Human-mediated landscapes of fear shape trophic cascades in shared desert ecosystems of the Middle East: elucidating the ecological roles of the Arabian wolf (*Canis lupus arabs*)

by Gavin Bonsen

Thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

under the supervision of Daniel Ramp and Arian Wallach

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Certificate of Original Authorship

I, Gavin Bonsen, declare that this thesis is submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Life Sciences at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

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List of Papers and Statement of Author Contribution

This thesis is a compilation of an introductory chapter and the following four manuscripts currently either published or in preparation for publication. Referencing style throughout this thesis is based on the journal *Biological Conservation*.

Chapter 2. Navigating a geopolitically complex landscape: the Arabian wolf's complicated plight.
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Chapter 4

Abstract

Grey wolf (*Canis lupus*) populations are increasing globally, thanks to a general rise in human acceptance. However, the smallest subspecies, the Arabian wolf (*Canis lupus arabs*), remains endangered across its wide range in the Middle East. Human land-use varies throughout its range, as do attitudes towards wolves, which range from acceptance to complete intolerance. Likely to have played a large part in the increase in acceptance of wolves in other regions is the knowledge of the important ecological roles they play as apex predators. Presence of wolves has been linked to profound, cascading effects, which have been claimed to benefit ecosystems across multiple trophic levels. This has consistently been demonstrated in temperate regions, where ecosystems are productive, but doubt has been cast over whether Arabian wolves play similar roles in the arid to hyper-arid ecosystems they inhabit. In this thesis, I begin by exploring the mechanisms and approaches that have previously gone into global wolf conservation efforts, assisting in their recovery, and then contextualise this within the geopolitical diversity of the Middle East. Realising that relatively little is known about Arabian wolves, from their ecology to their taxonomic status and distribution, I set out to discover whether they have the capacity to influence ecosystems in similar ways to their temperate counterparts. I conducted ecological studies in the deserts of Israel and Jordan to identify the ways in which Arabian wolves shape ecosystem structure and function through their interactions with other species, and how these are mediated by human-wolf relationships. Using non-invasive survey techniques (camera-traps and passive tracking surveys), I found that wolf occupancy and density are largely related to human land-use, where wolves use areas where they are accepted but avoid areas where they are not tolerated. This then has cascading effects through the ecosystem, influencing canid communities, landscapes of fear for mesopredators and prey, and behavioural responses of predators and prey. This thesis unearths the importance of Arabian wolves in desert ecosystems by showing their role in influencing spatial distributions and behaviours of species in lower trophic levels. The last half-century has already witnessed the loss of two other large predators throughout the region, and this functional role would disappear if the Arabian wolf was to follow suit. Through improved conservation efforts and working towards a peaceful co-existence between people and Arabian wolves, this unique and iconic subspecies of wolf can persist, along with its important ecological role.

Chapter 1. General Introduction

Grey wolves (*Canis lupus*) play pivotal roles in ecosystem structure and function by influencing species in lower trophic levels (Ripple and Beschta, 2011). The implications of these roles have become a hot topic of research in recent decades, and knowledge of this has arguably played a prominent role in wolf conservation. After widespread persecution led to large-scale extirpations into the 20th century, populations are now recovering in North America and Europe, largely due to an increase in human acceptance. Consequently, the grey wolf's global status changed from Vulnerable to Least Concern around the turn of this century (Boitani et al., 2018).

However, in other parts of the world, populations are yet to recover, particularly where human-wolf conflict occurs and tolerance of wolves is low, resulting in some grey wolf subspecies remaining imperilled. This is the case for the smallest grey wolf subspecies, the Arabian wolf (*Canis lupus arabs*), which remains endangered (Mallon and Budd, 2011), and its ecological roles are yet to be greatly considered. Adapted to life in Middle Eastern deserts, the Arabian wolf traverses one of the most complicated geopolitical landscapes on Earth; one in which human tolerance of wolves varies from acceptance to complete intolerance. The region recently lost two other large predators to large-scale extirpations, and we do not want the Arabian wolf to go the same way. To prevent this, we need to know more about its ecology and trophic interactions with other desert species throughout its distribution, as well as understand how relationships with people are key to its survival.

In this general introduction, I provide background into the mechanisms by which apex predators, like wolves, structure ecosystems through their trophic interactions with other species – both directly through predation and indirectly through instilling fear. I then discuss how these trophic interactions are mediated by humans playing similar, but far more pervasive, roles as 'super predators' (Darimont et al., 2015). After bringing the focus in on grey wolves, and the Arabian wolf in particular, I finish this chapter by providing an overview of the chapters within this thesis, which investigates the little-known ecological roles of the Arabian wolf and how these are influenced by human-wolf relationships.

1.1 The ecological importance of apex predators

Predators play pivotal roles in ecosystem functioning; a feat that is now well established in ecological theory (e.g., Estes et al., 2011; Ripple and Beschta, 2004a; Wallach et al., 2015b). Large-bodied 'apex' predators have the capacity to shape ecosystems by directly and indirectly influencing biota in lower trophic levels, through a process termed 'trophic cascades'. These top-down forces, driven by predators, limit the abundance and modify the behaviour of lower-trophic animals (Ripple and Beschta, 2006); which in turn influence a broad range of biotic and abiotic processes (Ripple and Beschta, 2004a). The cascading effects of apex predator removal can ultimately result in a reduction in ecosystem productivity (Ripple and Beschta, 2011).

Traditionally, research into trophic cascades has primarily focused on tri-trophic (three level) cascades, where predators affect vegetation community structure through influencing herbivore behaviour and density (Ripple and Beschta, 2011). For example, sea otters (*Enhydra lutris*) promote kelp forest development by limiting the abundance and distribution of herbivorous sea urchins (Estes et al., 1998). Similar evidence of predators reducing the impacts of herbivory on primary producers is widespread (e.g., Choquenot and Forsyth, 2013; Ripple et al., 2001). Perhaps the most noteworthy example comes from Yellowstone National Park in North America, where wolves were reintroduced following 70 years of extirpation (Ripple and Beschta, 2011). By influencing herbivore density and distribution throughout the landscape, wolves indirectly encouraged vegetation regrowth (Ripple et al., 2001).

It is now well-known that trophic cascades are more complex than short, linear chains of species interactions. Rather, they can involve multifaceted networks of various types and strengths of interactions (Wallach et al., 2016). For example, the suppression of herbivores in Yellowstone led to the regeneration of vegetation that then, somewhat unexpectedly, led to changes in stream morphology (Beschta and Ripple, 2011), restored the habitat of many species (Ripple and Beschta, 2011), and ultimately increased the complexity of interactions among many kinds of species (Smith et al., 2003). Predators also influence populations of other predators through intraguild predation (Polis et al., 1989), interspecific competition (Berger and Gese, 2007), and predation risk effects (Suraci et al., 2016). Thus, the removal of apex predators has been linked to widespread expansion of medium-sized predators (i.e., mesopredators; Ripple et al., 2013) through 'mesopredator release' (Crooks and Soulé, 1999), where mesopredator populations flourish due to a lack of top-down control from apex predators (Letnic et al., 2011).

This suppression of mesopredators by apex predators is likely as ecologically important as the suppression of herbivorous prey in shaping ecosystems as mesopredator release tends to lead to intensified predation on smaller prey species (Crooks and Soulé, 1999; Ripple et al., 2013). In regions such as Australia, where mesopredators have been introduced, their presence has been one of the most commonly cited causes of species extinctions (e.g., Dickman, 1996; Newsome et al., 2015). As a result, mesopredators are subjected to widespread, ongoing, and intense – yet unethical and largely ineffective – eradication efforts (e.g., Lazenby et al., 2014; Wallach et al., 2010). Evidently, dingoes (*Canis dingo*) provide small, endangered, Australian mammals with refuge from mesopredator predation (Gordon et al., 2015; Letnic et al., 2009; Wallach et al., 2010). However, the suppression of prey and mesopredators is not merely a result of direct predation by apex predators, but also the behavioural mechanisms these animals use to reduce the risk of predation. These non-consumptive, or indirect, effects are potentially more ecologically pervasive than direct mortality effects (Brown et al., 1999; Laundré et al., 2001).

1.2 Trophic cascades driven by fear

The anticipated risk of danger from predation, or 'fear' of predation, is integral to an animal's survival. Laundre et al. (2010) discuss the merits of using the landscape of fear as a conceptual model that explains how fear can influence an animal's use of habitat, and therefore, movement throughout the landscape. Landscapes are heterogeneous in both terrain and habitat; thus, predation risk may vary spatially throughout the landscape depending on the dispersion patterns of predators and their effectiveness at hunting in different habitats (Laundre et al., 2010). This variability in risk often results in a migratory shift in habitat use for prey, where prey animals occupy areas ('prey refugia', Taylor, 1984) that potentially minimize their chance of encountering predators (Ripple and Beschta, 2004b).

Much like the peaks and valleys in topographic landscapes, the landscape of fear is comprised of 'peaks' and 'valleys' of varying degrees of risk (Laundre et al., 2010). Areas of low risk to prey (i.e., the valleys) can thus be high risk to plants (Ripple and Beschta, 2004b), with escalated rates of herbivory in predator-free zones (Ripple et al., 2001). Similarly, areas of low risk to foxes are likely high risk to small rodents (Letnic et al., 2009). Hence, trophic cascades are not only driven by direct predation, but also by the perceived risk of predation, or an animal's fear of predation (Matassa and Trussell, 2011; Suraci et al., 2016).

However, predation risk not only varies in space, but also in time. Seasonal migration and changes in activity patterns (e.g., hibernation) of predators influence prey movement over seasonal timescales. For example, elk selectively separate themselves from wolves in summer when wolf activity is centred around dens and rendezvous sites (Mao et al., 2005). At finer scales (i.e., diel activity patterns), predators are often more active at certain times of the day, and evidence for prey adjusting spatio-temporal patterns of movement to lessen predation risk has been shown for many species (Valeix et al., 2009). As an example, ungulates often adjust their daily movements and foraging activity to coincide with times when predation risk is lower (Schmidt and Kuijper, 2015).

Where landscapes are more homogenous, or when food resources are scarce, it is not always possible for prey to find refuge by avoiding risky areas (Schmidt and Kuijper, 2015). In this case, individuals must alter their behaviour in ways other than migration or shifts in habitat use. Increasing group size in high-risk areas is common as it reduces an individual's chance of encountering a predator (Roberts, 1996). Animals also increase their vigilance, maintaining alertness in the event of a predatory attack (Eisenberg et al., 2014). Vigilance, which can be measured by the amount of time an animal searches for predators (Eisenberg et al., 2014), acts as a compromise between lowering the chance of predation and meeting other survival needs such as foraging.

1.3 Humans as agents of fear

Large predators like wolves and dingoes are not the only apex predators. The profound influence that humans have had on other species and entire ecological systems is unrivalled and has been at the centre of attention in conservation and environmentalism. Labelled 'super predators' (Darimont et al., 2015), humans have contributed to countless species extinctions (Estes et al., 2011; Vitousek, 1997) and have driven worldwide ecological change through global expansion and interactions with other species (Ciuti et al., 2012). Indeed, the global arrangement of today's biodiversity is largely a result of interactions between humans and the environment (Mcneely, 2003). Although the overall impacts of humans on wildlife and ecosystems are well documented (e.g., Tilman and Lehman, 2001; Vitousek, 1997), less understood is the manner in which humans shape and alter landscapes of fear. This is important because the effects of people in creating fear is decidedly non-linear: an increase in the density of people does not necessarily correlate with greater threat to wildlife. Attitudes and intentions matter. Indeed, risk to wildlife from people can change sharply across geopolitical or jurisdictional boundaries.

Human cultures are diverse and differ across borders, as do people's attitudes towards animals and the environment (Bekoff, 2013). Things that are deemed reasonable in one culture might be considered taboo in others. For instance, in Western cultures, the killing of chimpanzees for meat would likely be highly discredited by most people; however, in Cameroon, a smoked chimpanzee arm is a delicacy that sells for around four US Dollars (Peterson, 2013). Wildlife protection can vary country-to-country, region-to-region, and locality-to-locality. If wildlife are free to move across these borders, differences in persecution risk shape contrasting predicaments for wildlife. If protection is strong on one side of a border, but weak on the other, the border can act as an invisible barrier between life and death. Even in regions with strong protection, animals are not necessarily always safe from persecution. Management of wildlife often involves lethal control of 'pest' species: generally species that are considered to be overabundant or impinge on human lives or livelihoods (Ramp et al., 2013). As such, predators are a guild that are often directly targeted by people, and hence, experience fear of people.

People have conflicted with predators for millennia, decimating or entirely eliminating predators in both terrestrial and marine ecosystems (Terborgh and Estes, 2010). Vast expense goes into predator removal to reduce depredation on livestock (Bradley et al., 2015), but these attempts are often ineffective at meeting the proposed goals (McManus et al., 2015; Stone et al., 2017; Treves et al., 2016; Wallach et al., 2017). The widespread and highly promoted (e.g., Gibbs and Warren, 2014) persecution of predators has led to growing concern within the scientific community (e.g., Johnson and Wallach, 2016; Stone et al., 2017; Wallach et al., 2017) and the general public (Gibbs and Warren, 2015). Concern over the welfare of predators (Bekoff, 2013) and the loss of the functional role they play as keystone species has led to global interest in lowering the human toll on predators.

1.4 The grey wolf (*Canis lupus*) as apex predator

The grey wolf has been at the forefront of ecological research over the last few decades. After experiencing large-scale extirpations until the 20th century, populations are now recovering across North America and Europe (Boitani, 2003). While protective legislation and sophisticated conservation initiatives have certainly played a large part in these recoveries, perhaps more pervasive has been the general increase in public acceptance of wolves (Treves and Bruskotter, 2014). One of the most important bodies of research which has contributed to increased acceptance, and even appreciation, of wolves is that which elucidates their pivotal ecological roles as apex predators. Since the reintroduction of wolves at Yellowstone National Park in the United States throughout the 1990s, documentations of their benefits to ecosystem functioning have been profound. Further research from Europe has revealed how these roles play out in anthropogenic landscapes (Dorresteijn et al., 2015). However, wolves do not only exist in North America and Europe. With the widest historical distribution of any large terrestrial predator, their distribution extends across most of Eurasia (Nowak, 2003).

Thirty-two subspecies have so far been named throughout Eurasia and North America (Sillero-Zubiri et al., 2004). Nonetheless, as is often the case in taxonomy, debate around subspecific classification remains and is ever-changing (Nowak, 2003). Geneticists have identified several variations within *C. lupus* over the past thirty years (de Groot et al., 2016), and morphological differences have been documented over the last two and a half centuries (Nowak, 2003). Following Bergmann's Rule, smaller variations of wolves are found in warmer climates while larger variations are found in colder climates (Meiri, 2011). The smallest wolf subspecies are found in the Middle East, a geographical region lying at the southern extremity of the wolf's global range. Middle Eastern wolves are currently categorised as two distinct subspecies, with apparently little-to-no overlap between the two (Nowak, 2003). The Indian wolf (*C. l. pallipes*) has a broad distribution, ranging from the Indian subcontinent across to Turkey and down to Israel, while the smaller Arabian wolf (*C. l. arabs*) occurs solely within Middle Eastern deserts. Surprisingly, relatively little is known about Middle Eastern wolves compared to their North American and European counterparts.

1.5 The unique desert-adapted Arabian wolf

The Middle East has a rich tapestry of biodiversity. Situated at the intersection of Africa, Europe and Asia, the region is the only transition zone between three of the world's eight ecozones: the Palearctic, Afrotropical, and Oriental Realms (Krupp et al., 2009). As a result, the Middle East is a meeting point for a unique and diverse mix of species; only here is it possible to witness Eurasian wolves hunting African gazelle (e.g., *Gazella dorcas*). The majority of wolf habitat in the region could not be more distinct from that in the northern parts of Eurasia and North America. While snow-covered mountains exist, they are far from the predominant habitat type. Most of the land is characterised by steppe, semi-desert, and desert environments, with Mediterranean forests, woodlands, and scrub in the humid and northern regions.

The Arabian wolf inhabits the arid and hyper-arid ecosystems of the southern Levant and Arabian Peninsula. Being the smallest grey wolf subspecies, and solely occurring in low-productivity ecosystems, doubt has been cast as to whether Arabian wolves influence ecosystems like their counterparts in temperate regions. Dietary analyses have revealed that they mostly rely on small animals and agricultural food resources (Shalmon, 1986), and recent evidence suggests they are highly associated with human infrastructure (Barocas et al., 2018). However, most research on Arabian wolves comes from regions where they are generally accepted. The Arabian wolf must navigate one of the most geopolitically complex landscapes on Earth; one in which tolerance of wolves ranges from acceptance to complete intolerance (Cunningham et al., 2009; Khorozyan et al., 2014). Indeed, Arabian wolves have reportedly been shot after crossing from areas of acceptance to intolerance (Hefner and Geffen, 1999). As such, the persistence and ecological roles of the Arabian wolf are yet to be considered within the complexities and variation in top-down forcing by humans. This thesis aims to uncover the Arabian wolf's roles as apex predator, while focussing on the ways in which these are influenced by its relationships with people.

1.6 Thesis overview

Gaining an understanding of the conservation tools and strategies that have been developed in global wolf recovery, including those that have shaped acceptance of wolves, is paramount if we want to conserve the Arabian wolf. This includes increasing our knowledge of the potential ecological roles they play. Throughout this thesis, I borrow from global wolf conservation initiatives to learn how we can utilise these tools within the context of Arabian wolves. In Chapter 2, I review the available literature to gain a thorough understanding of conservation developments that have led to the recovery of grey wolf populations. I explore the benefits wolves provide to ecosystems, while considering the way knowledge of this has helped shift public attitudes towards acceptance of wolves. I then focus on the Arabian wolf, revising what is currently known about its distribution, ecology, and relationships with people throughout its range. Given that it traverses such a geopolitically complex region where wildlife protection and conservation efforts vary, I provide a detailed description of variations in current policy, legislation, and conservation effort pertinent to the Arabian wolf. I conclude the review by summarising what we have learnt from global wolf conservation efforts and recommending ways in which we could tailor these to the Middle East to ensure the ongoing conservation of this iconic subspecies of grey wolf.

Tolerance of Arabian wolves across their range is highly correlated with human land-use and agricultural practices throughout the region. In protected areas and agricultural regions dominated by crop farming, wolves are generally accepted by people (Barocas et al., 2018). However, pastoralism is the predominant form of land-use throughout Middle Eastern deserts, and tolerance of wolves is low in such landscapes due to the perceived impact wolves have on farmers' livelihoods. In Chapter 3, I set out to assess resource use and relative abundance of wolves in Israel and Jordan where land-use varies, and determine the potential top-down influence wolves have on desert canid communities. Through conducting occupancy surveys and assessing interspecific interactions and relative abundance of canids, I provide the first documentation of a trophic cascade in the Middle East in which canid communities are influenced by variations in tolerance of the Arabian wolf.

As trophic cascades are not only driven by direct predation and persecution, but also by indirect risk effects, these trophic cascades in the Middle East are likely driven by variations in perceived risk elicited by people and wolves to species in lower trophic levels. Chapter 4 explores the mechanisms by which these trophic cascades are triggered by determining how species distributions are driven by spatial responses to risk. With the use of single-species and two-species occupancy models, I show how suppressive interactions from wolves to prey and mesopredators are mediated by wolves' spatial responses to people in different scenarios of varying tolerance. While revealing how these relationships vary across land-use, I construct maps depicting variations in relative risk based on spatial responses of a lower-order species to the potential cooccurrence of a higher-order species to show how landscapes of fear alternate for species across trophic levels.

Within such landscapes of fear, responses of lower-order species to predation risk are shaped by two forms of knowledge: landscape knowledge (ambient risk) and immediate cues (imminent risk). Chapter 5 investigates these two types of knowledge by assessing responses of mesopredators and their prey to ambient and imminent risk across the landscapes of fear elicited by Arabian wolves. Through occupancy and foraging behaviour surveys across high and low risk areas, I show that foxes and rodents occur less, and reduce the amount of time they spend foraging, in high-risk areas compared to low-risk areas. With the use of imminent cues, I also show that agile responses of foxes and rodents to imminent risk may reflect adaptability and fitness trade-offs necessary to ensure survival.

In conclusion, this thesis provides the first piece of evidence suggesting that the Arabian wolf is as important as its temperate counterparts in regulating ecosystems. Its suppressive forces on species in lower trophic levels, whether they be through direct predation or instilling fear, shape cascading effects across multiple trophic levels. Through borrowing tools from wolf conservation efforts in other regions, we can begin working towards improving human-wolf relationships, particularly in pastoralist landscapes, and enhancing Arabian wolf conservation. Now is the time to act to ensure the persistence of this unique wolf and its important ecological roles.

1.7 References

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Chapter 2. Navigating a geopolitically complex landscape: the Arabian wolf's complicated plight

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Abstract

The grey wolf (*Canis lupus*) is one of the most adaptable predators but suffered major decline over the last few hundred years. Global wolf populations are beginning to recover, primarily through protective legislation and policy implementations, but also because of a general increase in public acceptance. Questions remain, however, about a little-known subspecies of the grey wolf, the endangered Arabian wolf, which is the only desert-adapted subspecies, residing in one of the most geopolitically diverse conflict zones in the world. In this review, we explore the plight of the Arabian wolf through the lessons of global conservation efforts, documenting what is currently known about this wolf and its taxonomic status, ecology, and distribution, and contextualise this within the geopolitical diversity of the Middle East. We stress that cross-jurisdictional planning and collaboration are likely to be vital to ensure the ongoing conservation of this keystone and iconic subspecies of grey wolf. However, any solutions to conserve the Arabian wolf must be cognisant of this complexity and strive to ameliorate the internal conflicts, attitudes, and values that are ingrained among the peoples that share this landscape.

2.1 Introduction

The grey wolf (*Canis lupus*) is perhaps the most adaptable large terrestrial predator on Earth (Nowak, 2003). With 32 subspecies identified across a historically Holarctic distribution (Sillero-Zubiri et al., 2004) – covering most of the northern hemisphere north of 20°N (Boitani, 2000) – wolves have inhabited every ecological biome from the arctic to the hyper-arid deserts of the Middle East. Through forming close bonds with humans (Germonpré et al., 2018) and adjusting to an increasingly human-dominated world, wolves have managed to outlast other large predators across much of their wide range (Wojtal et al., 2020). However, as the pervasiveness of global human dominance has progressed over the last several centuries, these adaptations that have helped wolves thrive for so long have proven to fall short. Habitat loss and increased conflict with humans, coupled with inordinate technological advances that have helped people deal with these conflicts, almost led to the demise of this formerly ever-adaptable, species.

Fortunately, there has been a growth in awareness of the overwhelming impact our dominance has had on the environment and species we share this world with. We now know that our actions have led to significant declines and range contractions of many species, particularly large predators, and appreciate the devastation this has caused to the world's ecosystems (Ripple et al., 2014). To combat this, conservation efforts have focussed on protection and rewilding (e.g., Yellowstone National Park), with some success. Yet conflict remains, and community attitudes toward predator protection are mixed, particularly within farming communities where depredation of livestock remains a hotly contested issue. Nevertheless, global wolf populations are beginning to recover (Boitani, 2003). Protective legislation and policy implementations have proven to support recovery, but perhaps even more permeating has been the general increase in public acceptance and appreciation of wolves (Treves and Bruskotter, 2014).

While there has been much focus on the conservation of grey wolves in North America and Europe, where their status is now Least Concern (Boitani et al., 2018), wolves across Asia have received little attention to date. The most southerly distribution of Eurasian wolves is dominated by two subspecies, both of which occur in the Middle East – the Indian wolf (*C. lupus pallipes*) and the Arabian wolf (*C. lupus arabs*). The Indian wolf has a broad distribution, encompassing much of southern and western Asia from India to Turkey, and favours Mediterranean or temperate climates. However, the Arabian wolf is the only desert-adapted subspecies and status reviews over the past few decades list it as either vulnerable or endangered (Boitani, 2003; Mallon and Budd, 2011). Coupled with the fact that the Arabian wolf resides in one of the most geopolitically diverse conflict zones in the world, the conservation of this unique and threatened wolf remains a considerable challenge.

The fact that wolves are now recovering in other parts of the world, after being on the verge of extinction, brings hope. But the circumstances for the Arabian wolf differ in two important ways: it resides in desert ecosystems that are far less productive than the temperate ecosystems of Europe and North America, and the geopolitical mosaic and distinct forms of human land use in the Middle East might be more complex than anywhere else in the world. Hence, the conservation challenges faced by the Arabian wolf are unique and require careful consideration of not just the ecology of the species, but also in the documentation and analysis of its role in shaping that of other species and in the way it accommodates variation in acceptance by the peoples of the Middle East.

To begin this process, it is necessary to borrow from our understanding of protection efforts of their northern cousins to ask how we can implement that knowledge in such a diverse conflict zone. In this review, we first examine global conservation efforts with a view to contextualising opportunities to understand and learn from those that can be used to strategise and conserve the Arabian wolf. We then document what is currently known about the Arabian wolf and its taxonomic status, ecology, and distribution. Finally, we contextualise this within the geopolitical diversity of the Middle East, highlighting areas of conflict and acknowledging opportunities for coexistence. We end by articulating how cross-jurisdictional planning and collaboration are vital to ensure the ongoing conservation of this keystone and iconic subspecies of the grey wolf.

2.2 Lessons from global conservation efforts

2.2.1 Ecology and importance of wolves globally

Emerging as arguably the most important body of research to inspire appreciation of wolves over the last few decades is that which elucidates the pivotal roles they play in the functioning and regulation of ecosystems (Ripple and Beschta, 2011, 2004a; Terborgh and Estes, 2010; Wallach et al., 2015c). As large-bodied 'apex' predators, wolves shape ecosystems both directly through predation, and indirectly by influencing biota in lower trophic levels – through a process termed 'trophic cascades'. These top-down forces limit the abundance and modify the behaviour of lower-trophic animals (Ripple and Beschta, 2011; Wallach et al., 2015c), in turn influencing a broad range of biotic and abiotic processes (Ripple and Beschta, 2004a). The loss of this function results in a series of cascading effects that can ultimately result in a reduction in biodiversity and ecosystem productivity (Ripple and Beschta, 2011). The most high-profile example of this comes from Yellowstone National Park in North America, where ecological transformation was documented over the two decades following the reintroduction of wolves (Ripple and Beschta, 2011, 2004a). Similar functional responses in Australia's arid region, where trophic interactions between dingoes (*Canis dingo*) as apex predators, herbivores like kangaroos, and vegetation have also been identified (Choquenot and Forsyth, 2013).

Trophic cascades are, however, more complex than the simple, albeit significant, three-level linear chains of species interactions these examples represent. Rather, they can involve multifaceted networks of species with various types and strengths of interactions (Wallach et al., 2016). For example, vegetation recovery in Yellowstone promoted the return of several species (Ripple and Beschta, 2011), and ultimately increased the complexity of interactions occurring there (Smith et al., 2003). Even stream morphology, which was believed to have been altered by excessive trampling from herbivores, returned to its previous meandering style (Beschta and Ripple, 2011). A further importance of apex predators, like wolves, is that they also interact with and shape the distribution and behaviour of other predators, through intraguild predation (Polis et al., 1989), interspecific competition (Berger and Gese, 2007), and predation risk effects (Suraci et al., 2016). One implication of this is that apex predators suppress populations of medium-sized predators (i.e., mesopredators; Ripple et al., 2013). This regulation effect becomes apparent when apex predators are controlled, resulting in 'mesopredator release' (Crooks and Soulé, 1999), where mesopredator populations flourish due to a lack of top-down control (Letnic et al., 2011).

The cascading effects of mesopredator release have been documented in many ecosystems around the world as apex predators, including wolves, are common targets for lethal control. For example, threatened small mammals in Australia are more susceptible to predation by mesopredators like cats (*Felis catus*) and foxes (*Vulpes vulpes*) in areas where dingoes are persecuted (Wallach et al., 2010, 2009a). Likewise, bird diversity is higher where coyotes (*Canis latrans*) are present, as they suppress predation on birds by cats and foxes (Crooks and Soulé, 1999). In this example, coyotes are acting as apex predators (Levi and Wilmers, 2012; Newsome and Ripple, 2015). However, medium-sized canids like coyotes and golden jackals (*Canis aureus*) are typically mesopredators – suppressed by larger predators – and continental range expansions of coyotes in North America and jackals in Europe occurred with widespread wolf removal (Krofel et al., 2017; Newsome et al., 2017).

Such shifts in trophic positioning can drastically affect ecosystem complexity, and thus biodiversity (Prugh et al., 2009). Trophic niche overlap is usually more pronounced between mesopredator species than between mesopredators and apex predators (Lanszki et al., 2006; Prugh et al., 2009). When suppression by wolves is reduced, competition increases between mesopredators, usually with the larger species becoming dominant (Levi and Wilmers, 2012). Foxes fare better in ecosystems where wolves and coyotes are present than in those where their sole competitors are coyotes (Levi and Wilmers, 2012; Newsome and Ripple, 2015). Wolves also suppress foxes, but not to the same extent as coyotes, who often reduce fox populations to unstable levels (Levi and Wilmers, 2012).

2.2.2 Conflict, persecution, and mitigation

Wolves experienced widespread persecution and extirpations during the last several centuries across Eurasia and North America. Various countries in Central and Western Europe had eradicated wolves over the 16th and 17th centuries, and by the early 20th century, wolves were nearly extinct across most of Europe and the 48 contiguous United States (Boitani, 2003). While the International Union for the Conservation of Nature (IUCN) now lists the grey wolf as Least Concern (Boitani et al., 2018), the conservation status of wolves around the world suggests that many subspecies remain imperilled. Included in these are the three subspecies with the most southern distributions, all listed as Endangered: the Arabian wolf (Mallon and Budd, 2011) and Indian wolf (Sharma et al., 2019) of Eurasia and the Mexican wolf (*C. l. baileyi*) of North America (Paquet et al., 2001).

Along with the loss of habitat and prey, pervasive lethal control and exclusion of wolves from agricultural landscapes have led to this demise. For millennia, predators like wolves have conflicted with people and their interests. People have long held beliefs that wolves are 'ruthless man-eaters', as can be acknowledged by their portrayal in a plethora of adages, nursery rhymes, and folk stories created throughout the world across centuries. During evolutionary history, people were most likely prey for wolves, driving people to fear them. Nowadays, it is wolves who, for the most part, are fearful of people (Dorresteijn, 2015; Oriol-Cotterill et al., 2015).

Today, livestock depredation is the most frequently reported reason for conflict between humans and wolves (Sillero-Subiri and Laurenson, 2001). While such conflicts are indeed a concern for agriculturalists, depredation by wolves is often minimal when compared to stock losses from disease (Ud Din et al., 2017) or exposure to extreme climatic conditions (Burns et al., 2010; Wallach et al., 2017); though these are highly dependent on geographic location. Wolves and other predators are also targeted because of other interests, related to aesthetics (Childes, 1988), fear of threatening encounters (Linnell et al., 2003), conservation concerns (Cohen et al., 2013), or simply because they 'don't belong' (Van Dooren, 2011; Wallach et al., 2015a). As a result of such conflicts, large predators have experienced substantial population declines and range contractions over the last two centuries (Ripple et al., 2014).

One conservation approach used globally as an attempt to combat such losses is 'land sparing' (i.e., the setting aside of land for conservation). During the last 100 years, more than 200,000 terrestrial protected areas such as national parks and nature reserves have been established worldwide, and they currently cover around 15 % of the Earth's surface (UNEP-WCMC and IUCN, 2016). This strategy of 'separating people from nature' can be effective for species whose movement and requirements are entirely contained within protected areas and where protection is enforced and regulated (Hill et al., 2020). However, protected areas are not sufficient to protect wide-ranging species with home ranges that exceed protected area boundaries from hunting and persecution (Johansson et al., 2016), which is often the case for large predators. Rarely are protected areas large enough to sustain viable populations of mobile species like wolves.

Protected areas are also not pristine environments outside of human influence. Management often involves pervasive and intrusive measures that disturb the ebb and flow of ecosystems: lethal control and harvest of unwanted or abundant species can cause cascading ecosystem effects (Colman et al., 2014); tourism and recreational activities bring pollution, environmental degradation, and wildlife disturbance (Pickering et al., 2003); and roads cut through protected areas, causing vehicular collisions with wildlife (Ramp and Ben-Ami, 2006; Roger et al., 2012), habitat fragmentation (Roger et al., 2011), and edge effects (Ben-Ami and Ramp, 2006). As such, other forms of human-caused wildlife mortality may not be altered by protection, and in some cases can be higher than non-protected areas. For example, roadkill and wildlife harvesting rates have recently been shown to be higher within national parks than elsewhere in North America (Hill et al., 2020). Recognition of the shortcomings of protected areas has led to broader social initiatives linked to coexistence and land sharing. It is widely accepted that humans and large predators can, in fact, successfully occupy the same landscapes (Lute et al., 2018).

2.2.3 Human attitudes and social research

As awareness and knowledge of the ecological roles of wolves have increased globally, so have intentions and efforts to conserve them. North America and Europe are prime examples, where wolf populations have made an incredible comeback thanks to efforts over the last 25 (Jimenez et al., 2017; Mech, 2017) and 40 (Chapron et al., 2014; Randi, 2011) years, respectively. Wolf populations have now recovered in seven of the 48 contiguous United States (Mech, 2017). In the Northern Rocky Mountains, the population recovered to over 1,600 wolves by 2008 (Jimenez et al., 2017) following reintroductions in the 1990s, ending more than 60 years of extirpation. While protected areas played a large part in this success story, similar recoveries have been documented in Europe where protected areas are few and far between (Boitani, 2003). Across much of Central and Western Europe and Scandinavia, wolves have recovered since the 1970s (Chapron et al., 2014). In refugia where wolves persisted, populations have since grown exponentially (Salvatori and Linnell, 2005). This success can be attributed in part to the development of transboundary policy initiatives (Epstein et al., 2016; Linnell and Boitani, 2012), where matching legislation is enforced across the continent through international collaboration (Linnell et al., 2008). However, these policies work because of a fundamental shift in public attitudes towards wolves (Bencin et al., 2016; Bruskotter et al., 2014; Kansky and Knight, 2014; Treves and Bruskotter, 2014).

Conservationists and wolf advocates have utilised social science to assist with large carnivore conservation efforts (Bruskotter and Wilson, 2014; Carter et al., 2012). Human attitudes towards predators, which range from tolerance to complete intolerance, are primary determinants of the success of long-term conservation of wolves (Bruskotter et al., 2014). Attitudes towards wildlife are shaped by social and cultural values, such as farmers across socio-political borders (Sagie et al., 2013) or varying education levels (Holsman et al., 2014; Manfredo et al., 2003; Williams et al., 2002), and vary across spatial (Bencin et al., 2016; Karlsson and Sjöström, 2007) and temporal (Fernández-Llamazares et al., 2020; George et al., 2016) scales. For example, people that live further from wolf territories (Ericsson and Heberlein, 2003; Karlsson and Sjöström, 2007) and have access to higher levels of education (Manfredo et al., 2003; Naughton-Treves et al., 2003; Williams et al., 2002) tend to hold more positive attitudes towards wolves. Conversely, people that live near wolves and have had direct experiences with wolves (e.g., through livestock loss or threatening encounters) tend to hold more negative attitudes towards wolf recovery (Ericsson and Heberlein, 2003; Karlsson and Sjöström, 2007).

Overall, public attitudes towards large carnivores shifted significantly during the latter half of the 20th century (Kellert et al., 1996). A driving factor in this shift is the transition of *wildlife value orientations* from 'domination' to 'mutualism'; where domination views that wildlife exist for human use, while mutualism emphasises that wildlife are capable of living in relationships of trust with humans, deserving of care and compassion (Manfredo et al., 2009). This transition is thought to have been triggered by social change from goals that are rooted in basic needs such as safety, survival, and sustenance, to goals such as environmental protection and free speech. These changes have been particularly prevalent in Western post-industrialised cultures after WWII (Inglehart and Baker, 2000), and generally in social groups with higher levels of education (Williams et al., 2002). Although general education has contributed to such change, carnivore education focussed on tolerance and ecological roles has been important for increasing support for predator conservation (Bruskotter and Wilson, 2014). Along this line, strategies promoting human-predator coexistence have been gaining traction (Wallach et al., 2015a).

2.2.4 Practical strategies for coexistence

For wolves, the frontline of coexistence is within agricultural landscapes. Fortunately, there is a growing global movement in 'predator friendly farming' which allows and even encourages predators to persist in these contested spaces (Johnson and Wallach, 2016). In both modern agricultural and traditional pastoralist systems of livestock production, a move to non-lethal predator control has enabled human-predator coexistence in intensive livestock growing regions (Ohrens et al., 2019; Stone et al., 2017). Non-lethal methods nearly always involve improved livestock husbandry practices, with the addition of tools that act as deterrents to prevent encounters between livestock and predators (McManus et al., 2015). Livestock guardian dogs have been used for millennia (Gehring et al., 2010) and continue to be an effective deterrent against predators (van Eeden et al., 2018); while modern deterrents such as fladry, livestock collars, and flashing lights (e.g., Foxlights®) have shown significant reductions in livestock depredations, are low cost, and require little effort to implement (McManus et al., 2015; Miller et al., 2016; Ohrens et al., 2019). Compensation schemes offered by governmental agencies or non-governmental organisations (NGOs) have also relieved agriculturalists from potential hardships associated with predator-related livestock loss (Naughton-Treves et al., 2003).

Improving human-predator coexistence is gaining increasing support, particularly in regions with targeted public education and conservation programs. However, it remains common for predators such as wolves to be viewed with widespread hostility in regions with strong traditional cultures (Seddon and Khoja, 2003). Knowledge of alternative methods of livestock protection is often lacking in such areas, and traditional beliefs based around fearful perspectives can take precedence over new, novel belief systems (Inglehart and Baker, 2000). Undeniably, it is doubly challenging to drive change in farmers' attitudes towards wolves where culture and traditional practices are entrenched.

2.3 State of Knowledge of the Arabian wolf

2.3.1 Toxonomy of *Canis lupus arabs*

The lack of knowledge on the wolves of Asia is epitomised by the continued speculation over whether the region's wolves deserve distinct subspecific taxonomic classification. Although inconsistencies exist within the literature (Afik and Alkon, 1983; Cunningham and Wronski, 2010; Mukherjee et al., 2009; Reichmann and Saltz, 2005; von Jaffa, 2013; Wronski and Macasero, 2008), it is generally accepted that there are two subspecies of wolves in the Middle East. *C. l. pallipes* occurs in temperate regions characterised by Mediterranean or semi-arid climates (Ferguson, 2002; Khosravi et al., 2013), while *C. l. arabs* inhabits the southern deserts of the Levant and Arabian Peninsula (Bray et al., 2014; Cohen et al., 2013; Hefner and Geffen, 1999; Nowak, 2003).

While the two subspecies share similarities – for example, both being small compared to conspecifics in northern regions (Ferguson, 2002; Nowak, 2003) – *C. l. arabs* is noticeably smaller than *C. l. pallipes*, with the latter being up to 1.5 times larger than the former (Ferguson, 2002). Morphological differences are particularly noticeable during the summer months when wolves lack their winter coats (*pers. obs.*). Clear genetic distinctions have also been documented between the two subspecies, where the wolves of Arabia were more closely related to Eurasian wolves (*C. l. lupus*) than *C. l. pallipes* (Bray et al., 2014). Within Israel, differences have been noted (Reichmann and Saltz, 2005) and observed (*pers. obs.*) between the two isolated wolf populations: the wolves in the southern deserts are smaller and have shorter hair than those in the Mediterranean landscapes of the Golan Heights.

Despite clear differences in climatic conditions between the distribution ranges of *C. l. arabs* and *C.l. pallipes*, it is unclear exactly where the two subspecies geographically diverge. The limited genetic and morphological evidence that is available suggests that only *C. l. pallipes* occurs in Iran (Khosravi et al., 2013, 2012) and *C. l. arabs* in Arabia (Bray et al., 2014). Furthermore, Khosravi et al. (2012) state that wolves are absent from the central deserts of Iran (i.e., Dasht-e Kavir and Dasht-e Lut); however, they do occur in semi-desert environments (Tourani et al., 2014). With the current literature as it stands, it seems most plausible that the range of the Arabian wolf extends more than 3 million km^2 throughout the arid region southward from the southern deserts of Iraq and possibly Syria, encompassing the Levantine and Arabian deserts (Figure 2.1). Some degree of overlap between the two subspecies may occur in the northern part of the Arabian wolf's range, however, no empirical data shows where or if this is the case. Further genetic testing across a broader range is required to truly understand the divergence between *C. l. arabs* and *C. l. pallipes*.

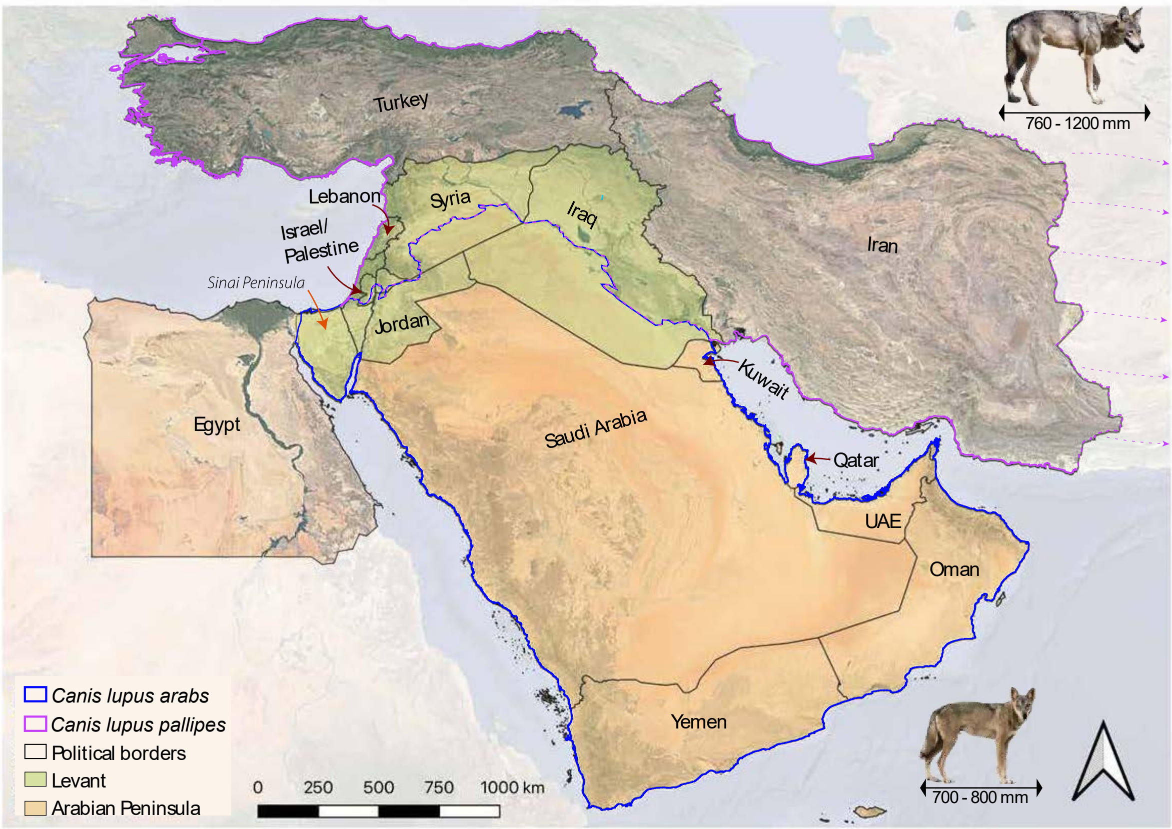

Figure 2.1. Likely distributions of the two grey wolf subspecies that occur in the Middle East. The Indian wolf (*C. l. pallipes*) inhabits temperate climates from India to Turkey while the Arabian wolf (*C. l. arabs*) resides in the deserts of the southern Levant and Arabian Peninsula.

2.3.2 Ecology and importance

Is it necessary to differentiate between the two subspecies? When it comes to setting conservation goals, it may be. The Arabian wolf is unique, as it is the only wolf specifically adapted to arid environments. While other wolves have ventured into deserts – the Gobi Desert in eastern Asia is home to populations of the Mongolian wolf (*C. l. chana*; Kaczensky et al., 2008), and the Mexican wolf used to occur in North American deserts (Hendricks et al., 2016) – neither of these subspecies are exclusive to arid regions, like the Arabian wolf. There are certainly similarities between Arabian and Mexican wolves: the Arabian wolf is the smallest subspecies in the Old World, while the Mexican is the smallest in the New World (Nowak, 1995). Sadly, the Mexican wolf is also the most endangered wolf subspecies, and it has been at the centre of conservation efforts in North America for the last 40 years (U.S. Fish and Wildlife Service, 2022, 1982). Efforts have included ongoing reintroduction programs and more stringent enforcement of protective legislation (Hendricks et al., 2016). However, it was concluded that the ultimate factor determining population viability is human attitudes (Paquet et al., 2001), largely shaped by the increase in knowledge of the ecological importance of wolves.

There is no doubt that the Arabian wolf is of considerable importance to the desert ecosystems of the Middle East (Bonsen et al., 2022). Since the widespread eradication of other large carnivores throughout its range, the Arabian wolf remains the last surviving apex predator. Until relatively recently, the wolf shared its role as apex predator with two large felids: the Asiatic cheetah (*Acinonyx jubatus venaticus*) and the Arabian leopard (*Panthera pardus nimr*). Today, with the cheetah extinct throughout the Arabian wolf's range (Farhadinia et al., 2017) and the leopard likely confined to a few protected areas (Spalton et al., 2006), the sole remaining large carnivore to fill a similar niche is the striped hyaena (*Hyaena hyaena*); albeit not as apex predator. While the Arabian wolf periodically hunts gazelle (*Gazella* spp.), ibex (*Capra nubiana*), and young onagers (*Equus hemionus*), the striped hyaena is not a successful hunter of ungulate prey (Kruuk, 1976). However, both share a largely omnivorous diet. Each actively hunts small mammals, birds, and reptiles, and scavenges from agricultural crops, carrion, and garbage (Afik and Alkon, 1983; Kruuk, 1976; Qarqaz et al., 2004; Shalmon, 1986). In regions where wild prey densities are low and free-range livestock farming common, domestic ungulates form a considerable part of each species' diet (Qarqaz et al., 2004; Shalmon, 1986).

The difference between the two lies in their methods of acquiring prey. The striped hyaena is primarily a scavenger, and mostly feeds on carcasses of livestock that have died from prior causes (Tourani et al., 2012). Wolves, on the other hand, are known to prey on livestock (Yom-Tov, 2003), especially where natural prey resources are diminished (Khorozyan et al., 2015). Throughout the Arabian wolf's range, ungulate abundance is low because Middle Eastern arid and hyper-arid environments couple low productivity with strong hunting pressure, pushing many of the region's ungulate species to extinction or extensive decline (Mallon and Kingswood, 2001). Local and regional efforts to revive ungulate populations are largely confined to protected areas (Amr et al., 2004; Barichievy et al., 2018; Mallon and Kingswood, 2001), leaving few suitable alternatives for large prey, other than livestock, outside of protected areas.

Historically, Middle Eastern deserts were predominantly farmed by Bedouins; nomadic or semi-nomadic tribal pastoralists whose shepherding methods often require them to travel for days on end without securely protecting their flocks of sheep and goats. Across much of the region's deserts, Bedouin pastoralism remains the primary source of agriculture. However, in the latter half of the 21st century, technological advances in groundwater acquisition and farming practices saw a rapid increase of agricultural land-use in arid regions. These transformed 'oases' provide an abundance of fruits, vegetables, and water to be scavenged by wolves, reducing their reliance on limited ungulate prey populations. In fact, diet analyses from high crop-growing regions reveal that vegetative material and garbage constitute most of the Arabian wolf's diet (Shalmon, 1986).

In such areas, and those where livestock are well protected, losses to wolves are negligible (Nemtzov and King, 2001). This is the case in Israel's hyper-arid Arava Valley, where shepherding is minimal and crop farming is the predominant form of agriculture. Here, wolves have developed such an affinity for human habitation, several GPS-tracked individuals were observed to seldom venture more than five kilometres from human infrastructure (Barocas et al., 2018). As a result of the reduced tendency to hunt, pack sizes are generally smaller than those reported in North America and Europe (Hefner and Geffen, 1999), with solitary or pair sightings of wolves common.

2.3.3 Distribution and abundance

Arabian wolf densities vary considerably throughout its wide distribution (Figure 2.2). Current evidence suggests the Negev Desert of Israel, which includes the Arava Valley, has the most stable population of Arabian wolves. The population here was estimated at 90 to 150 individuals (Cohen et al., 2013), a relatively stable number for an arid to hyper-arid region with an area of less than 15,000 km^2. West of Israel, the wolf's range extends into the Sinai Peninsula of Egypt. While it is unknown how far across Sinai wolves occur, they were recently recorded in St Katherine Protectorate in the south (Gecchele et al., 2017). They have been recorded in Sinai for some time (Ferguson, 1981) and continue to cross the border from Israel (Barocas et al., 2018), but no population estimates are currently available.

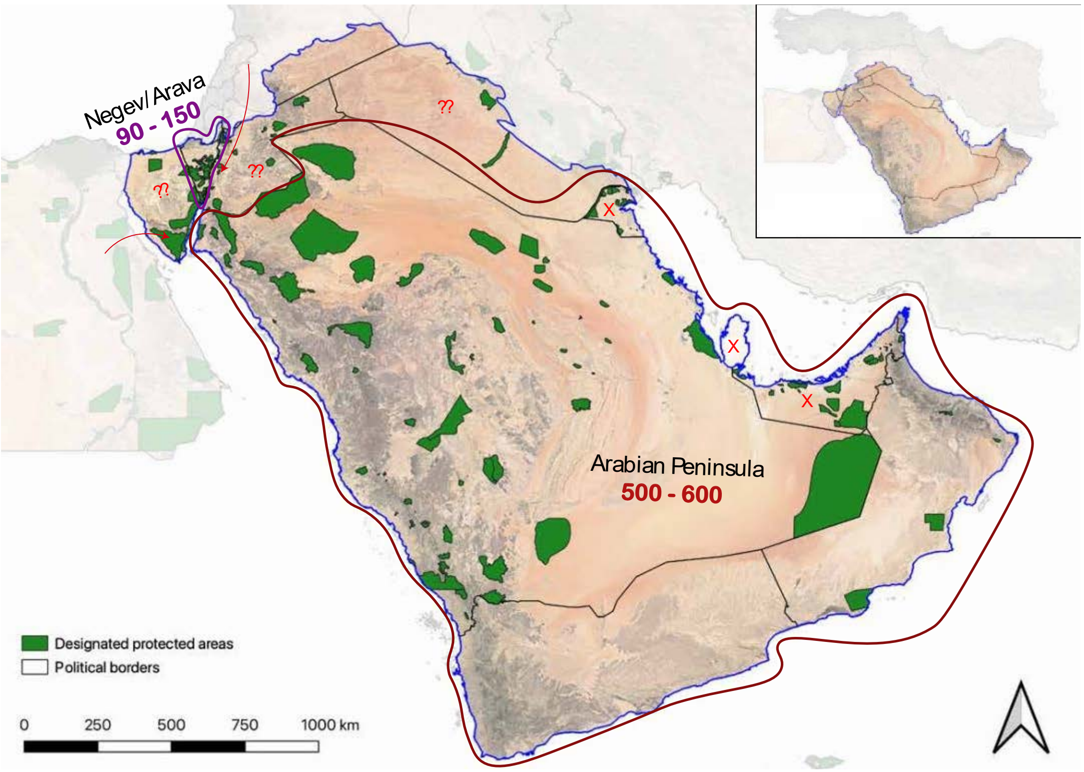

Figure 2.2. Population estimates of the Arabian wolf in Levantine and Arabian deserts within the Middle East (inset).

In the eastern part of its range, the estimated population size across the three largest countries on the Arabian Peninsula (i.e., Saudi Arabia, Yemen, and Oman) is 500 – 600 individuals, but is declining (Sillero-Zubiri et al., 2004). Wolves appear to be common in remote and protected areas of Yemen (Khorozyan et al., 2014). In Oman, wolves have been recorded throughout the country, but are again seemingly confined to remote and protected areas (Mazzolli et al., 2017; Spalton, 2002). Records are common throughout Saudi Arabia, however, the vast majority of these records derive from killed specimens (Aloufi and Amr, 2018; Zafar-ul Islam et al., 2019). The Arabian wolf is now thought to be locally extinct in Qatar (Mallon and Budd, 2011), the United Arab Emirates (Cunningham, 2004), and Kuwait (Mallon and Budd, 2011).

Jordan lies between the Negev/Arava and Arabian Peninsula populations, where wolf numbers are unknown but believed to be negligible (*N. Hamidan pers. comm.*). Past surveys confirmed wolf presence in the north-eastern Badia (Bunaian et al., 2001), and wolves were recently recorded during camera-trapping and passive tracking surveys in Dana Biosphere Reserve and Fifa Nature Reserve in Jordan's Wadi Araba region (Bonsen and Khalilieh, 2021). As such, Jordan provides an important stepping-stone between the stable Negev population and the dwindling population of the Arabian Peninsula. However, the most critical jurisdiction for Arabian wolf conservation is likely Saudi Arabia due to its large area and its geographic location. The country stretches 2.15 million km^2 and lies between the populations of the southern Levant (i.e., Sinai, Israel/Palestine and Jordan) and the southern and eastern extremities of Arabia (i.e., Yemen and Oman).

2.4 Geopolitical Diversity

2.4.1 Conservation of the Arabian wolf

The last two centuries have witnessed global extirpations and range contractions of large carnivores (Ripple et al., 2014). The Middle East is no exception. Of 20 carnivores known from Arabia, eight have been listed as threatened or near threatened: one being regionally extinct, another critically endangered, and two classified as endangered (Mallon and Budd, 2011). Although the global status for *C. lupus* is Least Concern (Boitani et al., 2018), status reviews for the Arabian wolf over the last few decades list it as vulnerable or endangered (Boitani, 2003; Mallon and Budd, 2011). This at least gives it the advantage of being stringently protected in Israel: aside from the authorised killing of almost 40 wolves to protect the critically endangered Acacia gazelle (*Gazella gazella acaciae*) in the mid 2000s, no legal killing of Arabian wolves is sanctioned (Cohen et al., 2013). While the subspecies is currently legally 'protected' across its range, the realistic definition of protected is not homogeneous. In areas of human-wolf conflict, this protection can be rather lax.

Small population sizes and low densities make the Arabian wolf particularly susceptible to stochastic events (e.g., disturbance, disease) and changes in protection status. Without concerted and coordinated conservation efforts, the Arabian wolf might end up following the path already traversed by the region's large felids. The critically endangered Arabian leopard (Stein, 2020), which had a range similar to the Arabian wolf, is now likely confined to small pockets of protected areas in Saudi Arabia, Yemen, and Oman (Khorozyan et al., 2014; Spalton, 2002; Spalton et al., 2006). The leopard's demise is recent, with extirpations in Israel/Palestine and Jordan likely to have occurred within the last 20 and 30 years, respectively (Farhadinia et al., 2019). The Asiatic cheetah, on the other hand, has been restricted to central Iran since the 1980s (Farhadinia et al., 2017). Iran is also the country in which the last known Middle Eastern sightings of an Asiatic lion (*Panthera leo persicus*) and Caspian tiger (*Panthera tigris virgata*) occurred in the 1940s and 1950s, respectively (Bailey, 2011).

The situation is rather grim for large carnivores in Arabia and the Levant. Remaining leopard populations are being closely monitored in the three countries they are known to remain, with little hope of widespread recovery (Farhadinia et al., 2019). Cheetahs are highly unlikely to return without the aid of reintroduction programs (Durant et al., 2017). For canids like wolves, the situation is potentially less dire as they are less fastidious, better adapted to human environments (Barocas et al., 2018), and have higher reproductive rates. Fortunately, wildlife conservation is on the rise across the Middle East. Governments have implemented protective legislations and biodiversity conservation plans, while advocacy organisations have become more involved in recent decades. Protected areas and governing bodies, as well as research and monitoring programs, have been established throughout the region, at least in some capacity. However, policy and practice are not uniform.

2.4.2 Scale of jurisdictional crossover

Without doubt, across its wide range, the Arabian wolf must navigate one of the most complicated geopolitical landscapes on Earth. Its distribution crosses a socio-politically complex region with a diverse historical and contemporary cultural heritage. For thousands of years, the region has been a melting pot of different tribes, ethnicities, races, and religions; each with its own value and belief systems. It is the birthplace of three of the world's most prominent monotheistic religions, and home to their most important holy sites. With half of the global population following one of these three religions, the region experiences millions of visitors each year making pilgrimage to fulfil their religious obligations (Luz, 2020). Economically, the Middle East is a stronghold of oil reserves and mineral resources, with local industries employing more than five million foreign workers annually (Sørli et al., 2005). As oil is a highly sought-after commodity, global interest in the region has dramatically increased over the last century (Goldschmidt, 2002).

As a result, the Middle East is a hotspot for intra-human conflicts. It is consistently recognised as one of the most conflict-prone regions on the planet (Sørli et al., 2005). During the last century, the region was an epicentre for both world wars, and has had constant internal wars ever since. Civil wars are commonplace, often resulting in countries lacking central governance. Challenges to state boundaries are continuously sought through militant campaigns or governmental agendas. Landmines are commonplace along some country borders for fear of military advancement from neighbouring states. These intra-human conflicts can directly impact upon wildlife and ecosystems. Armaments inadvertently kill wildlife, but also destroy habitats and cause environmental pollution and ongoing disruption (Lawrence et al., 2015). Furthermore, conflicts can have a long legacy, as remnant explosives represent an ongoing concern for wildlife (Eniang et al., 2007; Westing, 1996).

Conversely, wildlife can also benefit from areas with unexploded ordinance, which is the case for wolves who appear to successfully navigate landmines (*pers. obs.*). In fact, just like wolves in Germany who use military training areas as safe havens (Reinhardt et al., 2019), Indian wolves in the Golan Heights use minefields to escape lethal persecution (Wallach, 2015). In saying that, the opening of wildlife 'refuges' by creating human no-go zones can be an unexpected outcome of warzones (McNeely, 2003). Indeed, the demilitarised zone between North and South Korea contains untouched ecosystems with flourishing wildlife populations (Kim, 1997), while some military lands have been converted into wildlife sanctuaries in the United States (Havlick, 2011).

Land disputes play a major role in the region's political tensions (e.g., Bunton, 2013). As such, borders have experienced considerable changes over the course of the last century. It has even been suggested that governments in the region are using conservation strategies as political tools to expand their boundaries (Johnson, 2019). In the current political mosaic, the Arabian wolf's range covers eleven recognised states, intertwined with swathes of disputed land. Of course, each nation has its own set of legislations related to wildlife protection, and levels of enforcement. For nomadic wildlife with large home ranges, like the Arabian wolf, traversing this complex geopolitical landscape can be precarious and troublesome as actions and behaviours in one location may not cause conflict with people, but in another may result in them being shot. Arabian wolves must navigate this complexity daily.

2.4.3 Governmental and non-governmental conservation effort

Interest in wildlife conservation has proliferated throughout the Middle East, with governmental and non-governmental effort continuing to be established. The United Nation's Convention on Biological Diversity, launched during the 1990s, spurred many nations to become active participants. By the turn of the century, most nations across the region had ratified the convention and subsequently produced a National Biodiversity Strategy and Action Plan (NBSAP). With Iraq being the last to join in 2009, all eleven nations now have concrete plans to conserve biodiversity. These involve defining pitfalls within the current legal and institutional frameworks and developing solutions to improve strategies for biodiversity conservation and include many governments forming focused ministries or agencies to act as authorities for environmental affairs.

However, although protective legislation now exists throughout the region, awareness and enforcement vary considerably across and within state boundaries. An overview of the legal frameworks, governance, and conservation efforts within each country highlights key differences and similarities, pertinent to the conservation of the Arabian wolf (Table 2.1). Currently, all countries have legislation that prohibits or regulates hunting. It is universally illegal to hunt or kill protected species and to hunt or kill wildlife inside protected areas. However, legal frameworks vary between countries. For example, some countries have had consistent legislation relating to wildlife protection in place for decades, while the legal frameworks in others are still in their nascent stages. Some countries have had endless repeals and amendments, whereas others have had few regulations added to their long-standing laws (*see* Table S2.1 for a more detailed review of legislation and conservation effort[1]).

Inconsistencies in legal frameworks create confusion within policies; legislations that are present in some countries seem to exist solely on paper, but not in reality. Adding to this confusion is the fact that many governments continue to lack solid institutional structure attributed to biodiversity conservation or environmental matters. Such muddled institutionalisation often results in a lack of trained staff, funding, and infrastructure. Most nations acknowledge such shortcomings in their NBSAP's and aspire to improve (*see* Table S2.1 sources).

[1] Information was gathered from scientific literature, grey literature, governmental and non-governmental reports, and websites. Some websites were either no longer active or had not been updated for a number of years (noted in the table). Discrepancies were reduced by being as thorough as possible, however, some inconsistencies were worth noting. For example, a series of web articles stated that wolves are only legally protected in Israel and Oman, though this does not explicitly appear to be the case. 'Legal' protection occurs throughout their range and active protection occurs in Jordan (*pers. obs.*). It might be that particularly successful protection occurs in Oman; however, this is doubtful as poaching remains a common occurrence (Giangaspero and al Ghafri, 2015). In the case of legal frameworks, individual legislations were verified against official documents or their translated versions. Effort was made to enhance accuracy by reducing the number of official resources for legislation to avoid inconsistencies between countries. However, this was challenging as not all nations featured consistently in any one online resource. The FAOLEX database on the Food and Agriculture Organisation of the United Nations (FAO) website (http://www.fao.org/faolex/en/) was used as the primary repository for sourcing legislation as it was the most comprehensive. For additional legislation listed in governmental reports, legitimacy of the listed legislation and the cited source was assessed.

Table 2.1. Overview summary of Arabian wolf status, protection, and conservation effort in the eleven countries likely to be within its distribution. For further details, see Table S2.1 in Supplementary Material.

Country	Enforcement of protective legislation	Conservation effort	Protected areas (PAs) % Total land area	*C. lupus arabs* status (Density; trend; persecution)
Egypt (Sinai Peninsula)	Some inside PAs†	Active network of NGOs across Egypt working towards hunting reduction; however, the primary local focus (Sinai) is on marine and coastal biodiversity.	13.14	Rare†; unknown; widespread†
Iraq	Negligible	Signed Convention on Biological Diversity (2009) and produced National Biodiversity Strategy and Action Plan (2015). Has active network of conservation NGOs.	1.53	Unknown; unknown; widespread
Israel / Palestinian Territories (West Bank and Gaza)	Israel: Strong inside and outside PAs Palestinian Territories: Strong in some areas	Israel: Strong governmental and non-governmental support for wildlife protection and conservation. Palestinian Territories: Network of NGOs but many are inactive due to cuts in overseas funding.	Israel: 24.49 Palestinian Territories: 8.36	Israel: Common; stable; negligible Palestinian Territories: Unknown; unknown; unknown
Jordan	Strong inside PAs, some outside	Strong semi-governmental support for wildlife protection and conservation, and a large network of NGOs.	3.09	Occurs in PAs; declining†; widespread
Kuwait	Strong inside PAs	Well-established network of NGOs with an increase in prioritising biodiversity conservation.	17.10	Extinct; NA; NA
Oman	Strong inside and outside PAs†, but poaching common	Strong governmental and non-governmental support for wildlife protection and conservation.	2.57	Occurs in PAs; declining†; unknown
Qatar	Some inside PAs	An increase in governmental and non-governmental effort, however, the primary focus is on marine and coastal biodiversity.	13.23	Extinct; NA; NA
Saudi Arabia	Some inside PAs	Several governmental and non-governmental pushes towards wildlife protection and conservation, but difficulty in moving from policy to practice.	4.76	Common; declining; widespread
Syria	Negligible	A small network of NGOs exists, but civil and political tensions have caused conservation efforts to cease.	0.69	Unknown; unknown; unknown
United Arab Emirates (UAE)	Strong inside PAs, some outside	Strong governmental and non-governmental support for wildlife protection and conservation.	17.95	Extinct; NA; NA
Yemen	Negligible	Predator protection efforts increasing (e.g., critically endangered Arabian leopard), but civil and political tensions hinder sufficient expansion.	0.77	Occurs in PAs; declining; unknown

†Considerable level of uncertainty due to either a lack of, or conflicting, information

However, even with such institutional and strategic improvements being made, shortfalls remain in moving from policy to practice. For example, considerable effort went into implementing Saudi Arabia's conservation strategies and action plans. The relevant governmental authority engaged in dramatic transformation, prioritising the structured support for their protected area network and protected species lists. Yet, the country falls short in assigning protective status, enforcing laws, and acting upon violations (Barichievy et al., 2018). Although wolves persist within Saudi Arabia's designated protected areas (Abuzinada, 2003; Seddon et al., 1997; Wronski and Macasero, 2008), it is unclear how much protection they are actually afforded (Cunningham and Wronski, 2010; Seddon, 2000). What is known is that Arabian wolves are subjected to heavy persecution outside (Aloufi and Amr, 2018; Cunningham et al., 2009; Cunningham and Wronski, 2010; Wronski and Macasero, 2008; Zafar-ul Islam et al., 2019). In fact, it is not uncommon to see persecuted wolves hanging in trees while driving along desert roads in Saudi Arabia (Cunningham et al., 2009; Cunningham and Wronski, 2010).

Protected areas remain a key legislative protection for the Arabian wolf. However, the status and meaning of these protected spaces differs between countries. For example, while some countries have a single managing agency, authoritative control of protected areas can be variable within a country. Jordan's Royal Society for the Protection of Nature (RSCN) actively enforces protection laws in areas under their governance, however, they are not authorised to govern all the country's protected areas (UNEP-WCMC, 2020). Additionally, some protected areas allow livestock grazing, while others do not. In Israel, Bedouin pastoralists receive large fines for moving their livestock into protected areas, whereas livestock are the primary users of many protected springs in Jordan (*pers. obs.*). Another example of difference is in enforcement. On Yemen's mainland, protected areas appear to be 'protected' in name only (Schlecht et al., 2014). Although areas have been designated, they are not included in official registries and lack any institutional governance (Environmental Protection Agency, 2017). Along with the gulf countries, Yemen's mainstream conservation effort tends to focus on marine and offshore biodiversity (e.g., Socotra Island). Plans and proposals for extending the protected area network have been presented, however, action is yet to be taken (Schlecht et al., 2014).

To mitigate these differences, non-governmental conservation effort is increasing throughout the region and domestic NGOs have now been established in all countries (Table S2.1). In countries where conservation is yet to become a national priority, local NGOs fill the void to conduct much-needed research and monitoring surveys. The Foundation for the Protection of the Arabian Leopard in Yemen is a non-profit dedicated to Arabian leopard conservation within the country. In the case of Iraq, the primary conservation NGO works with governmental ministries towards implementing conservation strategies. Established in 2003, Nature Iraq has been at the forefront of governmental liaisons and policy change for any issues relating to wildlife protection and biodiversity conservation.

Implementing protective legislation and designating protected areas can only go so far towards the conservation of the Arabian wolf. Deeming it illegal to kill them does not necessarily stop people from doing so (Eid and Handal, 2018). It is more important to understand the needs and struggles of the people that share the land with such wildlife, and compassionately work with them towards a peaceful coexistence. Resolution of any conflict is only possible once the situation has been assessed from the perspective of those most affected.

2.4.4 Society, culture, and human-wolf relationships

Humans and wolves have shared a vibrant coexistence across the Middle East throughout history. Archaeological (Davis and Valla, 1978; Dayan, 1994) and genetic evidence (Freedman et al., 2014; Vonholdt et al., 2010) point to early domestication of wolves or a wolf-dog ancestor in the Levant at least 12,000 years ago, suggesting that humans and canids have been forming close relationships in the region for thousands of years. With the advent of agriculture not long after (Zeder, 2011), conflicts between humans and wolves would undoubtedly have ensued. From this point, dogs were being selectively bred for practical purposes such as livestock protection (Gehring et al., 2010) and hunting (Guagnin et al., 2018), leading to further isolation from their wild ancestors (Landry, 1999). Today, dogs are still used by Bedouins for livestock protection and to warn off predators like wolves around camps and villages.

Human-wolf conflicts still occur to this day. Pastoralists frequently lose unsecured sheep and goats to wolf depredation, often sparking retaliation (Cunningham et al., 2009). On top of livestock-related persecution, age-old beliefs that wolves endanger human lives (Seddon and Khoja, 2003), and that wolf body parts can be used for therapeutic purposes (Aloufi and Eid, 2016), persist. Moreover, widespread cultural ideals depicting canids as malevolent and impure have triggered large-scale eradication attempts (Subasi, 2011). In these same regions, legal and illegal hunting and persecution are common (Eid and Handal, 2018; Giangaspero and al Ghafri, 2015), and many threatened species, including Arabian wolves, are largely confined to protected areas (Amr et al., 2004).

Conversely, wolves are accepted and even appreciated in other regions. In Israel's Negev, particularly in the crop farming landscapes of the Arava Valley, wolves and people peacefully coexist. Farmers assist wolves and other wildlife by intentionally providing water in this hyper-arid landscape, where wolves are free to roam through agricultural fields. A series of incidents in 2017, in which a few wolves came uncomfortably close to people at a village adjoining a nature reserve, generated outrage amongst the locals; but this was quickly resolved with education programs around the importance and hazards of nature and wildlife. Likewise, villagers and pastoralists coexist with wolves in Yemen's Hawf district, the location of the country's only mainland designated protected area (Schlecht et al., 2014), where acceptance of wolves and other predators is reportedly higher than in other parts of the Arabian Peninsula (Khorozyan et al., 2014).

It has clearly been shown that coexistence between people and Arabian wolves is achievable. Like elsewhere in the world, strategies that assist in coexistence are required. Although livestock loss is not a major concern in Israel's crop farming landscapes, farmers are not free from economic costs of living with wildlife. However, they have learnt to adapt; strategizing to minimise such costs and ultimately appreciating the many benefits of having wildlife on their doorsteps. With improvements in cooperation and planning, coexistence is possible elsewhere.

2.5 Moving Forwards

2.5.1 Building collaborative planning

Primarily, it is important for conservation groups and authoritative bodies to form caring relationships with local stakeholders and cooperatively plan solutions for mitigating potential costs and hardships associated with coexistence. Rather than forcibly implementing policy and legislation, in which violators (often unwary) are automatically penalised, authorities should take a step back and understand the underlying issues and lend assistance. For example, Bedouin pastoralists are often marginalised when promoting conservation goals, with authorities failing to act on environmental damage reported by Bedouins and discriminately penalising them more than other societal groups (Gilbert, 2013). Jordan's RSCN, motivated by early flaws recognised when not considering pastoralists in the establishment of a nature reserve, began involving Bedouins as primary stakeholders and collaborators in developments of further conservation projects (e.g., Wadi Rum Nature Reserve), with escalated success (Chatty, 2002).

The cultivation of efforts and achievements from conservation groups and authoritative bodies throughout the Middle East is certainly promising, but these are largely confined to individual jurisdictions. For example, the UAE is currently one of the most committed Arab countries to wildlife protection: local NGOs have spearheaded international reintroduction projects and residents are encouraged to report any environmental or wildlife-related violations (Salama, 2018).

Likewise, Israel is quite conservation-minded, with clear goals and objectives, as well as strong public adherence to wildlife protection (Nemtzov and King, 2001). However, collaborative efforts across international borders must improve if Arabian wolf populations are to recover.

What is likely to have contributed the most to the successful wolf recovery in Europe is the development of transboundary planning initiatives. All European countries have subscribed to the Bern Convention (Convention on the Conservation of European Wildlife and Natural History, 1979), by which all wolf populations and habitats are fully protected (Boitani, 2003). During the 1990s, the Large Carnivore Initiative for Europe (within the IUCN's Species Survival Commission) was established to improve coexistence between people and wolves throughout the region, while prioritising heightened consideration of both parties. Although transboundary conservation initiatives have also been carried out within the Middle East, these have mostly focussed on local-scale projects across individual borders (Knight et al., 2011).

International research collaborations have increased over the last decade or so, however, large-scale applications and policy implementations are yet to be pushed. For example, the Middle Eastern Biodiversity Network was established in 2006 between universities and research institutes from Iran, Jordan, Lebanon, and Yemen in a collaborative effort to conserve biodiversity across the Middle East, but no information has been updated since 2009 (Krupp et al., 2009). More recently, Compassionate Conservation Middle East (CCME) was established as a research group collaboration between various institutes and NGOs in Israel/Palestine and the Centre for Compassionate Conservation at the University of Technology Sydney, Australia. CCME has developed wolf research and conservation projects across Israel and Palestine with the primary objectives of improving human-wolf coexistence and regional collaborations – a key tenet of CCME is that 'nature knows no borders'. Unfortunately, political tensions in the region currently make these visions and goals unattainable or hinder progress.

2.5.2 Concluding remarks

The Arabian wolf is likely to be an important trophic regulator of desert ecosystems of the southern Levant and the Arabian Peninsula. To ascertain just how important it is, there are significant knowledge gaps that need to be filled. Although populations are sparse across most of its wide range, the Arabian wolf remains the most widespread large predator inhabiting the deserts of the Middle East. Yet, little is known about its potential influence on these arid ecosystems. Considering its close association with human infrastructure (Barocas et al., 2018) and reliance on anthropogenic food resources (Shalmon, 1986) in Israel, there is some conjecture as to how important a role the Arabian wolf plays in shaping trophic cascades like their larger, temperate counterparts.

That it might do so, however, is only within the context of their acceptance by people. Demarcations of tolerance or persecution may override the trophic position of these desert-dwelling wolves. As has been previously noted, conservation conflicts are often interrelated to intra-human conflicts (Redpath et al., 2013), and the Middle East is one of the most complex geopolitical landscapes in the world. Any solutions to conserve the Arabian wolf must be cognisant of this complexity and strive to ameliorate the internal conflicts, attitudes, and values that are ingrained among the peoples that share this landscape.

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Chapter 2. Supplementary material

Table S2.1: Overview of legal frameworks, governance, and conservation efforts within the eleven countries considered to fall within the Arabian wolf's range.

Country	Legal Framework Relating to Biodiversity Conservation and Wildlife Protection	Enforcement (governing bodies, inside/outside protected areas, species)	Conservation effort / Non-Governmental Organisations (NGOs)	Terrestrial Protected Areas - km² (% of total land area)[φ]	*C. lupus arabs* status	Persecution
Egypt	Egyptian wildlife conservation was first acted upon in 1982 with the establishment of the Egyptian Environmental Affairs Agency (EEAA). The following year, Law No. 102 (1983) for Nature Protectorates was issued upon recommendation from the EEAA, which prohibited any actions that led to destruction or deterioration of the natural environment or harm to biota inside protected areas (PAs), including catching, transporting, killing or disturbing wildlife[1]. The EEAA was designated as the administrative body responsible for establishing regional offices within governorates where PAs exist, preparing and executing studies and programs to enhance protection within PAs, conducting wildlife monitoring surveys, and guiding and educating the public around nature conservation[2]. All societies and organisations regarding environmental protection were required to seek council from the EEAA, and a special fund was to be established to collect donations, grants, admission fees, as well as fines incurred	In 2002, it was recommended that the Nature Conservation Sector (NCS) of the EEAA become an autonomous institution under the Ministry of State for Environmental Affairs. It was envisioned that the NCS would become a properly resourced institution, with adequate staff, funds and policies; and would be able to manage the nation's PA network, helping to secure ecological integrity. However, the PA system remains seriously under-resourced. Almost none of the revenue raised has been reinvested within the system. Although laws support the executive role of the NCS, the sector operates largely within a policy vacuum, with few formal policies for nature conservation and protected areas. Enforcement of laws is poor due to low levels of government funding, few trained staff and limited training opportunities, poor infrastructure and conflict with local communities[5]. Law No. 9 (2009) that prohibits killing of wild animals only applies to either protected species or within protected areas. It is innocuously stated in the	The largest, oldest and most recognised environmental NGO in Egypt is the Hurghada Environmental Protection and Conservation Association (HEPCA). Established in 1992 by some concerned Red Sea divers, the NGO has since grown to become a large network of scientists, professional divers, industry and community experts proactive in protecting and preserving natural resources, as well as promoting conservation and sustainable tourism. However, while HEPCA focusses on both land and sea, projects are mostly confined to the Red Sea Governorate[9]. Several smaller NGOs exist today throughout Egypt[119]. Perhaps the one with the most nation-wide recognition is Nature Conservation Egypt (NCE). Established in 2005 by a number of Egypt's leading nature and biodiversity conservation experts, NCE works towards conserving Egypt's natural heritage and the promotion of its sustainable use. As an IUCN member, NCE collaborates with local experts, governmental bodies and international organisations in	129,390 (13.14) *Federal ministry/agency (48%)* *Not reported (52%)*	Only found on the Sinai Peninsula, where they are locally endangered and legally protected[5]. Found to be among the rarest species in a recent carnivore survey of three protected areas[11].	Widespread[11]

	by any violators of the new law. Legal and infrastructural authority within the EEAA remained weak. In 1994, attempts were made to strengthen the authority and address legal gaps by introducing the Environmental Law (Law No. 4/1994)[3]. The EEAA was then re-established under a cabinet of ministers as the highest national authority in charge of the environment and the roles and responsibilities of the Agency increased. The EEAA was then made solely responsible for enforcing the law and penalties for violating became more severe. Under the current law (Environmental Law No. 9 of 2009)[4], it is prohibited in any way to perform any of the following actions: hunting, killing, or capturing wild animals; as well as possessing, transferring, or trading wild animals, whether dead or alive.	'fine print' that the executive regulations of this law specify which species and areas to which provisions apply, however, these are not easily attainable[6]. PA managers do have the authority to enforce legislation, however, fines are seldom issued with a blind eye being turned on many incidents[7]. Still, with the limited enforcement that exists, patrolling and monitoring activities of the NCS have apparently led to a reduction in the hunting of large mammals within PAs; increases in some ungulate populations have been recorded[8].	scientific research, advocacy, education and outreach to support species, their habitats and local communities[10].			
Iraq	In 1979, Law No. 21 on the Protection of Wild Animals and Birds was issued to create protected areas by dividing Iraqi territory into three categories: prohibited zones, protected zones and hunting zones[16]. The law was repealed in 2010, by Law No. 17 (also 'Law of Protecting Wild Animals and Birds'), with an aim to protect wild animals and	Information regarding bodies governing nature conservation in Iraq is conflicting. Law No. 17 (2010) states that it is the duty of the Ministry of Agriculture to create PAs to protect endangered species, as well as to determine hunting grounds and the species allowed to be hunted[17]. However, articles quote the Ministry of Health	Nature Iraq was founded in 2003 as Iraq's first and only nature conservation NGO. Since its establishment, it has initiated and been involved in ongoing projects with aims of protecting and restoring the environment and biodiversity within Iraq. The NGO is active in conducting monitoring surveys, scientific research and education programs, and	6,714 (1.53) *Not reported (100%)* Currently, no national network of PAs exists, but plans for establishing such a network are underway[18].	Unknown[20]	Widespread[20,21]

	organise hunting grounds by regulating hunting licenses and determining which species can be hunted and which are protected[17]. Penalties for violating the law are also specified. In the autonomous Kurdistan region, Law No. 8 (2008) on Environmental Protection and Improvement states that it is prohibited to hunt, kill, capture, possess or transfer animals that are threatened with extinction[18]. The rest of Iraq followed suit the following year by issuing Law No. 27 (2009) on Protection and Improvement of the Environment. Article 18 of this law states that it is prohibited to hunt animals that are threatened or likely to be threatened with extinction or use them for trade[19].	and Environment as the body considering PA network plans[18, 19], with no information available regarding a change in governmental authorities. Updated information is difficult to obtain as official websites are currently out of use[14]. Still, although legislation exists around protected areas and species, protection appears to be in name only, with enforcement being negligible[19].	is the primary organisation involved in liaising with the government regarding any conservation issues. Their main objectives include improving the capacity of Iraq's institutions to protect biodiversity and to increase environmental awareness and stewardship within the public. Nature Iraq has helped with the establishment of several smaller NGOs through training programs[26]. Iraq only signed the Convention on Biological Diversity as late as 2009 and produced its first National Biodiversity Strategy and Action Plan in 2015[135].			
Israel / Palestinian territories (the West Bank and Gaza)	Israel was the first country in the Middle East to issue a law explicitly protecting wildlife. The Wildlife Protection Law (1955) prohibits the hunting of game or protected wildlife species, unless under a hunting licence or permit granted by the Ministry of Agriculture. Permits are not readily attainable but may be granted to hunt for scientific purposes; or to prevent agricultural damage, dangers to humans or other animals, and infectious diseases[22]. The Wildlife Protection Regulation was then implemented in 1971 to establish a national PA	The Israel Nature and Parks Authority (INPA) is a governmental organisation within the Ministry of Agriculture. The INPA is delegated to preside over any issues regarding nature and conservation throughout Israel, as well as some PAs in the West Bank† (Area C). The organisation was established in 1998, by merging two pre-existing organisations who had been managing PAs since the 1960s. The INPA is involved in forging national policies to protect biodiversity both inside and outside of PAs and employs proactive rangers with legal	The Society for the Protection of Nature in Israel (SPNI) was established in 1953 and is the largest non-profit organisation operating within Israel. The SPNI collaborates with the Ministries of Agriculture and Environmental Protection, as well as the INPA, zoos and universities to protect biodiversity and nature. With field schools scattered throughout the country, the SPNI coordinates ongoing programs for monitoring, research, education and eco-tourism to increase environmental awareness and stewardship[28]. Several	**Israel** 5,133 (24.49) *Federal ministry/ agency (98.5%)* *Not reported (1.5%)* **Palestinian Territories** 517 (8.36) *Federal ministry/ agency (100%)*	**Israel** Stable population throughout Negev Desert[27] **Palestinian Territories** *Unknown – not certain of occurrence, however, preliminary surveys are currently underway – NPS*	**Israel** Negligible; controlled cull between 2005 – 2008[27] **Palestinian Territories** Unknown

	network and set restrictions for hunting within PAs[23]. Further regulations were added in 1976, which defined the species to be protected by law[24]. Environmental legislation in the Palestinian Territories has been less organised. Between WWII and 1967, the West Bank was subject to Jordanian laws, while Egyptian laws applied to Gaza. Following the 1967 Arab-Israeli War, legal frameworks within the Palestinian Territories were established, however, they have remained rather scrambled. The Palestinian Environmental Law was issued in 1999, which gave the Palestinian National Authority (PNA) the right and responsibility to study and assess environmental implications of any project within the Territories. Under this law, the PNA designates and delineates PAs with the aim to protect biodiversity. The law prohibits hunting, shooting, catching or transporting of any wild animals specified in the regulations, as well as activities which cause any damage to the natural environment[31]. In 2003, Agricultural Law No. 2 was issued, which also addresses protection of nature and biodiversity. It gives clear definitions of PAs and places the Ministry of Agriculture in charge of the PA network. Under this law, the Ministry is responsible for cooperation with relevant authorities to	jurisdiction to enforce wildlife protection laws throughout the entire country[25]. Any lethal control of wildlife species is stringently coordinated with the INPA and permissible only in exceptional circumstances[27]. Governmental structure within the Palestinian Territories has been more muddled. After the Oslo Agreement* in the 1990s, the PNA established the Department of Environmental Planning, who were assigned to track environmental management within the PNA's territories (Gaza and areas A and B of the West Bank). Simultaneously, however, the separate Ministries of Health, Agriculture, and Local Government all formed departments covering environmental affairs, which resulted in duplicate authorities with overlapping responsibilities for environmental administration and decision-making. Until the turn of the century, attempts were made to establish a central body to govern environmental issues. There was limited success until 2002, when the Environmental Quality Authority (EQA) was designated as the primary authority working with the Ministry of Agriculture to manage biodiversity conservation and the PA network. In 2010, the EQA developed a comprehensive 3-year strategy with objectives to enhance	educational and research institutions exist within Israel, with varied environmental research projects including the fields of biodiversity conservation and human-wildlife coexistence[e.g., 32]. In the West Bank, conservation efforts only really began taking off around the turn of the century. Palestine Wildlife Society (PWS) was established in 1998 as the first Palestinian NGO focussing on wildlife conservation. Their main objectives were to be based around education, awareness and capacity building within the public in terms of wildlife and nature conservation[29]. The Biodiversity and Environmental Research Centre was another early NGO, established in 2001. However, their website does not appear to have been updated since the early 2000s[41]. The environmental sector continued to struggle until 2013 due to a lack of attention, structure and a clear vision, as well as low communication among NGOs. The NGO Development Centre (NDC) then created a framework encouraging NGOs to align their projects with common goals and objectives. Several environmental NGOs now operate; however, many are currently inactive due to a lack of interest and cuts in international funding[31].			

	develop cohesive and comprehensive management plans to conserve all organisms within the PA system[31].	environmental protection and institutional structure related to the environment. Performing the assigned duties remains overwhelming due to the current political situation, as well as a lack of human interest and financial resources. Violations are common, but action is rarely taken. There is an almost complete disregard within the public for the law that prohibits illicit hunting, and excessive bureaucracy and corruption further hinder effective governance[31].	Nature Palestine Society (NPS) was founded in 2017 with an explicit mission to protect, conserve and educate around nature and biodiversity. NPS has established national, regional and international collaborations with governmental, research and educational institutions to monitor and protect biodiversity, and promote responsible relations between people and the environment[30].			
Jordan	The first action taken by the Jordanian government towards environmental protection was in 1976, when the Department of Environment was established within the Ministry of Municipal, Rural Affairs and the Environment. The National Environment Strategy was then issued in 1991, paving the way for new environmental legislations, while making Jordan the first Middle Eastern country to adopt a clearly defined national strategy for environmental protection[33]. Since then, environmental protection laws have continually been replaced, with laws not remaining in place for much longer than ten years: The Environment Law No. 12 (1995) was repealed by the Environment Protection Law No. 52 (2006) and again by the Environmental Protection Law No. 6 (2017)[34]. The law prohibits	The Royal Society for the Conservation of Nature (RSCN) in Jordan is an independent organisation that functions via legal mandate under delegation from the Jordanian government. Established in the 1960s, the RSCN has a strong partnership with the country's public sector in hunting regulation and PA management, issuing hunting permits and enforcing legislation related to illegal hunting[36]. Rangers are employed throughout Jordan to patrol open areas, both inside and outside of PAs, and the organisation has spearheaded novel initiatives in attempts to curb illicit hunting (e.g., social media surveys of hunters with their kills[35]). Although considerable effort goes into enforcing wildlife protection laws, successful elimination of illicit hunting continues to struggle as a result of a general	The RSCN leads the country in terms of wildlife protection and conservation effort. Since the organisation's establishment, their primary objective was to coordinate with the government to regulate hunting. In the 1970s, the RSCN was given responsibility to issue hunting licences and establish patrols for enforcing hunting laws. They were involved in formulating the first Environmental Protection Law in 1995. Several PAs within Jordan have been established by the RSCN, with progressive ambitions and actions for both nature conservation and ecologically aware socio-economic development[37]. Reintroduction programs commenced in the early 1980s, where the once-extinct Arabian oryx was successfully bred in Shaumari Reserve[38]. The end of the decade saw the	2,774 (3.09) *Federal ministry/agency (3%)* *Not reported (28%)* *Local communities (16%)* *Government-delegated management (50%)* *Non-profit organisations (3%)*	Occur in protected areas[123, 126]	Widespread (*N. Hamidan pers. comm.*)

	hunting of protected species and hunting within PAs, with strict penalties applying for violations. The following year (2018) saw further institutionalised change with the issuing of the Regulation of the Department of Environmental Protection No. 37 and the Environmental Protection Fund Law No. 18.	inadequacy of existing legislation and institutional structure. Specifically, continuous amendments and repeals cause instability and scatter within the legal framework, making referring to the laws difficult and impractical[36].	establishment of Dana Biosphere Reserve, which on top of creating a PA, also created jobs and boosted the economy within the local community. The success of ecotourism at Dana encouraged the RSCN to help manage one of Jordan's biggest tourist attractions, the Wadi Rum PA. RSCN incorporated the local Bedouin community into decision-making and provided hundreds of jobs relating to eco-tourism[39]. Since the turn of the century, the RSCN has been actively involved in increasing awareness and capacity-building throughout Jordan and across the Middle East, and is one of the leading organisations in campaigning and advocating environmental protection across the region [37]. There is now over one hundred registered environmental NGOs within Jordan tasked with increasing environmental awareness throughout the general public [40].			
Kuwait	Kuwait started implementing legislations related to the environment during the 1960s, however, these largely centred around pollution, and marine and oil resource conservation[42]. In the 1970s, a supreme committee was established by a Decree of the Council of Ministers to integrate efforts of various organisations active in the field of environmental protection, resulting in the promulgation of Law No. 62	Concern for biodiversity conservation was lacking in Kuwait until 1998, when the newly established EPA released the National Biodiversity Strategy in collaboration with the United Nations Development Programme (UNDP) and the IUCN. Existing legislation was reviewed, and the Strategy outlined the gaps in policy and practice relating to biodiversity within the State of Kuwait. This was the first	The first NGO to touch on environmental issues in Kuwait was the Kuwait Fund for Arab Economic Development, founded in 1961. Since its establishment, environmental protection has been a major concern for the fund, although biodiversity conservation has only played a minor role in its aims and objectives. Nevertheless, the organisation has expanded since the 1970s, gaining	2,979 (17.1) *Federal ministry/agency (26%)* *Not reported (64%)* *Government-delegated management (8%)* *Joint governance (2%)*	Extinct[124]	NA

	(1980) on Environmental Protection[43]. In this law, the Environmental Protection Council was established as part of a unified legislative and institutional framework with explicit policies for environmental protection[44]. This law was then repealed in 1995 by Law No. 21 concerning the Establishment of Environment Public Authority (EPA)[45]. Major gaps remained in biodiversity related legislation, with no legislative arrangements to declare and gazette PAs, and no laws to regulate trade and hunting of wildlife until the turn of the century[46]. Resolution No. 93 (2003) regulating Sale and Trade in Endangered Wildlife Species was then issued, with an aim to protect endangered plant and animal species[47]. Previous provisions and legislations relating to the environment were then integrated in 2014 to form the Environmental Protection Law No. 42. This law prohibited harming or transporting wild animals and defined the species and areas to which this law applied[48]. Further regulations were then issued with Decree No. 3 (2017) on the Executive Regulations on Biodiversity[49], which was then amended in 2019 by Resolution No. 3[50]. This decree and its amendments set further regulations for hunting and delivered explicit definitions of PAs and protected species.	step towards wildlife protection in Kuwait[46]. The EPA is a public authority with legal jurisdiction over all environmental affairs. Supervised by the Supreme Council for the Environment, the EPA is attached to the Ministerial Cabinet and allocated a position within the State's budget to take care of environmental issues, including: setting and applying policies and composing strategies and action plans regarding environmental protection; preparing draft laws, regulations, systems and requirements for environmental protection; participate in environmental research, monitoring surveys and setting framework for environmental awareness programs[51]. The Environmental Protection Law No. 42 (2014) established the Environmental Police force within the Ministry of Interior, who are tasked with enforcing the environmental laws and regulations released by the EPA[42].	much success throughout the region and developing countries worldwide in a push towards sustainable development[52]. The Kuwait Environmental Protection Society was established in 1974 and is the leading NGO in dealing with biodiversity conservation. The organisation has evolved into a body of various cooperating committees dedicated to environmental protection: The Wildlife Protection Committee raises awareness of wildlife and the natural environment in Kuwait, and proposes programs and legislation to protect both; the Public Relations Committee participates in various environmental fairs and events; the Media Committee publishes work in media outlets; the Friends of Environment Committee is concerned with youth – participates in folk events, environmental activities, increases awareness and educates about environment; and the Wild Environment Protection Committee follows up and monitors negative activities and transfers to relevant authorities[53].			

Oman	Oman first issued legislation regarding biodiversity conservation in 1980 with Royal Decree No. 6 on the Law of Protection of National Heritage[54]. Not long after, the Law on Conservation of the Environment and Prevention of pollution was issued by Royal Decree No. 10 (1982). To fill in gaps in legislation two decades later, this law was repealed by Royal Decree No. 114 (2001)[55], setting the stage for a series of environmental legislations and regulations; most of which remain in place today[56]. This new law placed the Ministry of Regional Municipalities, Environment and Water Resources (MRMWR) in charge of ecosystems, natural processes and wildlife species and defines penalties for harming or spoiling nature conservation areas or wildlife. Over the following two years, provisions were explained more explicitly, clarifying regulations and definitions. Hunting, and any other form of killing, without permit was banned under Ministerial Decision No. 101 (2002) on the Prohibition of hunting, killing or capturing of wild animals and birds[57]. In 2003, the Law on Nature Reserves and Wildlife Conservation was issued, defining protected areas and species[58]. In 2007, under Royal Decree No. 90, the Ministry of Environment and Climate Affairs (MECA) was established to deal with all issues related to the	In 2001, the National Biodiversity Strategy and Action Plan was released to highlight issues relating to biodiversity conservation[61]. The plan describes protected areas and endangered species, however, it pointed to serious policy gaps within the existing legislation. Over the following years, a central body was established, and new laws were issued explicitly defining provisions towards enhanced wildlife protection. MRMWR held institutional authority over biodiversity related issues from 2001 until 2007, when it was split into two separate ministries, with MECA being assigned to exclusively govern environmental issues. Alongside the establishment of MECA came new regulations affording the ministry complete authority over protected area and species conservation. Among MECA's primary aims were increasing the number of wildlife PAs and the number of rangers in charge of monitoring PAs and wildlife[63]. However, although MECA acts as the institutional authority over wildlife protection, it seemingly does not hold full legal jurisdiction. Instead, the legal process operates in the 'old-fashioned way', where rangers are required to report violations to police to bring legal action in court[62]. Poaching remains a common occurrence both inside and outside of PAs[120].	Oman is depicted as being one of the Middle East's most engaged countries when it comes to environmental protection, as well as one of two countries leading the region in terms of wolf conservation[63 - 66]. It was apparently the first Arab state to create a special government body dedicated to environmental protection in 1974[63]. Oman played a large part in the Arabian oryx reintroduction program with the establishment of the Arabian Oryx Sanctuary in 1994[67], which had limited success[39]. Since then, eleven Royal Decrees have been issued to establish new PAs throughout the country[68]. Although a relatively recent development, Omani NGOs carry an astounding track-record today. Environment Society Oman (ESO) was founded in 2004 and remains the sole Omani NGO that supports the government's campaign for environmental protection and conservation on a national scale[70]. The organisation has established comprehensive monitoring and research programs and is active in increasing education and capacity building through various public and private sectors. Through its work with schools, Omani children are now among the 'greenest' in the world, with the world's largest children's initiative being established in Oman in 2012: Project Greenworld International[71].	7,985 (2.57) *Federal ministry/agency (94%)* *Not reported (6%)*	Occur in protected areas[125]	Likely widespread[120]

	environment and conservation[59]. In the same year, new regulations were issued under Ministerial Decree No. 110, enhancing the Law on Nature Reserves and Wildlife[60].					
Qatar	Qatar lacked specific legislation relating to biodiversity conservation until Decree No. 90 (1996) on the ratification of the Convention on Biological Diversity was issued, four years after signing the Rio Convention in 1992[73]. This decree established a force of law regarding the environment and biodiversity conservation, however, explicit provisions and legislations were still lacking until 2002 when the Environment Protection Law[74] and Law No. 4[75] regulating hunting of wildlife were issued, two years after the High Council for Environment and Natural Protected Areas was established under Enact No. 11[75]. Law No. 4 (2002) prohibited hunting within PAs and defined offences and penalties for violations. In 2004, Law No. 19 on the Protection of Wildlife and its Natural Habitat was issued, which prohibited hunting of protected species inside and outside of PAs, and promoted conservation and management approaches. Between 2006 and 2010, four sets of legislation were issued relating to wildlife conservation, trade, and hunting[78 – 81].	The Permanent Committee for Environmental Protection (PCEP) was created under Law No. 4 (1981)[76]. However, the State remained relatively idle in environmental protection until after the Rio Convention, in 1992. The Supreme Council for the Environment and Natural Reserves (SCENR) was then established in 2000 to replace PCEP. In 2004, the National Biodiversity Strategy and Action Plan was released, which outlined gaps in policy and practice regarding wildlife conservation[72]. It was noted that the country had not developed any clear management plans for PAs and objectives related to biodiversity conservation were still in their nascent stages. This plan explicitly outlined the responsibilities of SCENR, which covered everything related to the environment, including environmental protection and biodiversity conservation. The plan states that a network of rangers will be employed to enforce legislation implementing a hunting ban within PAs. In 2007, SCENR issued a Protected Area Action Plan, which describes the PA system and recommends future steps to	National conservation effort has stepped up since the turn of the century, following the Rio Convention. Although the predominant focus of Qatari conservation seems to be on marine and coastal biodiversity[85], the country is a significant player in the recovery of the Arabian oryx, with a number of reserves dedicated to their reintroduction programs[87]. Established in 1992, Friends of the Environment Centre is Qatar's most prominent NGO dedicated to environmental protection and conservation[86]. The centre works in collaboration with the SCENR towards conservation planning as well as public awareness and education initiatives. Among the primary objectives of the organisation are directing youth towards environmentally friendly approaches and developing conservation-orientated attitudes.	1,513 (13.23) *Not reported (100%)*	Extinct[124]	NA

		be taken[84]. The plan states that guards are deployed within PAs, however, they are not trained in PA management issues. The PA locations also encompass relatively large human populations, therefore, regulating hunting and enforcing wildlife protection remains difficult[85].				
Saudi Arabia	The Saudi government first recognised in the 1970s that biodiversity conservation was an issue in need of some attention. The Regulation of the Act on hunting wild animals and birds was implemented in 1979, which prohibited hunting within PAs, hunting certain ungulate species and hunting without first obtaining a licence[88]. The National Commission for Wildlife Conservation and Development (NCWCD) was then established under Royal Decree M/22 in 1986 as the governmental body in charge of wildlife conservation. The Wildlife Protected Areas Act was issued in 1995, which outlined the declaration process for PA establishment as well as management procedures. This included the establishment of a ranger network and defined acts to be prohibited in PAs[89]. In 1999, the Act on hunting wild animals and birds was repealed by the Game Law issued by Royal Decree No. M/8, which further defined hunting regulations, permits and protected species. The 1995 law on Protected Areas was also repealed in 2015 by	The NCWCD was established in 1986 with initial aims to develop biodiversity conservation strategies through protective measures and ongoing research and surveys[92]. They became the government authority responsible for establishing PAs and enforcing legislation related to the environment and conservation. The National Strategy for Conservation of Biodiversity in the Kingdom of Saudi Arabia was released by the NCWCD in 2005, outlining gaps and pitfalls in policy and practice related to biodiversity conservation. It emphasised that protection is necessary not only inside PAs, but also outside[93]. Although the NCWCD existed and held authority over wildlife protection, there were several other institutions under which conservation issues were appointed, leading to a muddled institutional structure through lack of a central body. The NCWCD was since reorganised to form the Saudi Wildlife Authority (SWA), which was given further, more focused responsibility and authority to deal with wildlife protection, but mainly	Soon after its establishment in the 1980s, the NCWCD established two wildlife research centres. The main objectives of the centres were to develop reintroduction programs for endangered native species, and conduct research around such species and rehabilitation of their habitats[100]. Captive breeding programs were relatively successful, with critically endangered Arabian leopards being successfully bred in the 2000s[129]. However, once it came to *in situ* reintroduction, many challenges arose. Hunting and persecution are widespread in Saudi Arabia, and enforcement of protection laws has been relatively lax within PAs. Several plans and strategies have been developed over the years towards achieving conservation and wildlife protection goals, however, the country has generally fell short in putting such strategy into practice[103]. Protection of large areas in Saudi Arabia is apparently only possible with support generated through a focus on flagship species that	92,064 (4.76) *Federal ministry/agency (73%)* *Not reported (3%)* *Local communities (6%)* *Joint governance (4%)* *Collaborative governance (4%)* *Sub-national ministry/agency (7%)* *For profit organisations (3%)*	Declining[127]	Widespread[128]

	Royal Decree No. M/66 issuing Ministerial Resolution No. 429 approving the Act on the Protected Zone of the Natural Primordial Wildlife. This new Act was issued to set the responsibilities for the Saudi Wildlife Authority (SWA) with the purpose to protect, conserve and develop wildlife within the Kingdom of Saudi Arabia. In 2019, Ministerial Resolution No. 416 was issued to establish the Environment Fund to contribute to achieving the national strategy for the environment[91].	focused on PAs. However, less than 50 % of PAs within the Kingdom were under SWA's jurisdiction. In 2012, the Action Plan for Implementing the Convention on Biological Diversity's Programme of Work on Protected Areas was released to fill gaps in the PA network and outline downfalls and areas for improvement in wildlife conservation[94]. Through the SWA, Saudi Arabia is ahead of benchmarks in planning PAs, but lags in designating them. Several government-designated PAs remained under jurisdiction of other governmental institutions. In terms of managing PAs, SWA suffers from lack of human and technical capabilities and is understaffed and underfunded[93,95]. Their jurisdiction also only covers PAs. Apparently, a Royal Decree was issued in 2018 to establish the Council for Protected Areas[98], as the first agency solely for biodiversity and tourism[99]. In 2019, it was announced that the General Authority of Meteorology and Environment Protection would be launching an environmental police force, with jurisdiction throughout the country to enforce wildlife protection legislation[96].	interest the general public or stakeholders[101]. Luckily, a biproduct is that PAs have become a refuge for other species that receive little public sympathy, however, it shows that effort must be made to shift public perception of such species. Since the turn of the century, research has been conducted to get a feel for attitudes and perceptions of local Saudi teenagers [102] and stakeholders [103] in terms of wildlife conservation and PAs. These studies promoted ecotourism as an important method to progress in conservation, which has since become a development, albeit has received relatively little attention thus far [104]. Also receiving little attention to date is the Saudi Environmental Society, which was established in 2006 as a national non-profit under the Ministry of Social Affairs to support the government in its environmental protection effort and enhance public participation.			
Syria	Syria introduced hunting regulations in 1970 with Legislative Decree No. 152 regulating hunting, establishing a Hunting Council to issue hunting permits[118]. The decree did	The Environment Protection Authority was established in 1985 to act as a platform for cooperation between different ministries and administrations in implementing environmental	A small network of NGOs has been established in Syria with a focus on environmental protection[131] and wildlife conservation[132]. However, due to civil war,	1,293 (0.69) *Federal ministry/agency (5%)* *Not reported (95%)*	Unknown	Unknown

	not explicitly prohibit hunting but contained lists of species that were allowed to be hunted at different times of the year, as well as species that were deemed harmful to human interests that were allowed to be hunted year-round. In 1991, Legislative Decree No. 11 was issued, establishing the General Committee for Environmental Affairs[105]. The committee was responsible for overseeing environmental issues, as well as planning and educating towards environmental protection; however, their primary focus at this stage was pollution rather than wildlife protection. Ministerial Declaration No. 41 was then issued in 1994 by the Minister of Agriculture and Agrarian Reform to prohibit hunting of wild animals throughout Syria for a 10-year period[106]. During the same year, the Law on Environmental Protection and Development (1994) was issued, with aims to protect plants and animals, and create PAs[107]. This law was then repealed in 2002 by Environmental Affairs Law No. 501[08, 122], which was to become the central legal tool for safeguarding the environment[109]. This law defined the objectives of the General Authority for Environmental Affairs such as conducting biodiversity-related research, laying down policies and preparing a national strategy for environmental protection, and developing public	protection plans[111]. Since then, several ministries and administrations have been established, and Syria currently has the institutional resources necessary for biodiversity conservation[106]. However, political tensions within the nation have hindered progress in recent years.	conservation efforts have temporarily ceased.			

	awareness campaigns. The law also established the Environment Protection Council and laid down the basis for creating PAs. In 2007, Legislative Decree No. 11 was issued[110], defining competencies for the Ministry of Agriculture and Agrarian Reform (MAAR), outlining the ministry's responsibilities in environmental protection, including protecting and maintaining natural resources, contributing to the development of research and monitoring programs, creating PAs and regulating the exploitation of deserts. A new constitution was adopted in 2012 in parallel with The Environmental Protection Law No. 12 (2012)[106]. This new law was issued to replace all preceding laws and gave the Ministry of State for Environmental Affairs (MSEA) more mandates and responsibilities related to environmental protection, though they should be executed in close cooperation with other related bodies.					
United Arab Emirates (UAE)	Hunting regulations were first brought into UAE legislation in 1983 with Decree Law No. 9 concerning Regulating the Hunting of Birds and Animals[112]. The law explicitly names taxa that it is forbidden to hunt. Federal Law No. 24 for the Protection and Development of the Environment was then issued in 1999[115], which prohibited hunting, killing or	Several authorities and agencies exist throughout the separate emirates of the UAE, ranging significantly in their roles and capabilities[113]. The majority of the federation's land falls within the emirate of Abu Dhabi, whose Environment Agency (EAD) was founded in 1996 and is now the largest environmental regulator in the Middle East[114].	The World Wide Fund for Nature (WWF) holds a prominent position within the UAE with Emirates Nature-WWF being the leading non-profit organisation within the country[134]. Over the last two decades, Emirates Nature-WWF has been at the forefront of environmental conservation in the region.	12,734 (17.95) *Government-delegated management (2%)* *Not reported (98%)*	Extinct[124]	NA

	capturing animals identified in the Executive Order, which shall also determine the areas licenced for hunting. I found the Exec. Ord., but no mention of species to be protected. In 2005, Law No. 22 was issued in regard to the prohibition of hunting within the emirate of Abu Dhabi[117], which comprises the majority of open space within the UAE. This law added further hunting regulations and defined requirements for hunting licence acquisition. However, it was not fully implemented for ten years until the Decision of the President of the Executive Council No. 69 to issue the Executive Regulation of Law No. 22 (2005). Federal Law No. 16 regarding Animal Welfare was issued in 2007 to encourage people to promote animal welfare and join voluntary activities related to animal protection[116].	In 2019, the Ministry of Climate Change and Environment signed an agreement with Emirates Animal Welfare Society and Emirates Park Zoo to devise a National Animal Welfare Plan, promoting animal protection and raising public awareness around animal welfare[133].				
Yemen	Law No. 26 on Environment Protection was released in 1995, with aims of protecting the environment (including local species) and organise the conservation of Yemen's natural ecosystems[136]. The Environment Protection Authority was established in 2001 as the regulatory body dealing with environmental/biodiversity concerns. However, legal frameworks regarding environmental/biodiversity conservation remain weak[137].	A large PA (Hawf Protected Area) has been designated, but official governance is lacking[138]. While national conservation efforts are improving, civil unrest and political tensions hinder progress[137].	The Foundation for the Protection of the Arabian Leopard in Yemen is the most active NGO on Yemen's mainland, dedicated to ensuring a "sustainably managed population of Arabian leopards living in harmony with local communities in Yemen"[139]. Protection of predators is increasing, however, humanitarian crises are currently widespread.	3,520 (0.77) *Not reported (100%)*	Occur in unofficial protected areas[130]	Unknown

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Chapter 3. Tolerance of wolves shapes desert canid communities in the Middle East

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Abstract

The grey wolf (*Canis lupus*) is recovering globally due to increasing human acceptance, which can drive trophic cascades. An endangered subspecies, the Arabian wolf (*Canis lupus arabs*), inhabits arid regions of the southern Levant and Arabian Peninsula where it remains widely persecuted, and little is known about its ecology. Most of the Arabian wolf's range is dominated by pastoralism, where tolerance of wolves is low. We assessed how acceptance of Arabian wolves, relative to human land-use and density, has cascading effects on other canids by comparing spatial and temporal interactions, and relative abundance of canids across a hyper-arid desert crossing the Israel-Jordan border. Canids responded by adjusting their spatial and temporal activity patterns in relation to human activity. Wolves were recorded significantly less in pastoralist landscapes, leading to cascading effects. We found that jackals (*Canis aureus*) and foxes (*Vulpes* spp.) are both suppressed by larger canids. Wolves and jackals both suppressed foxes, but wolves also facilitated foxes by reducing pressure from jackals. Representing the first documentation of the role of an apex predator in the Middle East, our findings highlight the strong ecological effects that Arabian wolves have on desert ecosystems. Conservation efforts should focus on increasing tolerance and working towards coexistence in pastoralist landscapes.

3.1 Introduction

The grey wolf (*Canis lupus*) is recovering across its global range, particularly in North America and Europe, largely due to a general increase in human acceptance of predators (George et al., 2016) and the transition of some farming regions to wild spaces (Chapron et al., 2014). The ecological implications of this recovery have been demonstrated in some protected areas like Yellowstone National Park, USA (Ripple and Beschta, 2011). However, persecution remains the greatest threat to large predators globally, including wolves (Ripple et al., 2014). Animal production, specifically of free-ranging domestic ungulates (i.e., pastoralism), remains one of the main drivers of predator persecution (Boronyak et al., 2020). Wolf-induced trophic cascades have gained much attention in areas where populations are recovering, but the removal of apex predators also triggers cascades (Colman et al., 2014; Heath et al., 2014). While the recovery and ecological effects of wolves in North America and Europe are well understood, less is known about the ecological roles of wolves in other regions.

The desert-adapted Arabian wolf (*C. l. arabs*), the smallest subspecies of grey wolf, was historically widespread across arid regions of the southern Levant and Arabian Peninsula, but it is now endangered due to persecution (Mallon and Budd, 2011). The Arabian wolf remains the sole apex predator across most of its range since the extirpation of the Asiatic cheetah (*Acinonyx jubatus venaticus*) and the near-eradication of the Arabian leopard (*Panthera pardus nimr*) during the last several decades. Elucidating the important ecological roles of Arabian wolves is likely to enhance the conservation of this endangered grey wolf subspecies (Sakurai et al., 2020). The only known stable population is confined to the Arava Valley and Negev Desert in Israel, where legal protection is enforced and acceptance of wolves is high (Barocas et al., 2018; Cohen et al., 2013). Wolves in this region also benefit from the legal protection of their prey, such as gazelle (*Gazella* spp.), and from water and food (e.g., dates and melons) resources available at crop farms (Barocas et al., 2018; Lewin et al., 2021). However, most of the Arabian wolf's range overlaps with semi-nomadic sheep and goat herders, and like most regions where pastoralism occurs, predators are killed to protect domestic animals from predation. The question remains whether Arabian wolves structure ecosystems in similar ways to their northern counterparts.

As apex predators, wolves are known to suppress populations of smaller canids in other parts of the world. In North America, wolves limit the distribution and abundance of coyotes (*C. latrans*) (Berger and Gese, 2007), while the ranges and densities of wolves and golden jackals (*C. aureus*) are negatively correlated in Europe (Krofel et al., 2017; Newsome et al., 2017). Likewise, across the deserts of Australia, the closely related dingo (*C. dingo*) has strong suppressive effects on red foxes (*Vulpes vulpes*) (Wallach et al., 2010; Wooster et al., 2021). The suppressive effects of large canids can cascade through the predator community. For example, the suppression of coyotes by wolves has released red foxes (Levi and Wilmers, 2012; Newsome and Ripple, 2015). In core agricultural areas of Israel, foxes avoid areas of high jackal density (Shamoon et al., 2017), and foxes also avoid jackals at fine spatial scales in agricultural landscapes of the Arava Valley (Scheinin et al., 2006). Humans influence canid communities through both agonistic and facilitative interactions in the Middle East. Wolves remain heavily persecuted in pastoralist landscapes on the Arabian Peninsula (Cunningham et al., 2009). In the southern Levant, golden jackals have expanded their range into arid regions along with agricultural development (Magory Cohen et al., 2013), and are often culled due to perceived economic impacts to agriculture and the spread of rabies (Nemtzov and King, 2001). Here, we ask whether contrasting human attitudes shape the cascading ecological effects that Arabian wolves may have on mesopredators. We hypothesised that when humans are tolerant of wolves, the ecological effects of wolves will be stronger than when humans persecute wolves.

To test this hypothesis, we assessed spatial and temporal interactions of Arabian wolves, golden jackals, and foxes between different human contexts based on human acceptance of wolves, with an aim to determine if acceptance of wolves shaped canid communities in a Middle Eastern hyper-arid desert. We quantified spatial and temporal avoidance of smaller canids toward larger canids across protected areas and agricultural landscapes dominated by either pastoralism or crop farming. Given that tolerance of wolves is low in pastoralist landscapes, we predicted a reduction in wolf activity, releasing jackals from top-down pressure and cascading to intensify suppression of foxes.

3.2 Methods

3.2.1 Study Area

We measured canid activity patterns across a ~6,000 km^2 region of desert in the southern Levant (Fig. 1) during the summer (June-September) of 2019. Almost all rainfall in this arid to hyper-arid region (e.g., < 50 mm in lowland, < 200 mm in highland areas) occurs within 6-month periods surrounding winter (October to March). Temperatures reach > 45°C in summer (< 10°C cooler in the highlands), so the study area was typically dry and hot during sampling. Our study area incorporated both highland and lowland areas, stretching across the Negev Desert from the Israel-Egypt border in the west (highest peak ~1,000 m) to Jordan's Edom Mountains in the east (highest peak ~1,200 m). Bisecting these two highland areas is the hyper-arid Arava Valley (Arabic: وادي عربة, 'Wadi Araba'; Hebrew: עֲרָבָה 'Arava'), which straddles the Israel-Jordan border, and its lowest point reaches 400 m below sea level at the southern shore of the Dead Sea. Our study area covered the northern section of the Arava Valley (spanning 50–70 km south of the Dead Sea), encompassing a contiguous lowland desert ecosystem averaging 20 km wide, and its adjacent arid highlands to the east and west.

The southern Levant is a socio-politically complex region encompassing parts of Israel, Palestine, and Jordan, where acceptance of wolves varies. The Arabian wolf is legally protected throughout the region, but protection is only enforced in limited areas and community support for predator protection in pastoralist landscapes is generally low. Arabian wolves have reportedly been shot after crossing into pastoralist landscapes in the past (Hefner and Geffen, 1999). Legal and illegal hunting is common in some pastoralist landscapes (Eid and Handal, 2018), and several threatened species, including the Arabian wolf (Bonsen and Khalilieh, 2021), can be confined to nature reserves (Amr et al., 2004). A severely depleted wild prey base outside of protected areas means that domestic ungulates (hence 'livestock') are now an important food source for wolves in some pastoralist landscapes (Bonsen and Khalilieh, 2021), often exacerbating conflicts (Gecchele et al., 2017). In crop farming landscapes absent of pastoralism, tolerance of wolves is high (Barocas et al., 2018), which expands the areas of protection for wolves.

The section of the Israel-Jordan border running through our study area had no physical barrier. Simple barbed-wire fences enclosing minefields along the Israeli side of the border are remnants of times before the ratification of the 1994 peace treaty. Unlike wildlife that can cross the border freely, human movement is controlled by the military on both sides. Within our study site, military activity in Jordan was concentrated predominantly within 5 km of the border, while Israel's military activity spanned the borders from Jordan to Egypt. The Negev contains extensive military training areas that are off limit to the public (including to pastoralists) apart from weekends (Friday afternoons and Saturdays) and Jewish holidays when they are open for hiking and camping.

Thus, pastoralism is more restricted in southern Israel compared to Jordan where pastoralists are granted considerably more freedom in their movement and temporary settlement when herding. In Jordan, herders are allowed to bring their domestic sheep and goats into protected areas to drink at springs, whereas in Israel, livestock are excluded from protected areas. Within this part of Israel, most livestock are confined to dairy factory farms, and the small agricultural villages ('moshavim' and 'kibbutzim') are surrounded by intensive crop fields. Common crops include dates and seasonal cultivars such as melons and peppers, which form a considerable part of the diets of the region's canids (Lewin et al., 2021).

3.2.3 Data collection and analysis

We used data obtained from various sources to generate GIS layers in ArcGIS 10.8 (Esri 2019) based on human land-use and population density (see Table S3.1 in Ch. 3 Supplementary Material). We then characterised the study area into the three following categories based on land-use. (1) *Protected areas*: National parks and nature reserves primarily used for benign recreational activities, in which wildlife are legally and actively protected. The risk of wolf persecution is low. (2) *Crop farming landscapes*: Agricultural landscapes devoid of pastoralism, where crop farming is the main land-use, and large vertebrate wildlife are legally and actively protected. The risk of wolf persecution is similarly low to protected areas, but human activity is higher. (3) *Pastoralist landscapes*: Agricultural landscapes in which livestock herding is a predominant form of agriculture. Wolves are perceived as a threat to livestock (Barocas et al., 2018) and are illegally persecuted in some areas (Eid and Handal, 2018; Hefner and Geffen, 1999).

We set up 1-3 Trophy Cam Aggressor no-glow camera-traps (Bushnell, Overland Park, KS, USA) at 27 water points (natural springs, leaky pipes, artificial dams, and troughs) – nine in each land-use category – for approximately one month to estimate use, as well as spatial and temporal interactions, of canids across human contexts (Fig. 3.1). The number of cameras at each water point was dependent on the size of the water point and number of access points. We focused on water points because this is where wildlife activity is highest, and where canids scent mark regularly (Wallach et al., 2009b). We categorised the water point to land-use by determining the predominant human activity, and calculated the mean human population density, within a 5 km radius. Camera-trap data were sorted into species (for *Canis* spp.) or genus (for *Vulpes* spp.). The red fox (*V. vulpes*) was the most frequently detected fox species, but we combined their detections with two other foxes (*V. cana* and *V. rueppellii*) as they constitute a similar trophic position (all weigh < 5 kg).

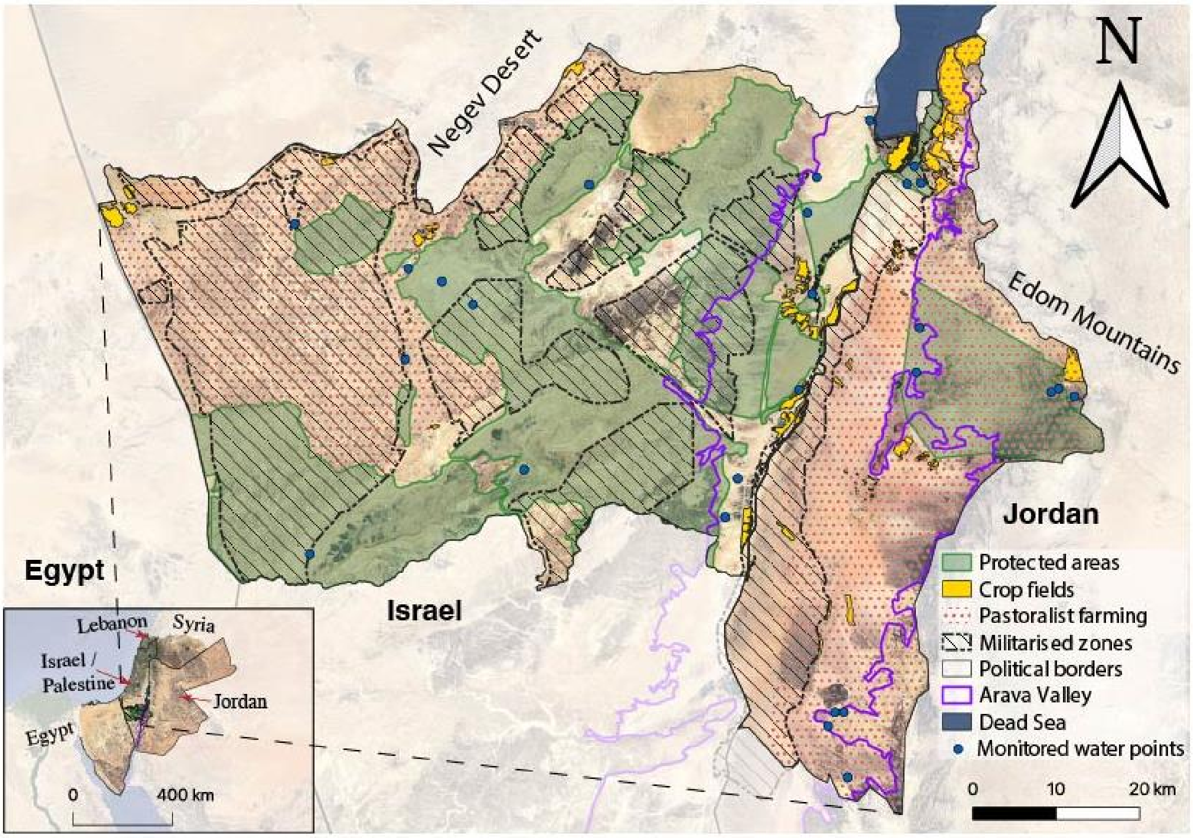

Fig. 3.1. Spatial distribution of monitored water points across three human land-use categories within a ~6,000 km² study area in the southern Levant (inset), highlighting the Arava Valley (outlined in purple) which straddles the international border between Israel and Jordan.

We conducted single-species and two-species occupancy models using the package 'Wiqid' in program R version 4.0.1 (R Development Core Team 2008). Given that water point availability was limited, and individual canid home ranges often consisted of multiple water points (the mean distance between adjacent water points was 6.5 ± 1.2 km), we interpreted the occupancy parameter (ψ) from the single-species models as the probability of resource use to accommodate the lack of spatial independence (Mackenzie, 2006). We calculated a Species Interaction Factor (SIF *or* φ) from the two-species models according to the equation proposed by Richmond et al. (2010):

$$\varphi = \frac{\psi^{A}\,\psi^{BA}}{\psi^{A}\,(\psi^{A}\,\psi^{BA} + (1 - \psi^{A})\psi^{Ba})} \qquad \text{Eq. 1}$$

where:

ψ^{A} = probability of the dominant species occurring,

ψ^{BA} = probability of the subordinate species occurring given the dominant species is present,

ψ^{Ba} = probability of the subordinate species occurring given the dominant species is absent.

The SIF indicated whether a smaller canid avoided ($\varphi < 1.0$) or was attracted to ($\varphi > 1.0$) a larger canid, or if the two canids occurred independently ($\varphi = 1.0$); the further the value is from the neutral value of 1.0, the stronger the interaction. The probability of resource use was modelled as a function of human population density within each land-use category, whereas a single SIF was calculated across the study area for each species pair.

We further explored interactions between canids by determining overlap in temporal activity patterns. We treated detection 'events' as independent if there were no other detections of the same canid for five minutes before or after the given event, and recorded the location, date, and time of each independent event. Using the 'overlap' package in R (Meredith and Ridout, 2020), we then estimated temporal activity patterns and fitted kernel density curves in radians (*r*). A coefficient of overlap ($\hat{\Delta}$) was calculated as the area lying under the overlap in density curves for each canid, returning a value ranging from 0 (no overlap) to 1 (complete overlap). Following the recommendations of Ridout and Linkie (2009), we used $\hat{\Delta}_1$ for small sample sizes (< 75) and $\hat{\Delta}_4$ for large sample sizes (> 75), and generated 1,000 smoothed bootstrap samples; estimating a mean $\hat{\Delta}$ and 95 % confidence intervals (CI; *as per* Meredith and Ridout, 2020) for each pair of density curves within each land-use category. Finally, we tested for any significant change in temporal activity patterns for a given canid between land-use categories using a Wald's Test in the 'activity' package in R. Temporal activity patterns of humans were also analysed using camera-trap detections to visualise temporal adjustments in wolf activity in response to humans. We used package 'camtrapR' in R to define detection events and create detection histories used in occupancy models.

We also conducted tracking surveys to estimate an index of relative abundance of canids between the two agricultural land-use categories. We concentrated efforts in the Arava Valley to draw direct comparisons between crop farming and pastoralist landscapes across the Israel-Jordan border, while reducing confounding spatial factors such as differences in elevation or accessibility to prey or resources. Protected areas are small in the Arava and largely influenced by the surrounding agricultural activities, so sampling conducted within protected areas was classified according to the corresponding agricultural activity. Thus, for relative abundance estimates, all sampling units in crop farming landscapes were in Israel, while all sampling units in pastoralist landscapes were in Jordan.

Following Wallach et al. (2010), we used two different tracking methods to assess two parameters for each species: relative density and relative distribution. We then multiplied these two parameters together to obtain an index of relative abundance [$IR_{ab} = R_{dens} \times R_{dist}$], which we compared across land-use categories by performing a Kruskal-Wallis test for each species. To determine relative density, we counted the number of fresh tracks along 500 m transects (21 in crop farming, 17 in pastoralist areas) across an average of three consecutive mornings. After counting, we cleared any previously deposited tracks by dragging a heavy metal object, with dried palm fronds attached, behind a slow-moving vehicle. We then converted the daily number of fresh tracks recorded per transect into the number of tracks/ha/day. Relative distribution (i.e., the proportion of area occupied) was estimated by scanning randomly selected 2-ha plots (31 in crop farming and 21 in pastoralist areas) and recording the presence or absence of tracks for each of the canid species.

3.3 Results

Based on a total of 418 canid events from 997 camera-trap days, we found that canid communities differed between human land uses (see Table S3.2). Most wolf (62.2 %) and fox (54.4 %) events were recorded in protected areas, whereas most jackal events were recorded in pastoralist landscapes (76.1 %). Probability of resource use was similar for wolves and foxes: highest in protected areas, significantly higher in crop farming than pastoralist landscapes, and declining as human population density increased in agricultural (crop farming and pastoralist) landscapes (Fig. 3.2). In contrast, the probability of resource use for jackals increased with human population density and was significantly higher in pastoralist landscapes than protected areas and crop farming landscapes.

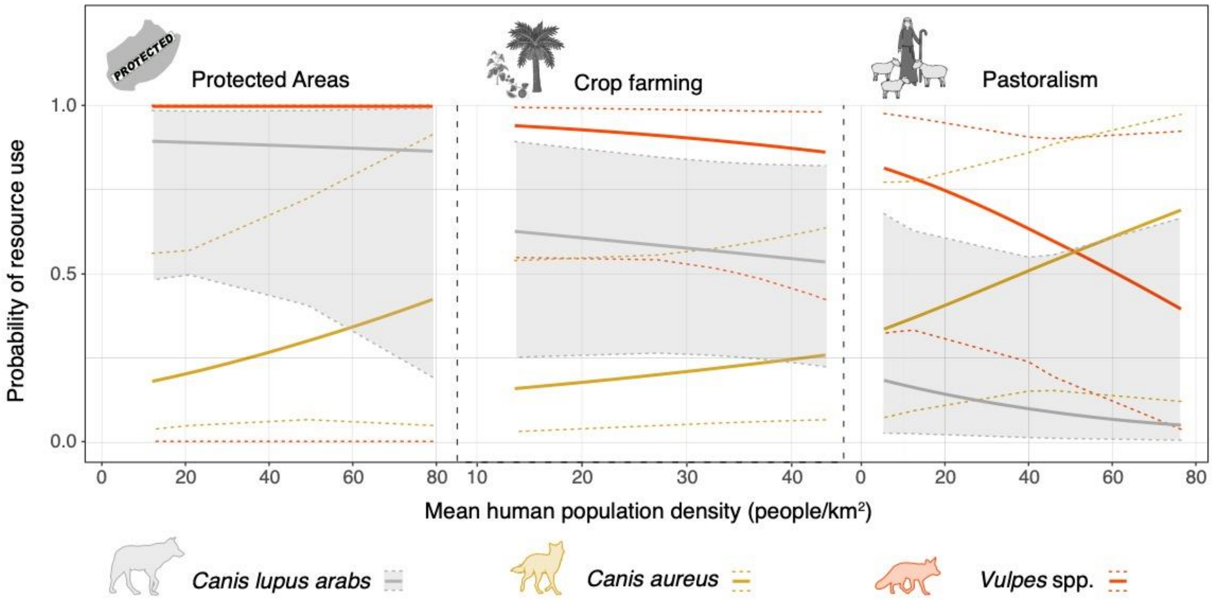

Fig. 3.2. Probabilities of resource use of canids across land-use categories as a function of human population density reveal that wolves (grey lines and shading) and foxes (red lines) are negatively influenced, while jackals (gold lines) are positively influenced, by human population density, particularly in pastoralist landscapes. Dashed lines represent 95 % confidence intervals.

All canids were mostly nocturnal, with crepuscular peaks in activity (jackal activity was slightly later in the morning), and temporal overlap was generally high between canid pairs (Fig. 3a). However, wolf and jackal activity shifted significantly in pastoralist and crop farming landscapes, respectively (see Table S3.3). Temporal overlap between wolves and humans was low overall ($\hat{\Delta} \pm$ 95 % CI = 0.39 ± 0.22 – 0.44) as humans were diurnal. However, overlap was particularly low in pastoralist landscapes where wolf activity shifted to a single peak in the middle of the night when humans were inactive ($\hat{\Delta} \pm$ 95 % CI = 0.01 ± 0.00 – 0.02; Fig. 3b; Wald's $\chi^2 = 33.6$, $p < 0.0001$). Likewise, temporal overlap between wolves and jackals was lower in crop farming landscapes where jackal activity shifted to times of low wolf activity ($\hat{\Delta} \pm 95$ % CI = 0.41 ± 0.19 – 0.53; Fig. 3c; Wald's χ^2 = 16.5, p < 0.0001).

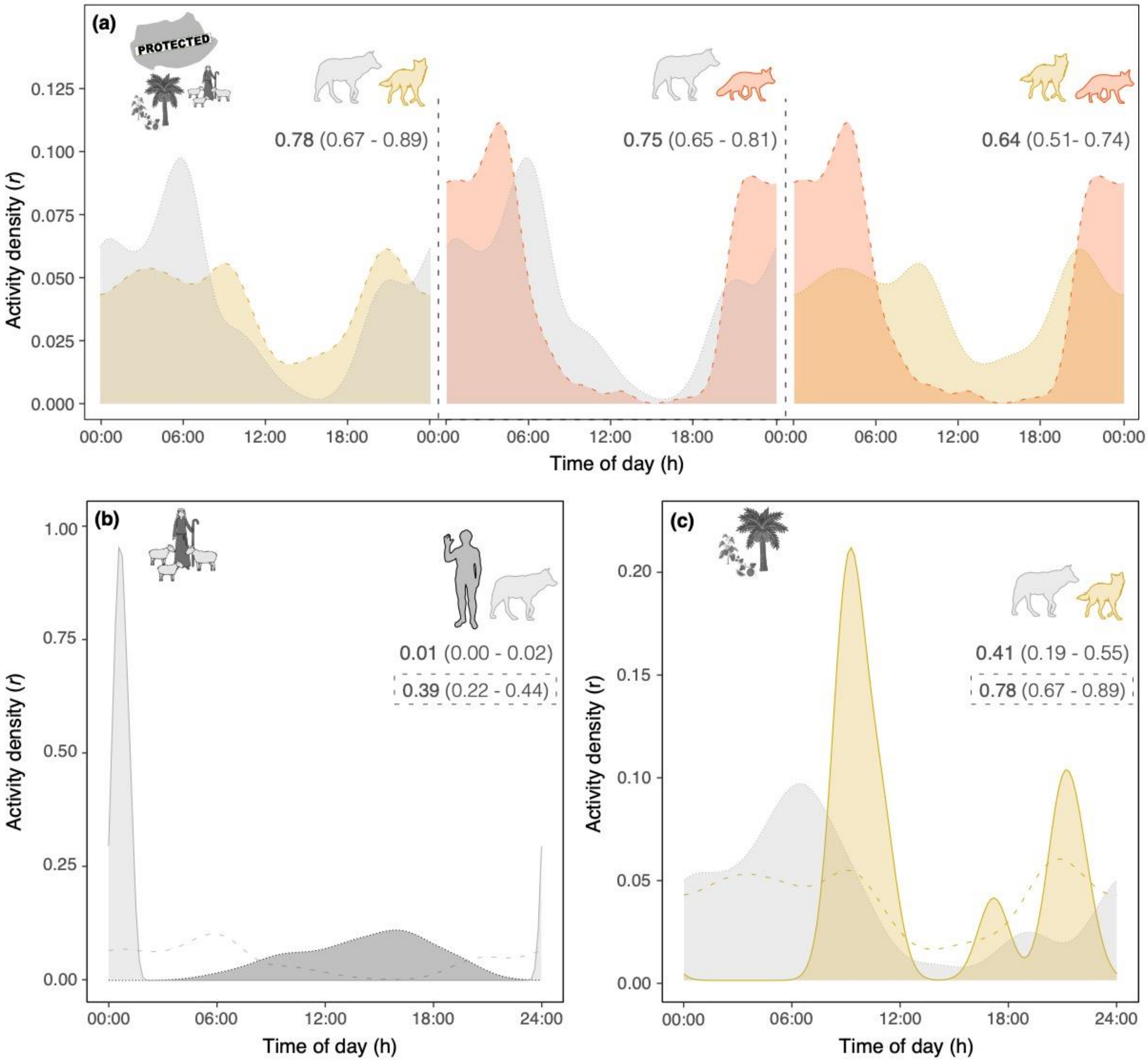

Fig. 3.3. Overlap in temporal activity patterns illustrating: **(a)** a relatively high temporal overlap between larger (dotted lines) and smaller (dashed lines) canids overall, where all canids are largely nocturnal with bimodal peaks in activity around dawn and dusk for wolves (grey lines and shading) and foxes (red lines and shading), and slightly later in the morning for jackals (gold lines and shading); **(b)** a significant shift in wolf (solid and dashed lines) activity in pastoralist landscapes to the middle of the night when people (dotted lines) were inactive; and **(c)** a significant shift in jackal (solid and dashed lines) activity in crop farming landscapes to times when wolves (dotted lines) were less active. Values denote bootstrapped coefficients of overlap ($\hat{\Delta} \pm 95$ % CI), while dashed lines in **(b)** and **(c)** represent overall temporal activity patterns of smaller canid [dashed boxes represent overall coefficient of overlap ($\hat{\Delta} \pm 95$ % CI)].

Both jackals and foxes spatially avoided larger canids. At water points, fox avoidance of jackals was strongest (φ ± 95 % CI = 0.34 ± 0.04 – 0.64), followed by jackal avoidance of wolves (φ ± 95 % CI = 0.72 ± 0.55 – 0.90), and fox avoidance of wolves was the weakest (φ ± 95 % CI = 0.82 ± 0.67 – 0.98). Although the probability of resource use for foxes was highest at water points used by wolves, tracking surveys revealed that wolf and fox relative abundances were inversely related across agricultural landscapes in the Arava (Fig. 4). Wolves were more abundant in crop farming landscapes (Kruskal-Wallis $\chi^2 = 8.68$, $p < 0.01$; see Table S3.4), while foxes were more abundant in pastoralist landscapes (Kruskal-Wallis $\chi^2 = 11.40$, $p < 0.001$; see Table S3.4). Jackal abundance was equal, and lower than other canids, across both crop farming and pastoralist landscapes (Kruskal-Wallis $\chi^2 = 2.42$, $p = 0.12$; see Table S3.4).

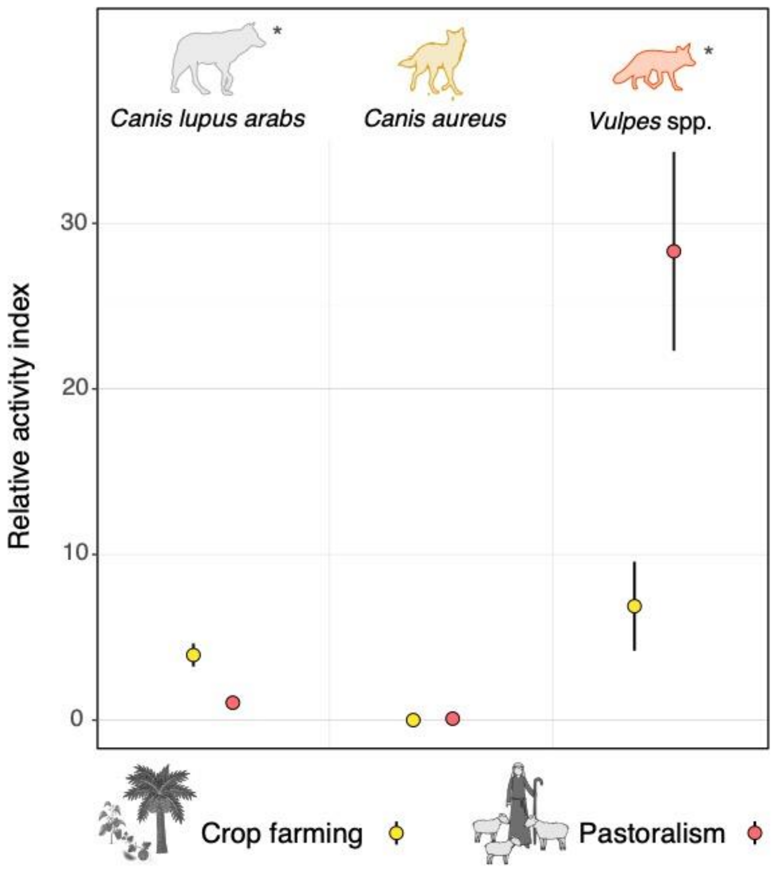

Fig. 3.4. Relative activity indices, calculated using the parameters estimated from tracking surveys, show that foxes in the Arava Valley are significantly more active in pastoralist landscapes than in crop farming landscapes where wolves are more active.

3.4 Discussion

Our study demonstrates that Arabian wolves structure canid communities in the Middle East, and that this effect is intertwined with human land use and acceptance. We show that wolf persecution in pastoralist landscapes releases golden jackals from top-down pressure, which has cascading suppressive effects on foxes. Both wolves and jackals suppress foxes. We found that the relative abundance of foxes was lower where wolves were more abundant, and foxes avoided water points most used by jackals. Although Arabian wolves suppress foxes, they also indirectly facilitate foxes by lessening the suppressive force of jackals. These interactions, which are likely to have implications across multiple trophic levels, are contingent on human behaviour in these arid anthropogenic landscapes.

Wolves used protected areas most. Within agricultural areas, the probability of resource use and relative abundance of wolves were higher in crop farming than pastoralist landscapes. Similar to wolves, foxes used protected areas and crop farming landscapes most, and the probability of resource use of foxes declined with human population density in pastoralist landscapes. In contrast, the probability of resource use of jackals was lowest in protected areas and in crop farming landscapes, and the few jackal events that were recorded in crop farming landscapes coincided with times of low wolf activity. Unlike wolves and foxes, the probability of resource use of jackals increased with human population density. This aligns with the abundance of jackals around densely populated Israeli cities (Shamoon et al., 2017). Similarly, Shahnaseri et al. (2019) noted that in arid parts of Iran, the slightly larger Indian wolf (*C. l. pallipes*) avoided humans while jackals concentrated in agricultural areas.

We argue that jackals suppressed foxes in pastoralist landscapes with the highest human population densities in our study. Red foxes are consistently reported to have a strong affiliation with human activity, including previously from our study area (Shapira et al., 2008). In the USA, a regional study showed that coyotes and red foxes were both positively correlated along an urbanisation gradient (Rota et al., 2016); meanwhile, a fine-scale urban parklands study showed that red foxes benefit from using areas of high urban development as spatial refugia to reduce the chance of interference competition from coyotes (Moll et al., 2018).

Our study joins the internationally consistent observation that large canids suppress smaller canids. As European wolves suppress jackals (Krofel et al., 2017) and North American wolves suppress coyotes (Levi and Wilmers, 2012), Arabian wolves suppress jackals. The effects of wolf persecution cascade from wolves to jackals and to foxes in these desert canid communities. Our observation that wolves suppress jackals, releasing foxes from top-down control, parallels findings in North America where wolves mediate coyote suppression of foxes (Levi and Wilmers, 2012). Wolves were found to have a negligible effect on mesopredators in forested anthropogenic landscapes of Romania (Dorresteijn et al., 2015). However, the fact that jackals inhabit the region (Banea et al., 2012), but only foxes were recorded in the study, could provide further insights into interactions within the region's canid communities. We found that wolves influenced fox abundance in a region of the Arava Valley where jackals do not occur. Wolves were also noted to reduce fox abundance in parts of Sweden where jackals are absent, but only where wolf packs are stable, and territories are well-established (Wikenros et al., 2017a) as in the crop farming landscapes of the Arava Valley (Cohen et al., 2013).

In Europe, wolves avoid human-dominated landscapes (Carricondo-Sanchez et al., 2020; Dorresteijn et al., 2015). However, in crop farming landscapes of Israel's hyper-arid Arava Valley, Arabian wolves have previously been reported to spend most of their time in proximity to human infrastructure (Barocas et al., 2018), where they are subsidised by anthropogenic food and water resources (Lewin et al., 2021). We stress that the ability of wolves to do this is dependent on whether they are accepted by humans. In pastoralist landscapes, wolves are driven away from humans, and our results highlight the importance of protected areas among pastoralist landscapes (Bonsen and Khalilieh, 2021). We recorded few wolves in pastoralist landscapes, and those that occurred were around midnight, when humans were least active. Wildlife often become more nocturnal in anthropogenic landscapes to avoid human encounters (Gaynor et al., 2018). In our study, Arabian wolves increased their nocturnality where they were persecuted.

3.4.1 Conclusions

Our results indicate that, like their temperate cousins, Arabian wolves structure canid communities, and are therefore ecologically significant in arid environments. However, their ecological effects are most notable under conditions of human acceptance. Previous research focussing on relationships between humans and Arabian wolves has been limited, and comparisons had not been made between areas of varying acceptance. We show that, despite their relatively small size and the low productivity of the ecosystems they inhabit, Arabian wolves play key ecological roles where populations are stable. In contrast, the effects of such roles are considerably reduced in pastoralist landscapes where tolerance of wolves is low.

With things as they stand, Arabian wolf populations remain imperilled as pastoralism prevails as a predominant form of agriculture throughout its range. Jordan is an important jurisdiction for its conservation, as it provides a steppingstone between the stable population of the Arava Valley/Negev desert and the declining population of the Arabian Peninsula. The discovery of wolves successfully using protected areas in Jordan is potentially promising. Conservation efforts should focus on increasing tolerance and coexistence within pastoralist landscapes by promoting education around the ecological importance of the Arabian wolf and strategies towards coexistence. Reducing hunting rates, not only of wolves, but also their prey, is imperative as it would lead to the recovery of the wolf's natural prey base and alleviate the need for wolves to rely on livestock for sustenance. We hope that our research enhances protection of these animals in this unique part of the world so that Arabian wolves are not added to the list of predators recently lost from the Middle East.

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Chapter 3. Supplementary material

Table S3.1: GIS layers used to categorise water point to land-use for occupancy and interspecific interactions.

Layer	Description	Source
Human land-use		
Protected areas	Polygon shapefile outlining designated protected areas (national parks and nature reserves) governed by the Israel Nature and Parks Authority in Israel and Royal Society for the Protection of Nature in Jordan.	Polygon vector data obtained from M. Silver, Arava Drainage Authority, Sapir, Israel, and the Royal Society for the Conservation of Nature in Jordan.
Crop farming	Polygon shapefile outlining agricultural fields that are used for intensive crop farming.	Polygon vector data partly obtained from M. Silver, Arava Drainage Authority, Sapir, Israel, and partly from scanning satellite imagery in ArcGIS.
Pastoralism	Polygon shapefile outlining regions in which pastoralism is a dominant form of agriculture.	Polygon vector data produced in ArcGIS through local knowledge of predominant land-uses in the region.
Human population density	Mean human population within a 5 km radius from each water point.	Means calculated from raster cells within a 5 km radius of each water point, using the Gridded Population of the World, Version 4 (GPWv4) raster of global human population density in ArcGIS.

Table S3.2: Summary of canid records from camera-trap data, showing the number of events overall and within each land-use category, the number of water points (*n*) at which each species was recorded (% of total), and the probabilities of resource use (ψ) and detection (*p*) of each canid overall and within each category.

Species	Land-use	No. of events (% total)	*n* (% total)	ψ (95 % CI)	*p* (95 % CI)
Wolves	*Overall*	*111*	*14*	*0.57 (0.37 – 0.75)*	*0.18 (0.14 - 0.22)*
	Protected Areas	69 (62.2)	8 (57.1)	0.89 (0.50 – 0.99)	0.21 (0.16 – 0.26)
	Crop farming	38 (34.2)	5 (35.7)	0.56 (0.25 – 0.83)	0.16 (0.11 – 0.22)
	Pastoralism	4 (3.6)	1 (7.2)	0.13 (0.02 – 0.57)	0.04 (0.01 – 0.14)
Jackals	*Overall*	*46*	*7*	*0.28 (0.14 – 0.49)*	*0.17 (0.12 – 0.23)*
	Protected Areas	3 (6.5)	2 (28.6)	0.22 (0.06 – 0.58)	0.05 (0.01 – 0.23)
	Crop farming	8 (17.4)	2 (28.6)	0.22 (0.06 – 0.58)	0.06 (0.02 – 0.27)
	Pastoralism	35 (76.1)	3 (42.8)	0.44 (0.13 – 0.81)	0.27 (0.19 – 0.37)
Foxes	*Overall*	*261*	*24*	*0.87 (0.67 – 0.96)*	*0.28 (0.25 – 0.32)*
	Protected Areas	142 (54.4)	9 (37.5)	0.99 (0.00 – 1.00)	0.34 (0.28 – 0.40)
	Crop farming	57 (21.8)	8 (33.3)	0.89 (0.50 – 0.98)	0.20 (0.15 – 0.25)
	Pastoralism	62 (23.8)	7 (29.2)	0.70 (0.34 – 0.91)	0.35 (0.27 – 0.45)

Table S3.3: Bootstrapped coefficient of overlap ($\hat{\Delta}$) estimates and Wald's Test outputs used to determine changes in temporal activity patterns in canids. Wald's Test output corresponds to temporal activity changes of the species within the pair in **bold** text.

Species pair	Land-use	Temporal overlap $\hat{\Delta}$ (95 % CI)	Wald's Test Difference	SE	χ^2	*p* value
People	*Overall*	*0.39 (0.22 – 0.44)*				
Wolves	Protected areas	0.32 (0.14 – 0.40)	0.04	0.08	0.28	0.60
	Crop farming	0.52 (0.39 – 0.88)	0.11	0.11	1.05	0.31
	Pastoralism	0.01 (0.00 – 0.02)	0.08	0.10	0.61	0.43
Wolves	*Overall*	*0.78 (0.66 – 0.89)*				
Jackals	Protected areas	0.34 (0.31 – 0.92)	0.04	0.09	0.23	0.63
	Crop farming	0.41 (0.19 – 0.53)	0.01	0.10	0.01	0.93
	Pastoralism	0.12 (0.03 – 0.22)	**0.38**	**0.07**	**33.64**	**< 0.0001***
Jackals	*Overall*	*0.64 (0.52 – 0.75)*				
Foxes	Protected areas	0.33 (0.17 – 0.88)	0.05	0.25	0.05	0.83
	Crop farming	0.30 (0.11 – 0.43)	**0.49**	**0.12**	**16.53**	**< 0.0001***
	Pastoralism	0.69 (0.56 – 0.85)	0.12	0.12	0.78	0.38
Wolves	*Overall*	*0.75 (0.64 – 0.81)*				
Foxes	Protected areas	0.74 (0.60 – 0.81)	0.05	0.04	1.13	0.29
	Crop farming	0.68 (0.51 – 0.79)	0.01	0.06	0.03	0.87
	Pastoralism	0.17 (0.08 – 0.31)	0.09	0.06	2.41	0.12

*Wald's Test returned a significant p value.

Table S3.4. Estimated parameters used to calculate indices of relative abundance from tracking surveys conducted in the Arava Valley.

Species	Land-use	R_{dens} [1] (tracks/ha/day)	R_{dist} [2]	IR_{ab} [3]	Kruskal-Wallis χ^2	Kruskal-Wallis *p* value [4]
Wolves	*Overall*	*6.93 (1.15)*	*0.37*		8.68	**< 0.01***
	Crop farming	8.13 (1.41)	0.48	3.93 (0.70)		
	Pastoralism	5.51 (1.82)	0.19	1.05 (0.36)		
Jackals	*Overall*	*0.84 (0.60)*	*0.08*		2.42	0.12
	Crop farming	0.00	0.10	0.00		
	Pastoralism	1.84 (1.29)	0.05	0.09 (0.06)		
Foxes	*Overall*	*32.52 (5.71)*	*0.50*		11.40	**< 0.001***
	Crop farming	14.22 (4.15)	0.48	6.88 (2.69)		
	Pastoralism	54.04 (8.23)	0.52	28.31 (6.01)		

[1]Relative density was estimated by counting the number of fresh tracks that were recorded on a transect and dividing the total number by the number of days the transect was sampled and standardised per unit area (ha). Values are means (± SE). [2]Relative distribution was determined by dividing the number of 2 ha plots in which tracks were recorded for each canid species by the total number of 2 ha plots within each land-use category. [3]An index of relative activity was calculated for each species in each land-use category by multiplying relative density by relative distribution. *Kruskal-Wallis Test returned a significant p value in IR_{act} between land-use categories.

Chapter 4. Interactions between Arabian wolves and people drive risk-mediated trophic cascades in a Middle Eastern desert

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Abstract

The cascading influence of the grey wolf (*Canis lupus*) on temperate ecosystems is well established; however, less is known of how these effects are replicated in other ecological systems. The smallest subspecies of grey wolf, the endangered Arabian wolf (*Canis lupus arabs*), inhabits the deserts of the Middle East, and its influence on lower trophic-order species is only now gaining attention. Recent evidence suggests that the abundance of Arabian wolves is strongly shaped by their relationship with people and use of human resources in this socio-politically complex region. Here, we explored the trophic influence of Arabian wolves on lower trophic-order species by recording their activity across the Negev Desert of Israel, documenting how they navigate land-use by people and how their resulting distribution influences desert trophic systems. Through camera trapping and occupancy modelling, we mapped the relative risk posed by people to Arabian wolves, and Arabian wolves to mesopredator and prey species. We found that wolves shaped the distribution and activity of other species, however, this varied based on human-wolf relationships. Humans create a 'landscape of fear' for wolves, based on varying levels of tolerance, which then cascade to other trophic levels. Our study highlights the important trophic role Arabian wolves play across Israel's desert landscapes and provides motivation for improving tolerance towards these apex predators.

4.1 Introduction

Little is known about the trophic ecology of the endangered, desert-adapted Arabian wolf (*Canis lupus arabs*), the smallest subspecies of grey wolf. The most stable population resides in Israel's arid to hyper-arid Negev Desert (Chapter 2), where Arabian wolves frequently exploit anthropogenic resources (Shalmon, 1986) and are often observed near human infrastructure (Barocas et al., 2018). Consequently, it is thought that their influence on ecological communities is unlikely to match that of their temperate counterparts in Europe and North America (Newsome et al., 2017). In temperate ecosystems such as Yellowstone National Park in North America, the top-down control of lower-trophic animals by wolves has been linked to multi-faceted cascading ecosystem effects (Wallach et al., 2016), including the return of many species since wolf reintroduction less than three decades ago. By influencing herbivore density and distribution across the landscape, wolves indirectly encouraged vegetation regrowth (Ripple et al., 2001), which led to changes in stream morphology (Beschta and Ripple, 2011), and restored important habitat (Ripple and Beschta, 2011). These trophic cascades are likely to be less recognisable in arid ecosystems as they are less productive, but nevertheless may still exist.

There is good reason to believe that Arabian wolves may shape the communities of Middle Eastern deserts, as the similar-sized dingo (*Canis dingo*) has been shown to drive cascades in arid Australia (Wallach et al., 2010). However, it is possible that the manner in which trophic cascades are mediated by the Arabian wolf may be subtly different. While the dingo suppresses red foxes (*Vulpes vulpes*) in Australia where mesopredator communities consist of few species, wolves have been shown to benefit foxes by reducing pressure from larger mesopredators like jackals and coyotes, which suppress (Levi and Wilmers, 2012). Like European (Krofel et al., 2017) and North American wolves (Newsome and Ripple, 2015), the Arabian wolf regulates golden jackal (*Canis aureus*) distribution and fox (*Vulpes* spp.) densities through suppression (Bonsen et al., 2022). But given that Arabian wolves feed mostly from agricultural crops, carrion, and garbage (Shalmon, 1986) –

only occasionally hunting ungulates (Hefner and Geffen, 1999), hares (Shalmon, 1986), and reptiles – there is debate as to how they might shape trophic cascades like their northern cousins.

To answer this, it is necessary to consider not only intraguild predation and interference competition among predators and prey (Fedriani et al., 2000), but also the risk responses species engage in to avoid predation (Creel and Christianson, 2008). The recovery of Yellowstone's vegetation was not solely a result of increased predation of ungulates, but also in the response of ungulates to predation risk by preferentially occupying areas that reduce encounters with predators (Ripple and Beschta, 2006). Analogous to the heterogeneity of topographic landscapes, the 'landscape of fear' that this risk represents is comprised of peaks and valleys of variations in perceived predation risk (Laundre et al., 2010). Responses to perceived risk include spatial or temporal avoidance of high-risk places or times (Moll et al., 2017), as well as behavioural adjustments such as increased vigilance (Wikenros et al., 2014) and group size (Moll et al., 2016). For example, if predators are known to occupy certain places at certain times, prey might respond by avoiding these places when predators are likely to be there (Kohl et al., 2018), or they might increase their vigilance when avoidance is impossible (Schmidt and Kuijper, 2015).

Trophic cascades are, thus, not only driven by direct predation, but also by the perceived risk of predation (Ripple and Beschta, 2004b). Just as areas of low risk to ungulates are high risk to plants; areas of low risk to wolves are likely high risk to jackals and ungulates. In arid agricultural landscapes of the southern Levant, wolves are less abundant where pastoralism dominates, favouring jackals (Chapter 3). Intolerance of wolves clearly shapes their presence in pastoralist landscapes, where people are acting as 'super predators' through the direct killing of species across multiple trophic levels (Darimont et al., 2015). The question is how variation in human tolerance of Arabian wolves, from acceptance to persecution, shapes the interactions wolves have with other species. Although wolves are protected from persecution in the Negev Desert, the perceived risk posed by humans is likely to differ in agricultural regions dominated by pastoralism where tolerance of wolves is low, compared to areas where they are accepted and encouraged to thrive. Elsewhere, fear is a significant driver of grey wolf distribution across its range (Theuerkauf, 2009).

In this study, we determined whether Arabian wolves adjust their spatial and temporal distribution across the landscape according to variations in perceived risk as a product of human land use and distribution. We then explored the cascading effects of this landscape of fear, based on spatial and temporal responses to perceived predation risk elicited by wolves, and other predators, to species in lower trophic levels. It is the first study, to our knowledge, to assess landscape-level trophic cascades of desert-dwelling wolves via super predator-apex predator, predator-mesopredator, and predator-prey pathways. We combined single-species and two-species occupancy models to determine the distribution and spatial responses of predators and prey to landscape-level variations in perceived risk posed by higher-order predators. We predicted that predators and prey would adjust their spatial and temporal activity patterns in areas of high risk to avoid predation, and that these interactions would change according to spatial variations in human acceptance of Arabian wolves.

4.2 Methods

4.2.1 Study Area

We conducted this study across a roughly 4,000 km^2 region of the Negev Desert in southern Israel, bounded by Israel's borders with Jordan to the east and Egypt to the west. Climatic conditions vary along vast differences in topography and elevation: steep slopes and escarpments lead eastward from the arid Negev Highlands (highest peak ~1,000 m) into the hyper-arid Arava Valley (400 m below sea level at its lowest point), which stretches north-south from the Dead Sea to the Red Sea along the Israel-Jordan border. While rainfall is infrequent throughout the study area, occurring solely within ~6-month periods surrounding the winter months, the Arava is considerably drier (annual precipitation ~20 mm) and up to 10 °C hotter than the highlands (annual precipitation ~50 mm). Nonetheless, natural water sources are extremely limited throughout the region, with few springs that provide water year-round. Instead, flash floods periodically fill intermittent waterholes within wadis (dry creek beds) after heavy rain events, which can last for several months. The scarce vegetation in the region is mostly restricted to these wadis and their surroundings.

Except for a small city (Dimona, population ~35,000) and two towns (Yeruham, population ~10,000; Mitzpe Ramon, population ~5,000), the sparse human population within the study area is predominantly confined to small agricultural villages (moshavim, kibbutzim, and Bedouin villages) and military bases. Agricultural practices vary with elevation: the Arava focusses primarily on crops such as dates and other seasonal fruits and vegetables, while the northern and central parts of the Negev are dominated by pastoralism, and to a lesser degree vineyards, citrus, and olive groves.

4.2.2 Study Species

Despite their high aridity, the deserts of the southern Levant hold a rich and unique mix of biodiversity due to the region's geographical setting at the junction of Africa and Eurasia. However, people have driven the decline of many species over the last two centuries (Mallon and Budd, 2011). Since the extirpation of leopards and cheetahs within the last several decades, the Arabian wolf is the sole remaining apex predator that hunts ungulates. While striped hyaenas (*Hyaena hyaena*) persist in the region and have been documented to associate themselves with wolf packs (Dinets and Eligulashvili, 2015), they are primarily scavengers, and we did not include them in our models. Golden jackals, on the other hand, have the capacity to prey on gazelle fawn (Borkowski et al., 2011). However, as they are largely centred around human habitation in these arid lands (Nemtzov and King, 2001), there is likely little range overlap, and hence, minimal interaction between jackals and ungulates within our study system. Jackals are also considered a recent arrival to the Negev and are subject to lethal control throughout the study area (Nemtzov and King, 2001). We therefore focussed on two, relatively simple, trophic cascade pathways, and determined whether these were influenced by human-wolf relationships: (i) wolf interactions with mesopredators (jackals and foxes), and their successive interactions with lower trophic-order species; and (ii) wolf interactions with prey (ungulates and hares).

We grouped the three fox species that occur in the Negev (red fox; Blandford's fox, *V. cana*; Rueppell's fox, *V. rueppellii*) into genus (*Vulpes* spp.), and these defined the lowest trophic order mesopredators. Cape hares (*Lepus capensis*) are common prey for canids (Shabbir et al., 2013) and the most common small herbivore (excluding rodents) in our study area. Hares constituted the bottom trophic level in both the predator-predator and predator-prey pathways examined within our study. Four free-ranging ungulate species are known to occur in the Negev. While we conducted single-species occupancy models to determine spatial distribution of ungulate species individually, we merged ungulate species into two separate guilds, based on size, to assess trophic interactions: large ungulates (Arabian oryx, *Oryx leucoryx*; onager *or* Asiatic wild ass, *Equus hemionus*) and small-medium ungulates, whose spatial distributions differ with disparate topographic landscape requirements (dorcas gazelle, *Gazella dorcas;* Nubian ibex, *Capra nubiana*). Arabian wolves are capable of preying on adult small-medium ungulates, and we have observed them chasing young wild ass in the Negev.

4.2.3 Design and Sampling

We selected 80 sampling points using a stratified random design to capture the full range of conditions considered to influence mammal movement across the landscape (Figure 4.1). We identified six spatial variables, that were not highly correlated, from a larger pool of potential variables pertaining to three categories (attractants, anthropogenic risk factors, topography; Figure S1). Euclidean distance rasters were created from vector data acquired from various sources (Table

S1), while we derived elevation from an SRTM digital elevation model (DEM). We used the same DEM to produce a topographic complexity raster using focal statistics, scoring differences in slope between raster cells within a 2,000 m neighbourhood. Rasters were produced using Spatial Analyst tools in ArcGIS 10.3 at a spatial resolution of 30 m. A vector layer was produced to define pastoralist areas (binary) by creating a polygon outlining a region, excluding designated protected areas, where the nearest agricultural practice involved pastoralism. Sampling point locations were distributed evenly across these six variables, with a mean minimum distance of 4 km between sampling points, to ensure spatial independence.

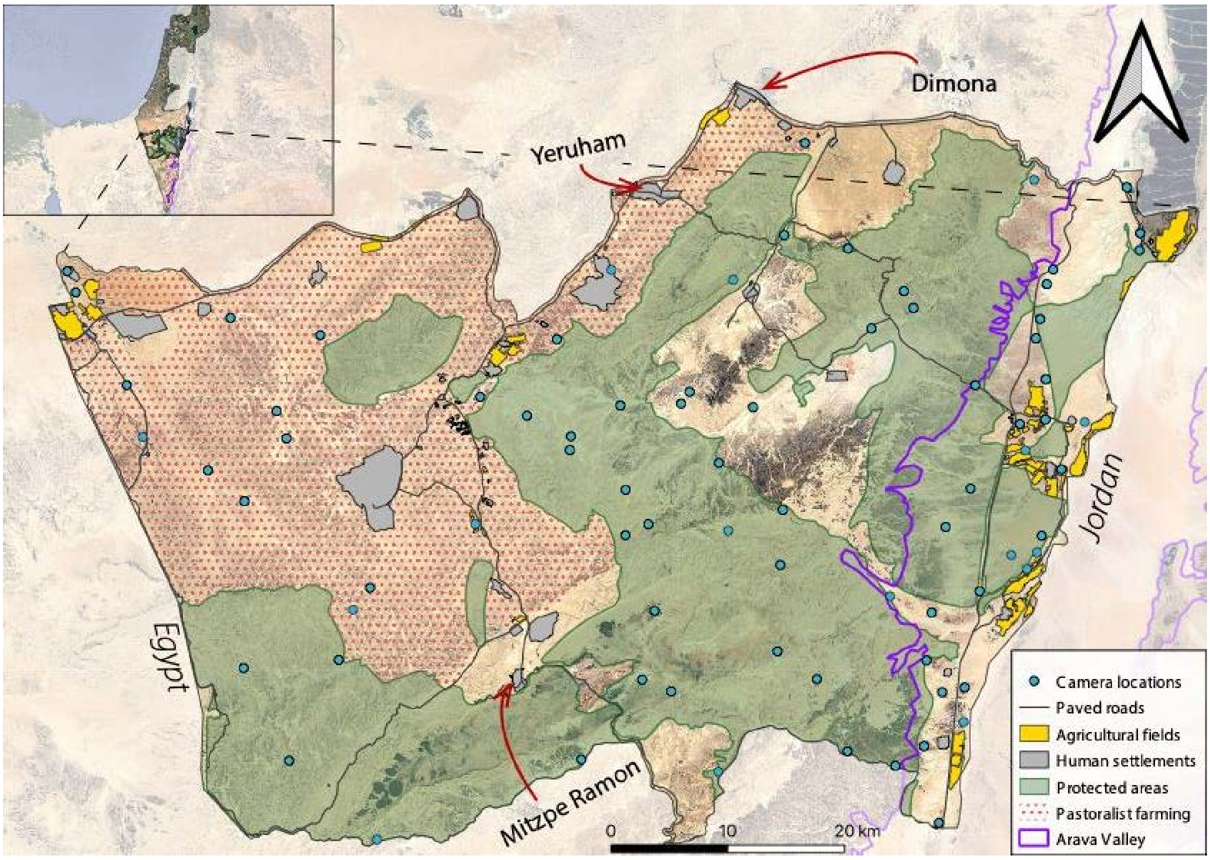

Figure 4.1: Spatial distribution of human land-use and infrastructure across the study area. Inset shows the location of the study area within Israel.

During three consecutive 'wet seasons' (~Oct-April) from 2016 to 2019, we deployed a single motion-sensing camera trap (Bushnell Trophy Cam Aggressor no glow) at each sampling point. We placed camera traps on the edge of wildlife trails within wadis, either disguised by rocks on the wadi's bank, or attached to trees or poles at 0.5 – 1.5 m above the ground. A uniform placement height was not possible to maintain as local context made some cameras conspicuous and subject to theft. Cameras were operational for a period of 30.4 (± 2) days for a single session each year, and were set to record a photo, or a short (10-15 second) video if the sampling point was close to a permanent water source, each time an animal moved in front of the sensor.

We retained camera-trap detections of mammal species of interest and sorted them into species or species complex (i.e., genus or trophic guild such as small-medium ungulates; hereafter 'species'). We defined a detection event as independent when no other detections of the same species occurred for five minutes before or after a single event, and collated independent events using the package 'camtrapR' in program R version 4.0.1 (R Development Core Team 2008). The location, date, and time of detection were recorded for each event.

4.2.4 Data Analyses

We used a three-step approach to map spatial responses of mammals to the landscape of fear using both single-species and two-species occupancy models in R package 'Wiqid'. We first used single-species occupancy models to determine the relationship between the probability of occupancy (Ψ) for a species with each of the spatial variables: namely distance to human habitation, permanent water sources, and paved roads, as well as elevation and topographic complexity. Continuous variables were scaled for modelling by subtracting the mean from each value and dividing the value by the standard deviation. The entire slate of spatial variables featured within the top-performing models for each species (i.e., those with $\Delta AIC < 2$), so we used the global model for all species other than gazelle, where distance from permanent water was excluded from the model (see Table S4.2 in Supplementary Material for details on model selection).

We then modelled trophic interactions using two-species occupancy models to determine the conditional occupancy probability of a subordinate species (i.e., prey or lower-order predator), given the probability of occupancy of a dominant species (i.e., higher-order predator). Like the single-species models, we used the global model for each species. The output from these models provided us with three parameters, from which we calculated a SIF using the equation proposed by (Richmond et al., 2010) (see equation 3.1 in Chapter 3). The SIF is an odds ratio based on overall occupancy across the entire landscape and describes segregation (avoidance) or aggregation (attraction) of two species after considering the spatial responses of the subordinate species to the dominant's presence or absence. SIF values ~1 indicate that the two species occur independently (i.e., occupancy of the subordinate species is not influenced by that of the dominant species), while values < 1 indicate avoidance and values > 1 indicate attraction. The strength of the interaction corresponds to the distance of the value from 1 (values further from 1 indicate stronger interactions). We calculated a SIF for each dominant-subordinate species pair, both within pastoralist landscapes and outside of pastoralist landscapes, and used the proportion of overlap of 95% confidence intervals to determine whether each SIF was different between pastoralist and non-pastoralist landscapes (Cumming, 2009).

To understand how variation in occupancy played out spatially, we used the models to predict occupancy across the landscape based on the spatial variables included in each model. Using the 'raster' package in R, we created output rasters at the same 30 m resolution used for the single-species models, as well as one parameter from the conditional two-species models (ψ^{BA}). Single-species model predictions produced a distribution map for each species, showing spatial variation in ψ, while ψ^{BA} predictions showed spatial responses of the subordinate species, given that the dominant species is present, based on the same spatial variables. Specifically, ψ^{BA} predictions did not state whether the dominant species was present at a location, but rather the response (change in ψ) of the subordinate species if the dominant species was to be present.

Finally, we produced maps depicting variations in 'relative risk' with the aim of capturing spatial variation in response to perceived risk across a landscape of fear for a subordinate species within a given dominant-subordinate species pair. We calculated relative risk using the following equation, which returned a relative risk index between -1 (high risk) and 1 (low risk; Figure S4.2).

$$\text{Relative risk} = \Psi^{BA} - \Psi^{A}$$

Rather than explicitly indicating variations in predation risk, our relative risk index is based on the spatial responses of a subordinate species to the potential cooccurrence of a dominant species. As relative risk is calculated across the entire landscape, we clipped the relative risk map for a given pair of interacting species to a polygon vector outlining an area in which the probability of occupancy of the subordinate species was ≥ 0.25. The resulting relative risk maps illustrate the variation in relative risk from safe (relative risk = 1) to risky (relative risk = -1) areas, based on the spatial responses of a species to perceived predation risk.

To determine whether animals adjusted their temporal activity (i.e., time of day individuals are active) in risky areas to avoid predation, we explored temporal activity patterns for each species within an interacting pair across relative risk levels. First, we split the camera-trap events by location for each species pair into 'high risk' and 'low risk' based on the 0.25 (high risk) and 0.75 (low risk) quantiles according to the spread of the data across the relative risk maps. After converting the time of each event into radians (*r*), we fitted kernel density curves and estimated the coefficient of overlap ($\hat{\Delta}$) between two curves using the 'overlap' package in R (Meredith and Ridout, 2020). Ranging from 0 (no overlap) to 1 (complete overlap), $\hat{\Delta}$ provides an estimate of overlap between two sets of samples (e.g., each species in a species pair) by measuring the proportion of area that sits concurrently below both curves. We followed the recommendations of Ridout and Linkie (2009) by using $\hat{\Delta}_1$ for small sample sizes (<75) and $\hat{\Delta}_4$ for large sample sizes (>75).

For each dominant-subordinate species pair, we estimated $\hat{\Delta}$ between species across high-risk and low-risk areas. To determine whether any change in $\hat{\Delta}$ was caused by temporal adjustments in activity of the dominant or subordinate species, we simultaneously estimated $\hat{\Delta}$ within each species across high-risk and low-risk areas. We then generated 1,000 smoothed bootstrap samples and estimated a mean $\hat{\Delta}$ and 95 % confidence intervals according to the procedure outlined by Meredith and Ridout (2020) for each pair of density curves. We tested for any significant change within a species' temporal activity patterns between high-risk and low-risk areas using a Wald's test in R's 'activity' package.

4.3 Results

From a total of 2,308 camera trap days, we recorded 1,587 events from the seven species or species complexes included in our analyses (Table 4.1). People (393 events from 46.3 % of sampling points) and small herbivores (378 events from 48.7 % of sampling points) were the most frequently recorded. However, foxes were the most widespread (304 events from 67.1 % of sampling points) and had the highest overall probability of occupancy ($\psi = 0.74 \pm 0.06$). Jackals (130 events from 15.8 % of sampling points) were recorded considerably more than wolves (64 events from 34.2 % of sampling points), but the probability of occupancy was significantly higher for wolves (wolf $\psi = 0.40 \pm 0.07$; jackal $\psi = 0.16 \pm 0.04$), with jackals being the least widespread species.

Occupancy probability of small-medium ungulates was equal to wolves (small-medium ungulate $\psi = 0.40 \pm 0.06$), but the number of events and sampling points was considerably higher for small-medium ungulates (283 events from 41.3 % of sampling points), due to the low probability of detecting a wolf ($p = 0.06 \pm 0.01$ compared to $p = 0.14 \pm 0.01$ for small-medium ungulates). The Asiatic wild ass was the only large ungulate species recorded and was the least recorded species (35 events from 17.1 % of sampling points), having a slightly higher probability of occupancy than jackals (large ungulate $\psi = 0.22 \pm 0.06$).

Table 4.1: Summary of species records from camera-trapping data, showing the number of events, the number of sampling points (n) at which each species was recorded (% of total sampling points), and the marginal occupancy (y) and detection (p) probabilities of each species (± SE).

Species/guild	Scientific name	No. of events	*n* (%)	ψ (± SE)	*p* (± SE)
People	*Homo sapiens*	393	37 (46.3)	0.49 (0.06)	0.13 (0.01)
Wolf	*Canis lupus*	64	26 (34.2)	0.40 (0.07)	0.06 (0.01)
Jackal	*Canis aureus*	130	12 (15.8)	0.16 (0.04)	0.17 (0.02)
Foxes	*Vulpes vulpes* *Vulpes cana* *Vulpes rueppellii*	304	51 (67.1)	0.74 (0.06)	0.11 (0.01)
Large ungulate	*Equus hemionus*	35	13 (17.1)	0.22 (0.06)	0.05 (0.01)
Small-medium ungulates	*Gazella dorcas* *Capra nubiana*	283	33 (41.3)	0.40 (0.06)	0.14 (0.01)
Small herbivore	*Lepus capensis*	378	37 (48.7)	0.52 (0.06)	0.19 (0.01)

4.3.1 Evidence of human-induced trophic cascades

Arabian wolves influenced the spatial distribution of prey and mesopredators, but this was largely dependent on the top-down influence of humans across pastoralist and non-pastoralist landscapes. All species in lower trophic levels showed some level of spatial avoidance towards wolves in at least one of the two landscape categories (Figure 4.2). In non-pastoralist landscapes where wolf avoidance of people was weak (φ ± 95 % CI = 0.80 ± 0.63 - 0.96), all herbivores (large ungulate φ ± 95 % CI = 0.52 ± 0.34 – 0.70; small-medium ungulates φ ± 95 % CI = 0.37 ± 0.20 – 0.54; small herbivore φ ± 95 % CI = 0.41 ± 0.22 – 0.59) strongly avoided wolves. In contrast, jackals were strongly attracted to wolves (φ ± 95 % CI = 1.32 ± 1.14 – 1.50). These interactions alternated in pastoralist landscapes, where wolf avoidance of people was significantly stronger (φ ± 95 % CI = 0.21 ± - 0.13 – 0.54). Jackals strongly avoided wolves (φ ± 95 % CI = 0.00 ± - 0.61 – 0.61) and main prey species no longer avoided wolves (small-medium ungulates φ ± 95 % CI = 0.87 ± 0.51 – 1.23; small herbivore φ ± 95 % CI = 1.37 ± 0.91 – 1.83), with small herbivores showing attraction towards wolves. While foxes avoided both wolves (φ ± 95 % CI = 0.72 ± 0.47 – 0.97) and jackals (φ ± 95 % CI = 0.21 ± - 0.13 – 0.54) across pastoralist and non-pastoralist landscapes, their avoidance of jackals was markedly stronger.

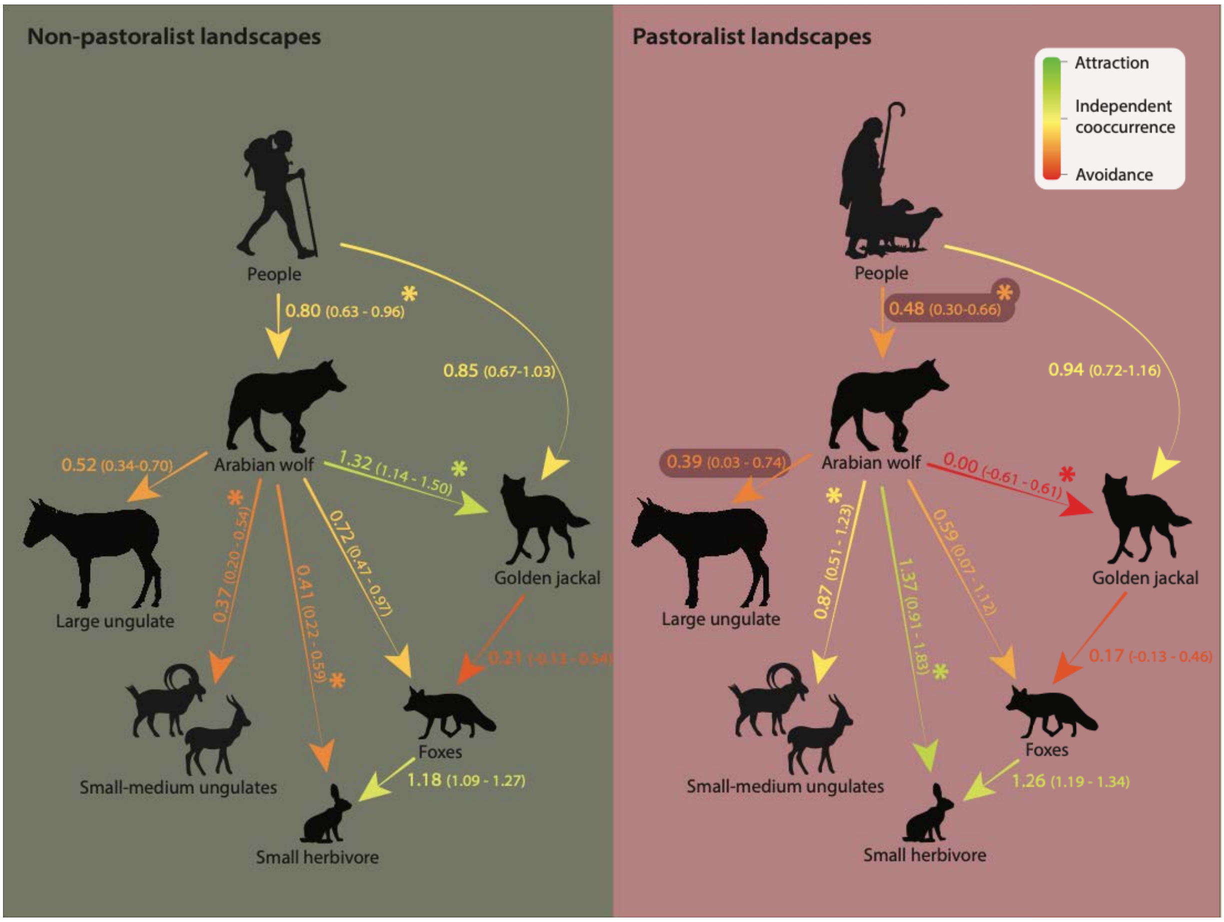

Figure 4.2: Conceptual diagrams illustrating Species Interaction Factors (SIFs) between a super predator–apex predator; apex predator–mesopredators; and predators–prey in non-pastoralist and pastoralist landscapes. The colour of each arrow corresponds to the strength and direction (attraction vs avoidance) of interaction between a pair of interacting species. *Significant difference in SIF between non-pastoralist and pastoralist landscapes (refer to Fig. S4.3 in Supplementary Material).

4.3.2 Predator-predator interactions

Landscapes of fear alternated through trophic levels for predators based on variations in relative risk imposed by higher-order predators (Figure 4.3). Relative risk of humans varied across the landscape for wolves, largely based on human land-use (Figure 4.3*a*). The safest areas for wolves were characterised by low elevation, and around human habitation where pastoralism was not the predominant land-use (e.g., close to nature reserves). The riskiest places were along the edges of protected areas in pastoralist landscapes, where wolves avoided human habitation (probability of occupancy < 0.25). Risk of wolves was highest for jackals at increasing distances from human habitation (i.e., the edge of their distribution) where wolves are safe from people (Figure 4.3*b*). Jackals strongly associated with human habitation (Figure S4.4) and the safest places for jackals were areas avoided by wolves, surrounding human habitation in pastoralist landscapes. Foxes were the most widespread predators, occurring throughout the study area. Risk of wolves was highest in small pockets immediately surrounding human habitation where wolves were safest from people (Figure 4.3*c*). Relative risk imposed by jackals on foxes was more pervasive, with sizeable risky areas in locations where jackals' risk of wolves was low, primarily near human habitation in pastoralist landscapes (Figure 4.3*d*). The probability of occupancy of all predators decreased with distance to human habitation, however, people were the only predator whose occupancy probability increased with distance to permanent water sources (Figure S4.5).

The only significant change in temporal activity between high-risk and low-risk areas for predators was in wolf activity where the relative risk imposed by wolves on foxes varied (Table 4.2). Wolves, jackals, and foxes were mostly crepuscular, with bimodal peaks in activity occurring around dawn and dusk, and higher levels of activity throughout the night than during the day (Figure S4.7). However, where foxes were safest from wolves, wolves were most active in the middle of the night, adjusting their activity from crepuscular to nocturnal (Wald's $\chi^2 = 4.26$, $p < 0.05$).

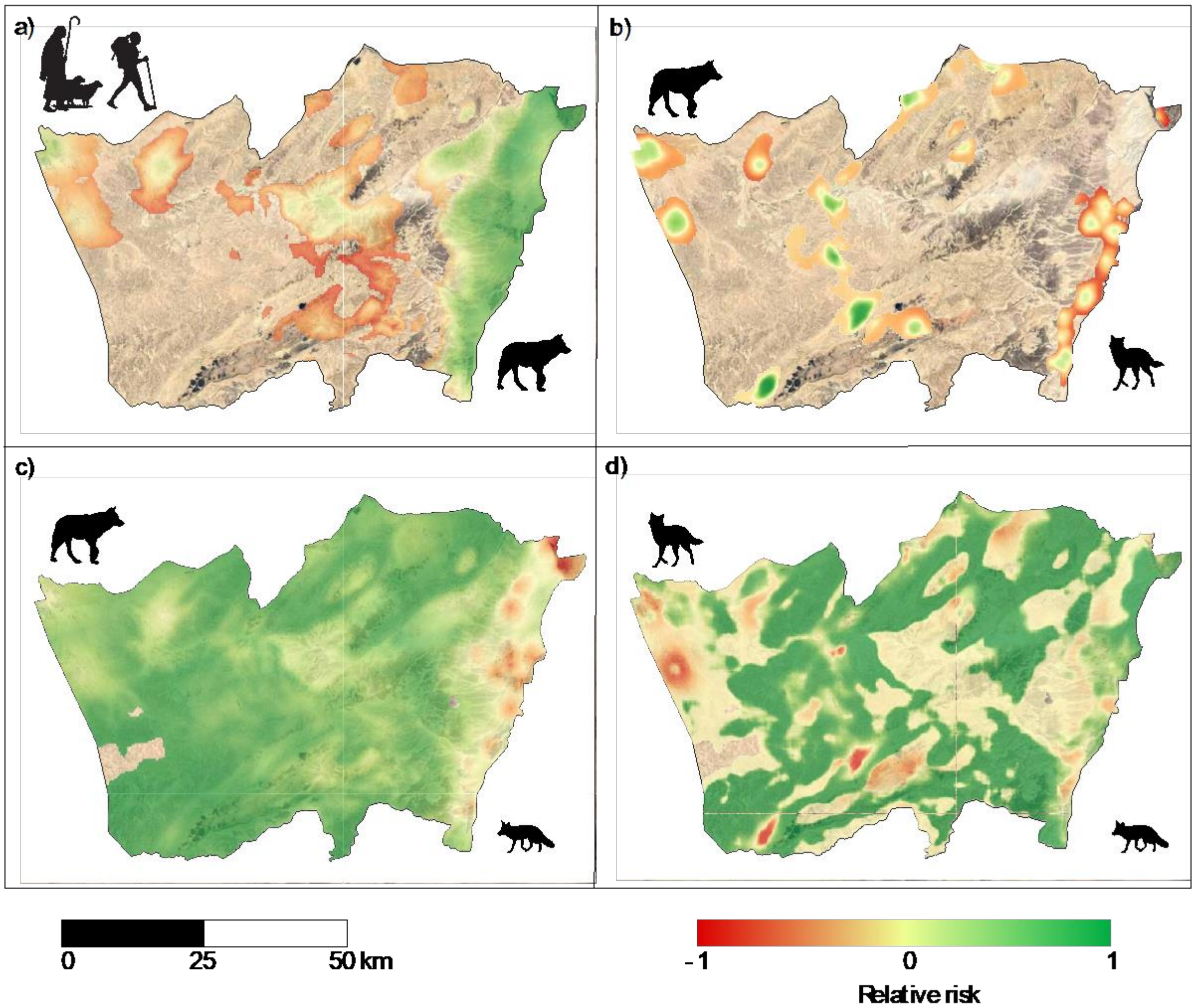

Figure 4.3: Relative risk maps depicting proposed landscapes of fear for a given subordinate predator species (bottom-right of each panel), based on spatial responses to the potential co-occurrence of a dominant predator (top-left of each panel) for a) people – wolf, b) wolf – jackal, c) wolf – foxes, and d) jackal – foxes. Colour scheme represents a gradient from low risk (green) to high risk (red).

Table 4.2: Bootstrapped coefficient of overlap ($\hat{\Delta}$) estimates for dominant-subordinate predator species pairs across risk levels (95 % CI). High risk and low risk columns compare $\hat{\Delta}$ between the two species within each risk level, while dominant and subordinate columns compare $\hat{\Delta}$ between high and low risk levels within each species. Grey cells indicate insufficient data.

Species pair	High risk	Low risk	Dominant	Subordinate
People Wolf	0.325 (0.167 - 0.443)	0.287 (0.093 - 0.379)	0.87 (0.805 - 0.957)	0.697 (0.543 - 0.914)
Wolf Jackal	0.770 (0.695 - 0.942)	0.688 (0.582 - 1.00)	0.579 (0.408 - 0.897)	0.672 (0.514 - 0.825)
Wolf Foxes	0.758 (0.656 - 0.931)	0.675 (0.522 – 0.858)	0.659* (0.466 - 0.877)	0.857 (0.826 - 0.991)
Jackal Foxes	0.770 (0.629 - 0.863)			0.836 (0.758 - 0.939)

* Wald's test returned a significant p-value

4.3.3 Predator-prey interactions

Similar landscapes of fear were demonstrated for prey species, with relative risk varying across the landscape based on the potential co-occurrence with predators (Figure 4.4). Large ungulates avoided low elevation areas where wolves were safest from people (probability of occupancy < 0.25); Figure 4.4*a*). Risk of wolves was highest in areas far from human habitation where wolves were relatively safe from people. However, large ungulates also responded negatively to potential cooccurrence with wolves outside of wolf distribution (probability of occupancy of wolves < 0.25; Figure S4.9). Risk of wolves for small-medium ungulates (Figure 4.4*b*) and small herbivores (Figure 4.4*c*) was also high where wolves were safe from people, but closer to human habitation and permanent water sources. While risk of wolves (Figure 4.4*c*) and foxes (Figure 4.4*d*) was high for small herbivores at local scales, particularly close to human habitation and permanent water sources, small herbivores were excluded from large areas (probability of occupancy < 0.25) where jackals were safest from wolves (Figure 4.3*b*), and risk of foxes was high surrounding these gaps in their distribution. Contrary to predators, the probability of occupancy of prey species increased with distance to human habitation and permanent water sources (Figure S4.5).

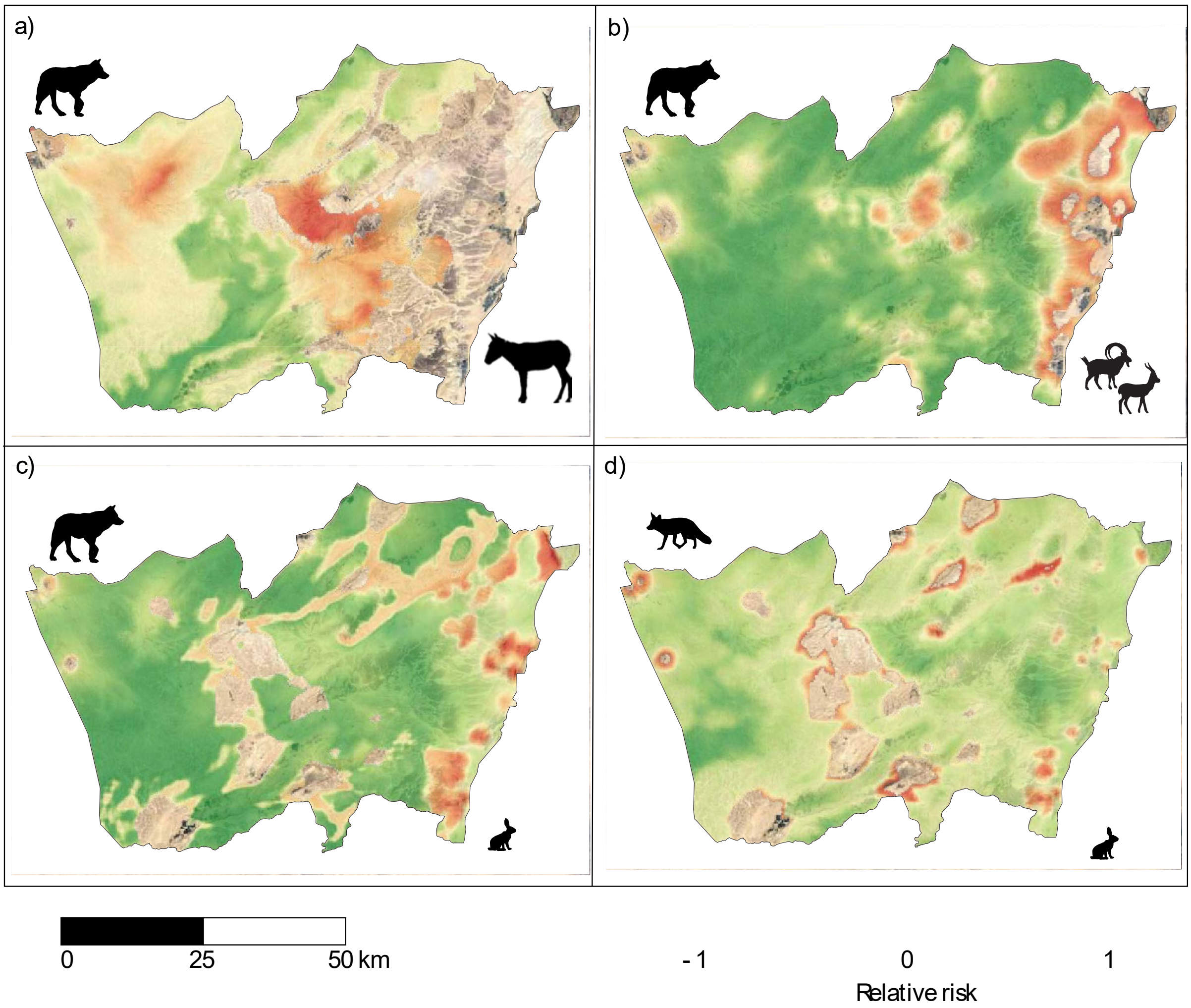

Figure 4.4: Relative risk maps depicting proposed landscapes of fear for a given prey species (bottom-right of each panel, based on spatial responses to the potential co-occurrence of a predator (top-left of each panel) for a) wolf – large ungulate, b) wolf – small-medium ungulate, c) wolf – small herbivore, and d) foxes – small herbivore. Colour scheme represents a gradient from low risk (green) to high risk (red).

Both small-medium ungulates and small herbivores adjusted their temporal activity significantly between high-risk and low-risk areas (Table 4.3). Temporal overlap between wolves and small-medium ungulates was higher in high-risk areas ($\hat{\Delta}$ 0.792) than in low-risk areas ($\hat{\Delta}$ 0.340). In low-risk areas, small medium ungulates were more active during the day, while they were mostly crepuscular, like wolves, in high-risk areas (Figure S4.7; Wald's χ^2 = 15.33, $p < 0.001$). Small herbivores, on the other hand, adjusted their temporal activity so overlap with foxes was significantly reduced in areas of high risk posed by foxes ($\hat{\Delta}$ 0.510 in high risk, $\hat{\Delta}$ 0.827 in low risk). Contrary to small-medium ungulates, small herbivores were crepuscular in low-risk areas, but shifted to a single activity peak in the middle of the night when fox activity subsided in high-risk areas (Wald's $\chi^2 = 8.67$, $p < 0.01$).

Table 4.3: Bootstrapped coefficient of overlap ($\hat{\Delta}$) estimates for predator-prey species pairs across risk levels (95 % CI). High risk and low risk columns compare $\hat{\Delta}$ between the two species within each risk level, while dominant and subordinate columns compare $\hat{\Delta}$ between high and low risk levels within each species. Grey cells indicate insufficient data.

Species pair	High risk	Low risk	Dominant	Subordinate
Wolf L ungulate		0.709 (0.579 – 1.00)	0.599 (0.428 - 0.865)	
Wolf S-M ungulate	0.792 (0.743 - 0.984)	0.340 (0.135 – 0.652)	0.588 (0.448 - 0.957)	0.556* (0.413 - 0.669)
Wolf Small herbivore	0.751 (0.633 - 0.909)	0.734 (0.663 – 1.00)	0.686 (0.594 – 1.00)	0.809 (0.708 - 0.909)
Foxes Small herbivore	0.510 (0.356 - 0.607)	0.827 (0.744 - 0.983)	0.681 (0.531 - 0.798)	0.690* (0.514 - 0.805)

* Wald's test returned a significant p-value. L ungulate = large ungulates; S-M ungulate = small-medium ungulates.

4.4 Discussion

Like its temperate cousins, we found that the Arabian wolf influences the spatial distribution of mesopredators and prey, and that this ecological role is clearly shaped by people. We found that wolves avoided both human habitation and areas occupied by people in pastoralist landscapes, where tolerance of wolves is low, while they were attracted to human habitation and co-occurred with people in areas where they are accepted. While previous accounts of the Arabian wolf's spatial distribution in the Negev have shown their increasing association with human infrastructure (Barocas et al., 2018), here we demonstrate the importance of human context in shaping the distribution of Arabian wolves in these desert landscapes (Haswell et al., 2016). We suggest that wolves respond spatially to variations in perceived risk by being cognisant of distinctions between benign and harmful human intentions, possibly as a result of associative learning (Austin and

Ramp, 2019). Their navigation of this landscape of fear then mediates trophic cascades by successively creating alternative landscapes of fear for prey and mesopredators.

The top-down pressure exerted by wolves on ungulates has previously been shown to be surpassed by direct and indirect top-down control from people in hunting landscapes (Dorresteijn et al., 2015). We similarly found that prey spatially avoid Arabian wolves in areas where wolves are tolerated, whereas in pastoralist landscapes prey occurred independently of wolves. In these pastoralist areas, both small-medium ungulates and small herbivores show less fear of wolves than they do in areas where wolves are not fearful of people. Jackals, on the other hand, are persecuted across this arid region (Nemtzov and King, 2001), but benefit nonetheless from the reduced competition with wolves in pastoralist landscapes (Chapter 3). While jackals and foxes both co-occurred with wolves in areas where wolves are safe from people, presumably because the three species share anthropogenic resources in these crop farming landscapes (Barocas et al., 2018; Shamoon et al., 2017; Shapira et al., 2008), jackals are far more active in pastoralist landscapes (chapter 3). This suggests that jackals may navigate the landscape of fear by occupying areas where risk of wolves is low, namely around human habitation in pastoralist landscapes, subsequently creating areas of high-risk to foxes and exclusion of small herbivores. While small herbivores adjusted their temporal activity patterns where foxes pose high risk, probably to avoid predation (Smith et al., 2019), small herbivore distributions were patchy in these same areas where jackals are safe from wolves, implying that high predation pressure from jackals leads to exclusion of small herbivores.

We argue that increased jackal activity, resulting from wolves avoiding high-risk areas in pastoralist landscapes, creates knock-on effects to species in lower trophic levels (Ripple et al., 2013). Although foxes do avoid wolves spatially, their avoidance of jackals is markedly stronger, confirming our previous research (Chapter 3). Likewise, small herbivores coexist with wolves by spatially avoiding wolves in high-risk areas. In these areas, where wolves are safe from people, jackals are exposed to risk from wolves except in the immediate vicinity of human habitation, where resources abound. Multiple predator species have been observed coexisting with relatively little aggression towards one another in resource-rich areas (Mueller et al., 2018), and we have recorded this between wolves, jackals, foxes, and striped hyaenas (*Hyaena hyaena*) at resource points within our study area (unpublished data). However, as interspecific competition is largely driven by resource gradients (Ullas Karanth et al., 2017), competitive exclusion is likely to escalate further from these resources, hindering expansions of jackals similar to those in pastoralist landscapes.

Several small herbivores (e.g., the Balochistan gerbil *G. nanus*) and mesopredators (e.g., Rueppell's fox, the sand cat *Felis margarita*) are already threatened throughout this region, largely due to increased human activity (Shapira et al., 2008). Agricultural expansion has caused the desiccation of numerous natural springs and, coupled with persecution of apex predators, has made way for the colonisation of generalist higher order mesopredators, increasing the risk of competition and predation for smaller species. Since the extirpation of the Arabian leopard (*Panthera pardus nimr*) and Asiatic cheetah (*Acinonyx jubatus venaticus*), the Arabian wolf is the only apex predator to remain in these deserts. While wolves inhabiting anthropogenic landscapes in Europe occupy high-elevation areas to avoid high temperatures at low elevations (Bassi et al., 2015), Arabian wolves are driven to the lowest and one of the hottest valleys on Earth (Pen-Mouratov et al., 2010), where they are accepted by people. Although we agree that species-specific responses to human influence depend on ecological and life-history traits (Suraci et al., 2021), we add that human acceptance is also a significant driver.

4.4.1 Depiction of the landscape of fear

Given the multitude of factors that influence landscape of fear dynamics (Gaynor et al., 2019) and the countless ways to interpret spatial variations in perceived risk (Iribarren and Kotler, 2012; Kauffman et al., 2013; Willems and Hill, 2009), landscapes of fear are difficult to represent visually.

While there is significant merit in conceptualising landscape-scale variations in perceived risk as a topographic map (Laundre et al., 2010), the various methods used to portray risk perception have led to confusion (Gaynor et al., 2019). One particular concern is that two species within an interacting pair often have disparate spatial distributions; something that is often overlooked. Our approach of estimating a relative risk index based on the modelled distributions of two species, paired with the spatial responses of one species to potential cooccurrence with the other, overcomes these concerns because it captures sources of variation in perceived risk. Our approach also accounts for where a single species must accommodate variations in risk associated with more than one predator.

We consider this an initial step in determining how landscapes of fear drive species distributions, and how perceived risk varies throughout these distributions. The resulting risk maps do not show absolute distribution (e.g., only showing areas where the species of interest has a probability of occupancy ≥ 0.25), but rather the variation in perceived risk across an area where a given species is likely to occur, and how this risk drives its distribution. This same method can also be used at smaller scales; for example, to see how perceptions of risk in prey vary with habitat or topographic complexity within a national park. Detailed studies can then be conducted to assess behavioural responses across risk levels.

4.4.2 Conclusion

We show that although Arabian wolves largely utilise human infrastructure (Barocas et al., 2018) and anthropogenic resources (Shalmon, 1986), they still play important ecological roles by influencing the spatial distribution of prey and mesopredators in desert ecosystems. While prey such as ungulates may not be subject to high predation pressure from Arabian wolves in these arid to hyper-arid ecosystems, wolves create landscapes of fear for prey and mesopredators, which has cascading ecosystem effects. Persistence of Arabian wolves is largely driven by their relationships with people, where they avoid areas where they are not tolerated by selecting for areas they are accepted. We have shown that through suppression of Arabian wolves – whether it be direct or indirect – people are driving species distributions across multiple trophic levels.

4.5 References

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Table S4.1: Types of explanatory variables used in site selection and as covariates in occupancy models.

Category	Layer	Description	Source
Attractants	Human habitation (m)	Distance to human settlements (cities, towns, villages, camp sites, and military bases) or agricultural fields.	Euclidean distance raster created in ArcGIS from settlement and agriculture polygon shapefiles obtained from M. Silver, Arava Drainage Authority, Sapir, Israel.
	Permanent water sources (m)	Distance to all permanent water sources (springs, water holes, leaking pipes).	Euclidean distance raster created in ArcGIS from permanent water point vector data acquired from local knowledge of the study area.
Anthropogenic risk factors	Paved roads (m)	Distance to paved roads.	Euclidean distance raster created in ArcGIS from roads vector data produced from scanning satellite imagery.
	Pastoralism (binary)	Polygon shapefile outlining an area in which pastoralism is a dominant form of agriculture.	Using a Euclidean distance raster of agriculture and knowledge of whether the nearest form of agriculture involved pastoralism, a polygon vector was created to outline agricultural areas dominated by pastoralism in ArcGIS.
Topography	SRTM digital elevation model (m)	Altitude above sea level (m).	Shuttle Radar Topographic Mission (SRTM) digital elevation model obtained from M. Silver, Arava Drainage Authority, Sapir, Israel.
	Topographic complexity (2km)	Difference in slope between cell neighbours within a 2,000 m neighbourhood (between 0^{o} and 90^{0}).	Generated from SRTM dataset using focal statistics in ArcGIS.

Table S4.2: Top-performing single-species occupancy models for each species. Models were selected from a set of 31 candidate models for each species by choosing those with ΔAIC < 2. As the entire slate of landscape variables featured in the top-performing models, we used the global model for each species[2].

	df	ΔAIC	ModelLik	ModelWt	Landscape variables included in model
People	3	0	1	0.101	roads
	3	0.05	0.975	0.099	topographic complexity
	3	0.336	0.845	0.085	elevation
	3	0.9	0.638	0.064	human habitation
	3	1.247	0.536	0.054	water
	4	1.353	0.508	0.051	roads + topographic complexity
	4	1.628	0.443	0.045	topographic complexity + elevation
	4	1.644	0.439	0.044	water + topographic complexity
	4	1.654	0.437	0.044	roads + elevation
	4	1.823	0.402	0.041	roads + water
	4	1.984	0.371	0.037	human habitation + topographic complexity
	4	1.988	0.37	0.037	human habitation + roads
Wolves	4	0	1	0.109	water + elevation
	4	0.022	0.989	0.108	water + topographic complexity
	3	0.327	0.849	0.092	elevation
	5	0.782	0.676	0.074	water + topographic complexity + elevation
	4	1.809	0.405	0.044	topographic complexity + elevation
	5	1.846	0.397	0.043	water + elevation
	3	1.922	0.383	0.042	water
	5	1.958	0.376	0.041	roads + water + topographic complexity
	5	1.964	0.375	0.041	human habitation + water + elevation
	5	1.978	0.372	0.04	human habitation + water + topographic complexity
Jackals	6	0	1	0.215	human habitation + water + topographic complexity + elevation
	5	0.687	0.709	0.152	human habitation + water + topographic complexity
	7	1.51	0.47	0.101	human habitation + roads + water + topographic complexity + elevation
Foxes	4	0	1	0.202	water + topographic complexity
	5	0.65	0.723	0.146	human habitation + water + topographic complexity
	5	1.262	0.532	0.107	roads + water + topographic complexity
	5	1.989	0.37	0.075	water + topographic complexity + elevation
Onager	4	0	1	0.127	topographic complexity + elevation
	3	0.131	0.936	0.119	elevation
	4	0.948	0.623	0.079	water + elevation
	5	1.042	0.594	0.076	human habitation + topographic complexity + elevation
	5	1.471	0.479	0.061	water + topographic complexity + elevation
	5	1.774	0.412	0.052	roads + topographic complexity + elevation
	4	1.97	0.373	0.047	human habitation + elevation
Gazelle	4	0	1	0.161	water + elevation
	3	0.925	0.63	0.102	water
	4	1.381	0.501	0.081	water + topographic complexity
	5	1.698	0.428	0.069	water + topographic complexity + elevation
	5	1.822	0.402	0.065	roads + water + elevation
	5	1.902	0.386	0.062	human habitation + water + elevation
Ibex	3	0	1	0.226	topographic complexity
	4	1.553	0.46	0.104	topographic complexity + elevation
	4	1.685	0.431	0.097	human habitation + topographic complexity
	4	1.711	0.425	0.096	roads + topographic complexity
	4	1.861	0.394	0.089	water + topographic complexity
Hare	4	0	1	0.245	water + elevation
	5	1.145	0.564	0.138	human habitation + water + elevation
	5	1.697	0.428	0.105	water+ topographic complexity + elevation
	6	1.777	0.411	0.101	human habitation + water + topographic complexity + elevation
	5	1.848	0.397	0.097	roads + water + elevation

[2]Distance to water was removed from the gazelle model as model predictions were skewed by this variable.

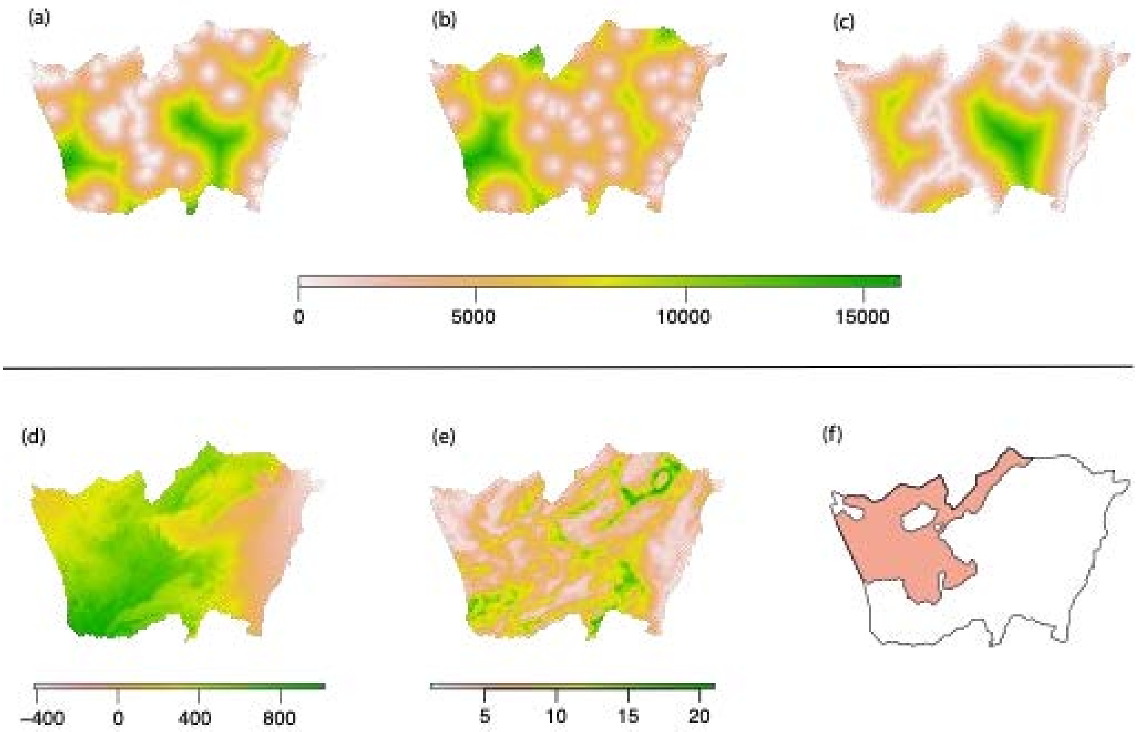

Figure S4.1: The six spatial variables included in site selection and occupancy model predictions, including: a) human habitation (m), b) permanent water sources (m), c) paved roads (m), d) elevation (m), e) topographic complexity (2 km), and f) pastoralism (binary).

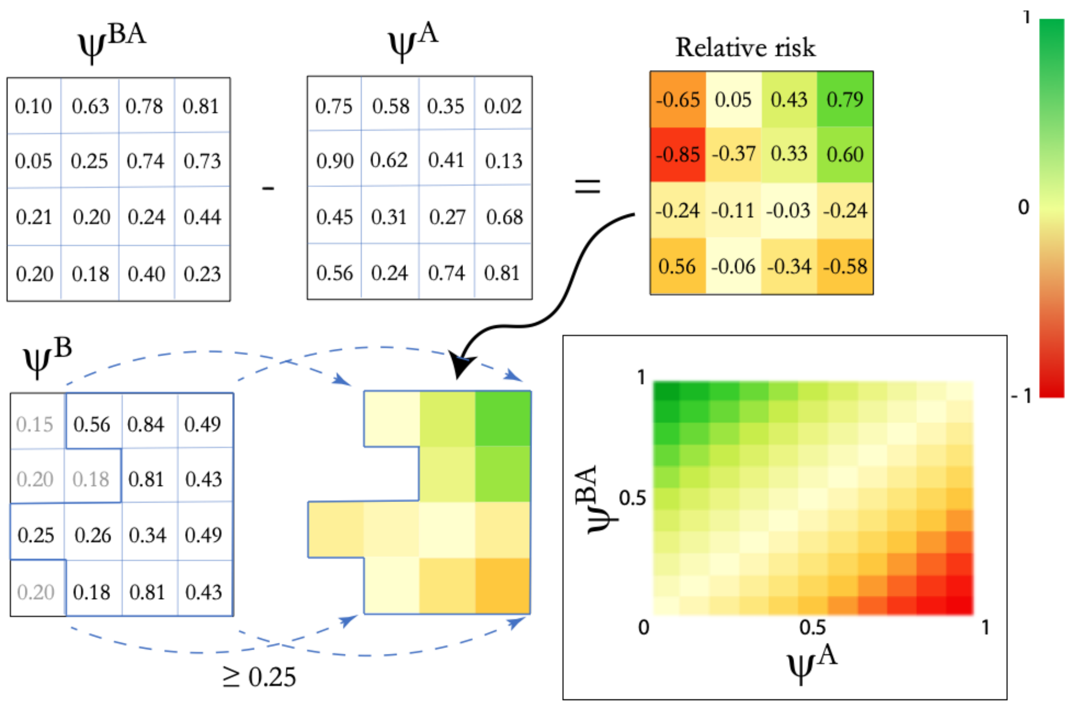

Figure S4.2: Schematic diagram illustrating the process used to calculate relative risk maps using single species and two-species occupancy model predictions. The colour scheme for the relative risk gradient was derived from the heat map in the bottom-right.

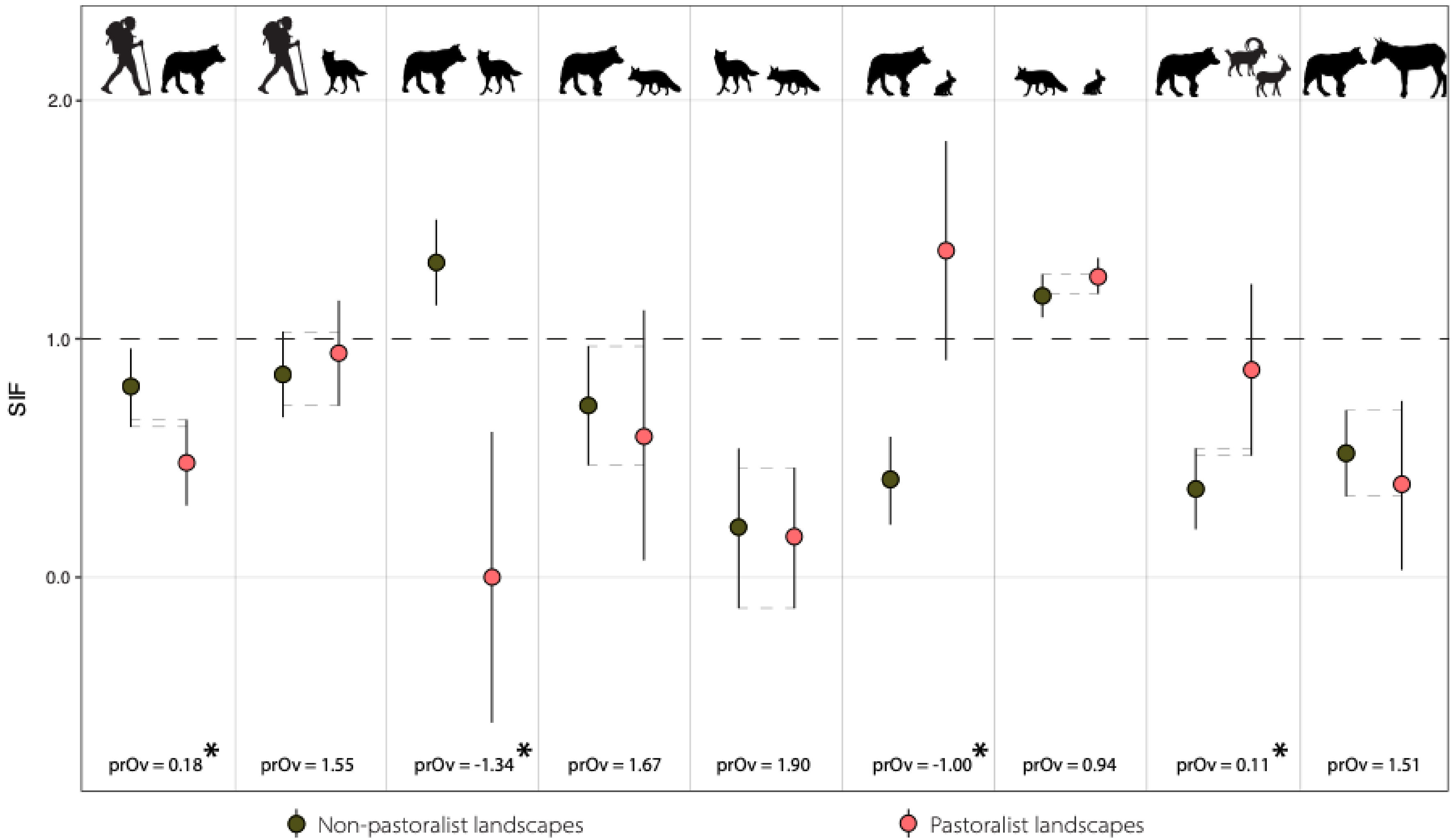

Figure S4.3: Species Interaction Factors (SIFs) between pairs of interacting dominant-subordinate species in non-pastoralist and pastoralist landscapes. *Significant difference in SIF between non-pastoralist and pastoralist landscapes based on the proportion of overlap of 95 % confidence intervals (prOv < 0.50).

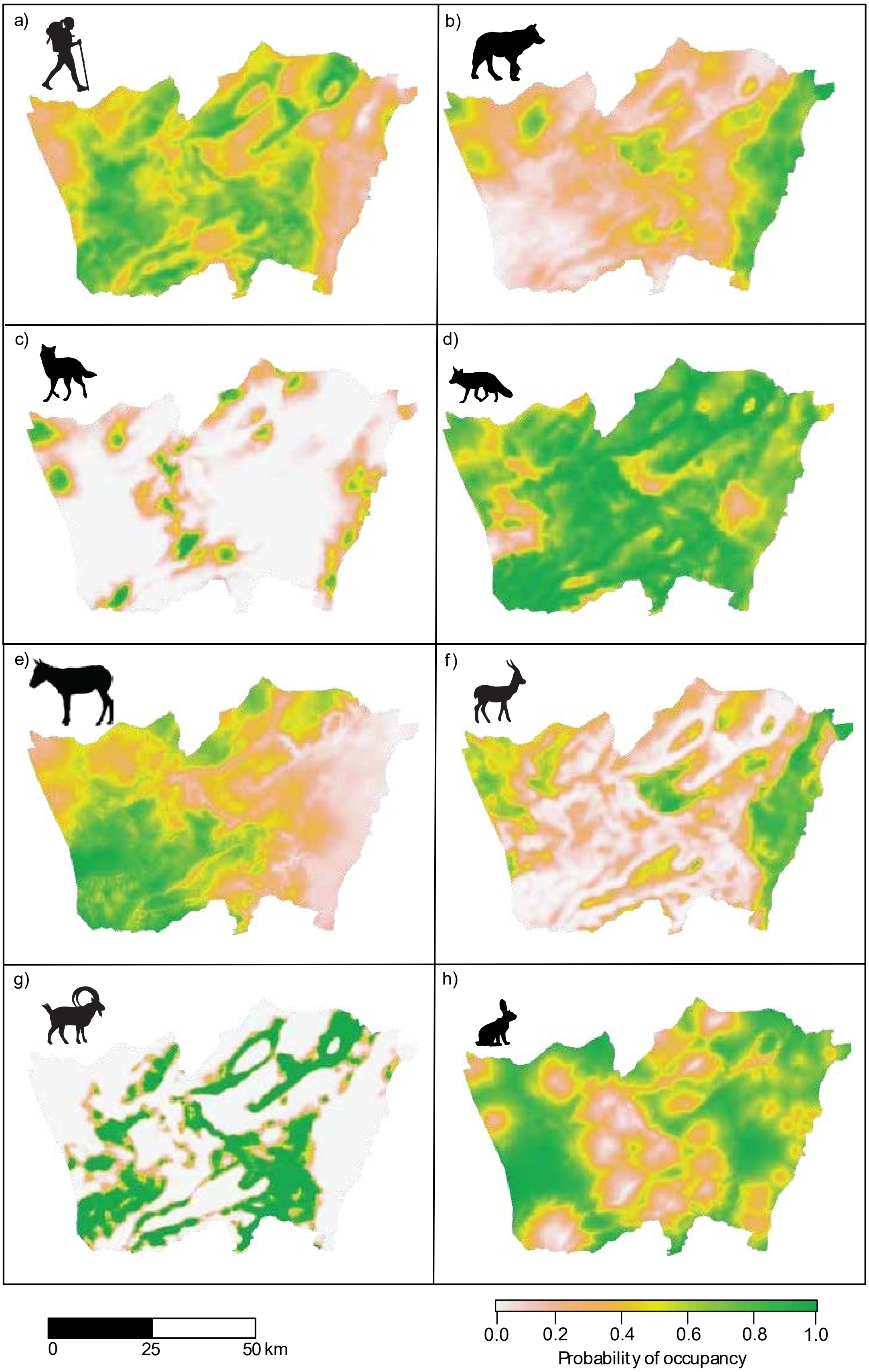

Figure S4.4: Single-species occupancy model predictions across the landscape based on spatial variables included in each model for: a) people, b) wolves, c) jackals, d) foxes, e) onager, f) gazelle, g) ibex, and h) hare.

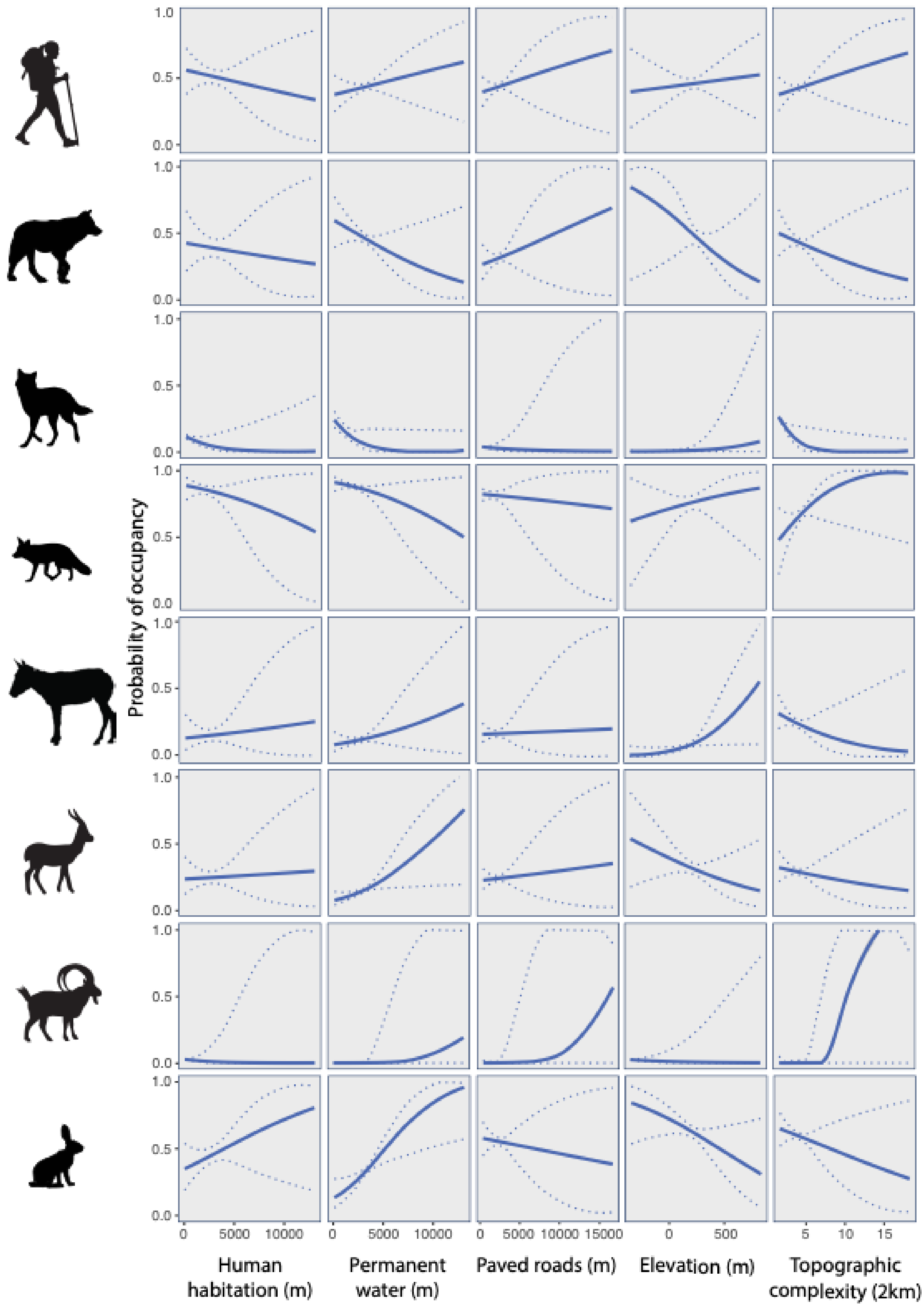

Figure S4.5: Single-species occupancy model predictions across the five continuous variables for each species.

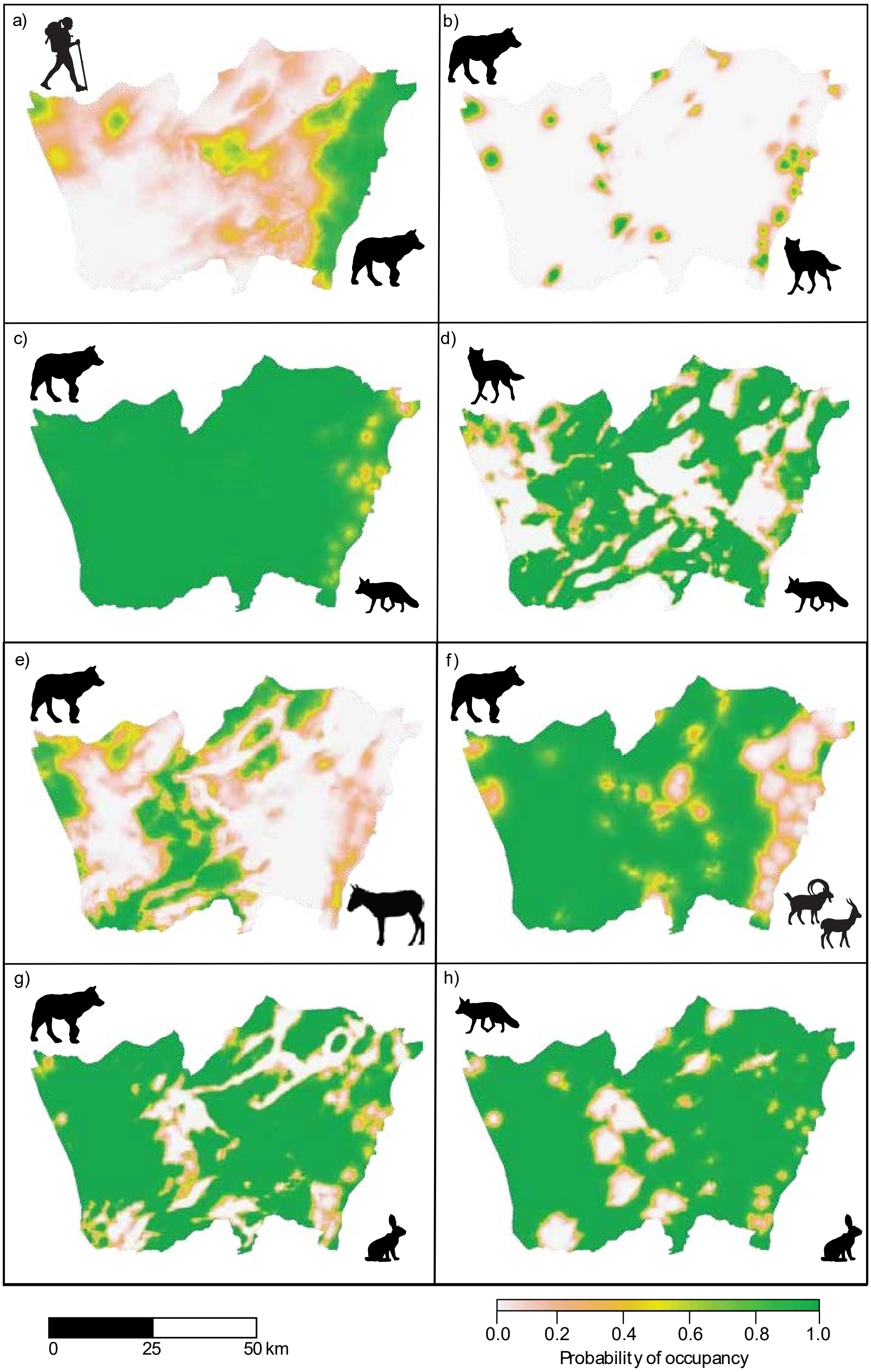

Figure S4.6: Two-species occupancy model predictions across the landscape based on spatial variables included in each model for dominant-subordinate species pairs: a) people – wolf, d) wolf – jackal, c) wolf – foxes, d) jackal – foxes, e) wolf – onager, f) wolf – small-medium ungulates, g) wolf – hare, and h) foxes – hare).

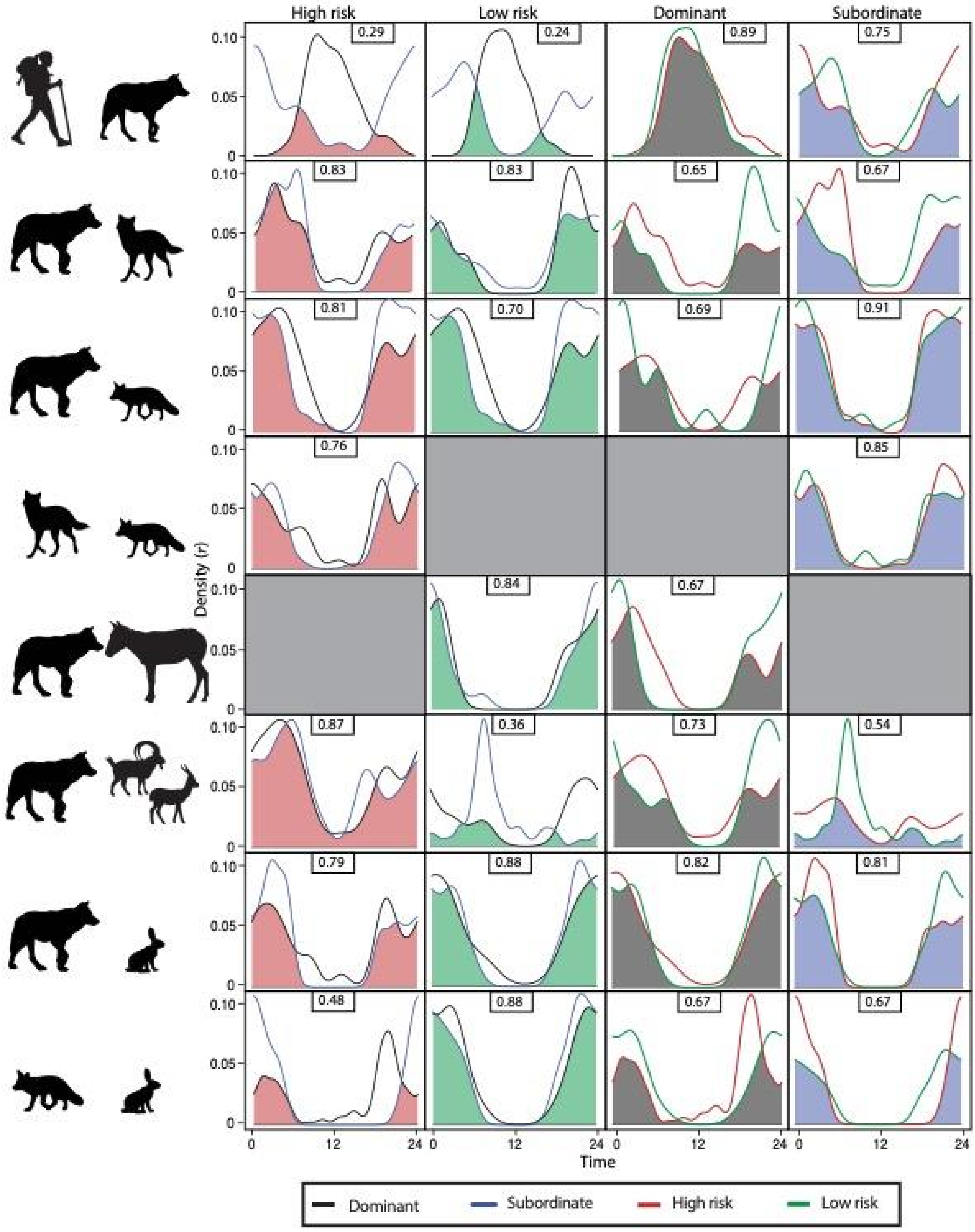

Figure S4.7: Overlap in temporal activity across high- and low-risk areas between each dominant-subordinate species pair.

Chapter 5. Agile responses of mesopredators and prey to ambient and imminent risk driven by Arabian wolves

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Abstract

Within trophic cascades driven by fear, there are two forms of knowledge that shape the responses of subordinate species to apex predators: landscape knowledge (ambient risk) and immediate cues (imminent risk). The density of apex predators, and the ambient threat they pose, is detectable via a wide range of cues and encounters that form experiential knowledge. Where apex predators are abundant, subordinate species should act to minimise risk of predation most of the time; whereas when apex predators are rare, subordinates should reduce the costs of risk aversion by engaging in risk assessment and mitigation less often, relying more on agile responses to immediate cues to dictate appropriate behaviour. Few studies examine responses to ambient and imminent risk simultaneously. In this study, we assessed the agility in behavioural responses of foxes and rodents to risk driven by Arabian wolves (*Canis lupus arabs*). We surveyed sites of high and low wolf density in the Negev Desert of Israel, where wolf density is influenced by human tolerance. We found that relative occupancy and time spent foraging of foxes were higher in low wolf areas, and that this trend was reversed in rodents. We then assessed whether immediate olfactory cues alter the behavioural responses of foxes and rodents in areas of high and low ambient risk. Our results confirm the role of ambient risk and highlight the implications of mesopredator release for desert rodents, but also find that agile responses of foxes and rodents to imminent risk may reflect adaptability and fitness trade-offs necessary to ensure survival in these desert ecosystems.

5.1 Introduction

Apex predators drive trophic cascades by creating 'landscapes of fear' for prey and mesopredators, where the perceived risk of predation varies spatially from high to low (Laundre et al., 2010). While this has consistently been demonstrated in protected areas such as national parks (Beschta and Ripple, 2013; Swanson et al., 2016; Ullas Karanth et al., 2017), less is known about how these roles play out in human-dominated landscapes (Dorresteijn et al., 2015). After all, fear of humans – 'super predators' (Darimont et al., 2015) who inspire fear across multiple trophic levels (Suraci et al., 2019) – often surpasses fear of other large predators (Clinchy et al., 2016). However, new landscape-scale evidence suggests that the Arabian wolf (*Canis lupus arabs*), an endangered subspecies of the grey wolf, has the capacity to influence the distribution and local abundance of prey and mesopredators by instilling fear in human-dominated desert ecosystems based on its own, human-induced, landscape of fear (Chapter 4). This has profound, cascading, implications for species in lower trophic levels.

'Mesopredator release', which results from relaxed suppression of mesopredators by apex predators, has been cited as a leading cause of bird extinctions (Crooks and Soulé, 1999) and reductions in small mammal abundance and plant diversity (Wallach et al., 2010). For example, in arid Australia, threatened mammals have a higher chance of survival in areas occupied by dingoes (*Canis dingo*), an apex predator who suppresses red fox (*Vulpes vulpes*) and cat (*Felis catus*) populations (Wallach et al., 2010, 2009a). Suppression of mesopredators is not necessarily always a result of direct predation, but also the mesopredators' avoidance of areas where the risk of encountering higher-order predators is high (Kauffman et al., 2007). While foxes avoid golden jackals (*Canis aureus*) more than wolves in the deserts of the southern Levant (Chapters 3 & 4), wolves also influence fox density (Chapter 3) and spatial behaviour (Chapter 4). By foxes avoiding areas of high predation risk, they reshape landscapes of fear for their own prey, such as rodents.

Of course, avoidance of high-risk areas is not always possible. Although awareness of background, or ambient, predation risk is vital at the landscape level (van der Merwe and Brown, 2008), predators are mobile and predation risk at local scales is dynamic (Kohl et al., 2018). Prey and mesopredators often need to share resources with their predators, particularly where resources are limited. Sometimes the risk of encountering predators can be overcome by spatio-temporal segregation; where individuals avoid high-risk areas at times when predators are active (Valeix et al., 2009), or consciously access such areas after predators have left (Swanson et al., 2016). However, this is not always feasible, as ecosystems often include multiple predator species with disparate temporal activity patterns, and individuals do not always have information on the whereabouts of their predators (Brown et al., 1999). In this case, individuals must employ risk-averse behavioural responses, such as becoming more vigilant, or reducing activity in risky areas (Clinchy et al., 2016). When wolves were reintroduced to Yellowstone National Park, USA, ungulates became more vigilant (Laundré et al., 2001). Such an increase in vigilance is appropriate for dealing with fine-scale alterations in predation risk, however, the benefits of behaving vigilantly wear off over time (Brown et al., 1999). Thus, individuals living in persistently high-risk areas, such as where predators have existed for a long time, should become accustomed to some ambient level of background risk (Laundre et al., 2010) and adjust their behaviour accordingly to reduce their chance of encountering predators.

While the entire Negev Desert of Israel is a stronghold for Arabian wolves (Chapter 2), their distribution is predominantly centred within the Arava Valley (Chapter 4), largely due to increased tolerance of wolves within this crop-farming region (Chapter 3). The presence of wolves influences the distribution of mesopredators by creating landscapes of fear (Chapters 3 & 4). For example, golden jackals, having recently become established in the Negev (Scheinin et al., 2006), are largely confined to the immediate surrounds of human habitation in pastoralist landscapes – areas avoided by wolves. In this study, we focussed on wolf interactions with foxes, and the subsequent cascading effects these have on rodents. We used camera traps to assess relative occupancy, as well as behavioural responses to predation risk in foraging foxes and rodents, to determine whether responses to the landscape of fear cascade through trophic systems. We compared the probability of occupancy, time spent foraging, and proportion of time spent vigilant in foxes and rodents between sites where wolf activity/occupancy was higher and lower, and then added olfactory cues (i.e., scats) to determine whether the local "presence" of a predator influenced these behaviours. We expected occupancy and time spent foraging of foxes to be higher in low wolf sites than high wolf sites, and the same variables for rodents to be higher in high wolf sites than low wolf sites due to cascading mesopredator effects. We then expected the addition of predator scents to trigger vigilant behaviours in both foxes and rodents but speculated that the rate of change may be different in high wolf versus low wolf areas.

5.2 Methods

5.2.1 Study Species

To study the influence of wolves on mesopredators and rodents, we targeted our research on the three fox species that inhabit the Negev: the red fox, Rueppell's fox (*V. ruepellii*), and Blandford's fox (*V. cana*). Red foxes tend to be more abundant close to farms, where they have access to anthropogenic resources (Shapira et al., 2008). However, our previous research suggests that red foxes are widespread throughout the Negev, possibly due to an increase in jackal populations near farms boosting fox dispersal (Chapters 3 & 2). The smaller Rueppell's and Blandford's foxes are specialised to sandy and rocky habitats, respectively (Ferguson, 2002). Rueppell's foxes are now rare throughout the study region (Shapira et al., 2008), while Blandford's foxes remain relatively common in rocky areas. Several rodent species occur throughout the study area (Shanas et al., 2006). We focused on small, nocturnal rodents, excluding the commonly observed fat sand rat (*Psammomys obesus*) from our analyses as they are large and diurnal, identifying them to genus (*Acomys*, *Gerbillus*, and *Meriones*). Besides canids, other potential predators of the Negev's nocturnal rodents include raptors, reptiles, and felids (e.g., caracal *Caracal caracal*, African wild cat *Felis lybica*).

5.2.2 Study Sites

We conducted surveys at four sites across Israel's Negev Desert (Figure 5.1). We selected sites based on the modelled probability of occupancy of the Arabian wolf (Chapter 4), coupled with prior knowledge of the wolf's spatial distribution throughout the region. We defined two sites in the Arava Valley as "high-wolf" (HW1 and HW2) and two sites in the western Negev as "low-wolf" (LW1 and LW2). All sites were located either within, or adjacent to, the boundaries of protected areas: HW1 was within the Sheizaf Nature Reserve; HW2 intersected the Makhteshim Ein Yahav and the lower reaches of the Mazuq Ha-Zinnim Nature Reserves; LW1 was within Ramon Nature Reserve; and LW2 was in the upper reaches of the Mazuq Ha-Zinnim Nature Reserve.

All study sites were located within geological depressions (e.g., river valleys, erosion cirques), yet climatic conditions varied between high and low wolf sites. Across all sites, rainfall occurred solely within ~6-months surrounding winter. Nonetheless, the Arava is considerably drier (annual precipitation ~20 mm) and up to 10°C hotter than the Negev highlands (annual precipitation ~50 mm). As such, vegetation communities varied subtly between sites: although desert herbs and shrubs (e.g., *Atriplex* spp., *Anabasis articulata*, and *Zilla spinosa*) dominate vegetation in wadis (dry riverbeds) at most sites, larger species (trees and large shrubs) are dominated by *Acacia* spp. at high-wolf sites and *Retama raetem* at low-wolf sites. In HW1 and LW1, all sampling was conducted within wadis, while sampling in HW2 and LW2 was conducted across a combination of wadis and rocky outcrops.

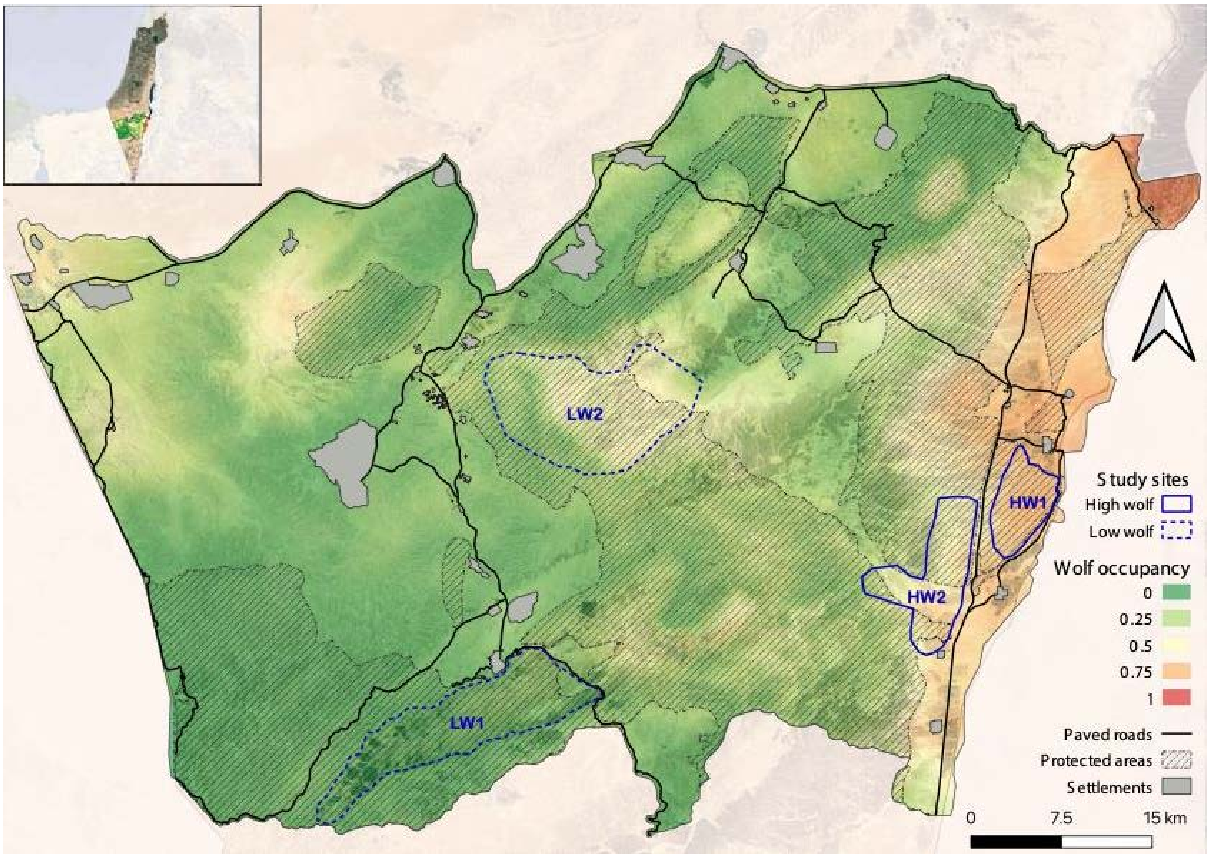

Figure 5.1: Locations of the four study sites (two "high-wolf" in the Arava Valley and two "low-wolf" in the Negev Highlands), within protected areas in the Negev Desert of Israel (inset), relative to the modelled occupancy probability of Arabian wolves and human infrastructure (paved roads and human settlements).

5.2.3 Data Collection

Between October 2018 and May 2019, we assessed relative occupancy and foraging behaviour of foxes and rodents with motion-sensing (Bushnell Trophy Cam Aggressor no glow) camera-traps. Cameras were attached to poles, facing a lure consisting of a tray containing crushed peanuts in sand for rodents, and a metal cage containing meat (chicken and tuna) for foxes. We defined each camera-lure setup as a "station" and designated a minimum distance between stations for both foxes and rodents. We established 21 fox stations at each site, approximately 1 km apart (actual mean distance between stations 936 ± 26 m) between stations. At one site (HW1), we initially used only chicken as a trial, and then added tuna and repeated sampling at this site and all others with this lure. All data collected were used for behavioural analyses, while occupancy modelling was only performed on samples using the modified lures (chicken and tuna).

We established rodent stations at HW1 and LW1 independently of fox stations. These two sites were selected as the most suitable for comparison as they were ecologically similar and had abundant rodent populations. We restricted sampling to wadis to reduce potential confounding factors and placed stations in the vicinity of rodent signs (e.g., burrows, tracks). With approximately 200 m between each station (actual mean distance between stations 183 ± 15 m), we established multiple sampling transects within each site (three transects each consisting of 30 stations in HW1 and two transects each consisting of 33 stations in LW1). Where no visual signs of rodents existed along the transect, we searched up to 100 m perpendicular to the proposed station location (within tributary wadis).

For both foxes and rodents, cameras were set to record short (10 – 15 s) videos with no interval over seven days. The first three nights of each session acted as an acclimation period to allow animals to adjust to the presence of the stations. The remaining four nights were divided into a 'control period' (to determine responses to ambient risk) and a 'scent period' (to determine responses to imminent risk). In the two-day control period, stations were unaltered and continued to lure foxes and rodents to the baits. In the two-day scent period, we randomly placed scat of either a higher-order predator (wolf scats for fox stations; red fox scats for rodent stations) or herbivore (domestic cattle scats) at each station to act as an olfactory surrogate for local predator or herbivore presence. Predator scats were collected from wildlife parks housing enclosed predators (Hai-Bar Yotvata and Ramat Gan Safari Park), while cow scats were collected from dairy factories. Scats were kept frozen from time of collection until we placed them in the field. We replaced lures at the beginning of each experimental period (i.e., acclimation, control, and scent) at fox stations and daily at rodent stations.

5.2.4 Data Analyses

Using the combined data from the acclimation and control periods, we conducted single-species occupancy models to determine the relative probability of occupancy of foxes and rodents at high- and low-wolf sites. To account for the actual presence of a higher-order predator nearby during the study (wolf for red foxes; wolf and red fox for Blandford's foxes and rodents) on modelled occupancy, we noted which stations detected a higher-order predator (for rodent stations, we noted whether the closest predator station detected a predator) and used local predator presence (binary) as a covariate in the model. As wolves were only detected at high-wolf sites, and Blandford's foxes were only detected at HW2, we only included data from high-wolf sites when assessing the influence of wolf presence, and data from HW2 for estimating relative occupancy of Blandford's foxes. We estimated rodent occupancy with red fox presence as a variable across HW1 and LW1.

Behavioural analyses were conducted by evaluating all independent camera-trap events, which we defined as being independent when no other detections of the same species occurred for five minutes before or after a single event. We measured the duration of each event as the amount of time an individual spent within the camera's field of view (in seconds) and evaluated video footage to score the following behaviours: vigilance, locomotion, foraging, sniffing the ground (foxes only), investigating (approaching the bait or lure to look but not attempting to access food), and other. We then determined the proportion of time that the individual was engaged in vigilant behaviour. We defined vigilance as an individual remaining still and alert, with attention directed away from the lure. Kruskal Wallis rank sum tests were used to compare event duration and proportion of time spent vigilant across six treatments: high-wolf control; low-wolf control; high-wolf predator scent; low-wolf predator scent; high-wolf herbivore scent; low-wolf herbivore scent. Where significant differences were found, we performed *post hoc* Dunn's tests to determine those treatments that were significantly different at a significance level of $p = 0.025$.

5.3 Results

We recorded a total of 300 fox events from 777 camera-trap days and 1,174 rodent events from 990 camera-trap days at fox and rodent stations, respectively (Table 5.1). The red fox was the most widespread and frequently recorded fox species and was recorded at all four study sites. However, the number of events, and percentage of stations within a site where detections were made, differed markedly between high- and low-wolf sites. In low-wolf sites, the number of red fox events (n = 218) was greater than in high-wolf sites (n = 31), and red foxes were detected at twice as many stations in low-wolf sites (> 90 % of stations) than in high-wolf sites (< 50 % of stations). Blandford's fox was recorded exclusively at HW2, where the number of events (n = 51) was more than double the number of red fox events (n = 19), but red foxes were recorded at more stations (red fox 47.6 %; Blandford's fox 33.3 % of stations). Rodents, on the other hand, were recorded significantly more in the high-wolf site than the low-wolf site, with 987 events from 64.8 % of stations in HW1 compared to 187 events from 53.0 % of stations in LW1.

Table 5.1: Summary of species records from fox and rodent stations showing the total number of events recorded, total number of stations (*n*), and occupancy (ψ) and detection (*p*) probabilities for each species (or group of species).

		Total no. of events		***n* (% of total stations)**		**ψ (± SE)**	***p* (± SE)**
Foxes		*V. vulpes*	*V. cana*	*V. vulpes*	*V. cana*	*V. vulpes*	*V. vulpes*
	HW1	12	0	7 (33.3)	0	0.15 (0.08)	0.026 (0.02)
	HW2	19	51	10 (47.6)	7 (33.3)	0.47 (0.11)	0.15 (0.04)
	LW1	78	0	19 (90.5)	0	0.73 (0.11)	0.31 (0.06)
	LW2	140	0	20 (95.2)	0	0.88 (0.11)	0.47 (0.05)
Rodents							
	HW1	987		57 (64.8)		0.66 (0.05)	0.55 (0.03)
	LW1	187		35 (53.0)		0.41 (0.06)	0.23 (0.04)

5.3.1 Relative occupancy

The probability of occupancy for red foxes was lower in high-wolf sites ($\psi = 0.31 \pm 0.07$) than in low-wolf sites ($\psi = 0.81 \pm 0.08$) (Figure 2). In contrast, the probability of occupancy for rodents was higher in high-wolf sites ($\psi = 0.66 \pm 0.05$) than in low-wolf sites ($\psi = 0.41 \pm 0.06$). When including the local presence of a higher-order predator as a covariate in the model (Figure S5.1), we found that occupancy probability of red foxes was higher at stations where wolves were absent ($\psi = 0.61 \pm 0.15$) than where they were present over the seven days ($\psi = 0.32 \pm 0.16$). Similarly, occupancy probabilities of Blandford's foxes ($\psi = 0.46 \pm 0.14$) and rodents ($\psi = 0.68 \pm 0.05$) were higher where red foxes were absent than where they were present (Blandford's fox $\psi = 0.20 \pm 0.13$; rodents $\psi = 0.52 \pm 0.06$).

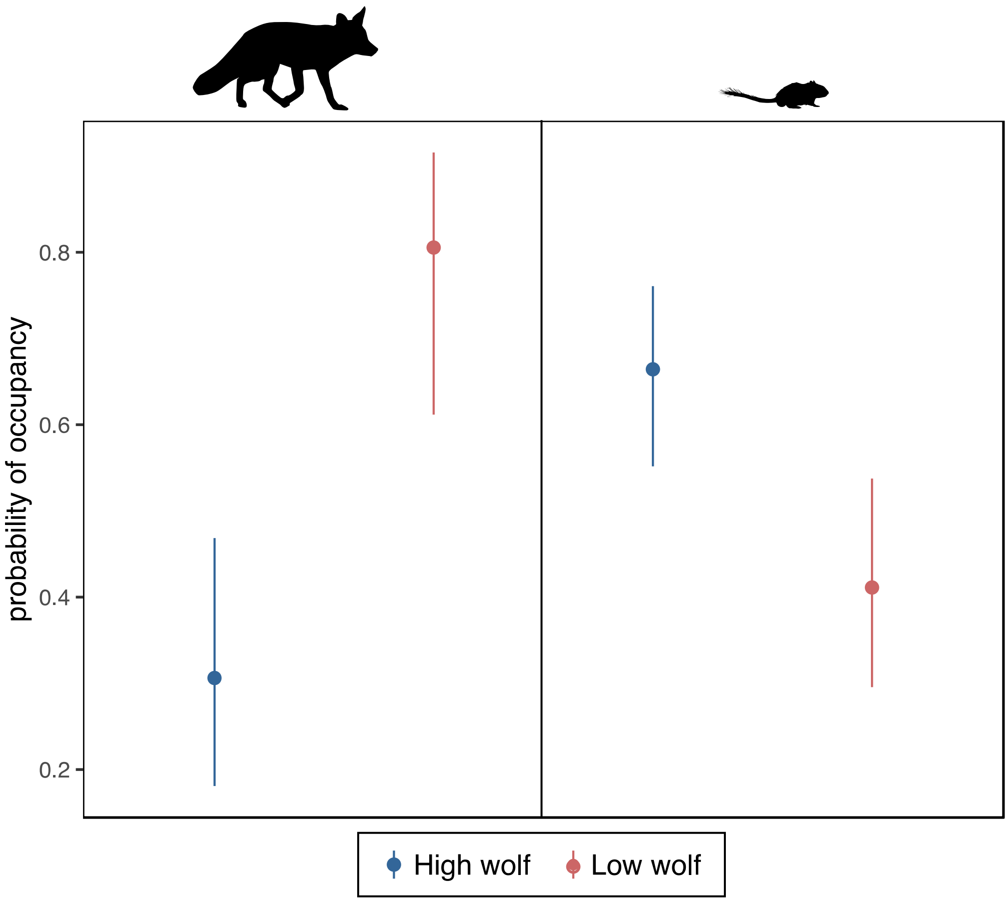

Figure 5.2: Modelled probability of occupancy for red foxes (*V. vulpes*) and rodents (*Acomys* spp., *Gerbillus* spp., *Meriones* spp.) across high-wolf and low-wolf sites (point = model estimate, line range = 95 % confidence intervals).

5.3.2 Event duration

Fox and rodent event durations differed between high- and low-wolf sites (fox: $\chi^2 = 17.17$, df = 3, $p < 0.001$; rodent: $\chi^2 = 16.84$, df = 5, $p < 0.01$; Figure 3). Foxes spent considerably more time at lures in low-wolf sites than high-wolf sites during the control period ($z = -3.76$, $p < 0.001$, Figure 3, interaction 'a'). At high-wolf sites foxes rarely approached lures, and if they did, were more likely to spend little time at the lure. After scent was added to low wolf sites, foxes spent significantly less time at stations marked with wolf scent, compared to the control period ($z = -2.22$, $p < 0.05$, Figure 3, interaction 'b'). Event duration at stations marked with cow scent was not significantly different to those marked with wolf scent or to the control period. However, the average duration of an event was considerably shorter at cow scented stations than in the control period, suggesting that foxes spend less time at stations marked with scents, regardless of whether the scent is from a predator or herbivore. We did not record enough fox events to make the same comparisons at high wolf sites during the scent period.

In contrast to red foxes, rodents spent significantly more time foraging at high-wolf sites than at low-wolf sites during the control period ($z = 2.65$, $p < 0.01$, Figure 3, interaction 'c'). After adding scent, no significant differences were found within high-wolf or low-wolf sites, however, the duration of events at high-wolf sites marked with fox scent were significantly longer than in low-wolf sites both during the control period ($z = 3.58$, $p < 0.001$, Figure 3, interaction 'd') and at stations marked with fox scent ($z = 2.21$, $p < 0.025$, Figure 3, interaction 'e'). While there was no significant difference in the duration of events between fox and cow scented stations at high- or low-wolf sites, rodents spent more time foraging at fox scented stations and less time at cow scented stations in high-wolf sites, and less time foraging at fox scented stations and more time at cow scented stations in low-wolf sites.

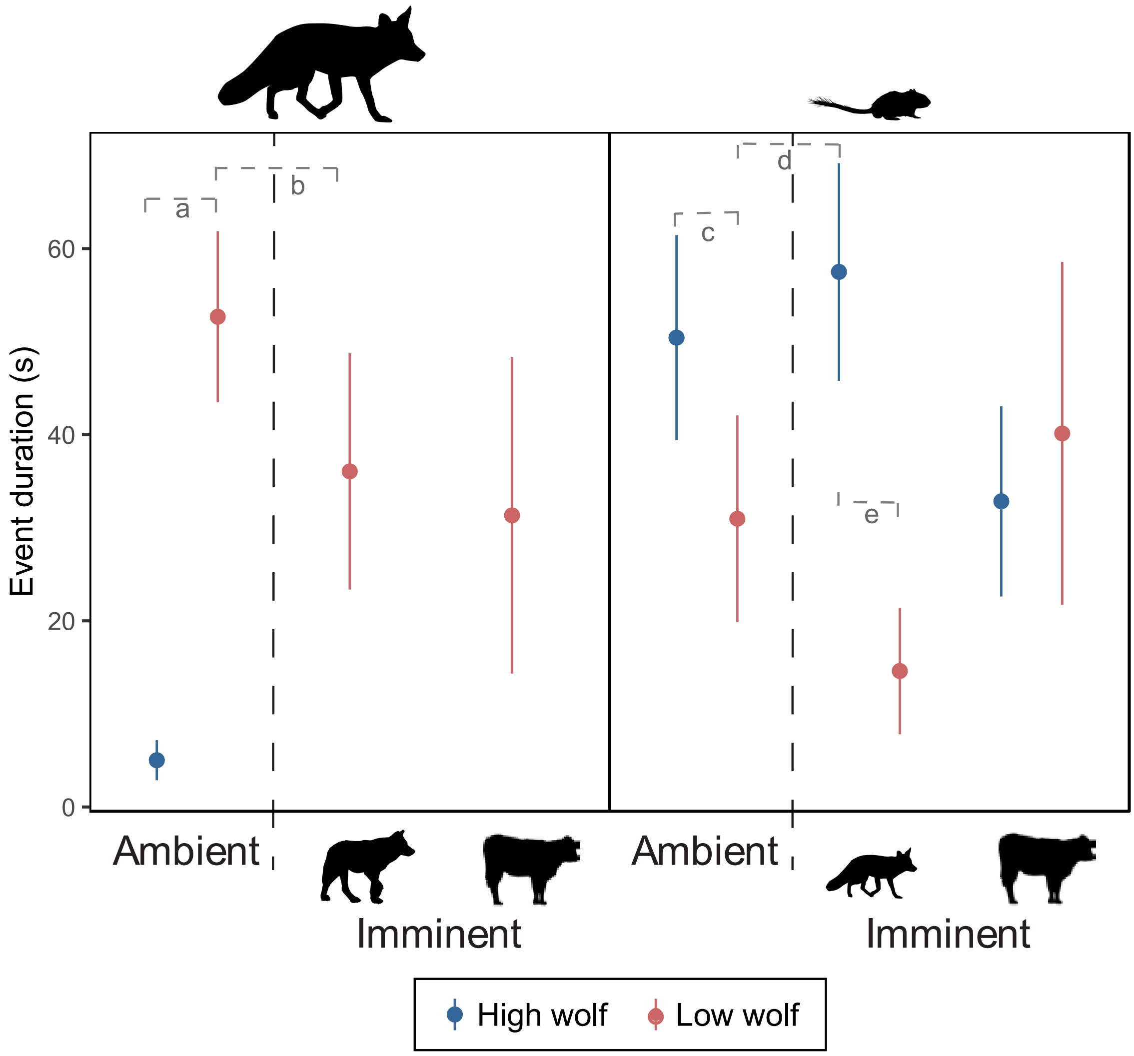

Figure 5.3: Differences in mean duration of red fox and rodent events across ambient (control) and imminent cue (scent from a higher-order predator and cow) treatments at high-wolf and low-wolf sites (point = mean, line range = SE). Letters denote significant interactions ($p < 0.025$).

5.3.3 Time spent vigilant

Fox or rodent vigilance did not differ across sites or treatments (fox: $\chi^2 = 4.42$, df = 3, p = 0.22; rodent: $\chi^2 = 4.12$, df = 5, p = 0.53). However, though not significant, foxes appeared to spend more time vigilant in low-wolf sites than high-wolf sites in the control period, but this is due to foxes not stopping to spend time at lures in high-wolf sites. After scent was added to low-wolf sites, foxes spent less time vigilant at scent marked stations than in the control period. The proportion of time rodents spent vigilant did not appear to change once scents were added to stations in high-wolf sites. However, they appeared to spend less time vigilant in low-wolf sites at stations where cow scent was added in low-wolf sites.

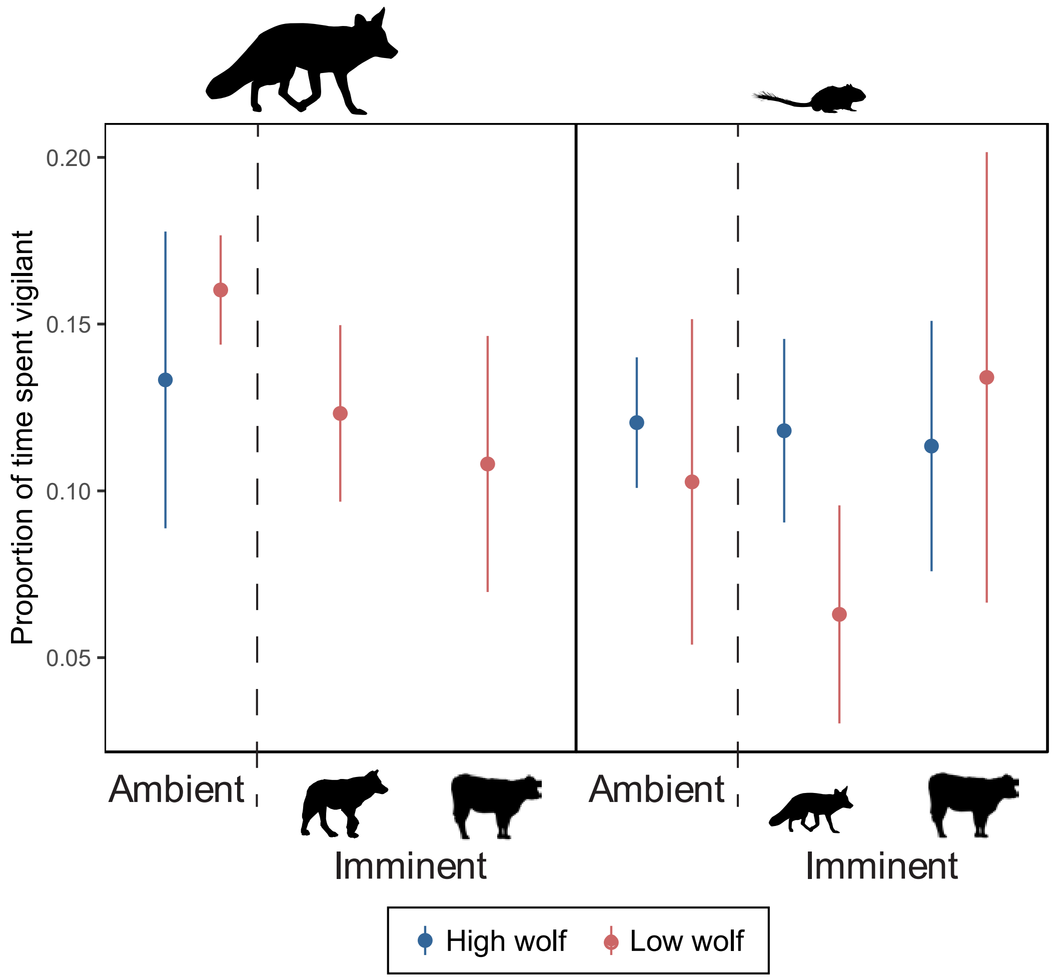

Figure 5.4: Proportion of time spent vigilant in fox and rodent events on control and scent (high-order predator and cow) periods across high- and low-wolf sites (point = mean, line range = SE).

5.4 Discussion

Arabian wolves shape trophic cascades in desert ecosystems by creating landscapes of fear for mesopredators and prey (Chapter 4). Here, we show that through engaging in risk-averse behavioural responses in areas of high ambient predation risk elicited by wolves, foxes create alternate landscapes of fear for rodents. Relative occupancies and times spent foraging of red foxes and rodents were significantly lower and higher, respectively, in high-wolf sites than in low-wolf sites. While the direct effects of top-down predation are indeed important in influencing species distributions (Newsome et al., 2017), we emphasise the importance of bottom-up avoidance of risky areas, and preferential use of safe areas ('refugia'; Taylor (1984), in generating these trophic cascades.

While the variations in occupancy probability between high- and low-wolf sites may be influenced by other factors, both foxes and rodents avoided risky areas by spending less time foraging in high-risk areas. For instance, rodent density and activity are highly variable across the Negev, with abrupt seasonal fluctuations in density (Sinai et al., 2003), and activity being dependent on various environmental factors (Kotler et al., 1993). However, given the strong behavioural responses of rodents to foxes in low-wolf sites, we suggest that rodents avoid areas where ambient risk of fox predation is high by selecting for refugia such as shrub cover (Brown et al., 1992).

When accounting for the actual presence of a higher-order predator, we found that relative occupancy of red foxes decreased at stations frequented by wolves, suggesting that red foxes spatially avoid places where wolves are active. Relative occupancies of foxes (both red fox and Blandford's fox) and rodents were consistently lower at stations where a higher-order predator was detected, but only if that predator was in the trophic level immediately above. For example, relative occupancy of Blandford's foxes appeared lower at stations visited by red foxes but was not influenced by wolf presence (see Fig. S5.1 in Supplementary Material), likely due to stronger trophic niche overlap within the mesopredator guild (Lanszki et al., 2007). In the Santa Cruz Mountains, USA, Wang et al. (2015) detected grey foxes (*Urocyon cinereoargenteus*), bobcats (*Lynx rufus*), and striped skunks (*Mephitis mephitis*) at sites occupied by pumas (*Puma concolor*) more than sites where pumas were absent, suggesting that these lower-order mesopredators benefit from pumas' suppression of coyotes (*Canis latrans*). This agrees with our previous work in the southern Levant's agricultural landscapes, where foxes found refuge from golden jackals by occupying areas where wolves occurred (Chapter 3).

In low-wolf sites, we also found foxes to spend significantly less time foraging at stations that were marked with imminent wolf scent cues. However, given that there was no difference in the time foxes spent foraging at these stations compared to stations marked with cow scent, it is likely that this is due to other factors. For example, foxes might spend less time foraging at stations marked with animal scats, regardless of whether the scat is from a predator or herbivore. Or the reason could simply be because the experimental (scent treatment) period chronologically followed the control period: foxes may have learnt from previous visits that they cannot access sufficiently more food by spending more time at the lure, or they may have already become satiated enough during previous visits.

Nonetheless, behavioural responses of foxes to olfactory cues from apex predators have varied in previous studies. While foxes in Croatia have been observed spending less time at foraging stations marked with wolf urine (Haswell et al., 2018), foxes in Australia and Poland spend more time drinking and foraging at stations marked with dingo (Leo et al., 2015) and lynx (*Lynx lynx*: (Wikenros et al., 2017b) scats, respectively. Ramp et al. (2005) found opposing responses to predator urine in two sympatric macropods, suggesting that responses to such cues are species-specific and depend on social and ecological characteristics. We posit that the variation in ambient risk across the landscape of fear is also an important driver of risk responses to sensory cues.

While we did not collect enough data to demonstrate how foxes respond to cues in high-wolf sites, given their low density in these areas, we found that rodents responded to fox scent differently in high-wolf and low-wolf sites; however, no significant differences were found within these sites. In high-wolf sites, where the risk of fox predation was low, rodents spent more time foraging at stations marked with fox scats compared to those marked with cow scats. The opposite was true in low-wolf sites, where the risk of predation by foxes was high. Responses to auditory cues have also varied according to ambient risk. Raccoons showed fear of dog sounds in playback experiments in the Gulf Islands where dogs are the only large predator (Suraci et al., 2016). On the other hand, badgers in the UK, where wolves are absent, showed no response to the playback of wolf sounds (Clinchy et al., 2016). Therefore, we postulate that the level of ambient risk has a stronger influence on risk responses than sensory cues, but responses to sensory cues are likely to vary according to the level of ambient risk. Dingoes are highly persecuted, and foxes are abundant, at the site where Leo et al. (2015) found foxes to spend more time drinking near dingo scats. If the authors were to repeat the study in an area where the risk of encountering dingoes is high, they might reach contrasting results.

We used scats as olfactory cues primarily for the purpose of assessing any increases in vigilance in response to imminent threat posed by local predator presence. Contrary to *a priori* expectations, neither foxes nor rodents increased their vigilance at stations marked with predator scent. We suggest that the use of olfactory cues is not the most suitable method to assess responses to imminent threat. Within our study area, where foxes show strong spatial avoidance of jackals, Scheinin et al. (2006) found that foxes did not respond to jackal scent but did show fear of jackals when presented with a visual cue (i.e., actual presence of a jackal). Auditory cues are also likely to be a trustworthy surrogate for imminent threat, as the sound of a predator implies closer proximity than predator scent – which implies a predator has previously been in the area. However, vigilance is not necessarily the most reliable metric for assessing responses to risk across the landscape of fear (Gaynor et al., 2019).

5.4.1 Conclusions

We show that ambient risk is an important driver of landscape-level risk assessment, but that potential risk signified by olfactory cues alters responses, suggesting agility. In the case of this study, landscapes of fear alternated through trophic levels, where foxes created landscapes of fear for rodents by navigating their own landscape of fear elicited by wolves. Both foxes and rodents showed significant responses, namely reductions in occupancy and time spent foraging, in areas where ambient predation risk was high. Areas that were risky for foxes became safe for rodents, and areas safe for foxes became risky for rodents. Given that Arabian wolves are highly persecuted throughout their range (Chapter 2), the ecological consequences of persecution are widespread. Many small mesopredators (e.g., Rueppell's fox, the sand cat *Felis margarita*) and rodents (e.g., the Balochistan gerbil *G. nanus*) are threatened throughout the region (Shapira et al., 2008). We show that by creating areas of high-risk to wolves, human actions cascade to species in lower trophic levels, ultimately leading to the loss of smaller species.

5.5 References

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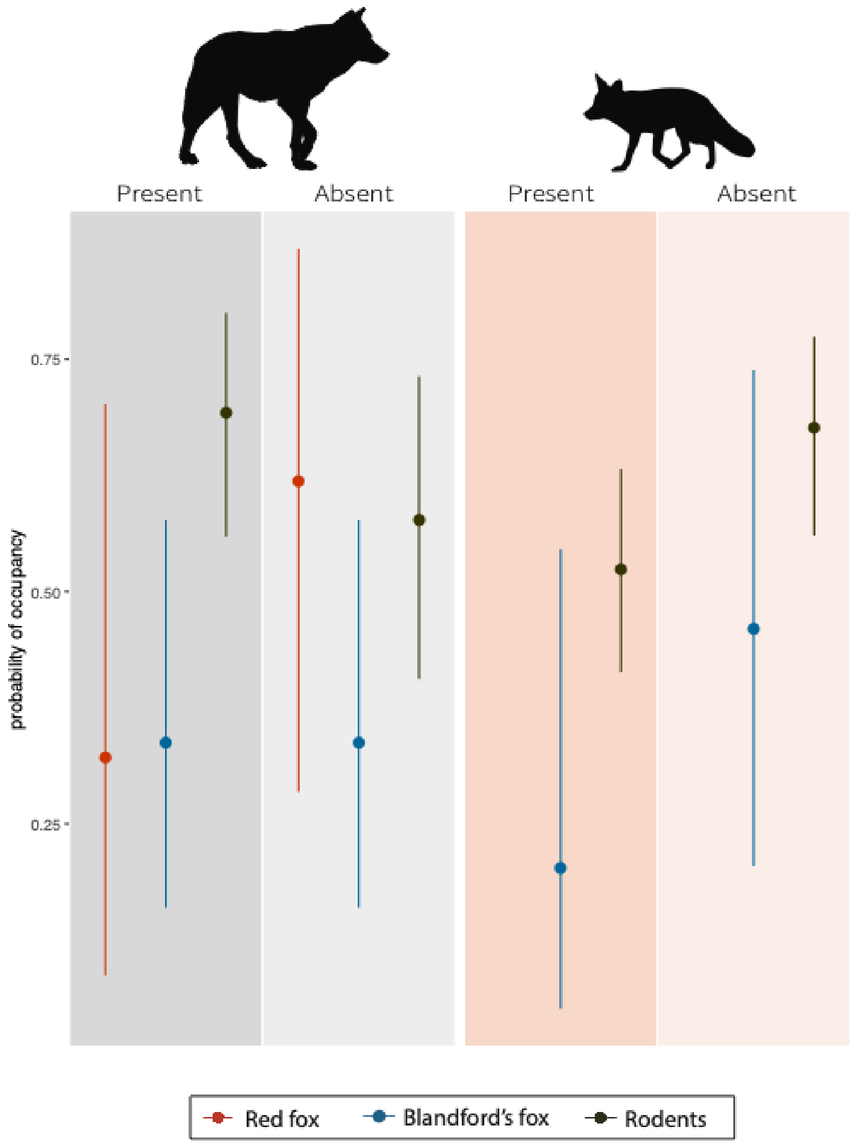

Figure S5.1: Probability of occupancy for foxes and rodents based on the local presence or absence of higher-order predators (wolf or red fox). We used data from HW1 and HW2 for red fox; HW2 for Blandford's fox; and HW1 and LW1 for rodents (point = model estimate, line range = 95 % confidence intervals).