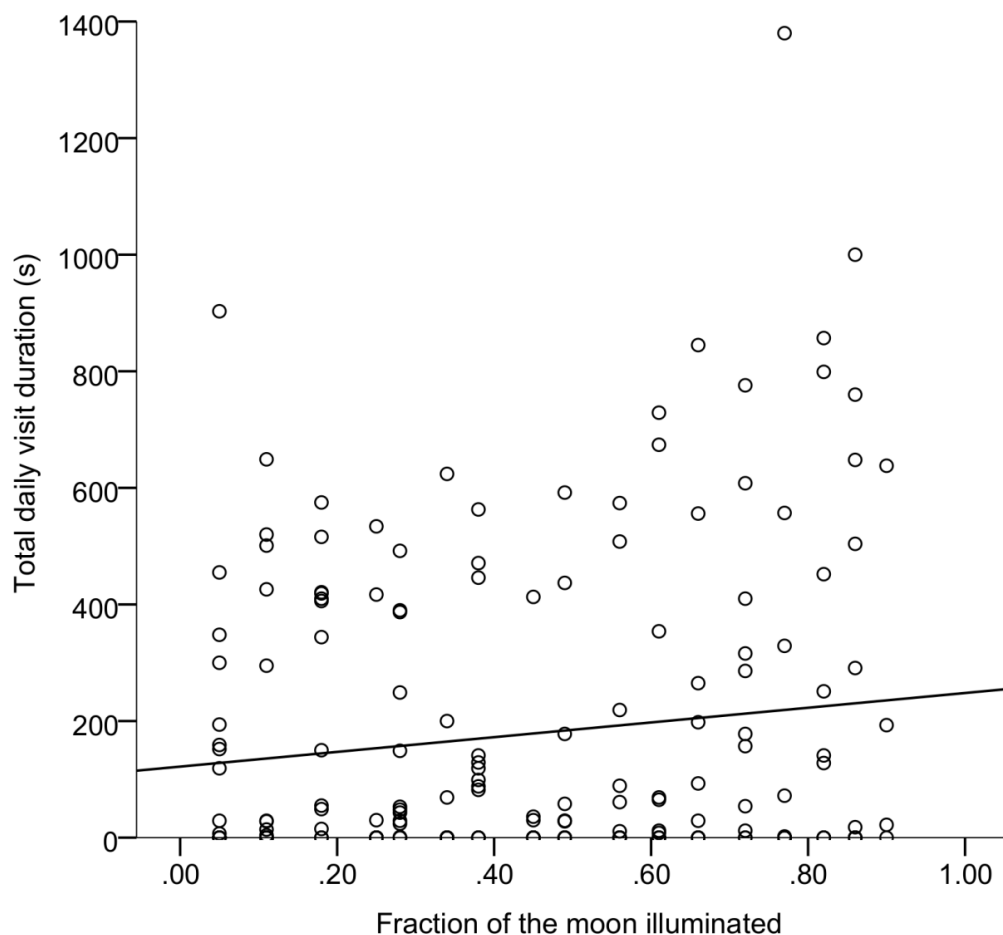
Figure. 2.1. Fox visit duration against moon illumination. Total visit duration by red foxes, *Vulpes vulpes*, to food patches each day had a positive relationship with fraction of the moon illuminated.

Behavioural analysis

Visit duration and frequency

In total, 790 videos of fox visits were used to calculate total visit duration (s) for 187 experiment days (camera malfunctions excluded N = 8). Scent treatment had a significant effect on total daily visit duration to the feeding patches ($F_{1, 9}$ = 10.570, P = 0.01). Visits were longer under the control scent (mint, 269.14 ±307.22 SD, N= 63) than with wolf urine (132.59 ±212.47 SD, N=124). Soil penetration ($F_{1, 10}$ = 0.279, P = 0.61) and percentage visibility to road ($F_{1, 6}$ = 1.396, P = 0.28) did not have a significant effect on total daily visit duration. Even though moonlight levels did not affect GUDs, total daily visit duration had a positive relationship with fraction of the moon illuminated ($F_{1, 11}$ = 7.388, P = 0.021, Fig. 2.1). No independent variables significantly influenced visit frequency per experiment day.

Percentage of time spent enacting behaviours

Behaviour was identifiable from 782 of the 790 videos of fox visits, providing behavioural data for 114 experiment days (72 patch avoidance days with no videos, 8 days with camera malfunctions, and 1 day with fox on video but behaviour identification not possible due to head being out of view). At patches, foxes spent significantly more of their time enacting major vigilance during wolf urine treatment than when the control scent was present ($F_{1, 26}$ = 31.996, P < 0.001, Fig. 2.2). Soil penetration ($F_{1, 9}$ = 3.679, P = 0.087), percentage visibility to road ($F_{1, 8}$ = 0.037, P = 0.85) and fraction of the moon illuminated ($F_{1, 104}$ = 2.493, P = 0.12) did not have a significant effect. No independent variables had a significant effect upon time spent enacting minor vigilance.

Foxes spent significantly less of their time foraging at patches with wolf urine than with the control ($F_{1, 52}$ = 6.132, P = 0.017, Fig. 2.2). Soil penetration ($F_{1, 24}$ = 2.128, P = 0.16), percentage visibility to road ($F_{1, 6}$ = 0.847, P = 0.39) and fraction of the moon illuminated ($F_{1, 29}$ = 0.121, P = 0.73) did not have a significant effect.

When at patches, foxes spent significantly more of their time sniffing the ground during wolf urine treatment than the control ($F_{1, 44}$ = 5.381, P = 0.025, Fig. 2.2). Percentage of time spent sniffing the ground had a negative relationship with increasing soil penetration ($F_{1, 4}$ = 20.530, P = 0.009, Fig. 2.3). Percentage visibility to road ($F_{1, 5}$ = 0.489, P = 0.52) and fraction of the moon illuminated ($F_{1, 109}$ = 2.892, P = 0.092) did not have a significant effect.
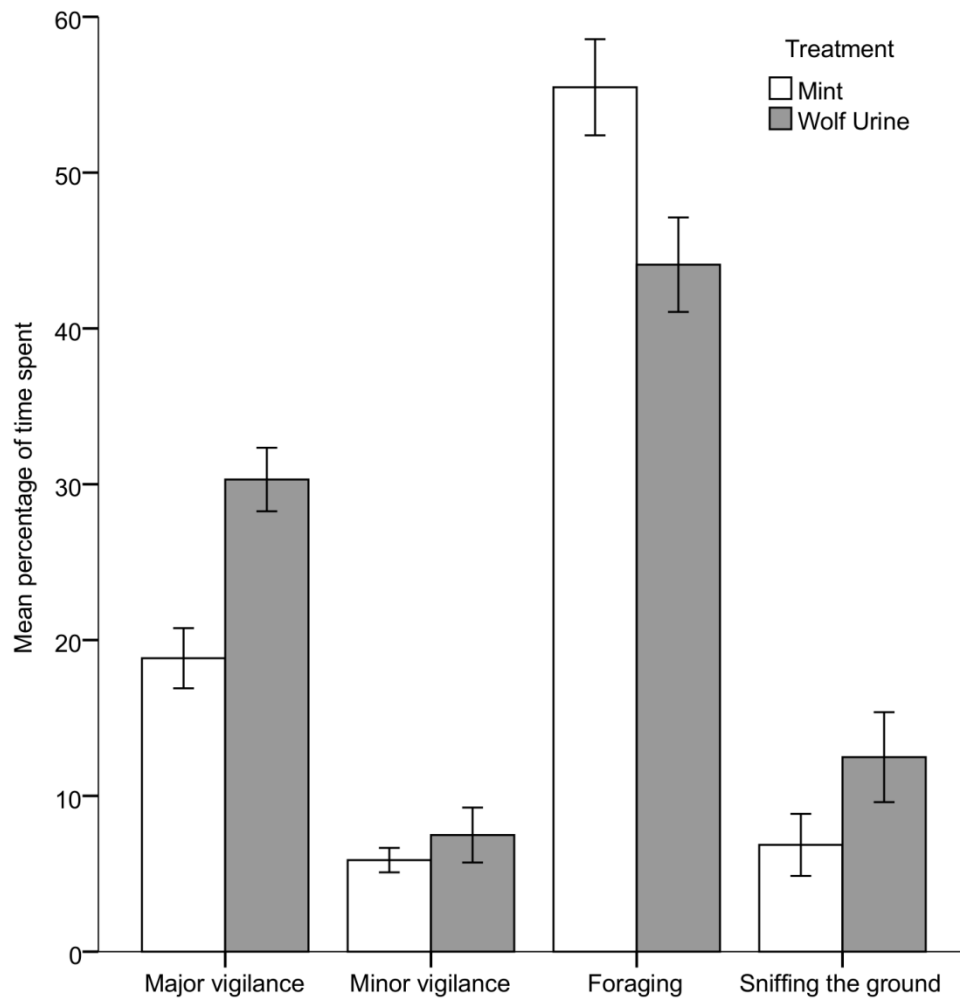
Figure. 2.2. Time spent by foxes enacting foraging or risk mitigation behaviour. Mean percentage of time spent by red foxes enacting major vigilance (mint, 18.83 ±13.37 SD, N = 48, wolf urine, 30.30 ±16.56 SD, N = 66), minor vigilance (mint, 5.88 ±5.44 SD, N = 48, wolf urine, 7.48 ±14.33 SD, N = 66), foraging (mint, 55.48 ±21.38 SD, N = 48, wolf urine, 44.09 ±24.64 SD, N = 66) and sniffing the ground (mint, 6.85 ±13.80 SD, N = 48, wolf urine, 12.48 ±23.46 SD, N = 66) at artificial feeding stations during two scent treatments, a control (mint) and wolf urine. Error bars represent ±1 SEM
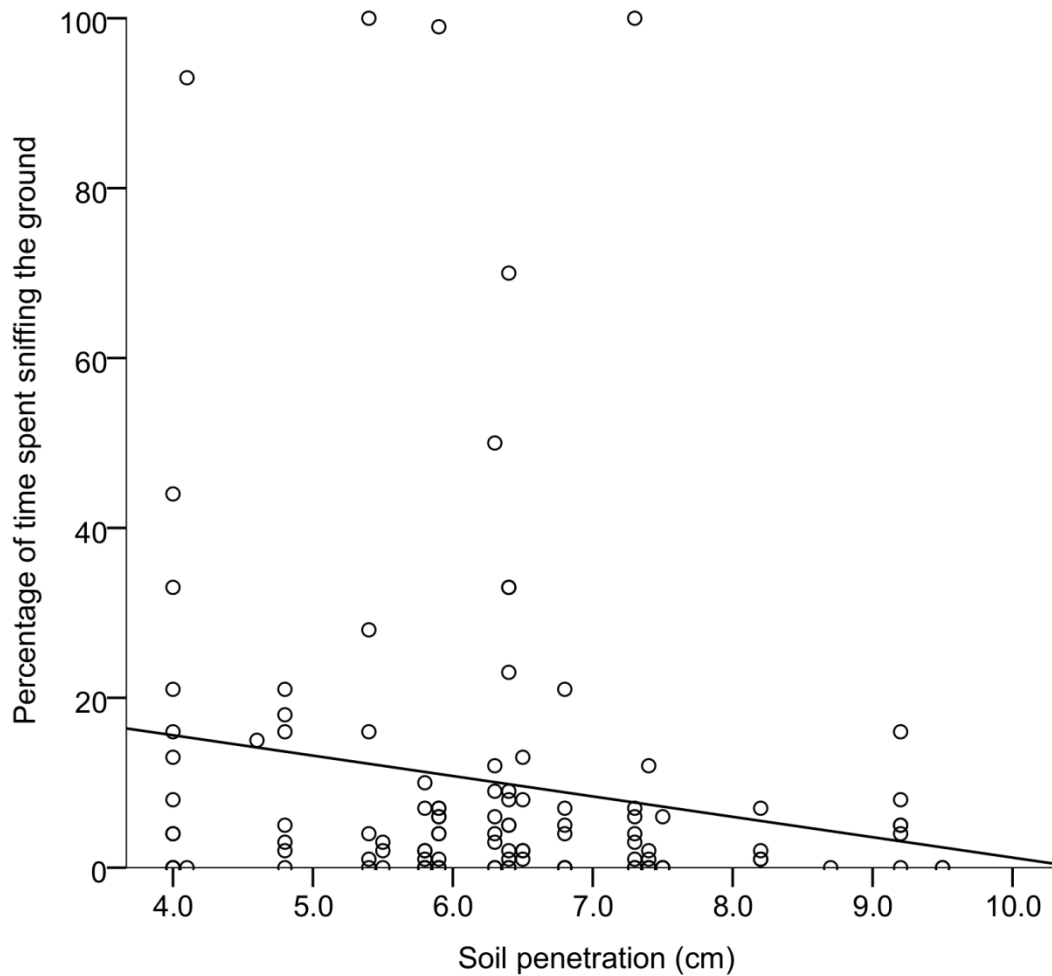
Figure. 2.3. Time spent sniffing the ground against soil penetration. Percentage of time spent by red foxes sniffing the ground had a negative relationship with soil penetration.

Quitting harvest rate curves

Lower mean GUD and characteristic quitting harvest rate (QHR) during mint treatment (0.034 food pieces /s) corresponds with greater time allocation (Fig. 2.4), as also shown by our analysis of time spent at patches. Higher characteristic QHR under wolf urine (0.044 food pieces /s) suggest foxes required higher remuneration when predation costs were higher. The QHR slope was however steeper and the attack rate higher under wolf urine (10.86 x 10^{-3}/s) than under mint treatment (6.97 x 10^{-3}/s), indicating quicker food harvest under wolf urine treatment.
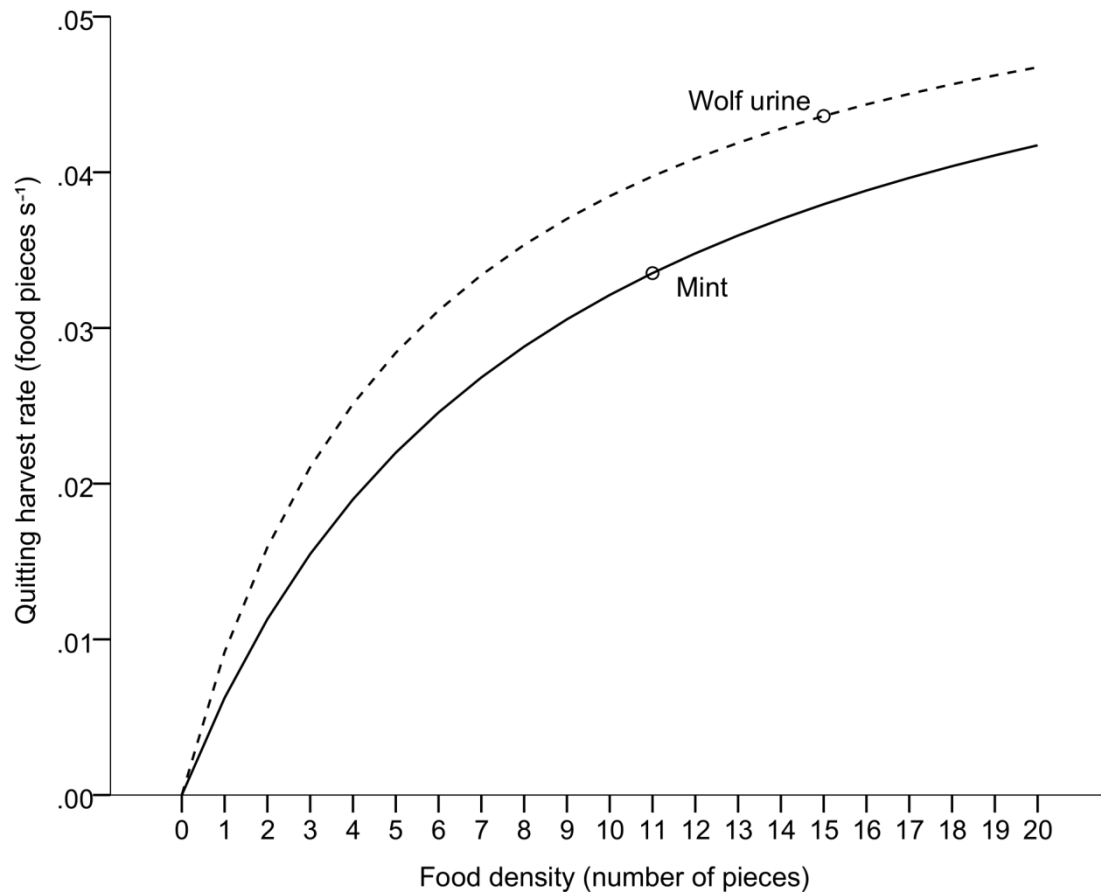
Figure. 2.4. Quitting harvest rate curves. Harvest rate curves for red foxes foraging under two scent treatments, a control (mint, solid line) and wolf urine (dashed line). Quitting harvest rates (QHR) were plotted as a function of the number of food pieces in the patch. Points represent characteristic QHR for mean GUD's under each scent treatment.

Discussion

We show that wolf urine signifies risk for foxes and olfaction is a mechanism by which foxes assess risk. The behavioural responses of foxes to wolf urine presumably reduced predation risk but also reduced their ability to utilise food resources. These behavioural strategies help explain how foxes are able to persist in sympatry with wolves, but also help explain some of the suppressive impacts wolves have on foxes.

When living in sympatry with larger carnivores, mesopredators often employ strategies such as vigilance, spatial or temporal avoidance, response to risk cues and adjustments in feeding behaviour (Durant 2000; Hayward & Slotow 2009; Wikenros, Stahlberg & Sand 2014). In the

presence of large carnivores, anti-predator strategies permit avoidance of danger but can carry costs such as decreased activity, restricted habitat use and reduced nutrient intake (Hernández & Laundré 2005; Lesmeister *et al.* 2015).

At least at a localised scale, wolves negatively affected red fox foraging efficiency with foxes exploiting patches less thoroughly in the presence of wolf urine. Reduction in time spent at patches came at a cost of lower food harvest from patches, with the amount of food left behind (mean GUD) being 34% higher under wolf urine and quitting harvest rates for mean GUDs being 29% larger under wolf urine than under mint treatment. This indicates that foxes required a higher payoff when olfactory cues suggested wolf presence. Such fitness costs of antipredator responses could affect survival and reproduction, ultimately impacting population dynamics (Creel & Christianson 2008). Such processes could contribute to the effect apex predators have on the distribution of mesopredators (Newsome *et al.* 2017b).

Contrary to expectation, additional strategies employed by foxes in response to wolf urine did not come at a cost to harvest rates. Kotler et al. (2010) proposed that a steeper QHR curve (quicker harvest) suggests less time investment in apprehensive behaviours. Our video analysis however shows that foxes spent a significantly greater percentage of time engaging in some forms of apprehension (major vigilance and sniffing the ground) and a lower percentage of time foraging under the wolf urine treatment, yet still achieved higher harvest rates. For some species harvest rates may be a product of more than just time allocation to apprehension and foraging. They may also be affected by how these activities are performed as well as time allocation to different types of apprehensive behaviour and other activities.

Having the head up in major vigilance, permits visual, auditory and scent based detection of danger and likely represents an effective, albeit costly, investment of time spent in risky food patches. Higher levels of predator detection behaviour do not always come at a cost to foraging performance and harvest rates can increase alongside proportion of time spent vigilant (Cresswell *et al.* 2003). It is feasible that foxes increased their digging speed and encounter rates when foraging under wolf urine in order to compensate for the reduction in time spent foraging.

Foxes were less casual and more focused about how time was spent under wolf urine, investing highly in major vigilance and spending less time engaging in "other" behaviours that were not productive to obtaining food or ensuring safety e.g. masticating without being vigilant (PMH *unpubl. data*). Mastication could not be measured in a comparable way to the

behaviours recorded in this study as the jaws could not always be seen, however we note that, where observable, mastication without vigilance appeared to be the dominant "other" behaviour. Herbivores have been observed to temporally and spatially partition their ruminating behaviour from their foraging behaviour (Nellemann 1998; Lynch *et al.* 2013). Mesopredators like foxes may also adjust their digestive behaviour in response to predation risk. Foxes may have chewed more quickly, chewed less or even swallowed pieces whole under wolf urine treatment, digesting away from risky patches instead of investing time aiding the digestive process by masticating while at patches. Mastication may also be reduced in risky locations because it can inhibit auditory vigilance (Lynch *et al.* 2013; 2015).

Mesopredators likely have a more complex olfactory landscape than organisms on the periphery of food webs and behavioural response to scent could be affected by scent strength, integrity and context (Jones et al. 2016). Previous works investigating the response of foxes to alternative risk cues have yielded varying results. Observations of red (Scheinin *et al.* 2006) and Indian foxes, *Vulpes bengalensis* (Vanak, Thaker & Gompper 2009) only showed significant reductions in food bait take in response to direct predator presence (golden jackal, *Canis aureus* and domestic dog *Canis lupus familiaris* respectively), but not to olfactory risk cues (urine, or scat and urine respectively). Observations were short and scents fresh so it could be concluded that foxes did not respond to these particular risk cues and only responded to immediate threats, or that foxes in these studies were bigger risk takers than in our study. However, these studies did not follow a GUD framework so responses to scent may have reflected experimental setup more than fox behaviour. Foraging may have been too easy or profitable and food to substrate ratios in these experiments may have only permitted observation of strong responses. Nonetheless, food take and behavioural responses towards live animals in both studies still suggest fearful responses of foxes towards larger predators. The studies also suggest that fearful responses to the actual presence of predators are likely to be stronger than to risk cues alone.

Under a GUD framework, Mukherjee et al. (2009) observed that foxes foraged more from patches with wolf scat present. They suggested that scat may provide information of a predator's whereabouts and could indicate that a predator has moved on and that the patch in fact carries less risk. The responses observed in this study suggest urine presents a more immediate predator presence cue. Scat can act as a territorial marker and conveyer of information about the depositor (Barja 2009a). Peters and Mech (1975) however concluded that raised leg urination was probably the most effective method of territory maintenance.

Competitors may associate higher risk with urine than with scat. Canids also preferentially faecal mark on visually conspicuous features, suggesting scat placement is an important aspect of communication (Barja 2009a; de Miguel *et al.* 2009; Hayward & Hayward 2010). Dependent on the context and placement, scat may communicate risk but could also be positively associated with scavengeable food sources.

Mukherjee et al. (2009) also suggested that the lower presence of wolves in the study area and higher presence of the larger striped hyena, *Hyaena hyaena*, could have been responsible for their observations. Aversion to foreign odours likely requires a social unit to have experience of antagonistic events (Peters & Mech 1975). At 1.4-1.6 wolves per 100 km^2 (JK *unpubl. data,* estimates based on 100% MCP polygons and snow tracking of two packs utilising PLNP during 2015), wolf density was higher in PLNP than the Croatian average of 1.3 (Štrbenac *et al.* 2005). Given fox responses to wolf urine and wolf density, encounter rates might also have been higher in PLNP.

Leo et al. (2015) examined fox GUDs in response to a combination of canid body odour (an indicator of close proximity and hence immediate threat) and scat (territorial demarcation and a less proximate threat). GUDs were higher under dingo, *Canis lupus dingo*, odour than control treatments. This is unsurprising given the threat dingoes pose to foxes through direct killing (Marsack & Campbell 1990; Moseby, Stott & Crisp 2009). The dingo has a different ecology to the wolf and exists in unique ecosystems (Mech & Boitani 2005; Purcell 2010). While interactions may vary depending on context, the findings of Leo et al. (2015) suggest that the combination of body odour and scat at locations such as den sites are likely to affect foxes as well.

Context can be an important driver of interspecific relationships between predators (Haswell, Kusak & Hayward 2017). The studies discussed suggest that cue type, species composition, experience and demography might be important factors in driving response to risk cues. A forager's response to risk may also vary dependent on factors such as social structure, food patch quality and energetic state (Fortin *et al.* 2009; Harvey & Fortin 2013; Hayward, Ortmann & Kowalczyk 2015). Nonetheless, cues informing of more immediate risk (direct predator presence, urine or body odour) should in general yield stronger behavioural responses. Inferences and responses to olfactory cues will depend upon selection pressures (Jones et al. 2016). Apex predator impacts may be weaker farther away from core areas such as den sites (Miller *et al.* 2012). The recently proposed "enemy constraint hypothesis" also

predicts weaker mesopredator suppression at peripheries of large carnivore range (Newsome *et al.* 2017b). At range edges, reduction in apex predator presence and risk cues would be expected. A reduction in behavioural suppression through mesopredator response to olfactory risk cues would thus also be expected. Factors affecting scent demarcation and landscape use by apex predators should in-turn affect risk perception and behavioural responses of mesopredators.

Suppression by larger predators can affect the abundance and behaviour of mesopredators, often but not always having consequent impacts upon mesopredator prey species (Ritchie & Johnson 2009). Mesopredator response to risk landscapes can have behavioural knock-on effects, influencing landscape and resource use by prey species (Palacios, Warren & McCormick 2016). Predator odours including those of foxes have a range of behavioural and physiological effects upon prey species (Apfelbach *et al.* 2005). Foxes can also have stabilising effects upon their prey populations (O'Mahony *et al.* 1999) or interact competitively with smaller carnivores (Bischof *et al.* 2014; Petrov, Popova & Zlatanova 2016). Behavioural interactions clearly play a part in maintaining functioning stable ecosystems. Anthropogenic disturbance or direct loss of processes through trophic simplification can however interfere with these complicated systems, leading to problems (Frid & Dill 2002; Prugh *et al.* 2009; Estes *et al.* 2011). Removal or disturbance of large carnivores may interfere with behavioural processes which also require consideration when managing human landscape use.

Chapter 3.

Chapter Two established that foxes perceive wolf urine as a risk cue and, at a cost to food harvest, adjusted their foraging and risk mitigation behaviour. Chapter Three makes use of camera trapping data with the occupancy modelling framework in order to understand the spatial extent of the risk imposed by large carnivores to foxes. A key problem in wildlife survey is variation in detectability and the labelling of false absences (MacKenzie *et al.* 2002; MacKenzie, Bailey & Nichols 2004). The occupancy framework attempts to incorporate this problem by simultaneously modelling occupancy and detection probability while accounting for site or survey characteristics (MacKenzie *et al.* 2006). We used the framework to investigate whether foxes are spatially restricted by large carnivores or more elusive in their presence. The effects of large carnivores were then explored alongside the influence of humans, seasonality and potential landscape drivers of detectability in order to ascertain strength of support for each potential explanatory variable.

A mesopredator is more detectable in the presence of large carnivores but elusive towards humans

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The following paper is prepared ready for submission to publish.

Author contribution statement

P.M.H conceived, designed and executed the study, wrote the manuscript, and also assisted with data collection. M.W.H contributed to the design, analysis and writing of the manuscript. J.K. conceived and executed data collection, obtaining permits and support from Plitvice Lakes National Park. Funding was acquired by P.M.H and J.K. Editorial advice was provided by M.W.H, K.A.J and J.K. All authors gave final approval for publication.

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Abstract

Large carnivores can suppress mesopredator abundance and behaviour. Understanding the implications, contextual variation and mechanisms behind mesopredator suppression is essential for conservation and land management. We used two-species occupancy modelling to examine the influence of gray wolves, *Canis lupus* and Eurasian lynx, *Lynx lynx* (apex predators) upon red fox, *Vulpes vulpes* (mesopredator) occupancy and detection probability in an ecologically intact European ecosystem (Plitvice Lakes National Park, Croatia). A single-season occupancy model was then used to examine the relative influence of wolf and lynx in comparison to anthropogenic and landscape drivers of fox detectability. Foxes occupied areas with and without large carnivores equally. Fox detectability fluctuated through the year and, against expectations, was positively associated with the presence of large carnivores (particularly lynx) but negatively with humans. Where large carnivore presence imposes foraging costs, foxes may need to visit more food patches to obtain sufficient nourishment, increasing detectability by moving and passing key travel routes more often. Increased fox detectability could also be indicative of facilitation by apex predators via scavenging opportunities, or increased food (small mammal) availability. In a protected area where food subsidies were minimal, foxes employed an elusive strategy towards human super predators. Mesopredator risk management behaviour is relative to competition, risk and benefits. As costs decrease and benefits increase, mesopredators will likely employ finer scale avoidance strategies to access resources. Understanding interspecific interactions and their trophic consequences across a range of contexts is fundamental to ensuring successful conservation outcomes in the face of anthropogenic change.

Introduction

Apex predators can affect the abundance, distribution and behaviour of mesopredators (Ritchie & Johnson 2009; Newsome & Ripple 2014; Newsome *et al.* 2017b). Large carnivores are thus considered to be of potential management utility for the regulation of mesopredators (Clarke 2007; Ritchie *et al.* 2012; Wolf & Ripple 2018). Humans however, kill carnivores at substantially higher rates than nonhuman predators (Darimont *et al.* 2015). Conflict with humans can lead to unfocused large carnivore culling programmes, even where targeting ultimate causes can provide more effective resolution (Proulx 2018). Where legislative protection exists, large carnivores can still be threatened by anthropogenic

mortality causes, such as poaching or traffic collision (Huber *et al.* 2002a; Sindičić *et al.* 2016). The conservation and restoration of large carnivores, as well as the ecological services they provide, are consequently of interest to practitioners and the wider scientific community (Ripple *et al.* 2014; 2017). The value and conservation of large carnivores need not be dictated by the services they provide, but managers and practitioners still require accurate knowledge of the implications, contextual variation and mechanisms of mesopredator suppression (Allen *et al.* 2017a;b; Haswell, Kusak & Hayward 2017).

The competitive exclusion of one species by another is thought to depend on the completeness of niche overlap, with ecological differentiation considered a prerequisite for coexistence (Hardin 1960). Sympatric coexistence does not however necessitate an absence of interspecific aggression or interference competition, particularly if niche differentiation evolved in allopatry (Connell 1980). Risk management behaviour, interspecific killing and interference are commonly observed where predators occur in sympatry (Palomares & Caro 1999; Ritchie & Johnson 2009; Haswell *et al.* 2018). Interspecific aggression may result from resource competition when previously isolated species come into contact, or could alternatively result from a legacy of similar agonistic cues or recognition mechanisms due to common ancestry (Grether *et al.* 2013). Interspecific aggression may also represent remnant behaviour from a more turbulent past where predator diversity, densities and food competition were likely greater (Sillero-Zubiri, Hoffmann & Macdonald 2004).

Interspecific aggression may modify characteristics that affect aggressive interactions, resulting in competitive exclusion and range shifts or changes in traits that enable coexistence e.g. spatial or temporal avoidance, fighting or defensive capabilities, competitor recognition (Grether *et al.* 2009; 2013). Defensive strategies can carry energetic, survival and reproductive costs (Preisser, Bolnick & Benard 2005). The effects of trait-mediated interactions upon prey can be at least as large as the act of killing (density-mediated interactions) and may provide substantial cascading effects to lower trophic levels (Werner & Peacor 2003; Preisser, Bolnick & Benard 2005).

At a regional or meta-community scale, apex predators and mesopredators may show divisional patterns of distribution, suggesting high levels of competition, mesopredator suppression and/or divergent habitat preferences (Newsome & Ripple 2014; Newsome *et al.* 2017b). Interactions between predators do however vary with context, and multiple system states are possible (Holt & Polis 1997; Ritchie *et al.* 2012; Haswell, Kusak & Hayward

2017). The strength of species regulation by carnivores is determined by both primary productivity and predator abundance (Letnic & Ripple 2017). Resource availability can be a key driver of interspecific aggression, with top-down effects weaker in more productive environments (Palomares & Caro 1999; Elmhagen & Rushton 2007; Elmhagen *et al.* 2010). Human activity also provides risk to animals and can additionally modify interspecific interactions (Frid & Dill 2002; Haswell, Kusak & Hayward 2017; Ladle *et al.* 2018). Motorised recreation, for example, can reduce site use by grizzly bears, *Ursus arctos,* potentially freeing up roadside habitat for black bear, *Ursus americanus,* which are generally more tolerant of anthropogenic activity and can also be spatially excluded by grizzly bear (Ladle *et al.* 2018). It therefore becomes important to examine how human context modifies ecological interactions but also to understand how strongly and in what capacity top-down suppression of mesopredators occurs.

Where predators occur in local sympatry (community scale), adaptive behavioural strategies, such as competitor recognition (e.g. through odour) or risk recognition through additional cues (e.g. moonlight levels), alongside direct avoidance of larger predators, may permit coexistence (Scheinin *et al.* 2006; Mukherjee, Zelcer & Kotler 2009; Haswell *et al.* 2018). Large scale spatial avoidance may carry significant costs in terms of access to resources, but behavioural strategies operating on a finer scale (e.g. diurnal temporal avoidance) may carry fewer costs and permit coexistence (Holt & Polis 1997; Swanson *et al.* 2016). As observed in African carnivores by Vanak et al. (2013), the use of large or fine-scale behavioural tactics may also vary throughout seasons of the year, as required, due to changes in conditions.

Donadio and Buskirk (2006) suggest that, while other factors are influential, body size is pivotal in determining rates of interspecific killing, with killing highest when body size difference is intermediate (41.4 − 88.3 %). The size differences between Croatian foxes *Vulpes vulpes* (6-8kg; (Janicki *et al.* 2007)) and wolves, *Canis lupus* (male ≈ 35kg, female ≈ 29kg; (Huber *et al.* 2002b)) or lynx, *Lynx lynx* (male ≈ 21.9kg, female ≈ 18.4kg; (Gomerčić *et al.* 2010)) are considered intermediate. Wolf and lynx morphology also suggests that attack or harassment of foxes is of low risk, so direct killing might be expected (Donadio & Buskirk 2006).

Foxes are a common scavenger of wolf and lynx kills (Selva *et al.* 2005; Wikenros, Stahlberg & Sand 2014). These apex predators might facilitate food for red foxes, leading to spatial association. Where the relationship is kleptoparasitic however, this may increase aggression

towards foxes, resulting in defensive strategies. Both wolves and lynx kill red foxes (Palomares & Caro 1999). Consumption of foxes has been observed by lynx in the Dinaric Mountains (Slovenia and Croatia), but not by wolves (Štrbenac *et al.* 2005; Krofel & Kos 2010; Krofel, Huber & Kos 2011).

Occupancy modelling offers an ideal framework to investigate spatial interactions between species (MacKenzie, Bailey & Nichols 2004; Richmond, Hines & Beissinger 2010). The method has been recommended following discrepancies in mesopredator studies that ignore differential detectability (Hayward *et al.* 2015). The system allows examination of the probability of species occurrence while estimating and accounting for the probability of detection alongside variables that may explain observed patterns (MacKenzie *et al.* 2006). Occupancy modelling investigations often focus on obtaining a desired level of estimate precision as efficiently as possible, minimising repeat survey effort (MacKenzie & Royle 2005). Longer detection histories (presence-absence data from more repeat surveys) can however provide useful information. Additional species interaction hypotheses can be tested by examining detectability patterns (Richmond, Hines & Beissinger 2010; Robinson, Bustos & Roemer 2014). We utilised a year-long dataset to examine the influence of apex predators, humans and landscape drivers on fox detectability and occupancy.

Methods

Study Site

Plitvice Lakes National Park (Plitvice), Croatia, is between 44° 44' 34" and 44° 57' 48" N and 15° 27' 32" and 15° 42' 23" E, in the central belt of the Dinaric Mountains (Šikić 2007). Approximately 1770 people live within 19 settlements inside the 297 km^2 park (Romanić *et al.* 2016). Tourism and recreation are the only permissible land uses (Firšt *et al.* 2005). Poaching is occasionally observed but its extent is unknown. The karst (limestone and dolomite) mountains and valleys are characterised by sink holes, caves and little surface water (~1%), however many underground drainage systems provision the iconic lakes and waterfalls (Šikić 2007). Ranging from 367 to 1279 m above sea level, topographical microclimates exist but generally temperatures fluctuate between winter minima of -3°C and summer peaks of 36°C with 1,550 mm annual precipitation (Šikić 2007; Romanić *et al.* 2016). Forest cover is predominantly Dinaric beech and fir trees (*Fagus sylvatica* and *Abies alba*), although one camera site also contained forests of Scots and black pine (*Pinus sylvestris* and *Pinus nigra*).

Camera trap deployment and sampling

Records from 20 passive infrared motion sensor cameras deployed on roads and trails between October 2015 and October 2016 in Plitvice were utilised in single-season occupancy models after collation in Camera Base 1.7 (www.atrium-biodiversity.org/tools/camerabase). Fox density in Croatia is estimated at 0.7 per km^2 with territory size of 1.43 km^2 (Slavica *et al.* 2010; Galov *et al.* 2014). Like Robinson et al. (2014), we assumed a circular territory size and utilised the radius (675 m) as the minimum acceptable distance between cameras. Camera locations and periods included in the analysis were selected *a priori* to data examination. Similarly to Santulli et al. (2014), we utilised data that was initially collected for other purposes. Original monitoring goals were to obtain lynx photographs for spot pattern identification and to ascertain large carnivore use of the national park. Camera station placement was ad-hoc, with locations targeted according to field sign surveys and travel routes, maximising detection of large carnivores.

Travel routes are commonly used to maximise detection in mammal camera studies (O'Connell, Nichols & Karanth 2011; Shannon, Lewis & Gerber 2014; Webster *et al.* 2016). Maximising detection can help reduce variance in parameter estimates (MacKenzie & Royle 2005). We acknowledge that predators use these thoroughfares differently (Mahon, Banks & Dickman 1998; Hayward & Marlow 2014), however, we accounted for variation in detection rates by using occupancy models. Cameras were checked monthly in summer but at the start and end of winter due to accessibility. Camera operation periods were considered from the first to the last picture, a period where a camera could confidently be considered operational. This accounted for potential camera malfunction or battery death after the last photo was taken, which could otherwise be misidentified as survey days without detection. During periods where two cameras were in operation at the same site (N = 3 sites), data from a single camera was selected at random to exclude this confounding variable.

To explore temporal fluctuations, data from the year was split into three survey periods of equal length based on carnivore life cycles (Lloyd 1980; Mech & Boitani 2005; Nowak 2005). Seasonal periods, named relative to fox life cycle, were dispersal (October – January 30th), denning (January 31st – May) and weaning (June – September). All twenty cameras were surveyed for more than eighty days per period (range 89 - 122 days), a design providing suitably low error for many mammalian species (Shannon, Lewis & Gerber 2014). Each period was utilised as a separate detection history, providing sixty (site-season) detection

histories in total. This method represents a compromise due to data availability and we acknowledge its limitations in underestimating confidence intervals. The approach however permitted the incorporation of detection probability and allowed temporal fluctuations to be modelled in single-season occupancy models.

It is reasonable to assume the wider system was closed to occupancy state change given the survey duration of one year (MacKenzie *et al.* 2003). As is common for highly mobile species, the assumption of changes in occupancy status was relaxed for large carnivores and humans with "occupancy" instead considered "use", and "probability of detection" considered "probability species were present and detected" (MacKenzie, Bailey & Nichols 2004; MacKenzie & Royle 2005; Webster *et al.* 2016).

Two-species interaction modelling: large carnivores and foxes

Firstly, we used occupancy modelling in PRESENCE 12.7 (Hines 2017) (https://www.mbr-pwrc.usgs.gov/software/presence.html) to test hypotheses regarding two-species interactions (MacKenzie, Bailey & Nichols 2004; Richmond, Hines & Beissinger 2010). To avoid over-parameterisation we ran relatively simple two-species models, examining the impact of wolves or lynx (Species A) and seasonal variation upon foxes (Species B; Table. 3.1). For each species pairing we compared the relative performance of a series of six candidate models utilising maximum likelihood methods (Appendix D), with the most supported models distinguished by AICc (Burnham & Anderson 2002).

Similar to Richmond et al. (2010), we tested two *a priori* hypotheses using conditional and unconditional two-species models. We predicted that fox occupancy in the presence of large carnivores (ψBA) would be equal to fox occupancy in their absence (ψBa). Because of potential scavenging opportunities and the resources available in Plitvice's mesic environment we did not anticipate models featuring ψBA $\neq$ ψBa to be strongly supported. Secondly, we predicted foxes would be more elusive and their detection probability would be lower at sites occupied by large carnivores (r^B) than at sites where large carnivores were absent (p^B). Foxes were detected during all site-season survey periods except two, so hypotheses regarding large carnivore detection probability in the presence (r^A) and absence (p^A) of foxes were not tested ($r^A = p^A$ for all models).

Fluctuation in parameter estimates throughout the year

We also hypothesised that fox detectability (p^B and r^B) might vary seasonally due to species life cycle (abundance and/or activity levels). Additionally, we checked closure assumptions by asking if fox occupancy (ψB) fluctuated seasonally. To test seasonal fluctuation in parameter estimates, we included two-species models where large carnivore impact was absent (unconditional) and either fox occupancy or detection probability was a function of season (dispersal (October – January 30th), denning (January 31st – May) and weaning (June – September)).

Table. 3.1. Parameters used in two-species conditional occupancy models.

Parameter	Definition
ψA	Probability of occupancy, species A
ψBA	Probability of occupancy, species B when species A is also present
ψBa	Probability of occupancy, species B when species A is absent
p^A	Probability of detecting species A when species B is absent
r^A	Probability of detecting species A when species B is also present
p^B	Probability of detecting species B when species A is absent
r^B	Probability of detecting species B when species A is also present

Notes: Species A is presumed dominant over species B. Table adapted from Richmond et al. (2010)

Single-species modelling: fox detection probability

To avoid inaccurate conclusions, it is important to investigate alternative explanatory variables when examining species interaction patterns (MacKenzie, Bailey & Nichols 2004; Allen *et al.* 2018). In complicated food web systems this should ideally include additional species, e.g. humans may have considerable effects (Kuijper *et al.* 2016; Haswell, Kusak & Hayward 2017). Humans were detected during all site-season survey periods except one, so two-species models would be ineffectual in understanding the influence of their presence. It was also desirable to know if one large carnivore had a stronger effect on fox detectability than the other and to see how the relationships changed with intensity of large carnivore detection.

Using a single-species model, the relative performance of 20 candidate models explaining fox detectability patterns were compared utilising AICc (Burnham & Anderson 2002). Values for the probability that humans, wolf and lynx were present and detected were obtained from single-species detection probability models (Appendix E). Detection probability reflects abundance, activity level and movement rates (Neilson *et al.* 2018). As such, these values were used to evaluate the intensity of other species presence upon fox detectability. We also

allowed for temporal fluctuation due to life history by including models where fox detection probability varied with season. In addition we included the influence of elevation (m), and forested area within a 1.43 km^2 (fox territory size) circle around the camera. We hypothesised that these landscape variables might affect territory quality and thus influence fox group size, activity and/or trail use. All numerical covariates were normalized before analysis (Hines 2017).

A Kendall's *tau-b* test was used to examine correlations between all numerical covariates prior to modelling (Robinson, Bustos & Roemer 2014). Lynx detectability and elevation ($\tau_b = 0.617$, *P* < 0.001), lynx detectability and forested area ($\tau_b = 0.637$, *P* < 0.001), lynx detectability and wolf detectability ($\tau_b = 0.322$, *P* = 0.001), human detectability and elevation ($\tau_b = -0.270$, *P* = 0.003), human detectability and forested area ($\tau_b = 0.540$, *P* < 0.001), wolf detectability and forested area ($\tau_b = 0.481$, *P* < 0.001) were all significantly correlated. These correlated covariates were not included as parameters in the same models to ensure a clear view of the main drivers of fox detectability and prevent loss in parameter estimate precision (Dormann *et al.* 2013; Robinson, Bustos & Roemer 2014). Correlated covariates were included in competing candidate models only.

A MacKenzie-Bailey goodness of fit (GOF) test (MacKenzie & Bailey 2004; Hines 2017) with 10,000 bootstrap resamples was performed on the most parameterised model with lowest -2 log likelihood for all single-season candidate model sets (Appendix E). AICc was adjusted to QAICc for wolf and lynx models where the overdispersion parameter ĉ > 1 (Burnham & Anderson 2002).

Results

During 6,833 camera trapping days, foxes were photographed on 934 days during 58 of the 60 site-season detection histories (presence-absence survey data). Wolves were photographed on 77 days during 28 histories; and lynx were photographed on 148 days during 33 histories. Humans were photographed on 1,786 days during 59 site-season detection histories.

Two-species interaction modelling: large carnivores and foxes

Effect of large carnivore presence on fox occupancy

Conclusions regarding fox occupancy being conditional or unconditional upon large carnivore presence were somewhat inconclusive (Table. 3.2). The most supported wolf-fox

model suggested fox occupancy was conditional upon the presence of wolves, being higher in wolf presence (ψBA) than in wolf absence (ψBa). The top lynx-fox model suggested fox occupancy was unconditional on lynx presence (ψB = ψBA = ψBa). In both cases however, the ΔAICc values for the competing hypothesis were less than two (Table. 3.2). While less supported, alternative possibilities remain highly plausible (Richards, Whittingham & Stephens 2011; Symonds & Moussalli 2011). For models where large carnivores did affect fox occupancy probability, the association was positive in both cases.

Table. 3.2. Top two-species models for red fox with wolf or lynx as the dominant species.

Model	Occupancy (Fox)	Detection (Fox)	ΔAICc	K	w	*-2logL*
Wolf (A), Fox (B)						
ψA, ψBA, ψBa, p^A, p^B, r^B	C	C	0	6	0.613	5960.22
ψA, ψB, p^A, p^B, r^B	U	C	0.92	5	0.387	5963.14
ψA, ψB, p^A, p^B (S)	U	U	127.46	6	0	6087.68
ψA, ψBA, ψBa, p^A, p^B	C	U	242.24	5	0	6204.46
ψA, ψB (S), pA, pB	U	U	282.37	6	0	6242.59
ψA, ψB, pA, pB	U	U	331.19	4	0	6295.41
Lynx (A), Fox (B)						
ψA, ψB, p^A, p^B, r^B	U	C	0	5	0.7221	6547.02
ψA, ψBA, ψBa, p^A, p^B, r^B	C	C	1.91	6	0.2779	6546.93
ψA, ψB, p^A, p^B (S)	U	U	72.41	6	0	6617.43
ψA, ψB, pA, pB	U	U	187.72	4	0	6736.74
ψA, ψB (S), pA, pB	U	U	187.85	6	0	6732.87
ψA, ψBA, ψBa, p^A, p^B	C	U	189.7	5	0	6736.72

Notes: The table shows all two-species models. C represents models where fox occupancy or detection was conditional on the presence of the large carnivore and estimated as two separate parameters. U represents models where parameters were unconditional and estimated as being equal. ψB denotes models where ψB = ψBA = ψBa and r^B where $r^B = r^{BA} = r^{Ba}$ (See Richmond et al. (2010) for use of these additional parameters). Models with p^B only, denote models where detection is unconditional upon the presence of the large carnivore ($p^B = r^B$). For all models p^A was held equal to r^A. Where no covariates are denoted in parenthesis, occupancy (ψ) or detection probability (p) were constant. The covariate (S) denotes that ψ or p parameters vary between seasonal periods of the year. ΔAICc is the difference in AICc relative to the best model, K is the number of parameters, w is the AICc weight, indicating the relative support for each model and *-2logL* is the -2 log likelihood.

Effect of large carnivore presence on fox detection probability

Models where fox detectability was conditional upon the presence of wolves or lynx both received extremely strong support. In both candidate sets, all of the most supported models

with ΔAICc less than two featured this structure (Table. 3.2). All top models (Table. 3.2) estimated fox detectability to be greater in large carnivore presence (r^B) than in large carnivore absence (p^B). For the top wolf-fox model, $r^B = 0.19 \pm 0.01$, $p^B = 0.04 \pm 0.01$. For the top lynx-fox model, $r^B = 0.18 \pm 0.01$, $p^B = 0.05 \pm 0.01$.

<u>Fluctuation in parameter estimates throughout the year</u>

There was no strong support for fox occupancy or detectability varying seasonally in the absence of large carnivore effects (Table. 3.2). Season did not provide a better explanation than the influence of large carnivores. Fox detection probability may still vary throughout the year as well as being affected by large carnivores but we lacked the data power to test this in two-species models. Single-species models were consequently used to test the effect of seasonality alongside that of large carnivores.

Single-species modelling: fox detection probability

From the top single-species models (Appendix E), humans were the species with the highest estimated probability of site use (0.98 ± 0.02 SE). Wolf use was lowest (0.75 ± 0.16 SE) and lynx use was 0.77 ± 0.10 SE. Estimated probability of fox occupancy was high (0.97 ± 0.02 SE).

Table. 3.3. Top single-species models for red fox detection probability.

Model	ΔAICc	*K*	*w*	*-2logL*
ψ, *p* (S+H+L)	0	6	0.54	5231.02
ψ, *p* (S+E+F)	0.76	6	0.37	5231.78
ψ, *p* (S+L)	3.66	5	0.09	5236.97
ψ, *p* (S+E+W)	8.83	6	0.01	5239.85

Notes: The table shows models where ΔAICc < 10, accounting for ≥ 0.99 of AICc weight (*w*).Where no covariates are denoted in parenthesis, occupancy (ψ) or detection probability (*p*) were constant. The covariate S denotes that *p* varies between seasonal periods of the year, W denotes the influence of the probability that wolves were present and detected, L, the probability that lynx were present and detected, H, the probability that humans were present and detected, E, elevation, F, forested area within a 1.43km^2 circle around the camera. ΔAICc is the difference in AICc relative to the best model, *K* is the number of parameters, *w* is the AICc weight, indicating the relative support for each model and *-2logL* is the -2 log likelihood.

Season was present in all plausible top models with ΔAICc < 10 (Table. 3.3), indicating its strong importance in explaining the patterns observed (Burnham & Anderson 2002). Fox detectability was lowest during dispersal (October – January 30th), highest during weaning (June – September) and slightly lower during the denning (January 31st – May) season (Fig.

3.1). The model where fox detectability was also positively associated with elevation and forested area had ΔAICc < 2 (Table. 3.3) so should not be completely discounted (Richards, Whittingham & Stephens 2011; Symonds & Moussalli 2011). Most support existed for the model where fox detectability varied seasonally and was positively associated with lynx detectability but negatively associated with human detectability (Table. 3.3; Fig. 3.1).
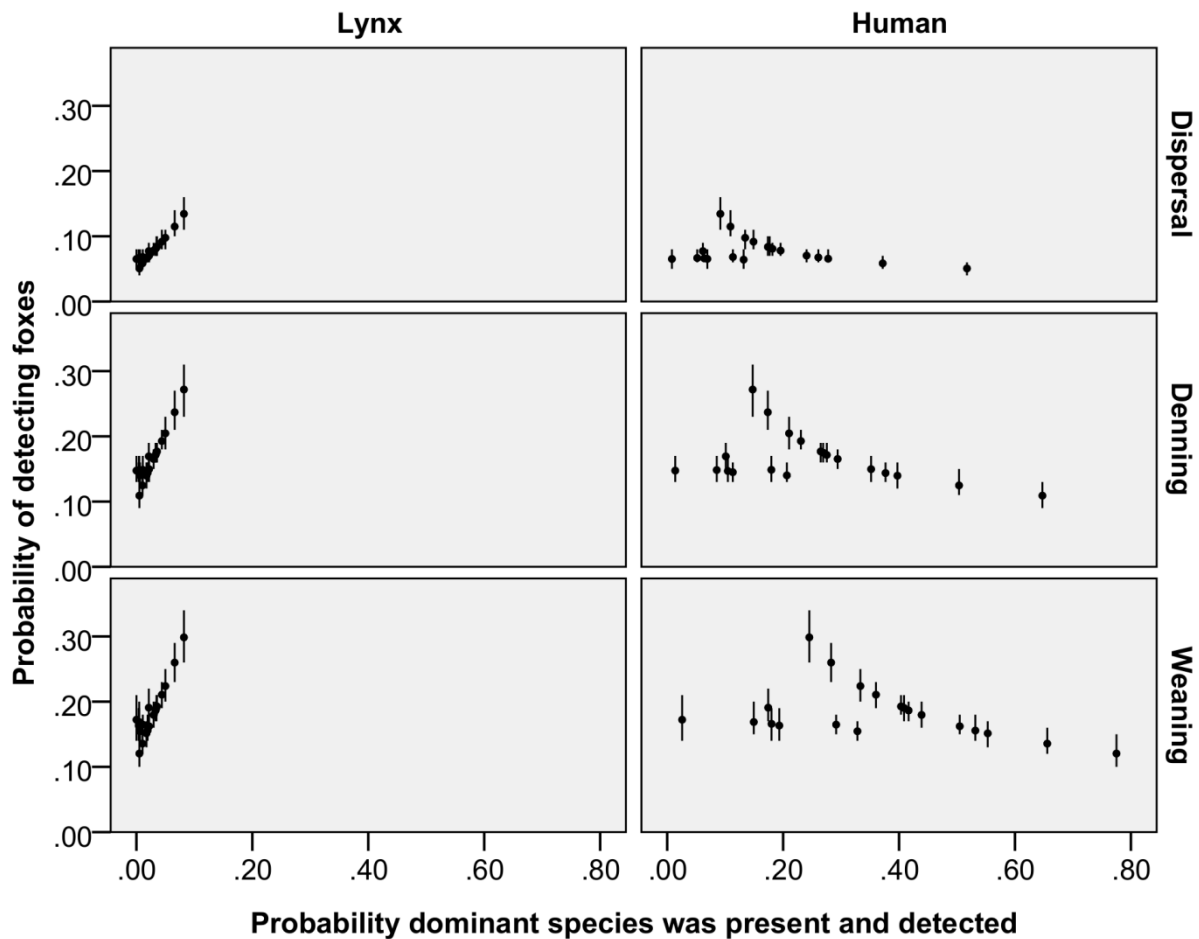
Figure. 3.1. Probability of detecting red foxes plotted against lynx or human detectability for each season. Strong support existed for fox detectability varying through the year, with detectability lowest during dispersal (October – January 30th). Most support existed for a model where fox detectability was also positively associated with lynx detectability but negatively associated with human detectability. Closed circles represent detection probabilities from the top model and bars represent 95% confidence intervals.

Discussion

In an intact European ecosystem (Plitvice), foxes were elusive towards human super predators but not towards apex predators. Foxes were not spatially excluded by larger predators. The probability of detecting foxes, however, fluctuated throughout the year and was positively associated with the presence of large carnivores (particularly lynx) but negatively with humans. Foxes can readily live in sympatry with larger carnivores (wolf and lynx) and may, in fact, be attracted to their presence (or the same factors that increase their presence) even though interspecific aggression poses a threat. All three predators may focus activity to areas of high food resource availability, or apex predators may facilitate foxes through carcass provisioning.

Alternatively, reasonable support also existed for fox detection probability being affected by elevaton and forested area instead of humans and lynx. Carnivores can travel faster and farther using linear features (Dickie *et al.* 2017). Foxes and lynx could make greater use of trails (and be more detectable) at higher elevations where terrain is rugged. Prey such as edible dormouse, *Glis glis,* availability in forested areas might also concievably increase fox activity (and thus detectability). Both human and lynx detectability values were however influenced by and correlated with elevation and forested area (Appendix E), so it is not surprising these variables achieved similar support. Most support existed for fox detectability being positively associated with lynx detectability but negatively associated with human detectability, so more confidence is given to this conclusion. Elevation and forested area could provide alternative drivers of fox detection probability but presumably just have indirect effects through the effect they have on humans and lynx.

Foxes can be spatially restricted by wolves and lynx (Fedriani, Palomares & Delibes 1999; Elmhagen & Rushton 2007). Spatial exclusion of mesopredators may not always be on a large scale however; in some contexts, avoidance may be on a finer spatial or temporal scale (Mitchell & Banks 2005; Vanak *et al.* 2013; Swanson *et al.* 2016). Fine-scale responses to changes in foraging patch predation risk previously observed for foxes by Haswell et al. (2018) did not translate to larger scale spatial avoidance in Plitvice. Environmental productivity can dampen the limiting effect of lynx and wolves upon foxes (Elmhagen & Rushton 2007; Elmhagen *et al.* 2010). Plitvice is an area high in biodiversity (Šikić 2007). Higher food availability, alongside resource partitioning and adaptive behaviour (e.g. fine-scale spatio-temporal avoidance) may permit co-existence (Durant 2000; Robinson, Bustos &

Roemer 2014; Swanson *et al.* 2016). Foxes are also well known for adjusting their activity patterns in response to risk (Baker *et al.* 2007; Diaz-Ruiz *et al.* 2016). Foxes in Plitvice may alternatively avoid large carnivores in time.

It has been suggested that mesopredators commonly avoid trails used by larger predators (Hayward & Marlow 2014). Carnivores can perceive humans as super predators, adapting their behaviour in response to disturbance (Frid & Dill 2002; Baker *et al.* 2007; Smith *et al.* 2017). Foxes are however often tolerant of human presence (Cove *et al.* 2012; Erb, McShea & Guralnick 2012; Ruiz-Capillas, Mata & Malo 2013). Anthropogenic habitat modification can benefit foxes, especially if accompanied by increased food availability (Hradsky *et al.* 2017; Reshamwala *et al.* 2018). Relative to carnivores, human detectability was high on trails within Plitvice (Appendix E, Fig. 3.1), and, against expectations, appeared to cause foxes to be more elusive (less detectable). In less modified landscapes where anthropogenic food subsidies are minimal and persecution exists outside protected area boundaries, foxes may be less tolerant of human presence.

Behavioural responses can provide early warning signals to anthropogenic pressures (Berger-Tal *et al.* 2011; Caravaggi *et al.* 2017). If unchecked, human disturbance can potentially alter the fitness value of behavioural strategies, affect population dynamics, evolutionary trajectories and, ultimately, community or ecosystem dynamics (Berger-Tal *et al.* 2011). Nature reserves offer desirable tourist destinations but some limitations are required to provide spatial or temporal wildlife refugia (Ngoprasert, Lynam & Gale 2017; Ladle *et al.* 2018). The necessity and accomplishment of suitable refugia will likely depend on reserve size, species sensitivity, tourist pressures and management goals. In many contexts however, human exclusion will need to be balanced against the level of human presence required to prevent illegal poaching (Rauset *et al.* 2016). Remote cameras may offer some assistance in apprehending and deterring poachers while also minimising disturbance.

Against expectations, fox detectability was positively associated with large carnivores. Positive associations between competitors observed in both North America and Africa suggest this is not anomalous (Richmond, Hines & Beissinger 2010; Lonsinger *et al.* 2017; Rich *et al.* 2017b). Detection rates often reflect animal abundance and activity (Allen & Engeman 2015). Neilson et al. (2018) suggest speed and scale of animal movements as well as population density strongly affect the temporal pattern of detection by camera traps.

Increased detectability could be indicative of greater fox movements, activity and/or abundance.

Across otherwise similar contexts, the home range size and travel movements of mesopredators such as long tailed weasels, *Mustela frenata*, cape foxes, *Vulpes chama,* and bat-eared foxes, *Otocyon megalotis,* can increase with pressure from a dominant predator (St-Pierre, Ouellet & Crete 2006; Kamler, Stenkewitz & Macdonald 2013). Mesopredators may also alter activity budgets, resting less when large carnivores are present (Switalski 2003). In the presence of wolf urine, red foxes reduced the amount of food taken and time spent at foraging patches (Haswell *et al.* 2018). Where large carnivores are present, foxes may need to visit more food patches, move around the landscape more and forage from a wider geographic range to obtain sufficient nourishment. Rather than becoming more elusive and avoiding trails, foxes may minimise risk by keeping moving, passing key travel routes more often and thus increasing the probability of detection.

Predator densities tend to scale to resource availability (Carbone & Gittleman 2002; Hayward, O'Brien & Kerley 2007). Higher fox detectability associated with large carnivore presence could simply reflect that all three carnivores are more abundant or active in resource rich areas. Similar to our findings, Wikenros et al. (2017a) observed positive associations between fox and lynx abundance. Wikenros et al. (2017b) also found foxes were attracted to lynx scats, concluding that investigating scats might provide information about risk, but also of scavenging opportunities. Kleptoparasitism can provide a reliable food supply for mesopredators (Wilmers & Getz 2005; Helldin & Danielsson 2007; Wikenros, Stahlberg & Sand 2014). Scavengers can however have detrimental effects upon large carnivore carcass utilisation, carrying the cost of increased hunting effort (Hayes *et al.* 2000; Kaczensky, Hayes & Promberger 2005). Mesopredator removal can free a top predator from the constraints imposed upon it by a smaller species (Bodey, McDonald & Bearhop 2009). Increased aggression towards scavengers might thus alleviate food loss. While providing an attractant for mesopredators, scavenging the kills of larger carnivores presents a trade-off between nutritional gain and risk of injury (Switalski 2003).

In a similar mechanism, fox detectability could be higher due to greater foraging opportunities for small mammals in areas used by large carnivores. Large herbivores may restrict their space use in response to predation risk from large carnivores (Ford *et al.* 2014). Spatial exclusion of large herbivores can result in vegetation structures that increase small

mammal richness and abundance, or at least maintain population levels where they may otherwise decline under heavier herbivory (Parsons, Maron & Martin 2013). Mesopredators may thus be attracted to risky places if small mammals are abundant. Though carrying foraging costs, risk management behaviour can enable nutrient acquisition in food rich areas where large carnivores present risk (Haswell *et al.* 2018). Avoidance of larger predators may not always necessitate large scale displacement from habitat or access to resources (Vanak *et al.* 2013; Swanson *et al.* 2016).

Knowledge and conservation of beneficial ecosystem services is vital in an era of vertebrate decline and extinction crises (Ceballos *et al.* 2015; Ceballos, Ehrlich & Dirzo 2017). Large carnivores, humans and the mechanisms underlying fox detectability could influence these ecological functions. Foxes affect prey species and other predators (O'Mahony *et al.* 1999; Apfelbach *et al.* 2005; Bischof *et al.* 2014). Fox effects on prey behaviour can consequently reduce tick-borne disease risk (Hofmeester *et al.* 2017). Increased activity or movement rates in response to large carnivores, or elusive trail use in response to humans could also affect less obvious functions such as primary (endozoochory) and secondary (diploendozoochory) seed dispersal (Cancio *et al.* 2016; Farris *et al.* 2017; Hämäläinen *et al.* 2017). Foxes may be particularly instrumental in seed dispersal and fleshy fruit shrub recruitment along linear travel routes (Suarez-Esteban, Delibes & Fedriani 2013a; Suarez-Esteban, Delibes & Fedriani 2013b).

Seasonal variation in detectability likely reflects fluctuation in fox numbers and/or activity. Fox detectability was much lower during the dispersal season (October – January 30th). Foxes can be more active in warmer months and have larger group sizes prior to juvenile dispersal (Lloyd 1980; Cavallini & Lovari 1991; Torretta *et al.* 2016). Vanak et al. (2013) proposed that seasonal changes in visibility through vegetation cover might affect mesopredator avoidance strategies. Sparser beech tree foliage and decline in trailside vegetation might also leave foxes more visually exposed in winter. This could feasibly contribute to lower detectability during the dispersal season. Temporal variation clearly requires consideration in research and monitoring programmes.

Conclusions

Spatial exclusion may be common where species compete closely and food availability is low, but mesopredator suppression may be more subtle where richer habitat and species attributes permit coexistence. Behavioural adjustments can enable coexistence between

carnivores but can carry costs as well as potential benefits. Instead of being elusive, foxes may be more active, more abundant or travel more often in localities with higher large carnivore detectability because food offers a benefit and keeping on the move permits safer resource acquisition where there is risk. In a less modified landscape where human activities were not associated with substantial food subsidies, foxes employed an elusive strategy to mitigate perceived risk. Ecological interactions are not homogenous. The risk management behaviour exhibited by mesopredators will be relative to the level of competition, risk and benefits. As costs decrease and benefits increase, mesopredators will likely employ finer scale avoidance strategies to gain access to resources. As costs increase and benefits decrease, mesopredators should employ larger scale avoidance strategies to the point of complete spatial exclusion. Accurate predictions are however essential to guide management decisions regarding interference, harvest, removal or restoration. Understanding interactions between organisms and their trophic consequences across a range of contexts will improve predictive capabilities.

Chapter 4.

The fine-scale risk mitigation behaviour observed in response to a large carnivore cue in Chapter Two did not translate into spatial restriction on a broader scale. Chapter Three showed that foxes were not spatially restricted by large carnivores and were in fact more detectable in their presence. It also suggested that humans caused foxes to become more elusive. Time is an often overlooked niche. Alongside subtle spatial avoidance, temporal avoidance could be highly important in enabling mesopredators to coexist with large carnivores that provide risk. Chapter Four uses recent methodological progressions for the study of temporal niche overlap as well as the exploration of animal propensity for nocturnal activity dependent on context (Ridout & Linkie 2009; Gaynor *et al.* 2018). Like Torretta et al., (2016), we also applied more traditional measures of comparing activity patterns with circular statistics to compliment the more recent developments (Meredith & Ridout 2018a). Importantly, activity patterns were made more biologically relevant by adjusting records according to the position of the sun (Nouvellet *et al.* 2012). The influence of time of day and dominant species activity on vigilance patterns were also explored as an indicator of risk.

Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality but humans moderate the interaction

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The following paper is prepared ready for submission to publish.

Author contribution statement

P.M.H conceived, designed and executed the study, wrote the manuscript, and also assisted with data collection. M.W.H contributed to the design, analysis and writing of the manuscript. J.K. conceived and executed data collection and contributed to writing, obtaining permits and support from Plitvice Lakes National Park. Funding was acquired by P.M.H and J.K. Editorial advice was provided by M.W.H, J.K. and K.A.J. All authors gave final approval for publication.

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Abstract

Coexistence among competitors requires differentiation along a niche axis, but an absence of top-down suppression is not essential. The temporal avoidance of interspecific aggression can enable access to resources without complete spatial exclusion. While somewhat constrained by endogenous rhythms, morphology and ecology, animals may still exhibit flexible activity patterns in response to external stimuli. We explored activity pattern overlap in large carnivores (gray wolf, *Canis lupus* and Eurasian lynx, *Lynx lynx*) and a mesopredator (red fox, *Vulpes vulpes*), alongside context dependent nocturnality and the influence of human disturbance in Plitvice Lakes National Park, Croatia. Humans were diurnal with activity peaking just before noon. Carnivores avoided this period and were predominantly nocturnal. Large carnivores were more active than foxes immediately after sunrise and before sunset. Carnivore activity patterns overlapped greatly but temporal distributions followed expectations based on interspecific killing, with significant differentiation occurring where body size differences were intermediate (foxes to large carnivores) but not when they were small (wolf and lynx). Risk ratios showed foxes were more nocturnal when large carnivore pressure was higher. Low light levels likely provide safer conditions by reducing the visual detectability of mesopredators, decreasing the likelihood of aggressive encounters. Mesopredators may be able to cope with interspecific aggression through fine-scale mechanisms without the need for substantial spatial or temporal avoidance. High human disturbance moderated the strength of top-down temporal suppression, which could carry consequences for the trophic interactions of mesopredators. If national parks are to play a part in providing ecological baselines and achieving conservation goals, then some limitation to recreation and development within them is required.

Introduction

Larger carnivores can suppress smaller carnivores through direct killing, harassment and by creating risk (Crooks & Soulé 1999; Palomares & Caro 1999; Ritchie & Johnson 2009). Aggressive encounters between species can be affected by body size differences, niche overlap, resource availability, physical characteristics, behavioural strategies and similarity in stimuli (appearance, behaviour, scent etc.) that trigger agonistic behaviour due to common ancestry (Donadio & Buskirk 2006; Grether *et al.* 2013; Haswell *et al.* 2018). Ecological differentiation along a niche axis is deemed necessary for coexistence (Hardin 1960).

Differentiation along spatial and dietary niche axes has received notable attention (Azevedo *et al.* 2006; Bassi *et al.* 2012; Newsome & Ripple 2014). The temporal niche and methodologies for its study has however recently received more focused attention, particularly with regard to fine-scale circadian patterns (Ridout & Linkie 2009; Frey *et al.* 2017; Gaynor *et al.* 2018).

Circadian clocks help maintain optimal activity and likely provide restrictions to activity patterns because divergence from endogenous rhythm can carry ecological and physiological costs (Kronfeld-Schor & Dayan 2003; Relógio *et al.* 2011). Intrinsic characteristics such as eye morphology and visual acuity may also restrict temporal niche (Veilleux & Kirk 2014; Banks *et al.* 2015). There is however substantial overlap in eye morphology among mammal groups with different circadian activity patterns, with most mammals retaining a scotopic (low-light) eye design and genomic patterns consistent with nocturnal origins (Heesy & Hall 2010; Hall, Kamilar & Kirk 2012; Borges *et al.* 2018). Anthropoid primates (e.g. humans), having eye morphology adapted to diurnality, are a notable exception (Ross & Kirk 2007; Heesy & Hall 2010; Hall, Kamilar & Kirk 2012). Additional advanced sensory systems (olfactory, auditory and tactile vibrissae) are prevalent in mammals, so a return to diurnal or cathemeral habits by some species may not have provided a strong enough selection pressure to re-evolve photopic eye morphologies (Hall, Kamilar & Kirk 2012).

Animal behaviour and decision making is contextual (Haswell, Kusak & Hayward 2017; Owen, Swaisgood & Blumstein 2017). Animals can exhibit flexible activity patterns in response to non-photic stimuli, although mismatching activity-rest cycles and circadian rhythms may incur severe costs (Kronfeld-Schor & Dayan 2003; Monterroso, Alves & Ferreras 2013; Heurich *et al.* 2014). Ambush predators like lions, *Panthera leo,* may hunt more successfully at night whereas cursorial predators like African wild dog, *Lycaon pictus*, and cheetah, *Acinonyx jubatus*, may rely on good light conditions to perform risky high speed chases (Cozzi *et al.* 2012). Time use can accordingly, although not always, be influenced by abiotic conditions, resource acquisition and foraging success but also by intraspecific or interspecific competition and risk (Reimchen 1998; Hayward & Slotow 2009; Theuerkauf 2009). Temporal partitioning of activity may be a mechanism allowing mesopredators to avoid costly interspecific interactions (Monterroso, Alves & Ferreras 2014; Diaz-Ruiz *et al.* 2016). Complete spatial avoidance of suitable habitat prevents access to resources, whereas avoidance of competitors or aggressors in time can permit coexistence and access to resources (Holt & Polis 1997; Swanson *et al.* 2016).

Observing changes in behaviour, such as activity patterns, can improve our understanding of ecological processes but can also provide early warning signals, e.g. temporal avoidance might be a precursor to spatial exclusion, population decline or regional extinction following growing anthropogenic pressure (Berger-Tal *et al.* 2011; Caravaggi *et al.* 2017). Humans (*Homo sapiens*) can place top-down pressure on carnivores, creating spatiotemporal risk (Darimont *et al.* 2015; Smith *et al.* 2017; Gaynor *et al.* 2018). Here, we aimed to understand how mesopredator suppression and human disturbance shape time use so explored activity patterns and contextual interactions between wolves, *Canis lupus*, lynx, *Lynx lynx*, foxes, *Vulpes vulpes* and humans in Plitvice Lakes National Park, Croatia.

Methods

Study Site

Plitvice Lakes National Park (Plitvice), is situated between 44° 44' 34" and 44° 57' 48" N and 15° 27' 32" and 15° 42' 23" E, in the Dinaric Mountains, Croatia (Šikić 2007). The mountainous karst (limestone and dolomite) landscape ranges from 367 to 1279 m and, excepting the iconic lakes and waterfalls, is characterised by scarce surface water (~1%), underground drainage systems, sink holes and caves (Šikić 2007; Romanić *et al.* 2016). Annual precipitation is 1,550 mm with temperatures fluctuating between winter lows of -3°C and summer highs of 36°C (Šikić 2007). One survey site contained planted stands of Scots and black pine (*Pinus sylvestris* and *Pinus nigra*) but forest cover is predominantly Dinaric beech and fir trees (*Fagus sylvatica* and *Abies alba*). Tourism and recreation are permissible within the 297 km^2 park where approximately 1770 people live within 19 settlements (Firšt *et al.* 2005; Romanić *et al.* 2016). The number of people visiting Plitvice has grown from 928,000 visitors in 2007 to over 1.72 million in 2017 (Smith 2018).

Data collection

We aimed to investigate the activity patterns associated with the spatial patterns of interspecific coexistence previously observed in Chapter Three. We utilised records from the same 20 passive infrared motion sensor cameras and periods. Cameras were placed on roads and trails between October 2015 and October 2016. Data were initially collated in Camera Base 1.7 (www.atrium-biodiversity.org/tools/camerabase).

Estimating activity patterns from camera data collected via a range of survey designs may be acceptable provided 100 detections are obtained (Lashley *et al.* 2018). We satisfied this

threshold for all species except wolf (80 records). The minimum acceptable distance between camera locations used was 675 m. When two cameras were present at the same site (N = 3), we only used data from a single camera selected at random. Cameras were checked monthly in summer but at the start and end of winter due to accessibility restrictions.

Data analysis

Activity patterns

Like Rowcliffe et al. (2014), we defined activity records as the times of day that cameras were triggered by a given species. Only independent triggers (>30 minutes apart) were utilised (Ridout & Linkie 2009; Linkie & Ridout 2011; Torretta *et al.* 2016). We labelled activity records as day (between sunrise and sunset) or night (before sunrise and after sunset) according to the corresponding sunrise and sunset times; we then conducted Pearson chi squared tests for each species to see if the distribution of observations was different to that expected from the proportion of day time and night time available during the survey year (http://aa.usno.navy.mil/data/index.php).

In longer term studies of behavioural timings, it is important to ensure that actual timings, as given by the position of the sun, are used instead of clock time to prevent the generation of false activity patterns (Nouvellet *et al.* 2012). Clock time does not have any biological or environmental meaning, whereas the sun's position in the sky does (Nouvellet *et al.* 2012). We adjusted clock time to sun time using the "overlap" package in R version 3.5.1 (Meredith & Ridout 2018b). Circadian activity patterns were then estimated as probability density functions using kernel density estimation (Ridout & Linkie 2009; Linkie & Ridout 2011; Meredith & Ridout 2018a).

Interspecific time use

We first explored overlap in species circadian trail use non-parametrically. Under the presumption that animals were equally likely to be photographed at any time they were active on trails, we fitted kernel density curves and estimated the coefficient of overlapping, Δ, which is the area lying under both curves (Ridout & Linkie 2009; Linkie & Ridout 2011; Meredith & Ridout 2018a). The coefficient of overlapping ranges from 0, indicating no overlap, to 1, indicating complete overlap (Ridout & Linkie 2009; Linkie & Ridout 2011). All sample sizes were >75 so, as recommended, we used the estimator $\hat{\Delta}4$ (Meredith & Ridout 2018a).

Within the "overlap" package in R, we generated 10,000 smoothed bootstrap samples to estimate a mean coefficient of overlap and 95% confidence intervals for each species pairing (Meredith & Ridout 2018a; Meredith & Ridout 2018b). The 2.5% and 97.5% percentiles of the bootstrap samples were adjusted to account for bootstrap bias (approach "basic0"), providing the 95% confidence intervals presented (Meredith & Ridout 2018a). We performed interval corrections on a logistic scale and back-transformed them to correct for any confidence interval estimates falling outside the possible range of 0–1 (Meredith & Ridout 2018a).

We then tested for significant differences between species activity patterns, conducting multiple comparisons using Watson's two sample test (U^2) for common distribution in the "circular" package using R (Pewsey, Neuhäuser & Ruxton 2013; Torretta *et al.* 2016; Lund *et al.* 2017). We controlled for type I errors with Bonferroni correction, adjusting significance criterion (α) by dividing the type I error rate (0.05) by the number of tests (McDonald 2009; Field 2013).

<u>Nocturnality risk ratios</u>

We split activity records into high and low human disturbance levels based on whether the human detection probability for the location and time period was above or below mean detectability (0.260; from Chapter Three, Appendix E). We also split fox records into high and low wolf or lynx pressure based on whether the corresponding detection probability for the location and time period was above or below average (wolf, 0.014, lynx, 0.025; from Chapter Three, Appendix E). For each carnivore, we calculated the risk ratio $RR = \ln\left(\frac{\bar{X}_{High}}{\bar{X}_{Low}}\right)$ proposed by Gaynor et al. (2018), with $\bar{X}_{High}$ being the proportion of night time observations when human disturbance was high and $\bar{X}_{Low}$ the proportion of night time observations when human disturbance was low. The risk ratio represents a measure of effect size, with a positive risk ratio indicating a relative shift towards greater nocturnality in response to increased human pressure and a negative risk ratio indicating reduced nocturnality. For wolves and lynx, the risk ratio was calculated from all data, but for foxes we calculated two risk ratios towards humans, one using a subset of records when pressure from both large carnivores was low and another when it was high. We also calculated risk ratios for foxes towards wolf and lynx. We did this for subsets where human disturbance was either high or low to see if high human disturbance moderated the impact of large carnivores. To

maintain a clear understanding of the impact of a given large carnivore, the detectability of the other large carnivore was kept low in both cases.

<u>Vigilance as a behavioural indicator of risk</u>

We classified carnivore photographs as a binary outcome dependent on whether they exhibited major vigilance (1) or not (0). We defined major vigilance following Haswell et al. (2018), whereby the top of the head is above the shoulders and the neck is angled above horizontal. Photos where vigilance was not identifiable were excluded. We conducted a binary logistic regression (generalized linear model with a binomial distribution and logit link function) to examine the effects of time of day, wolf, lynx and human disturbance level upon engagement in major vigilance. We hypothesised that carnivores would be less likely to exhibit major vigilance at night, when it is presumably less useful in risk detection given low light levels. We thought carnivores might also be more vigilant when human disturbance was higher. We hypothesised that foxes would likewise be more vigilant when pressure from a larger carnivore was higher.

Chi-square tests assessing nocturnal vs diurnal record distribution and generalized linear models examining vigilance patterns were conducted in IBM SPSS statistics 22. Risk ratios were calculated in Excel. Overlap between species activity patterns and differences in record distribution using Watsons two sample test were conducted in in R version 3.5.1.

Results

Activity patterns

During 6,833 camera trapping days, 1,197 activity records were obtained for fox, 80 for wolves, 156 for lynx and 3,715 for humans. Fox records (χ^2 = 717.98, d.f. = 1, p < 0.001), wolf records (χ^2 = 15.73, d.f. = 1, p < 0.001) and lynx records (χ^2 = 30.40, d.f. = 1, p < 0.001) were all significantly more nocturnal than expected through random activity (88%, 71% and 71% of records occurring at night respectively). Human records were significantly more diurnal (96% of records) than expected (χ^2 = 3016.55, d.f. = 1, p < 0.001).

Interspecific time use

Mean overlap for fox activity curves was lowest with human activity curves, 0.17 (95% CI, 0.14 to 0.17). Overlap with lynx was 0.75 (0.65 to 0.79), and with wolf was 0.73 (0.65 to 0.82). Wolf and lynx shared the highest temporal overlap of any species pairing, 0.79 (0.72 to

0.89). Lynx overlap with humans was 0.28 (0.22 to 0.32). Wolf and human overlap was also 0.28 (0.19 to 0.34).
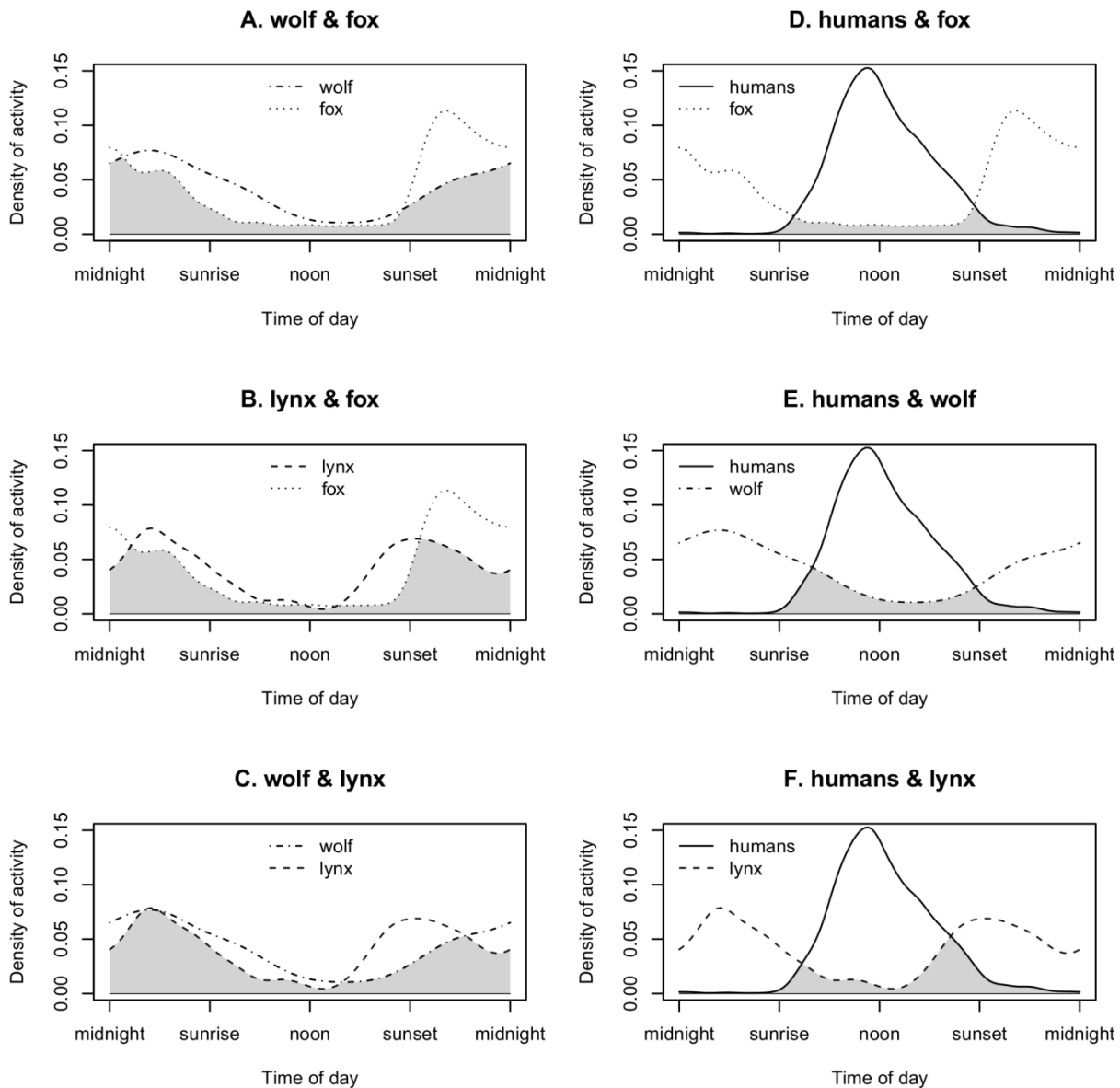
Figure. 4.1. Temporal niche overlap (grey area) between carnivores and humans in Plitvice lakes National Park, Oct 2015-Oct 2016. Dotted lines represent kernel density estimates for red foxes, *Vulpes vulpes*, dot-dash lines for gray wolves, *Canis lupus,* dashed lines for Eurasian lynx, *Lynx lynx,* and solid lines for humans, *Homo sapiens*. Kernel density estimates are plotted as a function of sunrise time.

Watson's two sample tests revealed fox activity patterns were significantly different to those of lynx ($U^2 = 1.13$, n = 1353, $P < 0.001$), wolves ($U^2 = 0.56$, n = 1277, $P < 0.001$) and humans ($U^2 = 60.47$, n = 4912, $P < 0.001$). Human activity patterns were also significantly different to those of lynx ($U^2 = 8.92$, n = 3871, $P < 0.001$) and wolves ($U^2 = 4.78$, n = 3795, $P < 0.001$). Wolves and lynx however did not have significantly different activity patterns ($U^2 = 0.17$, n = 236, $0.05 < P < 0.01$).

Foxes were very inactive during daylight hours with activity peaking after sunset and declining across the night, reaching low levels shortly after sunrise (Fig. 4.1.A, Fig. 4.1.B, and Fig. 4.1.D). The peak of fox activity did not coincide with activity peaks of larger species; however all carnivores were highly active during the night (Fig. 4.1.A, Fig. 4.1.B). Lynx activity peaked in the later part of the night between midnight and sunrise but higher activity was briefer than in wolves, with lynx utilising the early parts of the day at intermediate levels between wolves (Fig. 4.1.C) and foxes (Fig. 4.1.B). Lynx had a second peak of activity around sunset using the late afternoon more than wolves (Fig. 4.1.C) and foxes (Fig. 4.1.B). Wolves were more active than foxes during the early hours of the day (Fig. 4.1.A), with activity lowest after noon, rising after sunset and peaking similar to lynx in the later part of the night (Fig. 4.1.C). Humans dominated the daylight hours with activity peaking just before noon, this contrasted strongly to nocturnal carnivores (Fig. 4.1.D, Fig. 4.1.E, and Fig. 4.1.F).

Nocturnality risk ratios

When human disturbance and pressure from lynx was low, foxes were 1.13 (95% CI, 1.02 to 1.25) times more nocturnal in response to increased wolf presence. When human disturbance and wolf pressure were low, foxes were 1.11 (1.03 to 1.20) times more nocturnal in response to increased lynx presence. Effect size (risk ratio, *RR*) in response to wolves, 0.12 (0.02 to 0.22), (Fig. 4.2.E), was similar to that of lynx, 0.11 (0.03 to 0.18), (Fig. 4.2.G). All other risk ratios with confidence intervals overlapping zero were inconclusive, i.e. showing no significant difference in nocturnality between high and low conditions (Fig. 4.2). When human disturbance was high, the effects of increased large carnivore pressure upon fox nocturnality were not significant (*RR* Wolf, 0.03, -0.08 to 0.14, Fig. 4.2.F, *RR* Lynx, 0.08, -0.01 to 0.18, Fig. 4.2.H). No risk ratios showed significant responses to human disturbance. Wolves had the largest risk ratio, 0.19 (-0.09 to 0.46), (Fig. 4.2.A), lynx were intermediary, 0.06 (-0.14 to 0.27), (Fig. 4.2. B), and foxes had negative risk ratios (-0.02, -0.11 to 0.07,

when large carnivore pressure was low, Fig. 4.2.C and -0.07, -0.15 to 0.01, when high, Fig. 4.2.D) suggestive of greater diurnality when human disturbance was higher.
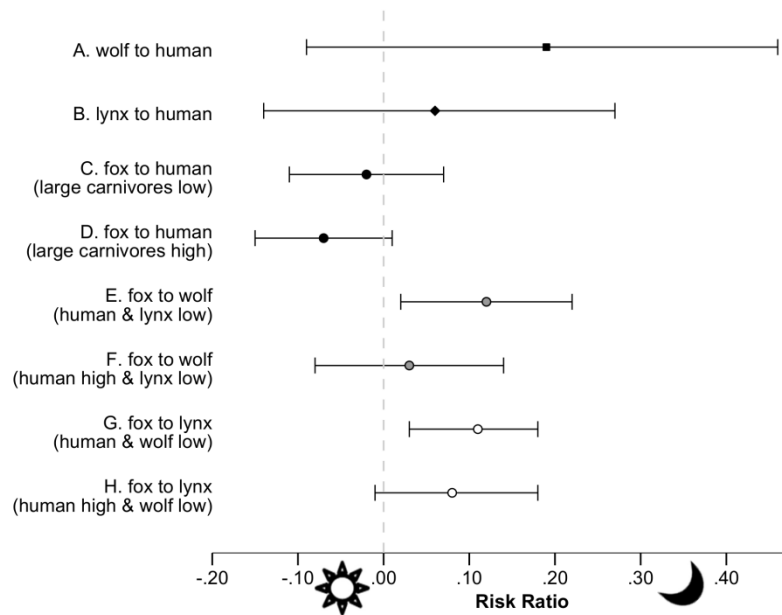
Figure. 4.2. Carnivore time use responses towards increased top-down pressure in different contexts. Points represent nocturnality risk ratios and bars 95% confidence intervals (Gaynor *et al.* 2018). Positive risk ratios represent a relative increase in nocturnal activity in response to increased top-down pressure, with negative records representing an increase in diurnal activity.

Vigilance as a behavioural indicator of risk

Foxes exhibited major vigilance in 34% of photos (N=1095). Generalized modelling revealed that no factor had a significant effect on whether foxes exhibited major vigilance (time of day, Wald χ^2 = 2.10, d.f. = 1, P = 0.15, wolf pressure, Wald χ^2 = 3.12, d.f. = 1, P = 0.08, lynx pressure, Wald χ^2 = 3.66, d.f. = 1, P = 0.06, human disturbance level, Wald χ^2 = 2.07, d.f. = 1, P = 0.15). Odds ratios suggest foxes were less likely to exhibit major vigilance at night (0.76, 95% CI, 0.52 to 1.10, times the odds during the day). Foxes were also less likely to exhibit major vigilance when wolf pressure was high, with the odds 0.78 (0.59 to 1.03) times that of when pressure was lower. The odds of foxes being vigilant were 1.31 (0.99 to 1.72) times higher when lynx pressure was high. The odds of foxes being vigilant were also 1.21 (0.93 to 1.56) times higher when human disturbance was high.

Lynx exhibited vigilance in 36.6% of photos (N = 145). The only significant driver of lynx vigilance patterns was time of day (time of day, Wald χ^2 = 11.47, d.f. = 1, P = 0.001, wolf

pressure, Wald $\chi^2 = 1.55$, d.f. $= 1$, $P = 0.21$, human disturbance level, Wald $\chi^2 = 0.88$, d.f. $= 1$, $P = 0.35$). Lynx were less likely to be vigilant at night, with the odds 0.27 (95% CI, 0.13 to 0.58) times those during the day. While not significant, odds ratios suggest lynx were 1.74 (0.73 to 4.18) times more likely to exhibit vigilance when wolf pressure was high than when it was low, and 1.49 (0.65 to 3.39) times more likely when human disturbance was high.

Wolves exhibited vigilance in 40.9% of photos (N = 66). No factors had a significant effect on whether wolves exhibited major vigilance (time of day, Wald $\chi^2 = 0.23$, d.f. $= 1$, $P = 0.63$, human disturbance level, Wald $\chi^2 = 2.07$, d.f. $= 1$, $P = 0.15$). Odds ratios suggest wolves were 1.33 (95% CI, 0.42 to 4.20) times more likely to be vigilant at night and 2.13 (0.76 to 5.96) times more likely to be vigilant when human disturbance was high.

Discussion

We observed temporal partitioning among carnivores and contextual differences in fox activity patterns. Our findings support the notions of a level of flexibility in activity patterns, with animals avoiding activity during high-risk periods (Lima & Bednekoff 1999; Kronfeld-Schor & Dayan 2003). Temporal differentiation between carnivores followed the patterns of interspecific killing associated with body size differences (Donadio & Buskirk 2006). We observed significantly different activity patterns between carnivores when body size differences were intermediate (fox-wolf, fox-lynx), but not when size differences were smaller (wolf-lynx). Our results also support the concept of humans dampening the ecological effects of large carnivores (Hebblewhite *et al.* 2005).

Large carnivores made use of parts of the day when humans were less active (wolves just after sunrise and lynx just before sunset), which, in turn, appears to have restricted day light use by foxes. Foxes made more use of daylight hours when large carnivore pressure was low, being more nocturnal when pressure from wolves or lynx was higher. Fox nocturnal activity also peaked during periods when large carnivores were less active. Foxes avoided risky periods but made greater use of a broader temporal niche in less risky contexts. Mesopredators can expand their niche axes in the absence of top-down pressure (Gese & Grothe 1995; Prugh *et al.* 2009; Kamler, Stenkewitz & Macdonald 2013). Monterroso et al. (2013) observed foxes to be the dominant daytime user in a Mediterranean national park void of larger carnivores (Cabañeros, Spain). Our findings suggest that foxes can readily adjust their activity patterns as required in response to localised variation in top-down pressure. Risk

perception may play a pivotal role in informing such flexible behaviour (Leo, Reading & Letnic 2015; Haswell *et al.* 2018; Kohl *et al.* 2018).

Fox activity pattern adjustment in response to large carnivore context did not result in dramatic temporal differentiation and a complete shift to diurnality as has been observed in rats, *Rattus norvegicus*, and American mink, *Neovison vison* towards dominant carnivores (Fenn & Macdonald 1995; Harrington *et al.* 2009). Predators that evolved under similar ecological conditions and share ecological traits may have similar activity patterns and co-occur often, limiting the potential for temporal avoidance (Kronfeld-Schor & Dayan 2003; Davis *et al.* 2018). This may be particularly true if humans also restrict diurnal activity. Low light levels and visual obstacles can increase spatial tolerance and reduce agonistic interactions between intraspecific competitors (Reimchen 1998). Presumably the same might be true of interspecific competitors. Animals may be less conspicuous in lower light levels; predation and harassment risk might therefore be lower at night, providing a time period where habitat and resources can be accessed more safely (Beauchamp 2007). Animals may consequently invest less in vigilance at night, although this could also be linked to reduced defensive efficacy of vigilance in low light levels (Beauchamp 2007; Le Saout *et al.* 2015). We found lynx vigilance was significantly lower at night and observed a similar albeit non-significant decrease for foxes.

While not significant, odds ratios suggested wolves were slightly more vigilant at night when humans were inactive. While often associated with interspecific defence, vigilance also functions in prey detection and conspecific monitoring (Caro 1987; Hirsch 2002; Pangle & Holekamp 2010). Having the head up may also serve auditory functions, particularly for species whose ears function directionally. Wolves are social foragers most likely to hunt during twilight when success is highest, except perhaps in areas of high prey density or carrion availability (Theuerkauf 2009). Ungulates are protected from human harvest in Plitvice and the surrounding area contains garbage dumps and wildlife feeding stations. Human disturbance also began after sunrise in Plitvice, whereas wolf activity peaked between midnight and sunrise. Wolves actively seeking food at night, or keeping track of conspecifics while moving as a social unit, might thus be more vigilant. The avoidance of foraging wolves might explain why fox activity declined when wolf activity peaked. Subordinate mesopredators may need to move their activity around the foraging bouts of larger carnivores (Hayward & Slotow 2009).

Avoiding interspecific aggression along the temporal niche axis could carry costs to individual body condition (Harrington *et al.* 2009). Behavioural responses to risk can thus result in significant demographic consequences (Preisser, Bolnick & Benard 2005; Creel & Christianson 2008). Demographic consequences may however be negligible when avoidance is on a very fine, moment-to-moment scale (Swanson *et al.* 2014; Swanson *et al.* 2016). The demographic consequences of fox responses to top-down risks require quantification but modified foraging behaviour, nocturnality and temporal partitioning did not prevent foxes from occupying sites used by large carnivores in Plitvice (Haswell et al. (2018) & Chapter Three). Foxes, like other mesopredators, fulfil key trophic functions (Smedshaug *et al.* 1999; Roemer, Gompper & Valkengurgh 2009). Temporal obstruction by larger carnivores could still inhibit mesopredator foraging, having indirect trophic consequences by offering respite to certain prey species. For example, when diurnal prey (Orthoptera) provide an important dietary component for red fox, this can drive increased diurnal activity (Cavallini & Lovari 1991). Small mammal prey may also be capable of altering their own activity patterns, becoming more diurnal to avoid encounters with red foxes (Fenn & Macdonald 1995).

Risk assessment and response to dynamic landscapes of fear can enable access to resources through the use of risky places at safe times (Palmer *et al.* 2017; Kohl *et al.* 2018). Mesopredators may alternatively optimise access to resources by coexisting in space and time through the use of fine-scale mechanisms. Species specific strategies may however be somewhat affected by locomotor modality (Hunter & Caro 2008). Partial or complete plantigrade foot posture (walking on toes and metatarsals) may reduce the effectiveness of high speed running, negating flight as an evasion strategy but perhaps benefitting fighting performance (Hunter & Caro 2008; Carrier & Cunningham 2017; Pagano *et al.* 2018). An inability to outrun faster predators might thus select for defensive adaptation. Armaments such as noxious secretions, accompanied by aposematic colouration visible in low light levels (e.g. skunks, Mephitidae) may mitigate aggressive encounters (Caro 2005; Hunter & Caro 2008; Caro 2009). The ability to differentiate (e.g. arboreal Procyonidae) along habitat strata may also enable finer scale spatial avoidance where activity overlaps (Hunter & Caro 2008).

Digitigrady (walking on toes) enables speed (Lovegrove 2004; Lovegrove & Mowoe 2014). Flight offers escape for digitigrade mesopredators, perhaps making stand and fight mechanisms less likely. The dominant competitors of digitigrade mesopredators are often however also digitigrades. Some mesopredators (e.g. cheetah, *Acinonyx jubatus*) may be able to mitigate aggressive encounters on a moment to moment basis if they are quicker than their

suppressors (Swanson *et al.* 2016). This is unlikely the case for foxes. Without superior speed or physical defences, foxes might thus rely upon nocturnal cover and temporal avoidance (this paper), alongside risk detection and fine-scale mitigation (Haswell *et al.* 2018). Some foxes (e.g. San Joaquin kit fox, *Vulpes macrotis mutica*) may alternatively make greater use of evasion to subterranean burrows (Cypher *et al.* 2001).

Context will dictate the efficacy of risk mitigation strategies. Habitat structure may be important, with complex habitats and the presence of visual obstacles potentially reducing aggressive encounters (Reimchen 1998; Harrington *et al.* 2009; Vanak *et al.* 2013). Escape strata availability and species traits could also affect coexistence likelihood. For example, gray fox, *Urocyon cinereoargenteus*, may successfully evade coyotes, *Canis latrans*, using arboreal strata when trees are readily available, but this may be less effective in sparser forest or when evading bobcats, *Lynx rufus*, which can climb trees (Lesmeister *et al.* 2015). The traits of mesopredators and their dominant competitors are likely to interact with local conditions, shaping risk mitigation strategies, predator community structure and diversity.

Humans can provide additional predation risk and function as super predators (Walther 1969; Smith *et al.* 2017). Benitez-Lopez et al. (2018) suggested that the human disturbance of apex predators from daylight activity might affect ecological interactions. In Plitvice, higher human disturbance mediated the top-down temporal restriction imposed upon foxes by apex predators. We found the effect of large carnivore pressure on fox nocturnality was insignificant when human activity was higher; risk ratios also suggested a much smaller effect of lynx (27% smaller) and wolf (75% smaller) pressure in this context. Interference with predator to predator interactions and consequent changes to mesopredator foraging activity could alter the pressure these efficient predators place upon prey communities (Vance-Chalcraft *et al.* 2007; Ritchie & Johnson 2009).

Gaynor et al. (2018) showed human activity can restrict diurnal activity in mammals. Carnivores, particularly foxes, were predominantly nocturnal, having little activity pattern overlap with humans. Humans were strictly diurnal with activity peaking just before noon. Nocturnality could suggest avoidance, particularly when humans present high risk to carnivores (Kusak, Skrbinšek & Huber 2005; Diaz-Ruiz *et al.* 2016). Limited temporal overlap might however be expected given species adaptations and evolutionary history (Heesy & Hall 2010; Hall, Kamilar & Kirk 2012). A lack of carnivore activity during the central parts of the day could reflect avoidance of heat but human activity during twilight

could still affect carnivore hunting success (Hayward & Slotow 2009; Theuerkauf 2009). Our contextual risk ratios were inconclusive. The obstruction of large carnivores from daylight hours by high human disturbance would however explain the moderation of large carnivore effects on foxes in this context, with foxes utilising the day slightly more to gain resource access or to avoid more nocturnal large carnivore activity.

Higher human activity modified ecological interactions in Plitvice. Intense human pressure is prevalent in almost a third of global protected lands and undermines biodiversity preservation (Jones *et al.* 2018). Furthermore, interference risks altering baselines, negating the function of reserves in detecting ecological change, but also distorting public understanding of intact ecological processes (Sarmento & Berger 2017). Increasing intensity, temporal or spatial coverage of human activities beyond species tolerance could also conflict with conservation goals (Firšt *et al.* 2005; Štrbenac *et al.* 2005). Human disturbance can negatively affect foraging success, territorial defence, mate acquisition and reproductive output, as well as causing spatial displacement, stress and reduced energy intake, which have the potential to ultimately affect body condition, survival, fitness and demography (Frid & Dill 2002; Strasser & Heath 2013; Pauli, Spaul & Heath 2017).

If national parks are to play a part in achieving wildlife conservation goals then some limitation to recreation and development within them is required. Excluding visitors from protected areas could diminish support and create conflict; restrictions to use accompanied by stakeholder collaboration and incentives may alternatively prove suitable (Soliku & Schraml 2018). Restriction to visitor numbers, human activity types, intensity, timing and spatial distribution should help to mitigate impacts within national parks (Rogala *et al.* 2011; Vujko *et al.* 2017; Ladle *et al.* 2018). Efforts have been made to manage visitor numbers in Plitvice, increasing ticket prices and directing space use through designated hiking trails and restricted road access. Pressure from increasing tourist developments and recreational encroachment however remain problems.

Lower impact recreational activities like hiking, often experienced in national protected areas, could however prove important in fostering interest in private land conservation (Farmer *et al.* 2016). Partitioning of conservation and recreational sites through the creation of private reserves and conservation easements could contribute valuable additional wildlife refugia (Rissman *et al.* 2007; Reed & Merenlender 2008; Hardy *et al.* 2018). Minimising visitor impact, while instilling stewardship, should assist the preservation of biodiversity and

ecological processes, both within and outside national parks, but this will only work where large areas of private land are also available for conservation.

Europe has a larger human footprint than almost anywhere else in the world (excepting some parts of Asia); there are positive trends towards reduced local footprint in Western Europe but this may be predominantly through shifting impact to other countries via resource imports (Venter *et al.* 2016). Given the lack of true wilderness areas compared to North American landscapes, many believe the most probable scenario of saving wildlife in Europe will be characterized by a dynamic interspersion of both wildlife and humans (Chapron *et al.* 2014). Biodiversity preservation still requires strictly protected areas, but these also need to be supported by favourable coexistence landscapes (Kremen 2015). Restrictions to visitor numbers and access are almost certainly needed in European protected areas. Restrictions may however also be necessary in the managed national forests of Croatia, particularly those within NATURA 2000. Emerging recreational threats such as all-terrain vehicles and snowmobiles should probably be banned from protected reserves outright and will need regulation in national forests. Such recommendations will be unpopular with recreationalists, but given competing demand for more essential human land uses such as food production, European nature conservation efforts need to carefully consider how non-consumptive recreation is managed (Reed & Merenlender 2008).

Chapter 5.

Conclusions

This thesis sheds light on the mechanisms of predator interactions that enable coexistence, foster predator diversity and perhaps encourage biodiverse communities. It also informs on human disturbance via non-consumptive landscape presence, by assessing whether European protected areas remain relatively undisturbed as is desired. Together this information provides guidance on the ecological role of apex predators, anthropogenic disturbance and land management in the Anthropocene.

Interactions between predators

The work of Davis et al. (2018) presents a recent development in global patterns of carnivore co-occurrence. They suggest that carnivores with similar ecological traits are more likely to co-occur but note depressed co-occurrence where one of the pair was large or medium-large. This somewhat supports the notion of top-down suppression, but also suggests that similar ecological requirements may cause similar geographic distributions, without competitive exclusion in many cases. Their work utilised broad categorical definitions of traits and they acknowledge an inability to examine finer scale differences as this thesis has. It is these fine-scale differences that may provide the answer to how predators with broadly similar characteristics can coexist. Interestingly they also found that omnivores co-occurred more often than expected with strict carnivores, as did species with similar categorical activity pattern types. In Plitvice, we found the omnivorous fox to spatially co-occur with larger carnivores and have broadly overlapping activity (Chapters Three & Four).

Complete spatial exclusion may not actually be as common as co-occurrence. This does not however disagree with concepts that mesopredators may be found in higher densities or under

less pressure on the peripheries of large carnivore range. The enemy constraint hypothesis suggests that top-down pressure will be strongest within the core range of larger carnivores (Newsome *et al.* 2017b). Spatial detectability patterns in Plitvice (Chapter Three) however suggest a positive association between fox detection probability and large carnivore presence, potentially suggesting the opposite. Large carnivores do facilitate smaller predator access to large herbivores via kleptoparasitism (Selva *et al.* 2005; Helldin & Danielsson 2007). This might counter the negative impacts of enemy constraint, with detectability being associated with greater fox numbers due to facilitation of food. Wolf pack size may have a negative effect on fox abundance, and accurate matching of group body mass to prey carcass mass reduces food availability to scavengers (Wilmers *et al.* 2003; Wikenros *et al.* 2017a). The amount of scavengeable food available at large carnivore kills could explain why fox detectability was more strongly associated with solitary lynx than with social wolves. Greater detectability does not necessarily represent greater fox densities but could alternatively be indicative of movement and activity (Neilson *et al.* 2018). This is something that requires reconciliation to establish whether Chapter Three's findings are contrary to the enemy constraint hypothesis or simply signify additional processes. As was suggested in Chapter Three, less exhaustive foraging patch utilisation observed in response to large carnivore cues (Chapter Two) might logically equate to greater landscape movement in order to obtain sufficient sustenance and thus cause greater detectability. Increased activity could alternatively be associated with foraging opportunities brought about by the cascading benefits large carnivores may have on small mammal communities (Creel *et al.* 2005; Parsons, Maron & Martin 2013). Understanding the mechanisms associated with elevated fox detectability (fox densities, scavenging, movement rates and prey abundance) will shed further light on the balance between enemy constraint and benefits.

Where predators occur in sympatry, temporal partitioning could provide a useful mechanism for alleviating competition and top-down suppression (Hayward & Slotow 2009). This may however only be necessary on a fine-scale (Chapter Four). Differing peak activity may be sufficient to enable co-occurrence (Davis *et al.* 2018). Where predator communities are more complicated however, peaks are more likely to converge and so temporal flexibility may play an increasingly important role as carnivore diversity increases (Monterroso, Alves & Ferreras 2014). Foxes became more nocturnal in response to increased large carnivore pressure in Plitvice (Chapter Four); suggesting darkness offers increased safety (Beauchamp 2007;

Benitez-Lopez 2018). Larger predators may well place stronger temporal limitations on day time activity.

Although differing in peak activity, almost three quarters of fox activity overlapped with that of wolf and lynx (Chapter Four). Predators may prioritise hunting success over temporal avoidance of dominant competitors (Cozzi *et al.* 2012; Mugerwa *et al.* 2017). Preference for different habitat characteristics may also enable smaller predators to share landscapes with larger predators, without substantial temporal partitioning (Bender, Rosas-Rosas & Weisenberger 2017; Mueller, Drake & Allen 2018). Alternatively, prey may access risky habitats at times when likelihood of encounter is low (Kohl *et al.* 2018). The risk detection and mitigation behaviour observed at a fine-scale in Chapter Two would enable foxes to read and respond to dynamic fluctuations in spatio-temporal risk landscapes. Avoiding spaces only immediately after an aggressor has used them may provide ample access to resources with minimal additional adjustments or demographic costs (Swanson *et al.* 2014; Swanson *et al.* 2016). Our findings also further support the notion that animals adjust their behavioural strategies when in high risk scenarios (Lima & Bednekoff 1999; Moll *et al.* 2016).

Spatio-temporal risk mitigation may be complimented or perhaps even superseded by mechanisms that enable successful and economic avoidance of aggression upon encounter. Animals may minimise predation via escape by concealment and locomotion or via self-defence (Lovegrove 2001). Differentiation along fine habitat strata or the ability to evade predators using strata that the aggressor cannot utilise, might enable landscape sharing without temporal avoidance (Hunter & Caro 2008). For example, burrow use by kit, *Vulpes macrotis*, and swift foxes, *Vulpes velox*, or tree use by racoons, *Procyon lotor*, (Cypher *et al.* 2001; Gehrt & Prange 2007). Larger mammals tend to be quicker than smaller limbed mammals but smaller mammals may speed match larger predators through higher than average basal metabolic rates or limb specialization (Lovegrove 2001). Slower carnivores may survive or prevent aggressive encounters through aposematic colouration (e.g. skunks, Mephitidae) and defensive adaptations (e.g. armour or weaponry) or perhaps simply through overly aggressive responses regardless of size (Lovegrove 2001; Prange & Gehrt 2007; Hunter & Caro 2008). Foxes do not possess specialist physical adaptations. This thesis suggests that instead, foxes rely upon spatio-temporal risk detection and mitigation in order to coexist alongside large carnivores.

The mesopredator release hypothesis, enemy constraint hypothesis and general patterns of interspecific aggression offer useful guidelines, but do not cover all of the complexity that yields the resultant interactions between carnivores (Crooks & Soulé 1999; Donadio & Buskirk 2006; Newsome *et al.* 2017b). This thesis concludes that fine-scale risk mitigation and temporal avoidance did not prevent foxes from occupying localities used by wolf and lynx. The consequences and cost benefit trade-offs of strategies ranging from broad to fine-scale spatio-temporal avoidance and physical adaptation require further investigation at both the individual and population level. Understanding how species traits may interact with local context to shape mammal communities and local diversity are important areas of exploration that may highlight strategic options for productive conservation interventions.

Mesopredators can offer important predation, seed dispersal and scavenging services of their own (Hofmeester *et al.* 2017; Hämäläinen *et al.* 2017; O'Bryan *et al.* 2018). Following the effects of coexistence strategy down through food web systems will further highlight whether the effects of large carnivores occurring in sympatry foster diversity, as seems plausible. With recent suggestions that cascading effects from apex predators may not be as substantial, or as permanent, as previously thought, gaining a firmer understanding of cascade theory seems ever crucial (Kohl *et al.* 2018; Shelton *et al.* 2018). It is also highly possible that, where carnivores coexist, top-down pressure, alongside the strategies studied and described in this thesis, may ultimately affect and drive, not only behavioural, but also evolutionary diversification. The potential for aggressive character displacement requires much greater study (Grether *et al.* 2009; Grether *et al.* 2013). Further exploration is crucial if we are to understand the implications of conservation threats to carnivores, calls for rewilding and anthropogenic species translocation (Rich *et al.* 2017a; Lundgren *et al.* 2018; Wolf & Ripple 2018).

Anthropogenic disturbance

Very little of the globe has escaped anthropogenic influence (Kareiva *et al.* 2007). The Anthropocene epoch signals an era where much of the globe, its biological communities and their behaviour have been substantially modified by human action (Venter *et al.* 2016; Bar-On, Phillips & Milo 2018; Tucker *et al.* 2018). Humans can be considered a super predator with global ecological implications, an integral part of food webs but importantly the only species with the ability to make ethical judgements and purposeful choices based on an awareness of the outcomes (Lewis, Burns & Jones 2017). Alongside intrinsic and resource

based motivations, there are additional arguments for nature derived human self-improvement (e.g. freedom, self-reliance, imagination and humility) that have encouraged wilderness preservation (Cafaro 2001). Biosphere reserves face demand to function not just environmentally but also economically and socially (Reed & Massie 2013). These three priorities can however be somewhat in conflict with each other. The human desire to interact with nature provides a level of conflict for parks and protected areas due to an increasing demand for recreation (Reed & Merenlender 2008; Sarmento & Berger 2017).

Visitors to protected areas require accommodation, provisions and infrastructure, which in turn require land modification. Recreational demand can lead to dramatic changes in land value, use and cover; risking degradation within national parks (Garrard *et al.* 2016). Anthropogenic landscape modification can create wildlife winners and losers, restructure ecological processes, and lead to less diverse communities (McKinney & Lockwood 1999; Fisher & Burton 2018). Human actions will often attenuate the density driven impacts of large carnivores, limiting predator densities and promoting prey densities through nutrient subsidies (Kuijper *et al.* 2016). Human disturbance can create prey refugia through predator exclusion, but open linear features and fencing can also facilitate predator movement, prey encounter and hunting efficiency (Neilson & Boutin 2017). Roads can further fragment landscapes and prevent horizontal processes such as foraging movements and dispersal (Forman & Alexander 1998). Anthropogenic infrastructure can also channel predator movements, having additional knock on effects such as increased scent marking rates (Krofel, Hocevar & Allen 2017). As was seen in Chapter Two, predator urine can affect the behaviour of mesopredators, as well as prey species (Apfelbach *et al.* 2005; Wikenros *et al.* 2017b; Haswell *et al.* 2018). Importantly, human infrastructure allows access to otherwise pristine areas, which alongside resource extraction, hunting and development, also brings sub-lethal anthropogenic disturbance (Forman & Alexander 1998; Basille *et al.* 2013; Venter *et al.* 2016).

Outdoor recreation can have marked effects on wildlife behaviour (Frid & Dill 2002; Blanc *et al.* 2006; Shannon *et al.* 2016b). Human disturbance can be erratic and of higher intensity than that of other predators, resulting in elevated stress levels (Zbyryt *et al.* 2018). Human detection probability was far higher than that of large carnivores in Plitvice (Appendix E). Increased stress may not always necessarily translate to demographic consequences (Creel *et al.* 2002). Investment in anti-predator behaviours like vigilance and reactions to different types of human disturbance may be dependent on factors such as individual status, a species

ability to distinguish threat level and the acoustic characteristic of the local environment (Shannon *et al.* 2016a; Lesmerises, Johnson & St-Laurent 2017). Understanding the species assemblage of protected areas and their characteristics will help with determining when, where and what types of human activities to allow. In general, flight responses are often stronger towards pedestrians than vehicles or noise, heightened in females with offspring and more pronounced in predators than ungulates (Stankowich 2008; Rogala *et al.* 2011). Where national parks support sensitive carnivore species, human activity will need to be cleverly guided to avoid negative impacts, especially during the breeding season. While European carnivores may be more adapted to anthropogenic disturbance than their North American counterparts, breeding site refugia, completely free of disturbance, agriculture and urbanisation are however essential (Chapron *et al.* 2014; White *et al.* 2015; Sazatornil *et al.* 2016).

Recreational risk can affect spatio-temporal patterns of habitat use, resulting in avoidance and reduced habitat access (Filla *et al.* 2017; Lesmerises *et al.* 2018). Individuals with higher energy requirements (females with young) may in some cases become more tolerant of human presence, investing less in anti-predator behaviour and benefitting from the presence of human shielding (Steyaert *et al.* 2016; Lesmerises, Johnson & St-Laurent 2017). In other circumstances human shielding may provide a scarecrow effect, mitigating the impacts of invasive species on those of conservation concern (Leighton, Horrocks & Kramer 2010). While human disturbance may provide some spatio-temporal protection for tolerant prey, it can also cause large carnivores to spend less time feeding from their kills, resulting in increased predation rates (Smith, Wang & Wilmers 2015; Smith *et al.* 2017). Human use of protected areas could greatly alter predator prey dynamics.

Examining occupancy during day-long survey periods, we found that human activity in Plitvice was not currently spatially excluding foxes, nor was it a key driver of large carnivore detection probability (Chapter Three, Appendix E). Spatial avoidance of human disturbance may however be on a much finer temporal scale, with the intensity of hourly human activity influencing site use (Rogala *et al.* 2011). Chapter Four showed that carnivores were predominantly active during the night in Plitvice, differing greatly from humans whose activity peaked just before midday. Increased nocturnality may be a common response to anthropogenic risk (Benitez-Lopez 2018; Gaynor *et al.* 2018). Carnivore nocturnality may not necessarily be driven by anthropogenic disturbance however (Theuerkauf *et al.* 2007; Heesy & Hall 2010). While the effects of human disturbance on carnivore propensity towards

nocturnality were inconclusive, risk ratios are suggestive of large carnivores becoming more nocturnal and foxes more diurnal under higher disturbance. A loss of access to successful hunting hours during twilight might be costly for large carnivores (Hayward & Slotow 2009; Theuerkauf 2009). The aforementioned human impacts presumably explain the negation of large carnivore impact upon increased fox nocturnality when human disturbance was high. While the ecological significance of temporal restriction placed upon foxes requires investigation, what is clear is that higher human activity in Plitvice altered this ecological process. Even in fairly remote protected areas, the maintenance of unmodified activity patterns may require human activity to be managed (Barrueto, Ford & Clevenger 2014).

Human activity further affected the behaviour of foxes in Plitvice. Fox detectability declined with human disturbance, signifying spatial elusiveness in response to disturbance. Dog walking is not common in Plitvice, although hikers with dogs could further exacerbate reductions in trail use (Banks & Bryant 2007; Doherty *et al.* 2017). We predict that the negative association of fox detectability with human disturbance was due to an absence of anthropogenic food provisioning. Food might override fear in circumstances where positive associations are observed (Hradsky *et al.* 2017; Reshamwala *et al.* 2018). Lower use of trails and roads in the presence of anthropogenic disturbance could influence the ecological role of mesopredators, particularly their role as seed dispersers (Suarez-Esteban, Delibes & Fedriani 2013a; Suarez-Esteban, Delibes & Fedriani 2013b).

The use of food subsidies to mitigate disturbance effects is not advisable. Predators can play an important role in nutrient distribution, facilitation for scavengers and the creation of nutrient pulses through kill sites (Wilmers & Getz 2005; Bump, Peterson & Vucetich 2009; Reimchen & Fox 2013). As such, food provisioning (e.g. for tourist viewing) could also have marked effects on carnivore habitat selection, movements and ecological function (Masse, Dussault & Ibarzabal 2014; Cozzi *et al.* 2016). Food subsidies can decouple the suppressive impacts of top predators and provide ecological traps if food encourages colonization but disturbance causes reproductive failure (Rodewald, Kearns & Shustack 2011; Strasser & Heath 2013). Recreational disturbance may of course also lead to reproductive failure in the absence of food provisioning (Pauli, Spaul & Heath 2017). Changes to species communities can consequently occur in the highly disturbed accommodation areas that support recreation, but effects are likely lessened near lower impact land uses such as trails and campfire sites (Huhta & Sulkava 2014). Habituation, adaptation to human landscapes and growing human encroachment in wilder areas is likely to alter the ecological functions of carnivores and

could ultimately lead to speciation events through hybridization, domestication and niche divergence (Newsome *et al.* 2017a).

The effects of large carnivores will be modified by the effect humans have both on large carnivores but also upon their prey and competitors (Kuijper *et al.* 2016). It is thus essential to consider human involvement when exploring how species interact. It is also useful to obtain information that adequately reflects the scale of anthropogenic threat (Cadotte *et al.* 2017). Disturbance from recreation in national parks is a localised impact of which this thesis has provided insight. Even where landscape use is non-extractive, human presence may still mediate ecological interactions (Chapter Four). Observing disruption to ecological process under the influence of low-level non-consumptive human disturbance also indicates that greater disturbance could further mediate top-down effects. Human disturbance can lead to the exclusion of predators from the landscape once tolerance thresholds are exceeded, resulting in cascading ecological effects (Hebblewhite *et al.* 2005; Ladle *et al.* 2018). The effects of human disturbance on species survival, fecundity, demography and composition within national parks require further investigation. Given European national parks are intended to provide core wildlife refuges, they must be cautious of the potential pressure that recreation might place upon refugia. The maintenance of pristine ecological interactions absent of human interference may prove difficult in many European contexts.

Acting appropriately to achieve management and conservation goals, alongside balancing political and public desires, is no simple task. To cultivate conservation in an era of rapid change, practitioners require a framework that enables them to know how, when and where to act (Heller & Hobbs 2014). This thesis provides insight into ecological considerations that managers of protected areas need to take into account. Such considerations do of course only provide part of a much more complex picture. Most national parks are generally expected to deliver conservation value, economic benefit and visitor experience. Determining the carrying capacity for visitors to protected areas is an essential beginning to ensuring sustainability (Vujko *et al.* 2017). This is not only important for conservation but also for visitor satisfaction, with many visitors disliking overcrowding (Rathnayake 2015; Rathnayake 2016). As this thesis highlights, humans can affect the behaviour of carnivores and interfere with ecological interactions. In order to mitigate these impacts, protected areas must consider, and implement, context appropriate restrictions to the spatio-temporal extent and types of human activities within their borders (Rogala *et al.* 2011; Ladle *et al.* 2018). Given the competing needs and rapidly changing circumstances facing national parks,

collaborative conservation schemes with private land owners and indigenous communities may prove increasingly valuable accompaniments to protected area networks (Rissman *et al.* 2007; Sarkar & Montoya 2011; Hardy *et al.* 2018). These additional options for the provisioning of protected areas will face similar requirements in mitigating human impacts. Managing a consolidated user group, with presumably less diverse or conflicting demands, may however prove more straightforward than mitigating multiple user interests in national parks. We recommend that national parks utilise and replicate studies such as those within this thesis to help guide their decisions on opening times, visitor intensity, spatial access, and activity types.

"First, tell yourself what you want to be, then act your part accordingly."

Epictetus

Appendices

Chapter 2: supplementary resources

A. **Fear foraging & olfaction, online resource 1:**

Table. A. Chapter Two, Methodological considerations proposed for the application of the giving-up density framework in field research and how the methodologies created in this paper accounted for these considerations.

Considerations	Author(s)	This study
Patches aren't natural.		Natural substrate (soil), patches were used by foxes during the 2014 pilot study.
Inappropriate food resources offered.	Brown (1988)	Food was consumed by foxes during the 2014 pilot study.
Foragers may become satiated.		Sargeant (1978) found captive kept adult daily food consumption ranging from 266 – 541g per day. Wild foxes presumably consume more food and each site contained 480g per day. All food was consumed from a site during the 2014 pilot study; the volume of food unlikely satiates as foxes continued to visit before patches were replenished (PMH *unpubl. data*).
Visits by more than one forager.		Camera identification of last visiting species but individual identification by pelage not possible.
Curvilinearity between harvest rate & energy/ diminishing returns.	Bedoya-Perez et al. (2013)	Depletable food in a suitable volume of inedible matrix (pilot study). Patches were only harvested to empty on 11 occasions from 195 GUDs suggesting diminishing returns were experienced.
Energetic state of forager.		Signs of mange or parasite grooming behaviours were not observed from videos. Data collected on multiple occasions. Single national park. No hunting sites or human food subsidies in study area.
Effects of group foraging.		Almost entirely solitary foraging, 2 foxes were only observed on 3 out of 790 videos and even when observed together only the behaviour of one fox at a time was identifiable, i.e. one fox departed from or was only part in camera shot as the other arrived.
Food quality & substrate properties.		Target species utilised both during the pilot study.
Predictability of patch.		Duration was limited to avoid the magic pudding effect. Conservative use of wolf urine as the second treatment. We deemed that there was less expectation of a response to wolf urine given its application later in the test procedure when foxes would be more familiar and reliant upon food patches.
Behavioural traits.		Analysis of behavioural/ temporal strategies from video observations.
Non-target species.		Camera identification of last visiting species.

B. Fear foraging & olfaction, online resource 2:

Table. B. Chapter Two, Ethogram describing behaviours recorded (Bold font). Other behaviours that might accompany or be performed alongside those recorded are described in plain text.

Category	Behaviour	Description / indicator	May include or be accompanied by
Environmental assessment	**Major Vigilance**	**The eyes are directed anywhere but the bucket or ground. The top of the head is above the shoulders. The neck is held above the horizontal plane.**	**Tilting of the head to one side. Focused/pricked ears. Mastication (rarely). Locomotion (rarely).**
	Minor Vigilance	**The eyes are directed anywhere but the bucket or ground. The top of the head is level with the shoulders. The neck is horizontal.**	**Tilting of the head to one side. Focused/pricked ears. Mastication. Locomotion.**
	Focused/ pricked ears	The ears/pinnae are upright with the inner surface area of the pinnae focused forwards.	
	Sniffing the Ground	**The nose is outside of the bucket and lowered 45° or more below the horizontal plane. The neck is angled below the horizontal plane and the eyes are directed at the floor. Not masticating. Nose is ≤15cm (half bucket width) from the ground.**	**Side to side or up down movements of the head. Locomotion.**
Foraging	**Foraging from the bucket**	**The muzzle may be inside the perimeter of the bucket or within a buckets width (30cm) of its edge. The neck is angled below the horizontal plane with the eyes directed towards the bucket. The fox may be digging with front paws close to (within 30cm) or within the bucket. It may alternatively be biting the bucket, moving its head around inside the bucket or removing a food item with its jaws.**	**Mastication (rarely), standing.**
	Mastication	Repeated upwards and downwards movement of the lower jaw.	Up down movements of the head.

C. Camera traps & giving-up densities

The following excerpt, written by Haswell[1] and Caravaggi[2], was first published in press, June 2017:

Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M.V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J. & Wood, M.D. (2017) A review of camera trapping for conservation behaviour research. *Remote Sens Ecol Conserv,* **3,** 109-122.

The giving-up density (GUD; i.e. the amount of food left behind from a known starting quantity; Brown 1988) is one such behavioural indicator that has been used to study predation risk (Orrock, Danielson & Brinkerhoff 2004; Severud *et al.* 2011), energetic costs (Nolet, Fuld & van Rijswijk 2006), forager state and forage quality (Hayward, Ortmann & Kowalczyk 2015), plant toxins (Emerson & Brown 2015), competition (Brown, Kotler & Mitchell 1997) and predator-prey dynamics (Andruskiw *et al.* 2008). It is also central to describing the "landscape of fear" (i.e. relative levels of predation risk within an area of use) of an animal and its habitat preferences, which are direct behavioural indicators with significant conservation implications (Kotler, Morris & Brown 2016). Camera traps offer a relatively reliable way of using the GUD technique to ask more in-depth questions of conservation relevance. For example, cameras have been used to calculate GUDs for multiple species (Lerman *et al.* 2012), examine personality (Mella *et al.* 2015), and differentiate individual versus group foraging habits (Carthey & Banks 2015). These observations can then be used to inform the development of hypotheses relating to the broader effects of local food and predator abundance, predation pressure and inter- and intra-specific competition. With advancements in camera trap technology and creative experimental design, a wealth of conservation-focussed GUD applications are now possible.

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Chapter 3: supplementary resources

D. Spatial interactions: statistical approach

An information theoretic approach permitted comparison of competing biological hypotheses, identification of key mechanisms and useful approximations of reality (Richards, Whittingham & Stephens 2011). By using AIC values, we acknowledge that reality is infinitely complex and the true model explaining the ecological phenomena in its entirety is not present within our candidate set (Wagenmakers & Farrell 2004). Ecological management and biological theory require focused inferences but must also maintain awareness of competing possibilities. We presented model ranking tables for all plausible models with ΔAICc < 10 (Richards, Whittingham & Stephens 2011; Symonds & Moussalli 2011). Akaike weight provides a useful tool for inferring relative support of conclusions but was not discussed because model structures and variable contribution to candidate sets was unbalanced. Model averaging is sometimes recommended for parameter estimation but there is methodological uncertainty and debateable utility (Richards 2005; Richards, Whittingham & Stephens 2011; Dormann *et al.* 2018). Estimation of model weights brings additional uncertainty to model averaging and much is unresolved (Claeskens *et al.* 2016; Dormann *et al.* 2018). Our interest was in parameter estimates from distinct mechanistic processes, so visualisations and estimates were presented from the most supported models.

E. Spatial interactions: single-species models

Human & large carnivore detection probability covariates

A single-season occupancy model was used to examine the influence of combinations of the variables season, elevation and forested area upon the probability that humans were present and detected. Occupancy was held constant. Values from the top human detection model (containing season, elevation and forested area) were then used as a variable for human detection probability in single-season detection models for large carnivores and foxes.

A single-season detection model for wolves was conducted with the aforementioned environmental variables plus the variable human detection probability. Estimates for probability of wolves being present and detected from the top model (season and forested area) were then used as a variable in single-season detection models for lynx and foxes.

A single-season detection model for lynx was conducted with the same variables as the wolf model plus the addition of the variable wolf detection probability. Estimates for probability of lynx being present and detected from the top model (elevation and forested area) were then used as a variable in single-season detection models for fox.

Single-species detection probability: full model ranking tables & top model estimates

Notes: Where no covariates are denoted in parenthesis, occupancy (ψ) or detection probability (p) were constant. The covariate S denotes that p varies between seasonal periods of the year, W denotes the influence of the probability that wolves were present and detected, L, the probability that lynx were present and detected, H, the probability that humans were present and detected, E, elevation, F, forested area within a 1.43km^2 circle around the camera. ΔAICc is the difference in AICc relative to the best model, *K* is the number of parameters, *w* is the AICc weight, indicating the relative support for each model and *-2logL* is the -2 log likelihood. For wolf and lynx models where AICc was converted to QAICc a value of one was added to K to account for the estimation of the overdispersion parameter ĉ.

Table. E.1. Single-species detection models. Humans

Model	ΔAICc	K	w	-2logL
ψ, p (S+E+F)*	0	6	1.000	6792.51
ψ, p (E+F)	243.75	4	0.000	7040.79
ψ, p (S+F)	362.24	5	0.000	7157.04
ψ, p (S+E)	481.38	5	0.000	7276.18
ψ, p (F)	611.14	3	0.000	7410.37
ψ, p (E)	708.8	3	0.000	7508.03
ψ, p (S)	794.98	4	0.000	7592.02
ψ, p	995.02	2	0.000	7796.39

*ĉ = 0.98

Table. E.2. Single-species detection models. Wolf

Model	ΔQAICc	K	w	-2logL
ψ, p (S+F)	0.00	6	0.295	782.96
ψ, p (S)	0.23	5	0.263	789.47
ψ, p (S+E+F)*	2.31	7	0.093	782.86
ψ, p (S+E)	2.38	6	0.090	789.10
ψ, p (S+H)	2.49	6	0.085	789.38
ψ, p (H)	2.98	4	0.067	802.33
ψ, p (E)	3.34	4	0.056	803.25
ψ, p (E+F)	3.47	5	0.052	797.83
ψ, p (F)	13.75	4	0.000	830.12
ψ, p	16.92	3	0.000	843.93

*ĉ = 2.58

Table. E.3. Single-species detection models. Lynx

Model	ΔQAICc	K	w	-2logL
ψ, p (E+F)	0.00	5	0.682	1276.90
ψ, p (S+E+F)	2.37	7	0.209	1274.01
ψ, p (S+E+W)	4.32	7	0.079	1276.48
ψ, p (E+W)	6.89	5	0.022	1285.64
ψ, p (E)	9.99	4	0.005	1292.42
ψ, p (S+H+W)*	11.02	7	0.003	1284.99
ψ, p (S+E)	11.82	6	0.002	1288.99
ψ, p (S+F)	30.16	6	0.000	1312.26
ψ, p (S+W)	30.78	6	0.000	1313.05
ψ, p (S+H)	33.13	6	0.000	1316.03
ψ, p (H)	35.04	4	0.000	1324.22
ψ, p (H+W)	36.17	5	0.000	1322.81
ψ, p (W)	37.94	4	0.000	1327.90
ψ, p	40.20	3	0.000	1333.54
ψ, p (S)	41.22	5	0.000	1329.21
ψ, p (F)	62.04	4	0.000	1358.49

*ĉ = 1.27

Table. E.4. Single-species detection models. Fox

Model	ΔAICc	*K*	*w*	*-2logL*
ψ, *p* (S+H+L)	0.00	6	0.538	5231.02
ψ, *p* (S+E+F)	0.76	6	0.368	5231.78
ψ, *p* (S+L)	3.66	5	0.086	5236.97
ψ, *p* (S+E+W)	8.83	6	0.007	5239.85
ψ, *p* (S+H+W)*	12.38	6	0.001	5243.40
ψ, *p* (S+E)	13.17	5	0.001	5246.48
ψ, *p* (S+F)	31.30	5	0.000	5264.61
ψ, *p* (S+H)	39.99	5	0.000	5273.30
ψ, *p* (S+W)	41.45	5	0.000	5274.76
ψ, *p* (S)	48.34	4	0.000	5283.89
ψ, *p* (E+W)	93.10	4	0.000	5328.65
ψ, *p* (E+F)	113.78	4	0.000	5349.33
ψ, *p* (H+L)	115.06	4	0.000	5350.61
ψ, *p* (L)	120.39	3	0.000	5358.13
ψ, *p* (E)	129.40	3	0.000	5367.14
ψ, *p* (W)	131.65	3	0.000	5369.39
ψ, *p* (H+W)	133.23	4	0.000	5368.78
ψ, *p* (F)	142.28	3	0.000	5380.02
ψ, *p* (H)	162.46	3	0.000	5400.20
ψ, *p*	211.60	2	0.000	5451.48

*ĉ = 0.80

Table. E.5. Probability of detecting each species from their top single-species models

Season	Camera site	Fox *p*	SE	Human *p*	SE	Lynx *p*	SE	Wolf *p*	SE
	2	0.070	0.006	0.241	0.011	0.022	0.004	0.030	0.008
	3	0.068	0.005	0.261	0.012	0.019	0.004	0.030	0.008
	10	0.065	0.006	0.008	0.002	0.000	0.000	0.002	0.004
	11	0.068	0.006	0.113	0.007	0.011	0.004	0.019	0.007
	14	0.098	0.008	0.135	0.008	0.050	0.005	0.030	0.008
	15	0.092	0.007	0.149	0.009	0.044	0.004	0.030	0.008
	16	0.077	0.006	0.062	0.005	0.021	0.007	0.018	0.007
	17	0.115	0.010	0.109	0.008	0.066	0.008	0.030	0.008
	20	0.065	0.006	0.069	0.006	0.004	0.002	0.012	0.007
	23	0.078	0.006	0.196	0.010	0.030	0.004	0.030	0.008
Dispersal	25	0.066	0.006	0.064	0.006	0.005	0.003	0.012	0.007
	26	0.051	0.006	0.517	0.023	0.005	0.002	0.030	0.008
	30	0.081	0.006	0.182	0.010	0.033	0.004	0.030	0.008
	33	0.064	0.005	0.132	0.008	0.006	0.003	0.017	0.007
	34	0.066	0.005	0.278	0.013	0.017	0.004	0.030	0.008
	35	0.084	0.006	0.174	0.009	0.036	0.004	0.030	0.008
	36	0.134	0.013	0.092	0.007	0.082	0.011	0.030	0.008
	37	0.059	0.006	0.372	0.017	0.011	0.003	0.030	0.008
	38	0.083	0.006	0.177	0.010	0.035	0.004	0.030	0.008
	40	0.067	0.006	0.052	0.005	0.005	0.003	0.012	0.007

Season	Camera site	Fox p	SE	Human p	SE	Lynx p	SE	Wolf p	SE
	2	0.150	0.008	0.352	0.012	0.022	0.004	0.020	0.007
	3	0.144	0.008	0.377	0.013	0.019	0.004	0.020	0.007
	10	0.148	0.012	0.014	0.003	0.000	0.000	0.001	0.002
	11	0.149	0.008	0.180	0.009	0.011	0.004	0.013	0.005
	14	0.205	0.011	0.210	0.010	0.050	0.005	0.020	0.007
	15	0.193	0.009	0.231	0.010	0.044	0.004	0.020	0.007
	16	0.169	0.010	0.101	0.007	0.021	0.007	0.012	0.005
	17	0.237	0.015	0.174	0.010	0.066	0.008	0.020	0.007
	20	0.145	0.010	0.113	0.009	0.004	0.002	0.008	0.005
Denning	23	0.165	0.008	0.294	0.011	0.030	0.004	0.020	0.007
	25	0.147	0.010	0.105	0.008	0.005	0.003	0.008	0.005
	26	0.109	0.012	0.647	0.021	0.005	0.002	0.020	0.007
	30	0.172	0.008	0.275	0.011	0.033	0.004	0.020	0.007
	33	0.140	0.008	0.207	0.011	0.006	0.003	0.012	0.005
	34	0.140	0.008	0.397	0.013	0.017	0.004	0.020	0.007
	35	0.177	0.008	0.265	0.011	0.036	0.004	0.020	0.007
	36	0.272	0.020	0.148	0.010	0.082	0.011	0.020	0.007
	37	0.125	0.010	0.504	0.017	0.011	0.003	0.020	0.007
	38	0.175	0.008	0.269	0.011	0.035	0.004	0.020	0.007
	40	0.148	0.010	0.086	0.007	0.005	0.003	0.008	0.005
Season	Camera site	Fox p	SE	Human p	SE	Lynx p	SE	Wolf p	SE
	2	0.162	0.009	0.505	0.013	0.022	0.004	0.004	0.003
	3	0.156	0.009	0.532	0.013	0.019	0.004	0.004	0.003
	10	0.172	0.017	0.026	0.006	0.000	0.000	0.000	0.000
	11	0.165	0.009	0.292	0.011	0.011	0.004	0.002	0.002
	14	0.224	0.012	0.333	0.012	0.050	0.005	0.004	0.003
	15	0.211	0.010	0.360	0.012	0.044	0.004	0.004	0.003
	16	0.191	0.012	0.174	0.009	0.021	0.007	0.002	0.002
	17	0.260	0.016	0.283	0.013	0.066	0.008	0.004	0.003
	20	0.163	0.012	0.193	0.013	0.004	0.002	0.002	0.001
Weaning	23	0.180	0.009	0.439	0.012	0.030	0.004	0.004	0.003
	25	0.166	0.012	0.180	0.011	0.005	0.003	0.002	0.001
	26	0.121	0.013	0.775	0.016	0.005	0.002	0.004	0.003
	30	0.187	0.009	0.417	0.012	0.033	0.004	0.004	0.003
	33	0.155	0.009	0.328	0.013	0.006	0.003	0.002	0.002
	34	0.151	0.010	0.553	0.013	0.017	0.004	0.004	0.003
	35	0.193	0.009	0.403	0.012	0.036	0.004	0.004	0.003
	36	0.299	0.022	0.245	0.013	0.082	0.011	0.004	0.003
	37	0.136	0.011	0.656	0.015	0.011	0.003	0.004	0.003
	38	0.190	0.009	0.409	0.012	0.035	0.004	0.004	0.003
	40	0.169	0.013	0.149	0.011	0.005	0.003	0.001	0.001

Note: For wolf and lynx estimates the original standard error estimates were multiplied by the square route of the corresponding ĉ value.

Supplementary manuscript: Foraging theory & livestock predation

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F. Foraging theory provides a useful framework for livestock predation management

Abstract

A societal shift toward plant dominant diets and a reduction in livestock rearing could have broad social, environmental and conservation benefits. Livestock husbandry, however, has a wealthy cultural history, strong support and high consumer demand. It is therefore likely to continue as a major land use and conservation issue for predators. From a producer's perspective, the primary goals of livestock protection are maximising, or at least maintaining, production by minimising losses and mitigating detriment to stock welfare. Lethal removal of predators remains a commonplace solution. Such management measures are questionable as they raise animal welfare and conservation concerns, risk inhibiting ecological processes, are often expensive, and in some circumstances, exacerbate livestock predation problems. Non-lethal alternatives can facilitate co-existence between livestock farmers and predators, ideally reducing the ecological impact of pastoralism and achieving conservation goals. The need for rigorous study of non-lethal approaches has however been recently highlighted. Tools and methods involved in livestock protection, as well as the theoretical basis of how we perceive and manage the problem, require deeper consideration. Non-lethal approaches require knowledgeable implementation and an effective decision making system is a prerequisite for successful practice. Livestock predation and its prevention are fundamentally influenced by the underlying principles of foraging ecology and risk theory. We propose that manipulating elements of Brown's (1988) quitting harvest rate model provides a useful conceptual framework for reducing livestock predation and encouraging coexistence.

Introduction

While perhaps politically and industrially unfavourable, there is justifiable discourse and concern regarding the social and environmental footprint of the livestock industry (Westhoek *et al.* 2014; Hallström, Carlsson-Kanyama & Börjesson 2015). Public concern with livestock welfare presents a longstanding contention (Deemer & Lobao 2011). Resource efficiency and issues relating to health and nutrition present direct concerns for effectively meeting nutritional needs of a growing human population through livestock products (Baroni *et al.* 2007; Westhoek *et al.* 2014; WWF 2016). Disease transmission and antibiotic resistance pose

additional health concerns for humans, livestock and wildlife (Thompson 2013; Gottdenker *et al.* 2014; Hudson *et al.* 2017). Pastoralism's freshwater consumption and land use are also intensive, with habitat modification, ecological degradation, emissions, effluent and contribution to climate change all providing grave concerns (Baroni *et al.* 2007; Westhoek *et al.* 2014; Hallström, Carlsson-Kanyama & Börjesson 2015). Alongside indirect implications for wildlife conservation, livestock directly compete with and have replaced much wild biodiversity (Bar-On, Phillips & Milo 2018).

Some champion the potential conservation benefits of well managed livestock but often neglect to place such benefits in context, failing to draw comparisons with unmodified systems (Franzluebbers *et al.* 2012). The overall benefits for wildlife conservation are however contentious; livestock grazing, for example, can adversely affect species conservation, ecosystem structure, function and composition (Reading & Jofre 2015; Eldridge *et al.* 2016; Sharps *et al.* 2016). Livestock biomass now far exceeds that of wild mammals and competition for forage can negatively impact both wild herbivores and their predators (Latham 1999; Bar-On, Phillips & Milo 2018).

Native predators can be completely excluded from pastoral landscapes or exterminated altogether, e.g. large carnivores in the British Isles (Brown, McMorran & Price 2011). Cultural and social bias against predators may often exist in rural areas, regardless of personal experience with livestock predation (Chavez, Gese & Krannich 2005). Actual impacts can be small relative to other factors including disease, birthing problems, weather and accidents (Breck & Meier 2004; Dar *et al.* 2009). A small proportion of producers in predation hotspots may, however, absorb the majority of losses, increased husbandry costs and decreased animal performance (Breck & Meier 2004; Shelton 2004). Damage to livelihoods can reduce support for conservation initiatives (Anthony 2007; Anthony, Scott & Antypas 2010). Livestock predation often results in disproportionate deaths of the animals deemed responsible and persecution of predators is common (Meriggi & Lovari 1996; Shivik 2006; Eggermann *et al.* 2011). Lethal control of predators to pre-empt or in response to livestock predation has become common management in many contexts (Macdonald & Baker 2004; Treves *et al.* 2006).

The simplest way to resolve many of these problems would be to substantially reduce livestock production and move to plant dominant diets on a societal level (Eshel *et al.* 2014; Poore & Nemecek 2018). Changing consumer habits should not be overlooked as a potential

nature conservation tool. Suitable damage related taxation may offer some assistance to this end (Springmann *et al.* 2017). Discouraging unnecessary consumption and encouraging financial divestment by consumers offers an additional route to achieving sustainability (Ripple *et al.* 2017). Such a large-scale transition may, however, prove difficult where habitat, technology, international trade, culture, affluence or knowledge makes livestock products one of few viable food production methods or an easily accessible dietary option. Livestock farming also has a long and enduring cultural significance (McClure 2015; Holmes 2016; Pitikoe 2017). High levels of meat, egg and dairy consumption are prevalent in many societies and a global shift away from this is currently unlikely, with human populations and demand for animal products increasing globally (Kearney 2010; Westhoek *et al.* 2014). Livestock production is likely to continue as a major land use and livestock predation remains an issue for both pastoralists and conservationists.

The ecological impacts, efficiency and morality of lethal control are questionable (Treves, Krofel & McManus 2016). Lethal control of predators and decline in their numbers can result in loss of ecological services and stability (Wallach *et al.* 2010; Ripple *et al.* 2014). Lethal control may not always be economically viable if loss of regulatory services by predators results in high costs where wild herbivores compete for forage with domestic stock (Wicks & Allen 2012). Lethal control can also disrupt social structure, exacerbating livestock predation problems (Wallach *et al.* 2009), or lead to compensatory reproduction, thereby minimising the effect of control (Minnie, Gaylard & Kerley 2016; 2017). A range of non-lethal alternatives exist that can assist mitigation of livestock predation problems and encourage coexistence (Shivik 2006; Stone *et al.* 2017). Societal preference for coexistence has led to greater adoption of such approaches (Chapron *et al.* 2014). Non-lethal livestock predation management can, although may not always, be equally or more effective than lethal control of predators (McManus *et al.* 2015; Stone *et al.* 2017; van Eeden *et al.* 2018a). Some non-lethal tools have been well tested but further robust experimentation is required to assess efficacy, encourage producer adoption and guarantee return on investments (Eklund *et al.* 2017; Scasta, Stam & Windh 2017; van Eeden *et al.* 2018b).

We refer readers to van Eeden et al. (2018b) for a useful synthesis of the current evidence base but recognise that in practice, one approach is rarely used in isolation of others, effectiveness will be context dependent and action is still required while the necessary testing of tools is conducted. Practitioners require a holistic and adaptive management system to more easily and effectively implement non-lethal programmes across a broad range of

contexts. Applying existing scientific theory to real world issues should prove productive for both study and practice. The predation and protection of livestock are fundamentally influenced by the principles of both foraging and risk theory. We propose that Brown's (1988) quitting harvest rate model provides a useful theoretical framework for managing livestock predation and achieving conservation goals.

Brown's (1988) quitting harvest rate model as a management framework

Foraging theory suggests animals attempt to make the best of foraging scenarios by trading-off costs against benefits (Emlen 1966; MacArthur & Pianka 1966; Charnov 1976). Decisions to prey upon livestock instead of wild prey may be based in energetics (Polisar *et al.* 2003), but there is little evidence of predators preferentially hunting livestock where it has been tested (Lyngdoh *et al.* 2014; Hayward *et al.* 2017). Brown's (1988) quitting harvest rate model provides a useful framework with which to examine the mitigation of livestock harvest by predators. Where food patches are depletable, animals should abandon patches once gains (H) become equal to or fall below costs (Brown 1988; Brown & Kotler 2007). The concept is described in the equation $H = C + P + MOC$, where H = harvest rate (food gain per unit time), C = energetic costs (to obtain food), P = predation costs (cost/likelihood of losing fitness by interacting with predators) and MOC = missed opportunity costs (food or fitness enhancing benefits available elsewhere) (Brown 1988; Brown & Kotler 2007). Like Berger-Tal et al. (2009), we also included risk of injury (RI) or mortality (e.g. from objects like electric fencing, terrain ruggedness, the stock themselves, or a device worn by stock) as an additional cost that may be incurred during livestock predation but discuss it alongside P for ease of discussion and implementation.

From a producer's perspective, the primary goals of livestock protection are maximising, or at least maintaining, production by minimising losses and mitigating detriment to stock welfare. Practitioners and wildlife managers should aim to manipulate predator foraging behaviour to reduce livestock predation; intentionally causing predators to quit livestock patches more quickly and harvest less, or ideally, no stock (Table. F). Ideally, livestock could be made so unprofitable comparable to wild prey that they become less preferable and are rarely preyed upon. Here we highlight considerations that may offer some utility but should be contemplated only in relation to individual context by giving thought to all model components.

Table. F. Management options for reducing livestock predation utilising Brown's (1988) quitting harvest rate model, H = C + P + MOC. H = harvest rate, food available per unit time, C = energetic costs, P = predation costs, MOC = missed opportunity costs, alternative fitness enhancing activities e.g. foraging elsewhere, we also add RI = risk of injury. Predators should give up foraging from patches of livestock when the available gains (H) are equal to or less than the costs (C + P + RI + MOC). Managers can manipulate and alter components of the model in order to manipulate predator behaviour, reducing livestock harvest or preventing it beginning in the first place.

Livestock predation management

Decrease H
Reduce herd size, remove carcasses, remove anthropogenic food sources, any intervention which increases time taken for predation

Increase MOC	Increase P or RI	Increase C
Ensure wild prey stocks - Ensure suitable habitat and access to forage - Decrease wild herbivore harvest - Keep wild prey and livestock separate - Deter wild prey from pastoral areas **Monitor seasonal fluctuations in wild prey** - Increase P, RI or C if wild prey stocks decline, become less accessible to predators or if predator food needs increase e.g. when predator young are weaned	**Guardians** - Use when possible. Humans, dogs or other animals e.g. donkeys - Use stock with natural defences - Ensure appropriate numbers and behaviour - Increase use when needed e.g. during mobile grazing **Scare devices / risk cues e.g. air horn** - Avoid predator habituation - Use sporadically and when most needed - Ensure stock are not startled by devices and are habituated **Aversive conditioning e.g. taste aversion collars worn by stock** - Ensure reinforcement	**Fencing** - Use corrals when vulnerable e.g. at night or during lambing - Consider solid stationary or electric mobile corrals as well as positioning - Apply additional deterrents (P or RI) when needed e.g. fladry **Livestock attributes** - Use more agile & less docile livestock - Use stock with natural defences e.g. armament or behaviour - Breed for attributes - Herding regime, dispersed or herded **Guardian patrols** - Increase when needed e.g. when predator young are weaned

Additional considerations

Terrain
- Avoid known hotspots or landscape contexts where livestock predation is more likely
- If unavoidable increase P, RI or C

Predator monitoring
- Avoid areas well visited by predators e.g. known breeding sites
- Increase P, RI or C when predators are in the vicinity

Harvest rate (H)

Initial harvest rate (H) of livestock patches could be reduced to increase how quickly predators give up on livestock patches. Predators can be attracted to anthropogenic food subsidies, adapting their behaviour to utilise them (Ciucci *et al.* 1997; Newsome *et al.* 2014; Morehouse & Boyce 2017). Refuse sites in pastoral areas are likely to attract predators and lead to increased conflict (Wilson *et al.* 2006; Kolowski & Holekamp 2008). Removal of carcasses, livestock pits or waste dumps in the vicinity of livestock would provide sensible starting points to reducing patch attractiveness. Herd size (i.e. food availability) may also provide an attractant. Farms with larger herds may be more likely to experience livestock predation (Treves *et al.* 2004; Bradley & Pletscher 2005; Pimenta *et al.* 2017). Herd size could potentially be reduced, although there is likely an economic disincentive to do so (Pimenta *et al.* 2017).

Missed opportunity costs (MOC)

Costs to predators of foraging in livestock patches can also be increased. Raising or ensuring high missed opportunity costs (MOC) relative to livestock patches should accelerate giving up on livestock. Often overlooked as a mitigation measure, ensuring viable wild prey populations (e.g. via harvest regulations, habitat restoration, reinforcement or reintroduction) is pivotal in sustaining large carnivore populations and minimising livestock predation (Meriggi & Lovari 1996; Polisar *et al.* 2003; Barja 2009b). Predators will increasingly target livestock, which increase in relative value, as wild prey decline (Kolowski & Holekamp 2006). Low energy state foragers also tend to take higher risks (Brown 1988; Brown, Morgan & Dow 1992). Ensuring higher predator energy states by maintaining suitable wild prey stocks could reduce the marginal value of livestock as a food source.

Livestock production and the maintenance of wild prey stocks are however most likely best kept somewhat apart. Abundant wild prey in pastoral areas could cause increased livestock predation (Stahl *et al.* 2001; Bradley & Pletscher 2005; Amirkhiz *et al.* 2018). Carnivores are attracted to high quality habitat and conflicts may be more likely to occur where human activities, including livestock farming, overlap (Wilson *et al.* 2006; Odden *et al.* 2008). Livestock could be kept away from preferable wildlife habitat or better protected where this is not feasible. Habitat improvement and suitable limitation to wild herbivore harvest could also be employed in areas set aside from pastoralism. Excepting large land owners, this will require regional level intervention. Livestock producers can however make their properties

less attractive to wild herbivores, e.g. protecting hay supplies, using livestock guardian dogs, *Canis lupus familiaris*, or hazing habituated wildlife (Bradley & Pletscher 2005; Kloppers, St. Clair & Hurd 2005; Gehring *et al.* 2010).

Seasonal declines in wild prey availability (MOC) driven by environmental conditions, seasonal migrations and prey habitat use, especially if coinciding with increased stock availability can lead to prey switching and increased livestock predation (Cavalcanti & Gese 2010; Valeix *et al.* 2012). In a similar fashion the relative value of livestock may increase following seasonal predator food demand and decreases in wild prey vulnerability due to maturing young (Ciucci & Boitani 1998). Practitioners should accordingly increase other costs (C, P or RI) and avoid increasing potential attractants (e.g. young livestock) during these more vulnerable periods.

Energetic cost (C)

The energetic cost (C) of preying on livestock could be increased, especially during periods of vulnerability. Fencing can provide an energetically costly barrier for carnivores to overcome. Fencing, albeit a barrier to wildlife movements, likely reduces losses; however its general efficacy will depend on the problem carnivore's abilities, fence maintenance and the presence of other fence damaging wildlife (Breitenmoser *et al.* 2005; McManus *et al.* 2015). Keeping livestock in predator proof corrals at night can efficiently minimise losses, although crowding can necessitate additional health care, and poor maintenance risks severe losses (Breitenmoser *et al.* 2005; Schiess-Meier *et al.* 2007; Weise *et al.* 2018). Corrals and fencing can also be made more disruptive through the addition of perceived or real injury related risk via fladry (Fig. F.1) and/or electric current (Musiani *et al.* 2003; Lance *et al.* 2011).

Livestock attributes could also affect the energetic costs of predation. Young, sick and injured animals may incur minimal energetic costs to hunt and can thus be more vulnerable to predation (Chavez & Giese 2006; Cavalcanti & Gese 2010). Producers should monitor and be mindful of herd vulnerability relative to alternative wild prey sources, targeting additional interventions accordingly. Vulnerable livestock, such as sheep, *Ovis aries*, can also be bonded to or housed with herd animals possessing better defensive capabilities (greater aggression, size, strength, armament). For example, llama's, *Lama glama*, long-horned cattle, *Bos taurus*, or donkeys, *Equus africanus*, can provide protective services by increasing injury related risk (RI) and the energetic costs (C) of accessing livestock (Smith *et al.* 2000b). Stock breed could perhaps be altered by selecting more agile or defensive breeds, which retain anti-

predator behaviour. Anti-predator defence could also be encouraged within current stocks, for example, some producers attribute fewer wolf, *Canis lupus*, related livestock losses to keeping protective mother cows and encouraging defensive herding behaviour, instead of removing protective mothers and allowing herds to fragment across remote areas (H.Z. Anderson, Tom Miner Basin Project, *Pers comm*).

Predation risk (P) and risk of injury (RI)

There is good evidence to suggest that animals assess and respond to risk (Lima & Dill 1990; Creel & Christianson 2008; Heithaus *et al.* 2009). Fear ecology suggests such interactions may affect landscape use and foraging (Brown, Laundré & Gurung 1999; Brown & Kotler 2007; Laundré, Hernández & Ripple 2010). The mesopredator release hypothesis suggests predators too have things to fear (Crooks & Soulé 1999; Ritchie & Johnson 2009; Newsome *et al.* 2017b). Humans are a key factor that alters the context within which predators exist (Haswell, Kusak & Hayward 2017). Humans may be viewed as super predators whose presence provides substantial risk to carnivores, consequently modifying predatory behaviour (Smith *et al.* 2017).

Increase in perceived or actual predation costs (P), as well as risk of injury (RI) from other causes, have received most attention in the development of non-lethal mitigation strategy (See Breitenmoser et al. (2005) and Shivik (2006) for comprehensive reviews). Wild animals, especially predators, can be particularly sensitive to new stimuli; scare devices using disruptive mechanisms such as neophobia, irritation or pain have consequently been utilised as primary repellents (Shivik, Treves & Callahan 2003; Shivik 2006). Secondary repellents establish a link between a behaviour and a negative outcome through aversive conditioning, e.g. electronic training collars worn by predators or taste aversion collars worn by livestock (Shivik, Treves & Callahan 2003; Shivik 2006). Excessive use of primary repellents risks habituation whereas secondary repellents can require substantial logistical effort and may need to be regularly reinforced to remain effective (Smith *et al.* 2000a; Shivik 2006). Harassment (e.g. rubber bullets) may offer simple implementation but linking aversion and behaviour might prove difficult and thereby limit effectiveness; consistent secondary repellents such as electrified fladry may however prove more efficacious in both application and reinforcement (Shivik 2006). Use of primary and secondary repellents will depend on local laws, additional conservation concerns, and the ethical views of the practitioner.

Manipulating risk perception could still prove useful alongside the provision of direct threats. Visual assessment of habitat and its interaction with escape strategies provides one means by which animals may assess and respond to risk (Wirsing, Cameron & Heithaus 2010; Kuijper *et al.* 2013; Camacho 2014). Landscape characteristics, such as vegetative cover or woodlands adjacent to pastures, can be associated with higher levels of livestock predation (Ciucci & Boitani 1998; Stahl *et al.* 2001). Mapping risk hotspots could provide an effective decision making tool (Treves *et al.* 2004).

Animals also assess risk through auditory means (Berger, Swenson & Persson 2001; Lynch *et al.* 2015). Many technological scare devices work through visual or auditory disruptive stimuli, e.g. flashing lights, high beam lights, air horns, propane cannons, and sometimes through a combination, e.g. radio activated guard (RAG) boxes. Repellents such as flashing lights can significantly reduce predation but may not be effective against all carnivores (Ohrens, Bonacic & Treves 2019). Practitioner strategy will need to be context specific as well as adaptive. For example, when nocturnally flashing lights were applied to livestock bomas (protective night pens) in Kenya, Lions, *Panthera leo*, switched to attacking bomas where intervention was not implemented, and subsequently, when installation of lights increased, shifted to diurnal attacks (Lesilau *et al.* 2018).

The scent of dominant predators can communicate increased risk to carnivores (Leo, Reading & Letnic 2015; Haswell *et al.* 2018). Manipulation of scent could be useful in manipulating predator landscape use but may not always yield intended outcomes due to the context in which scent is encountered (Jones *et al.* 2016). Placement of scent manipulations could ideally be optimised if context relations are understood, i.e. what scent to place, when, where and how much. Identifying effective components of olfactory communication such as producer diet or social status and their associated compounds could also improve effectiveness (Parsons *et al.* 2018).

Direct presence of predation and injury risk are likely to elicit stronger responses than cues such as olfaction alone (Scheinin *et al.* 2006; Vanak, Thaker & Gompper 2009). Livestock guardian animals may provide multiple benefits through olfactory and auditory risk cue provision as well as direct presence (van Bommel & Johnson 2012; McManus *et al.* 2015). Livestock guardian dogs (Fig. F.2) can increase predation risk (P) and intimidate predators by protecting stock directly or creating landscapes of fear when used in a patrolling manor (Rigg 2001; Hansen, Staaland & Ringso 2002; Rigg *et al.* 2011). Guardian dogs may protect

livestock without entirely excluding predators from foraging nearby (Allen *et al.* 2017c). In some circumstances, the use of dogs may be spatially or seasonally problematic depending on wildlife sensitive periods, farming practices and other landscape users e.g. hikers or hunters. Livestock guardian dogs show good potential in mitigating pastoral wildlife conflict but the most effective methods for their use requires further investigation (Gehring, VerCauteren & Landry 2010; Gehring *et al.* 2010; Lescureux & Linnell 2014).

Figure. F.1. Electrified fladry. Sheep in a temporary night time corral made of electrified fladry as part of the wood river wolf project in Blaine County, Idaho.

Figure. F.2. Livestock guardian dogs can be raised with, and kept with stock, or used in a patrolling capacity, with a handler or range rider. Karakachan female pictured, a rare breed being conserved by S. Sedefchev, Bulgarian Biodiversity Preservation Society, Semperviva.

Conclusions

Scientific theory can offer useful frameworks for applied conservation issues. Understanding patterns and processes involved in livestock predation, developing effective ways to mitigate predation and rigorously testing non-lethal deterrents have been identified as areas requiring advancement (Breck & Meier 2004; Purcell *et al.* 2012; Eklund *et al.* 2017). All could be assisted by inclusion of foraging theory and risk ecology frameworks as part of study design and theoretical underpinning for management decision making.

It is important to understand that there is no 'silver bullet' strategy (Treves *et al.* 2006). Interactions between species are context-dependent (Haswell, Kusak & Hayward 2017). Success of non-lethal tools will vary in time and space depending on the structure of the quitting harvest rate model in a given scenario. There will of course also be scenarios where animals don't follow the model or non-lethal tools aren't applied correctly. Habituation to repellent devices can also prove problematic (Musiani *et al.* 2003; Shivik 2006; Lance *et al.* 2011). Adaptive, location and time specific management strategies are likely to prove most effective in ensuring protection techniques do not lose risk value (Stone *et al.* 2017; van Eeden *et al.* 2018a). Understanding changes in model components will also help with timing management interventions, e.g. increase in P in unison with seasonal fluctuations of MOC and predator nutritional needs. Identifying areas where predation likelihood is higher and circumstances tip the equation in favour of harvest will prove additionally useful (Treves *et al.* 2004; Treves & Rabenhorst 2017). Foraging theory can provide a useful framework for studying and managing livestock predation. If components of Brown's (1988) model are understood and can be manipulated through management practices then it should be feasible to tip the equation in favour of coexistence.

Acknowledgements

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