Predator-prey interactions through the lens of coevolution and ecological context

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the degree of Doctor of Philosophy

under the supervision of Daniel Ramp and Arian Wallach

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Certificate of Original Authorship

I, Eamonn Ivor Fraser Wooster, declare that this thesis is submitted in fulfilment of the requirements of the award of Doctor of Philosophy, in the School of Life Sciences, Science 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.

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This thesis is a compilation of chapters and 5 published/publishable manuscripts. Each paper is formatted for their destination journals, except for referencing styles which feature as a single list at the end of the thesis.

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Thesis Abstract

The red fox (*Vulpes vulpes*) is one of the world's most widely distributed mesopredators. They influence ecosystems primarily through the predation of prey species, driving cascading effects on plant and animal communities. In modern times, red foxes have been introduced to new locales, forming part of native and non-native conglomerates. The resulting amalgamation of native and non-native predator communities have been described as producing novel trophic cascades. While some acknowledge the important rewiring of lost functions due to extinction, there remains widespread concern about the negative role introduced species might play as they lack coevolved traits and relationships with native prey. To that end, the introduction of novel predators, like foxes, has been suggested to be a leading cause of decline and extinction of small mammal prey, especially in Australia. Rather than detailed consideration of the niche that introduced predators fit into, and their functional similarities with lost species, foxes and other introduced mesopredators like cats (*Felis catus*) are maligned by conservation values that promote native prey and the prevention of extinction. Negative connotations around alien and invasive species frequently override sound ecological assessment and cloud the establishment of evidence-based environmental policy.

Rather than absorbing narratives of harm, what happens when we suspend our assumptions that introduced species are ecologically damaging? Is it possible that the role of introduced mesopredators in driving extinctions is overstated? Is it also possible that long histories of coevolution are less important than the contextual and functional

roles predators play in trophic cascades? Asking these questions is vital if we are to find transparent and peaceful ecological solutions to improve nature conservation and prevent extinction and harm. Within this thesis, I explore these questions with a desire to understand how the red fox shapes the behaviour and ecology of their prey and how this compares to the foxes native range. Further, I explore how the fox fits into Australian novel ecosystems but exploring their interactions with dingoes and how these are shaped by human hunting.

Red foxes, like any other predator, play important ecological roles, however, assumptions of their harm, have prevented us from fully exploring their ecologies within novel ecosystems. By dropping assumptions that foxes are inherently harmful, I show that the foxes biotic nativeness has very little to do with their ecological interactions, the foxes ecology and behaviour may, instead be better predicted by ecological context.

Chapter 1: Introduction

The human-assisted dispersal of species outside of their historic native ranges is a hallmark of the Anthropocene. This has created novel globalised ecosystems of native and introduced species. The human assisted dispersal of species has generated significant alarm among conservationists. Introduced predators in particular have been subjected to numerous conservation killing programs, as these novel predators predate upon native prey, sometimes resulting in their decline (Doherty et al., 2016). The role of introduced predators within these declines have resulted in them being considered inherently harmful (Chew and Hamilton, 2010). However, when we relax these assumptions, we are presented with the reality that these species influence their ecosystems in complex ways. We see that introduced species restore lost ecological function (Lundgren et al., 2020) and that the inclusion of introduced species drastically changes our perceptions of biodiversity change (Wallach et al., 2020b). These discoveries may never have seen the light of day, had perceptions of 'nativeness' not been suspended. However, introduced species are still implicated in the decline and extinction of their native prey (Doherty et al., 2016). This begs the question, can we suspend ideas of inherent harm and still be mindful to not cause extinction?

Many have argued that this is not possible, that welcoming introduced predators, like foxes (*Vulpes vulpes*) and cats (*Felis catus*) to a country like Australia will only result in declines in their prey (Hayward et al., 2019). However, locations, like Australia are considered permanently invaded, where the eradication of many introduced species is

unfeasible (Carroll, 2011), leaving the promotion of coexistence as the most realistic option to prevent decline and extinction. Proponents of *Compassionate Conservation* have shown that the protection and promotion of apex predators enables not only native non-native coexistence (Wallach et al., 2015b), but ecosystem functioning (Wallach et al., 2010). The perceptions of harm that surround introduced predators have led research to primarily focus on how to best control their populations (Harding et al., 2001; Mahon, 2009), leaving many aspects of the ecologies of predators outside of their native range unexplored. This thesis thus asks, if we relax ideas that introduced predators are inherently harmful, how do introduced mesopredators interact with their native predators and prey?

Biotic globalisation has created novel ecosystems

Human assisted biotic globalisation has created what are known as *novel ecosystems*. Novel ecosystems are conceptualised to have undergone significant, relatively recent, human-induced changes in composition and function, usually in comparison to "historic" or "native" ecosystems that reflect late Holocene conditions (Hobbs et al., 2009). The introduction of predators and prey can rewire the ecologies of native and introduced species, creating novel ecological interactions, and altering previously existing ones.

Many species introduced by humans throughout the last few centuries are small to medium bodied (<15kg). Some species were introduced accidentally (e.g., rats – *Rattus rattus* jumping ship), while many were introduced purposefully for recreation (e.g., foxes - *Vulpes vulpes* for sport hunting) or as biological control agents (e.g., cats – *Felis catus*

introduced to control rodents) (Wodzicki, 1973). Many of these species, however, are mesopredators. Mesopredators are a diverse trophic group that display a wide range of functional traits that enable them to thrive in a diverse range of ecosystems (Prugh et al., 2009). Due to their expansive human aided redistribution, mesopredators are among the most common constituents of novel ecosystems (Prugh et al., 2009). As such, they serve as the perfect vector to understand them.

Mesopredators often live risky and opportunistic lives. Many must contend with sharing habitats with apex predators (e.g., Carnivora species >15 kg; Wallach et al., 2015b) that hunt them while competing for resources with other mesopredators and simultaneously acting as predators themselves (Prugh et al., 2009). The effects apex predators have on mesopredators can be understood through *trophic cascade theory,* which has shown how apex predators can directly reduce the densities of mesopredators (Ripple et al., 2014). Additionally, the threat of predation forces mesopredators to alter their behaviour to reduce the risk of predation, which they do by avoiding their predators spatially and temporally (Karanth et al., 2017; Wooster et al., 2021), or when avoidance is not feasible, increasing their vigilance or caution (Haswell et al., 2018).

Trophic cascades have been observed across the globe, however, the most pertinent example exists within Yellowstone National Park in North America. After the extirpation of wolves (*Canis lupus*) from Greater Yellowstone, elk (*Cervus elaphus)* and bison (*Bison bison*) were able to forage without the threat of predators. When wolves were reintroduced in 1995, they began reducing the number of elk, bison, and mesopredators

such as coyotes (*Canis latrans*). The wolves also altered the behaviour of the elk and bison, as they began to avoid meadows where the wolves congregated and increased their vigilance when foraging (Laundré et al., 2001). The reintroduction of wolves resulted in increases in both faunal and floral biodiversity (Beschta and Ripple, 2012).

Australia, colonised by European settlers in 1788, is a globalised, novel ecosystem. Introduced mesopredators, herbivores and small mammals, are found across the continent. Trophic cascades within Australia are inherently *novel trophic cascades*. In Australia, dingoes (*Canis dingo*) are the sole mammalian apex predator, as such they can structure ecosystems by limiting populations of mesopredators such as foxes and cats and herbivores such as kangaroos (*Macropus spp.*) (Glen et al., 2007; Johnson and VanDerWal, 2009). Dingoes safeguard biodiversity, as their presence is linked to the survival of endangered small mammals within the Australian arid zone (Johnson et al., 2007; Wallach et al., 2010). However, dingoes are subjected to human persecution across the continent, altering their ecology and behaviour (Brook et al., 2012; Wallach et al., 2009) and hampering their ecological influence (Wallach et al., 2010).

Coevolution and novel ecological interactions

The introduction of foxes and cats to Australia is widely considered to be a driver of decline and extinction in Australian small mammals (Woinarski et al., 2015). This is posited to be due to the lack of coevolutionary history shared by introduced predators and their small mammal prey (Carthey and Banks, 2014). Coevolution is the process of two or more organisms reciprocally altering the evolutionary path of one another (Janzen,

1980). The "prey naivety hypothesis" has been put forward as an explanation for why non-native mesopredators sometimes cause the decline of native animals (Anson & Dickman, 2013). The prey naiveté hypothesis posits that as native prey lack long-term coevolutionary history with introduced predators they fail to recognise the threat posed by them (Banks et al., 2018). The validity of the prey naiveté hypothesis has recently been challenged (Gerard et al., 2014; Wallach et al., 2015c). While a lack of coevolutionary history can influence the outcomes of ecological interactions, native and non-native species are known to adapt through rapid behavioural changes in response to novel stimuli (Carroll et al., 2007). However, the universality of this hypothesis requires testing, as studies have not compared predator—prey interactions between foxes in their introduced and native range.

Australian ecosystems are almost ubiquitously made up of novel species assemblages and as such, serve as a pertinent location to study how the introduction of predators can shape these systems. However, many aspects of Australia's novel trophic cascades remain unexplored.

The red fox, a globalised mesopredator

The red fox is one of the Earth's most successful carnivores. In the face of constant, ever-increasing persecution, they remain. The fox has even established populations in nine new countries in modern times, attesting to their remarkable ability to adapt (Long, 2003). In their native range, foxes are considered key to ecological functioning, limiting densities of their prey and limiting disease transfer (Levi et al., 2012). While in the foxes introduced

range, they are widely accepted as a predator that drives declines and extinction (Doherty et al., 2016). However, foxes outside of their native range can also prevent extinction and decline through the very predation they are valued for in their native range (Hanna and Cardillo, 2014). As foxes have such wide geographic distributions they serve as the perfect species to understand how ecological context can shape the behaviour and ecology of a mesopredator.

Thesis overview

In this thesis, I examine how foxes shape the behaviour and ecology of their global prey and how their behaviour is influenced by their predators. Using both ecological and ethological methods, this thesis broadens our understanding of how predators and prey come to coexist.

Within Chapter 2, I evaluate how small mammals respond to foxes in both their introduced and native range. While we understand a great deal about the responses of Australian small mammals to introduced and native predators, this relationship has not been contextualised with interactions in the native range of the red fox. I thus test the prey naiveté hypothesis by studying how prey respond to foxes across their native and introduced ranges, finding that prey respond with vigilance, regardless of their coevolutionary history with the predator. As the strength of prey responses did not differ across the foxes native and introduced range, I suggest that prey naiveté is an unlikely cause of decline and extinction in Australian small mammals.

I then evaluate how the ecological contexts of apex predation can shape the behaviour of foxes. Chapters 3-5 explore the behaviour of the fox in response to their primary predator in Australia, the dingo. Foxes are supressed by dingoes across the continent, while the relationship between the abundance of the two predators is clear, the mechanism of suppression remains unknown (Letnic et al., 2011; Wallach et al., 2010). Given the focus on the dingo as a regulator of diversity, our knowledge of these interactions does not stem beyond the ecology of the two species. Understanding this, I explored the non-consumptive mechanisms of suppression that dingoes exert on foxes, quantifying how dingoes shape their behaviour across a range of ecological states.

In chapter 3, published in *Animals*, I begin by combining behavioural ecology and ethological methods to develop an ethogram for measuring the behavioural and attitudinal states of foxes. This was done in collaboration with fox carers and canid behaviour experts. Within Chapter 4, now published in *Behavioral Ecology*, I employ the methods from the previous chapter, combined with ecological and behavioural analysis to explore how foxes respond to dingoes when they are protected from human killing. I found that foxes avoided dingoes in space and time, however, against expectations, they did not increase their levels of caution with increasing indices of dingo activity. I conclude by suggesting that protection from human killing may enable foxes to develop knowledge of the activity patterns of their predators, enabling confident avoidance. Given this unexpected result, I expanded my focus, to explore how foxes were avoiding dingoes across a range of protected and persecuted areas, testing predictions made under the landscape of fear framework. Within chapter 5, I examine how predator persecution,

protection and the absence of a predator can shape the behaviour of the fox. I found that foxes strongly avoided dingoes in protected areas, however, dingoes did not inspire the most fear in the mesopredator. Instead, foxes were the most fearful where they (and dingoes) experienced human persecution. I conclude by highlighting that mesopredators living with socially stable apex predators may adapt their behaviours to avoid risk and reduce the need for constant fear. These behavioural adaptations promote knowledge rather than fear as the driving antipredator behaviours in stable and protected systems, this may turn landscapes of fear into *landscapes of knowledge*.

Within chapters 4 and 5, I found that fear-based mechanisms were not adequate to explain fox behaviour in the face of predation. This mirrored examples from around the globe that highlight that coexistence between predators may be driven by more than fear alone (Karanth et al., 2017; Mueller et al., 2018; Swanson et al., 2016). Knowing this, I began to look beyond ecological explanations as to the foxes confidence in the face of danger. Within the final chapter of my thesis, I explore the incorporation of animal cognition into predator-prey ecology, with the primary goal of elucidating that the complex cognition and emotional states of non-human animals are ecologically consequential.

Within my final chapter titled "*Animal cognition has cascading ecological effects*", I explore the theoretical and mechanistic underpinnings of the incorporation of animal cognition science into predator-prey ecology. I review literature relevant to the landscape of fear, and build beyond, exploring ecological interactions and phenomena that cannot be explained by fear alone. I provide evidence and theorise as to how the cognition of

individual animals has cascading ecological effects. I present the landscape of knowledge, a framework aimed at incorporating animal cognition into predator-prey ecology. I end the thesis with future questions and research directions, aimed at understanding how, with the incorporation of tenants and methods from animal cognition science we can better understand how predators and their prey come to coexist.

Chapter 2: Australian Small Mammals are fox savvy

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Abstract

Predator populations established outside their native range are considered drivers of extinction of their prey worldwide. The *prey naiveté hypothesis* has become the most widely accepted explanation for why native prey are vulnerable. It proposes that animals can be naïve to predation risk posed by introduced predators because they share a relatively brief coevolutionary history, too brief for adaptation to have occurred. In Australia, red foxes *(Vulpes vulpes)* have been implicated in the decline and extinction of small mammals due to prey naivety. However, the role of coevolution in these interactions remains unclear, as previous research regarding prey naiveté has been limited to a single geographic region. We compared native small mammal responses to predation risk where foxes are introduced (Australia) to small mammal responses where they are native (Israel and USA). We measured small mammal behaviour at food patches treated with the fox

scent as a predation cue, compared to the scent of a local introduced herbivore as a control. We established all study sites in deserts, to correspond with the type of environment where small mammals have declined the most in Australia. All study sites contained apex predators, and excluded human hunting, to reduce variability of predation pressure. We found that Australian small mammals were as wary of foxes as Israeli and American small mammals were. In response to the scent of foxes, small mammal vigilance increased, and food consumption remained unchanged, at all study sites. We conclude, therefore, that Australia's small mammals are fox savvy. The prey naiveté hypothesis is an unlikely explanation for the decline and extinction of Australian small mammals.

Introduction

Mammalian predator populations that have established outside their historic native range are believed to have caused the decline and extinction of terrestrial small vertebrates globally (Doherty et al., 2016). In Australia, the introduction of red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) is considered the primary cause of decline and extinction of their native small mammal prey (Woinarski et al., 2015). The decline of small mammal populations following fox and cat establishment (Short, 1998); their increase where these predators have been suppressed (Kinnear et al., 2002); and, the fact that cats and foxes include native animals in their diet (Stobo-Wilson et al., 2021), all point toward predation by foxes and cats as a plausible cause of decline. Yet, to ascertain that these predators are driving declines, a causal mechanism is required. The mechanism that has been proposed is that native animals are predator *naïve* (Carthey and Banks, 2014).

Australian small mammals have long coevolved with a wide range of vertebrate predators, thus it is necessary to explain why they would be unusually vulnerable to foxes and cats in particular. Invasion biology relies on the 'prey naivety hypothesis' to argue that Australian small mammals are vulnerable to introduced predators because their relatively brief shared history means they do not effectively recognise them as a threat (Carthey and Banks, 2014). Prey naivety of Australian small mammals toward foxes has been tested since at least 1998 (Banks, 1998), and toward cats since at least 2000 (Haythornthwaite and Dickman, 2000). A lack of effective anti-predator behaviour has been reported in prey populations that are allopatric (Jones et al., 2004) with their predators or in captivity (Blumstein et al., 2002). However, the accumulated research has generally found that Australian native small mammals that are sympatric with foxes respond with the same wariness as they do toward native predators (Banks et al., 2018). For example, Russell and Banks (2007) found that bush rats (*Rattus fuscipes*), swamp rats (*Rattus lutreolus),* eastern chestnut mice (*Pseudomys gracilicaudatus*), and brown antechinus' (*Antechinus stuartii*) all display the same level of avoidance toward the odours of the red fox and native tiger quoll (*Dasyurus maculatus*). Similarly, Bytheway and Banks (2019) demonstrated that northern brown bandicoots (*Isoodon macrourus*) living sympatrically with foxes reduced their foraging and increased their vigilance in response to fox scent, while those living allopatrically did not. Despite these studies, naiveté remains the proposed mechanism that ties introduced predators to the declines observed in their prey (Anton et al., 2020; Banks et al., 2018; Meyer et al., 2021).

It has been suggested that beyond the ability to recognise introduced predators, declining native mammals still lack the ability to appropriately respond to them (Banks et al., 2018) or that species that do respond appropriately are but a small subset of a naïve whole (Meyer et al., 2021). Yet, to comprehend whether the responses of Australian small mammals to introduced predators are appropriate, we must understand how they compare to small mammals where these predators are native. However, as research has solely focused on comparisons of small mammal responses to their native and introduced predators in Australia, it remains unknown how the responses of Australian small mammals compares to those in regions where introduced predators are native.

Understanding how coevolution drives the responses of small mammals to predators remains a hurdle in understanding how best to promote their populations across Australia. To address this, we conducted giving-up density (GUD) experiments and explored the behavioural responses of small mammals to foxes in Israel and North America, where foxes are native and in Australia where they are introduced. In doing so, we provide the first comparative study exploring how coevolution shapes the behavioural responses of prey to predators. The prey naiveté hypothesis predicts that small mammal anti-predator responses should be stronger within the foxes native range than outside it, while if Australian small mammals do recognise and respond to the fox, the strength of behavioural response should not differ across the foxes range.

Methods

We compared the behavioural responses of small mammals to the fox in and outside of its historic native range. All study sites were in arid systems, where apex predators were present, and all predators protected (Table 1). In Australia, study sites were situated in the Painted Desert, South Australia, and the Simpson Desert, Northern Territory; in the US, two study sites were located in Death Valley National Park, California; and in Israel two study sites were in the Arava.

The Painted Desert study site consisted of two conjoined properties, Evelyn Downs, a 2,300 km2 cattle station and Mount Willoughby a 5,600 km2 protected area, part of which is a cattle station. Predators have been protected on both properties since 2012, prior to this, predators were regularly killed across both properties (Wallach et al., 2017). The Simpson Desert study area is hyper remote, it is unlikely predators have experienced persecution at all. Small mammal species at both study sites have coexisted with foxes for >100 years, as foxes likely arrived at both Australian study sites around 1910 (Saunders et al., 1995). The Arava, is a hyper-arid valley, located on across the Israel-Jordan border. The area is used for agricultural purposes with small agricultural villages and fields of intensive crop and dairy farming surrounding nature reserves. Predators throughout this region have been historically protected from human persecution by law.

Table 1. Descriptions of ecological context of each field site. Columns indicate region and whether each location was in or out of the foxes' native range, the locations within each region, the average rainfall within each site, the small mammal study species at each site and the number of trays each was present at for both control and experiment period (sample size), reflected by identification from camera trap videos and the predator assemblage present at each of the sites. * Indicates the mesopredator scat used to simulate predation risk within the GUD experiment.

Region (In/out fox's native range)	Study Site	Average rainfall (mm)	Study species	Predator's present
Australia (out)	Painted Desert, South Australia	160	Notomys alexis	Canis dingo
	Simpson Desert, Northern Territory	125	Pseudomys hermannsbugensis Sminthopsis crassicaudata	Vulpes vulpes* Felis catus
Israel (in)	Shezaf Reserve, Arava Shahaq Reserve, Arava	40-60	Acomys alexis Psamommys obesus. Gerbillus gerbillus Gerbillus nanus	C. lupus C. aureus V. Vulpes* Felis silvestris
North America (in)	Butte Valley, Death Valley National Park, California Saline Valley, Death Valley National Park, California	25-50	Dipodomys merriami Peromyscus maniculatus	Puma concolor C. latrans V. macrotis* Urocyon cinereoargenteus

Death Valley National Park is the largest protected area in the continental United States and is located in eastern California. Mountain lions (Puma concolor), the local apex predators, are protected from most forms of persecution. Death Valley may thus harbor the world's most protected mountain lion population. Small mammals within both Israeli and North American study sites, where the fox is considered native, have coevolved coexisting with the predator.

To quantify the responses of small mammals to the fox, we used the GUD framework. The GUD framework provides a method to quantitively measure how individuals make foraging decisions (Brown et al., 1999). Upon a review of the literature, we found that GUDS have been the primary method used to assess the naiveté within Australian small mammals (Banks et al., 2018). As outlined within the GUD framework, prey individuals foraging at foraging trays should quit searching for food when the metabolic or predation costs outweigh the potential benefits from continued foraging (Pyke et al., 1977). We therefore used the amount of food left by foragers at each foraging tray as a metric of 'risk' perceived by individuals (Brown and Alkon, 1990).

Within each region we established between 40-56 small mammal foraging trays. Within Israel and North America, foraging trays were set a minimum of 200m apart along roads. However, at Australian study sites, attracting enough small mammals to foraging trays to ensure a sufficient sample size proved unfeasible, given their very low densities. Instead, within Australia we established foraging trays in hotspots of small mammal activity, such as pathways or colonies. Each foraging tray was filled with 30 peanut fragments mixed

into 2L of sand and a Bushnell MKII or Browning Dark Ops Pro camera was pointed at the foraging tray. The number of nuts placed in the trays was increased by 10 nuts if small mammals consumed 100% of the nuts given. All foraging trays were placed within 5m of vegetation.

Each session included a period 2-6 acclimatisation day, to ensure small mammal foragers were present at the foraging tray prior to the commencement of data collection. To measure the response of small mammals to their predators, we placed predator cues on the outside corner of the foraging tray. Upon review of the literature, we found that small mammals were most likely to respond to the scats of their predators, given this, we used the scats of predators to represent the threat of predation (Carthey, 2012). Scats are deposited by predators to represent ownership and territorial boundaries and as such present an excellent medium for conveying the risk of predation (Wallach et al., 2009). Understanding this, we conducted two control days followed by two experimental days where a fox or herbivore scat was added. In Australia and Israel, we used scats of the red fox. Within North America we were unable to locate an appropriate study location within an arid area with apex predators present and protected where red foxes were abundant, given this, we chose to use the scats of the kit fox (Vulpes macrotis), a close relative of the red fox and a mesopredator abundant within Death Valley. Control days served as a baseline for GUDs and vigilance to which experiment days were compared. In light of this, we used the scats of local herbivore species as a control: camel (Camelus dromedarius) in the Simpson Desert, cow (Bos taurus) in the Painted Desert and Arava, donkey (Equus asinus) in Death Valley.

Herbivore scats were collected in the field, fresh (moist) scats were located and immediately frozen at -20 C. Fox scats were sourced from captive individuals and frozen at -20 C. Scats were collected from local rescues or sanctuaries, from a mix of genders and ages. Scats were kept frozen until they were placed at foraging trays, within a month of collection. We treated foraging trays as replicates of odour treatments for GUDs and behavioural analysis.

We combined the GUD framework with behavioural analysis conducted on footage gathered from motion-sensing camera traps monitoring activity at foraging trays (Carthey and Banks, 2016). Based upon a review of the literature we identified the seven most relevant behaviours to assessing the level of fear felt by small mammals at foraging trays. We assessed videos for time spent foraging, vigilant, grooming, locomoting, investigating and engaging in social behaviour (See detailed ethogram in supplementary table 1). All behaviours were treated as mutually exclusive. Behaviour was scored by E.W and a team of four supervised interns. Behavioural analysis was primarily focused on scoring the amount of time small mammals spent vigilant. All behaviours were considered mutually exclusive with the exception of inside and outside the tray, which were scored alongside all other behaviours,

We analysed two variables related to how small mammals respond to predator cues: consumption rate and time spent vigilant. Given that moon phase has been shown to alter the foraging behaviour of small mammals (Navarro-Castilla and Barja, 2014), we also explored the relationship between small mammal nut consumption and vigilance and

moon phase across each of our study regions. For each, we calculated the difference between control periods (prior to scat placement) versus experimental periods (following scat placement). We then analysed how nativeness, scat type, their interaction, and total moon illumination influenced changes in consumption rate and vigilance using linear mixed effect models, treating sites as random effects in the R package lme4 v1.1-23. We used multimodel inference techniques (AIC) to find the most parsimonious model by dropping spurious predictor variables. We log-transformed response variables as necessary (after adding a constant to make values non-zero centred) to approximate normality. As vigilance was derived from trail camera videos, we constrained comparisons to trays with the same species before and after scat treatments and filtered out species with <10 independent observations (e.g., separate trays).

Results

Small mammals significantly increased their time spent vigilant in response to the addition of fox scats ($\chi^2 = 7.7$, p = 0.005) both in and out of their historic native range ($\chi^2 = 3.6$, p = 0.06, interaction: $\chi^2 = 0.50$, p = 0.50, Figure 1a). However, neither nativeness nor the addition of fox scat had an effect on nut consumption rates of small mammals, both in and out of the fox's native range. The final, most parsimonious model to explain changes in nut consumption, included only scat type, which was not significant ($\chi^2 = 0.44$, p = 0.50, Figure 1b). Moon phase did not influence the nut consumption or vigilance of small mammals both within and outside of the fox's native range. To verify that species identity did not influence the results, we also analysed the effect of species on changes in

behaviour for each region. The genus of small mammal did not significantly alter the behavioural response for any region (p = 0.07-0.5, Figure 2).
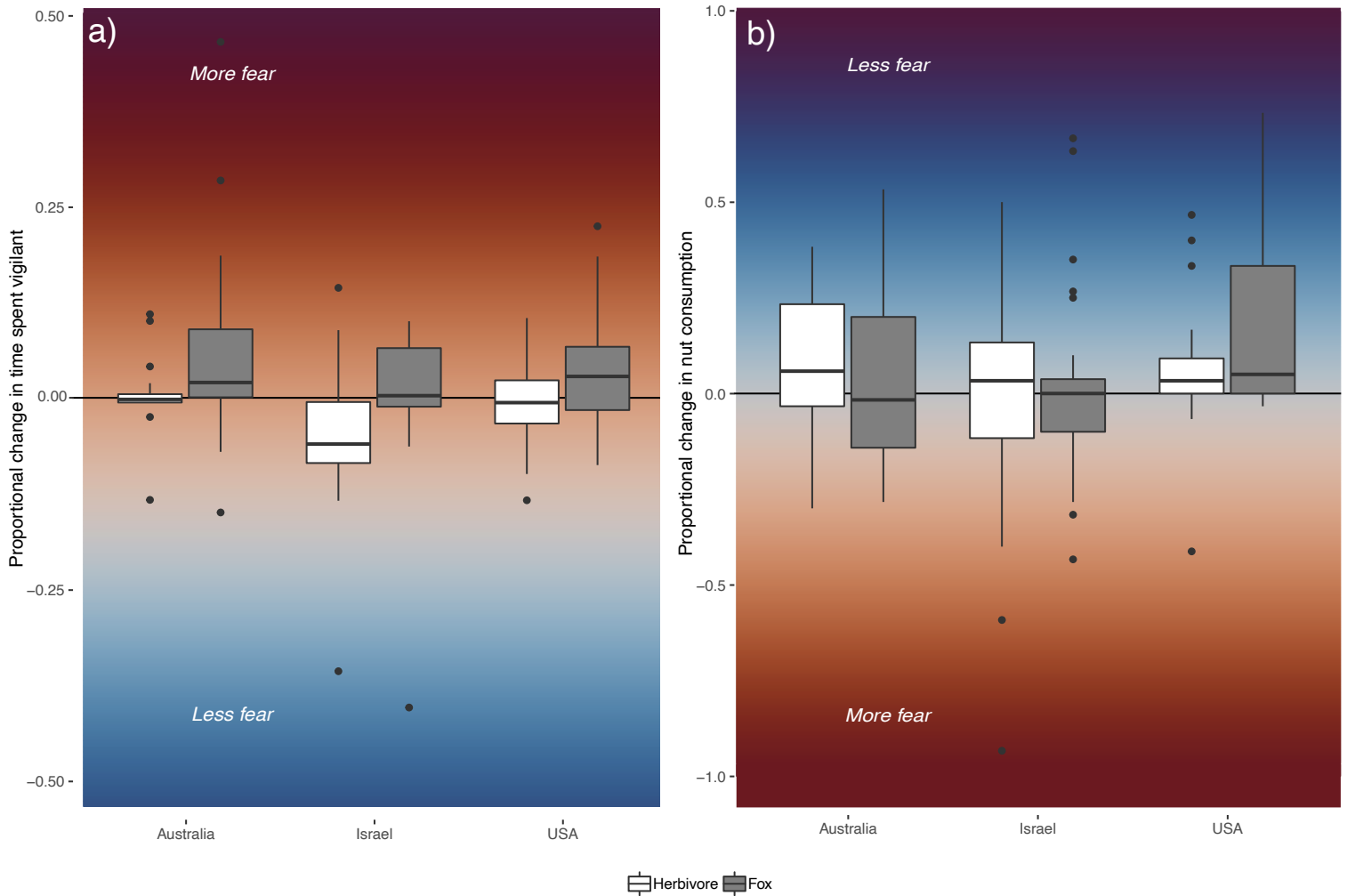
Figure 1. Behavioural responses of small mammals to addition of fox and herbivore scats, outlining changes in a) change in proportion of time small mammals spent vigilant in response to fox and herbivore scats. Positive values (red fill) indicate presumed increase in fear, through proportional increases in time spent vigilant. Horizontal line indicates no change between control days and experimental days (e.g., post scat placement). b) small mammal nut consumption rates in response to the addition of fox and herbivore scats. Negative values (red fill) indicate a decrease in proportional nut consumption (defined as higher fear).

Horizontal line indicates no change between control days and experimental days (e.g., post scat placement).

Figure 2. Behavioural responses of small mammal species to addition of fox and herbivore scats, outlining changes in the proportion of time small mammals spent vigilant in response to fox and herbivore scats. Positive values (red fill) indicate presumed increase in fear, through proportional increases in time spent vigilant. Horizontal line indicates no change between control days and experimental days (e.g., post scat placement).

Table 2: Outputs from the most parsimonious linear mixed effects models for each small mammal behaviour metric measured. Linear mixed effect models were conducted within the R package lme4 v1.1-23. * denote significance ($P < 0.05$).

Parameters included	Chi square	df	P
Giving up density			
Scent	0.407	1	0.523
Vigilance			
Nativeness x Scent	0.459	1	0.0564
Nativeness	3.640	1	0.0562
Scent	7.700	1	0.0055*

Discussion

The prey naiveté hypothesis predicts that the behavioural responses of small mammals to predators should vary based on whether the fox is native (Carthey and Banks, 2014). With a globalised field study, we demonstrate that Australian small mammals share the anti-predator responses of those in long-term coevolved predator-prey systems. We suggest that Australian small mammals are savvy to the threat posed by the red fox. Understanding this, prey naiveté is an unlikely driver of small mammal decline in Australia.

Upon first encountering eutherian predators, Australian small mammals were likely unaware of the threat they posed given their ecological and evolutionary distinction from

the marsupial predators they evolved with (Carthey et al., 2017; Luo et al., 2011). This initial naiveté may have contributed to small mammal decline as non-native predators first established across the country (Short, 1998). However, our results demonstrate that in the relatively short period of time since introduction, Australian small mammals have rapidly developed anti-predator behaviour that mirrors those in long term co-evolved systems. As a result, Australian small mammals are no longer naïve to the threat posed by the fox. This rapid adaptation can be elucidated by contemporary evolution (Carroll et al., 2007). Described as evolution occurring on ecological time scales, contemporary evolution explains the process by which organisms rapidly evolve traits or behavioural adaptations in response to environmental change, such as species introduction (Stockwell et al., 2003). The arrival of novel species can shape the behaviour (Parrott et al., 2020) and morphology (Cattau et al., 2018) of predators as they hunt novel prey species and the behaviour of prey as they avoid predation (Tortosa et al., 2015). Understanding this, it is not surprising that Australian small mammals have developed behavioural strategies that allow them to minimise the risk posed by foxes.

Regardless of their lack of naiveté, Australian small mammals remain in decline, and it is believed that non-native predators are responsible (Kinnear et al., 2002; Short, 1998; Woinarski et al., 2015). However, the effects that non-native predators have on their prey can be ameliorated by the presence and protection of dingoes (*Canis dingo*), Australia's primary mammalian apex predator. Dingoes limit the densities (Letnic and Dworjanyn, 2011; Letnic et al., 2012) and alter the behaviour of mesopredators (Brook et al., 2012; Wooster et al., 2021), which alleviates predation pressure on their small mammal prey,

promoting both their diversity and richness (Letnic et al., 2012). However, in Australia predators are subject to intense eradication programs (Philip, 2019). These programs hamper the dingoes ecological influence as they lose the ability to pack hunt and maintain territory (Wallach et al., 2009), resulting in increased densities of mesopredators and reductions in their small mammal prey (Wallach et al., 2010). This has resulted in areas of predator persecution across the continent being highlighted as hotspots of small mammal decline and endangerment (Fisher et al., 2003; Wallach and O'Neill, 2009b). Similarly, there is strong evidence for the negative effects of habitat degradation on small mammal prey species (Fisher et al., 2003). Complex vegetative cover is essential to small mammals facing predation, allowing them cover and safety (Pedersen et al., 2014). However, the prevalence of intensive agriculture within Australia has resulted in drastic land clearing and unsustainable livestock herbivory, further, the presence of sheep farming is one of the best predictors for the decline of Australian small mammals (Fisher et al., 2003). The introduction of sustainable pastoralist and livestock grazing practices, the promotion of apex predators, more conservative land clearing and fire management policies may all help the promotion of Australia's small mammals.

Non-native species are considered among the leading causes of decline and extinction globally (Simberloff, 2010). However, this paradigm continues to lose traction as non-native species restore ecological function lost to extinction (Lundgren et al., 2020) and native species evolve to face the challenges of novel ecosystems (Carroll et al., 2007; Cattau et al., 2018; Wallach et al., 2015c). Our work provides a pertinent example of native prey species rapidly evolving anti-predator responses to novel predators. This

suggests that coexistence between native prey and non-native predators is possible, however, identifying and promoting ecological conditions that facilitate coexistence remains a hurdle.

Supplementary material

Supplementary table 1. Ethogram used to score rodent behaviour at foraging trays from camera trap videos.

Behaviour	Modifiers	Description
Locomotion	Walk	Slow Quadrupedal or Bipedal Movement
	Run	Fast Quadrupedal or Bipedal Movement
	Jump	Vertical Or Horizonal Jump
	Perch	Sitting On the Edge of The Foraging Tray
Foraging		Individual Is Actively Digging, Looking for Or Consuming Food. Head Angle Below Horizontal.
Vigilance	Stage 1	Low to moderate level of alert. Quadrupedal species have all four legs on the ground with their head above horizontal. Bipedal species remain in neutral posture with head horizontal. Rodent is not doing anything else
	Stage 2	High level of alert. Quadrupedal species are on hind two legs with body extended. Bipedal species have body as extended as possible; posture is vertical. Individuals are listening/looking/sniffing and not doing anything else.
Grooming		Individual licks of bites own fur
Social		Two or more individuals interacting at foraging trays

Investigating		Individuals sniffing the tray or ground around surrounding the foraging tray
Inside Tray		Individual has at least two paws in the foraging tray
Outside Tray		Individual has all four paws outside of the foraging trat

Supplementary table 2. Unused data from GUD experiments using cat scent conducted in the Shezaf and Shahaq Reserves, Arava, Israel.

Treatment	Sample size sites	Sample size replicates	Mean change	Standard error
Cat	4	36	0.213	0.2865
Control	4	34	0.0074	0.2839

Chapter 3: The Wily and Courageous Red Fox: Behavioural Analysis of a Mesopredator at Resource Points Shared by an Apex Predator

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Simple Summary: The red fox is one of the Earth's most widespread mammalian predators. Human globalisation further expanded its range, so that today they are found on most continents. Despite their abundance, knowledge of fox behaviour remains limited. Most studies have observed foxes either in captivity or in their native range where both they and their predators are killed by humans. We conducted a behavioural study on foxes outside of their native range in Australia, at a unique location where all wildlife are protected. We developed an ethogram to explore fox behaviour at resource points shared with a potentially deadly apex predator, the dingo. We were surprised to find that foxes were in a confident state more often than in a cautious state, even leaving territorial markings over those of dingoes. One possible explanation for the confidence of foxes is that the social stability of both foxes and dingoes makes their world more predictable.

Abstract: The red fox (*Vulpes vulpes*) is a widespread and ecologically significant terrestrial mesopredator, that has expanded its range with human globalisation. However, we know relatively little about their behaviour under the wide range of ecological conditions they experience, particularly how they navigate the risk of encounters with apex predators. We conducted the first ethological study of foxes outside their historic native range, in Australia, where both the foxes and their main predator were protected from human hunting. Using remote camera traps, we recorded foxes visiting key resource points regularly utilised by territorial dingoes (*Canis dingo*), their local apex predator, in the Painted Desert, South Australia. We constructed an ethogram sensitive to a range of behaviours and attitudes. Since foxes are suppressed by dingoes, we expected that the foxes would primarily be in a cautious state. In contrast, we found that foxes were in a confident state most of the time. Where human hunting is absent, social stability of predators may increase predictability and therefore decrease fear.

Keywords: vulpes vulpes; canis dingo; landscape of fear; trophic cascades; mesopredator

Introduction

"Look at him. His coat is russet with sufficient gold in it to make him glow. He has just enough of a ruff to please a very young lion and enough tail to be the pleasure of any animal that grows a tail. His snout is a bit pinched-looking and would be mean if there wasn't so much pride in his carriage—he walks the Australian earth as though it was a carpet especially laid for him" (Rolls 1969).

The red fox (*Vulpes vulpes*) is one of the most widespread of all carnivores, having populations on all continents except Antarctica and South America (Macdonald and Reynolds, 2004). They inhabit a wide range of habitats, including tundras, temperate woodlands, coasts, and deserts. Foxes have adapted to, and benefited from, the ecological changes of the Anthropocene, exploiting anthropogenic resources (Contesse et al., 2004) and experiencing release from predation through the extirpation of apex predators in both urban and agricultural landscapes (Prugh et al., 2009). Furthermore, foxes have significantly expanded their historic range through introductions by humans, establishing populations in nine new countries over the last 170 years (Long, 2003). Studying the behaviour of animals outside of their historical ranges provides a unique opportunity to explore how species and individuals adapt to the challenges and opportunities of new environments.

One population that has flourished due to human-assisted migration is in Australia. Foxes were first introduced to Australia in the 1830s, brought to Victoria for hunting. Within a century they had expanded their range throughout much of the continent (Dickman, 1996). Bounty programs and "pest" status were first established in the 1890s, both of which continue today. Foxes are routinely shot, poisoned, trapped, and gassed, everywhere from national parks to farms and urban parklands. This control program exists alongside a similar lethal campaign against dingoes (*Canis dingo*), leading to the considerable decline of Australia's only remaining mammalian apex predator. This has arguably left foxes in a state of "mesopredator release", removed from top-down pressure

(Wallach et al., 2010). Hence, although foxes are heavily targeted by control programs, these efforts have not led to local or functional extirpation.

Apex predators limit the densities and spatial distribution of smaller predators, through competition, predation, and intraguild competitive killing (Haswell et al., 2017) . The ecology and behaviour of foxes, in both their historic and introduced ranges is actively shaped by the predation and interference by apex predators (Prugh et al., 2009) . Within their historic range, foxes are suppressed by coyotes in North America (*Canis latrans*) (Mueller et al., 2018)and wolves in Europe (*Canis lupus*), while in Australia they are suppressed by dingoes (Newsome et al., 2017). In response to the presence of apex predators, foxes are known to alter spatio-temporal activity patterns and increase vigilance behaviour, helping them to detect and avoid risky encounters (Scheinin et al., 2006). This creates a "landscape of fear", represented by "peaks" (high risk) and "valleys" (low risk) (Laundre et al., 2009b). In North America, foxes have been shown to exploit urban areas to avoid coyotes (Mueller et al., 2018), while in the Australian desert, foxes have been shown to avoid water sources where dingo activity is concentrated (Brawata and Neeman, 2011).

A review of the literature focused on studies that had significant behavioural aspects revealed that most ethological research on wild foxes has occurred where apex predators were absent (80%) and where foxes and their predators were subjected to lethal control (83%) (Table 1). Only two studies were conducted where both foxes and their predators were protected (Haswell et al., 2018; Scheinin et al., 2006), both within the fox's historic

range. A further eight studies were conducted in the wild that did not report whether apex predators were present, protected, or killed; three studies were conducted in captivity; while the rest were conducted without apex predators present. To the best of our knowledge, no study has been concerned solely with understanding fox behaviour outside their historic range without an overarching view of promoting suppression efforts. Although there has been much research on foxes in Australia, most of it has been concerned with how to suppress populations (Harding et al., 2001; Mahon, 2009) . Our interest, therefore, was in developing a suitable ethogram of fox behaviour and then implementing that ethogram to study wild fox behaviour in an introduced setting without interference from human persecution of themselves and/or their predators. To do this, we made use of a rare 'predator friendly' landscape in the Australian desert to observe fox behaviour where they are at risk from deadly encounters with dingoes. Due to the high level of risk dingoes pose to foxes, we expected that foxes would be highly cautious when accessing resource points shared with dingoes.

Table 1. Review of fox behaviour literature highlights the most common ecological contexts foxes are studied under. Data gathered for this review comes from a Web of Science search, using "Red fox behaviour" as the search term, the search was refined for "behavioural Sciences". Reference trails were also included in the review. Unstated was noted if authors did not mention whether the variable in question was present during their study. N/A refers to a variable not being applicable to the study (e.g., Foxes killed is not relevant to a study conducted in captivity).

Behavioural Study	Country	Wild/Captive	Foxes killed	Apex predators	References
Anti-predator behaviour	Australia	Wild	Yes	Dingo (*Canis dingo*)	(Leo et al., 2015)
	Canada	Wild	Unstated	Coyote (*C.latrans*)	(Voigt and Earle, 1983)
	Croatia	Wild	No	Wolf (*C.lupus*)	(Haswell et al., 2018)
	Israel	Wild	No	Golden jackal (*C.aureus*)	(Scheinin et al., 2006)
	North America	Wild	Unstated	Coyote	(Mueller et al., 2018)
	Poland	Wild	Unstated	Lynx (*Lynx lynx*)	(Wikenros et al., 2017)
Fox kit ethogram	Switzerland	Wild	Unstated	Unstated	(Meyer and Weber, 1996)
Reproduction	North America	Wild	Yes	Unstated	(Zabel and Taggart, 1989)
Sociality	England	Wild	Yes	No	(Baker et al., 1998)
	England	Captive	N/A	N/A	(Blizard and Perry, 1979)
	North America	Captive	N/A	N/A	(Fox, 1971)
Scent marking	Canada	Wild	Unstated	Unstated	(Henry, 1977)
	Israel & North America	Both	Unstated	Unstated	(Macdonald, 1979B)
	Spain	Wild	Unstated	Unstated	(Monclús et al., 2009)
	England	Wild	Yes	No	(Baker et al., 2007)
	England	Wild	Yes	No	(Soulsbury et al., 2011)
Temporal and Spatial patterns	England	Wild	Yes	No	(Tolhurst et al., 2016)
	England	Wild	Yes	No	(Tolhurst et al., 2016)
	Italy	Wild	Yes	No	(Iossa et al., 2009)
	Italy	Wild	Yes	Unstated	(Cagnacci et al., 2004)
	Italy	Wild	Yes	Unstated	(Lucherini et al., 1995)
	Japan	Wild	Yes	Unstated	(Cavallini, 1992)
Feeding behaviours	Switzerland	Captive	N/A	N/A	(Kistler et al., 2009)
	Sweden	Wild	Unstated	Unstated	(Jarnemo, 2004)

Methods

Our study was conducted across two contiguous predator friendly properties in the Painted Desert, South Australia. The properties include a 2300 km^2 cattle station and a 5600 km^2 Indigenous Protected Area, utilised in part for cattle and horse grazing. Foxes are likely to have been resident in the area as early as 1940, by which point they were already present in over two-thirds of Australia (Saunders et al., 1995) . The landscape is arid, with average rainfall around 160 mm annually, and is dominated by chenopod shrublands, tall Acacia woodland, and Eucalyptus species along ephemeral creeks. Reliable sources of drinking water for stock, predators are limited to semi-permanent rain-filled dams and permanent bores, spread evenly across the landscape approximately every 10 km. Historically, predators had been regularly poisoned, shot, and trapped across the region, but non-lethal predator friendly practices were established on both properties in 2012 (Wallach et al., 2017).

We remotely filmed foxes at water sources, rabbit warrens, and large carcasses, resource points known to be utilised by territorial foxes and dingoes (Wallach et al., 2009). Predators are highly elusive and thus, behavioural data is difficult to obtain as direct observations are not possible. This makes camera trapping the only source of gathering such data. Camera traps were placed at water points approximately 10 km apart, however, rabbit warrens and carcasses were regularly located within the 10 km between water points. As we were unable to identify individual foxes, and foxes home ranges vary

between 8.3 and 33.2 km^2 in arid environments (Moseby et al., 2009a), we caution that it is possible that we observed the same individuals across multiple resource points. Water sources in the arid zone are important resources for predators for drinking, socialising, communicating, and hunting (Wallach et al., 2009). The highest concentration of dingo scent marking occurs at arid zone water sources, with some waters having over 100 dingo scats. Dingo scent marking concentrates in areas where they are socially stable (Wallach et al., 2009). Scent marking is a good indicator of social stability in canids and is a common method of communication and territoriality. Large carcasses are important as resource points for food and as focal points for scent marking for both foxes and dingoes. Foxes readily scavenge carcasses of large prey killed by apex predators (Mitchell and Banks, 2005), and both foxes and dingoes scavenge domestic animals discarded by humans (Coman, 1973). Both predators are also significant predators of rabbits (Oryctolagus cuniculus) (Glen et al., 2007) and use rabbit warrens to locate prey and for scent marking (Monclús et al., 2009). Rabbits warrens are burrows dug and utilised by rabbits for shelter and raising young, they are identified through tracks or scats present at their entrance. We focused this study on resource points as they are both essential parts of life within the desert for both foxes and dingoes and as they represent potential points of conflict between them. We monitored fox behaviour through 3 winters (June–July; 2016–2018). In 2016, we monitored 10 water points; in 2017, we monitored 18 water points (of which eight were monitored across 2016 and 2017), 17 rabbit warrens, and five carcasses; while in 2018 we monitored 10 water points (of which six were monitored across 2017 and 2018 and three were monitored over all three years), eight rabbit

warrens, and four carcasses (two of which were monitored for three years). We strapped camera traps (Bushnell MKII and Browning Dark Ops Pro) to trees and posts at 30–60 cm high for 1–3 weeks set to record time-stamped 15–20 s videos, with one second delays. Cameras were hidden to the best of our ability to reduce the chance of behavioural responses being influence by the camera traps themselves. Cameras were active 24 h a day and were checked at least once a week. We set up to three cameras per water source, up to two cameras per rabbit warren, and up to two cameras per carcass, with the number varying based on the size of each resource point. We treated points independently for temporal analysis, if foxes were present on more than one camera at a single resource point within 30 min of each other, we considered them part of the same activity event.

We identified and described discrete fox behaviours to create an ethogram sensitive to wariness of foxes to predation while accessing resource points. We characterised fox behaviours from literature in ethology (Fox, 1971; Ghaskadbi et al., 2016; MacNulty et al., 2007; Way et al., 2006), animal personality (Biro and Stamps, 2008), and animal welfare (Mellor and Beausoleil, 2015), and from assessments made by captive fox carers (Sydney Fox Rescue). The ethogram was first organised into base behaviours, describing key actions such as locomotion and foraging (Table 2). Base behaviours were classified as either state events or point events for purposes of measurement. State events were defined as continuous behaviours (e.g., locomotion) and were measured in units of time (>1 sec), while point events were defined as instantaneous behaviours (e.g., startled jump) and were measured in units of frequency (<1 sec). All base behaviours were further

refined through modifiers, which were descriptive terms used to contextualise base behaviours both physically and mentally [35]. For example, 'locomotion' was modified by a range of both physical states, such as walking, running, jumping, or perching, and by attitudinal states, such as whether the actions were engaged in confidently or cautiously. Attitudinally modified behaviours were classified as either confident or cautious based on the body position of the foxes observed. Cautious behaviour is primarily categorised by the tail being positioned below the height of the back, torso positioned close to the ground and legs spread far apart. Cautious behaviour shares body positions with vigilant behaviour. Confident behaviours were primarily classified in opposition to body positions present within caution and vigilance, foxes are observed with the tail held above or level to the back, legs are extended and positioned close together (Figure 1, Table 3, Supplementary material Table S1).

Behavioural analysis of videos was performed using the Behavioural Observation Research Interactive Software version 7.9.15 (Friard and Gamba, 2016). We analysed observed behaviours for duration and/or frequency, according to the definitions in our ethogram. We calculated the proportion of time each base behaviour and modifier combination contributed to the total time of fox behaviour. Point events were analysed exclusively for their frequency of occurrence. Where more than one fox was present, behaviour was analysed separately. We tested for differences in the proportion of time allocated to base behaviours between the surveyed resource points and for differences in proportions of confident and cautious behaviour within each resource point and between all 3 resource points using separate negative binomial regressions, one per

behaviour (link function: log). All proportions were modelled as integers. In each regression, we set the proportion of time allocated in a given behaviour as the response variable. We included resource type as the predictor variable. We tested significance of the predictor through a Tukey post hoc test. Behaviours with only one attitudinal modifier (e.g., vigilance and scent marking) were removed from this analysis. Digging was also left out as it was only observed once cautiously. Negative binomial regressions were performed through the R version 3.4.1 using the package MASS.

We analysed fox activity patterns at each of the three resource points (i.e., water sources, rabbit warrens, and carcasses). Temporal activity patterns were compared using kernel densities, enabling us to estimate activity overlap between the three resource point types by calculating the area under the curve where all three temporal patterns overlapped. We did this by calculating the densities at which each temporal pattern intersected and then integrated the area where all resource points overlapped, compared to the total curve area. Finally, we recorded the frequency foxes were observed alone or in company. All analyses were performed in R version 3.4.1.

Table 2. Ethogram for foxes at resource points. Modifiers further describe the behaviour observed Point events describe instantaneous behaviours (P). State events describe continuous behaviour (S).

Behaviour state	Modifiers	Description
Locomotion (S)	A) Walk/Run/Jump/Perch B) Cautious/Confident	All spatial movements
Sniffing (S)	Cautious/Confident	Exploring area of interest leading with the nose, the head moves up and down with neck extended
Digging (S)	Cautious/Confident	Investigation of ground utilising the front two paws to remove a layer of dirt or sand
Vigilance (S)	Low/High	Examination of the surrounding environment in a state of alert or heightened awareness, the head moves directionally, head is moving rapidly or focused on an object or location. Individuals are positioned low to the ground with legs positioned far apart (see Figure. 1D)
Foraging (S)	A) Scavenging/Drinking/Hunting B) Cautious/Confident C) Alone/Social	The act of feeding on carrion, ingesting water from a natural or anthropogenic water source or hunting for prey
Scent marking (S)	A) Defecation/Raking/Rubbing B) Alone/Social	The raising of a hind leg or leaning into a squat position in order to deposit urine or scats onto a point of interest, using a paw to rake the ground or the act of rubbing face, paw or tail glands on an object
Flight (P)	Startled Jump/Startled Flee	Dramatic and exaggerated responses to environmental or camera born stimuli. Body movements are rapid, legs, torso and head perform sudden and reckless movements to jump or flee away from the location where they were startled
Investigating (S)	Cautious/Confident	The act of surveying the environment. Head moves directionally, can be performed stationary or during locomotion
Frustration (P)		An outburst of frustration manifested by biting or gnawing on an object in the Environment
Head shake (P)		A rapid shaking of the head in an attempt to remove or dislodge an item of irritation
Salivating (P)		A display of hunger at the anticipation of food involving the licking of the outside of an individual's mouth
Resting (S)		An absence of discernible activity. An individual laying on the ground with all four legs relaxed or sitting down on back end with front paws fully extended, supporting the individual. Individual is motionless. Head may be focused on the ground, sky or on nothing in particular but is motionless
Greeting (S)	Facial/Posterior/Denial	The act of sniffing a conspecific to identify and communicate with the individual
Play (S)	Jump/Chase	One individual actively solicits a non-agonistic interaction, with random and exaggerated movements

Results

We identified 14 base behaviours useful for categorising behaviour around resource points: locomotion, sniffing, digging, vigilance, foraging, flight, investigating, frustration, salivating, head shake, play, greeting, and resting (Table 2, Figure 1). We also identified five modifiers for those behaviours: type (e.g., locomotion modified as walking or running), attitudinal (e.g., locomotion modified as cautious or confident), intensity (e.g., vigilance modified as high or low), and social (e.g., foraging modified as social or alone) (Table 3).

We gathered a total of 55.33 min of fox footage (1.33 min from 2016, 42 min from 2017, and 12 min from 2018). Dingoes were present at all resource points surveyed, with evidence of scent marking by dingoes recorded at all carcasses, at 97% of water points, and at 47% of rabbit warrens. While accessing resource points, foxes spent most of their time engaged in the relevant foraging behaviour associated with that resource (i.e., scavenging at carcasses, drinking at water, and hunting at rabbit warrens), as well as sniffing and locomoting (Figure 2). There were no major differences in behavioural activity between the three resource types. On average, foxes spent only 12 s on camera, with the longest recorded at 65 s.

The average proportion of time allocated to a behavioural state was independent of the attitude of the fox (i.e., the time did not change whether the behaviour was done confidently or cautiously) (Figure 2). Similar trends were detected across resource points,

although at carcasses, foxes spent a significantly higher amount of time to cautious locomotion than confident (p = 0.022) (Figure 2). Foxes foraging at rabbit warrens (i.e., hunting) were always observed to be in a confident behavioural state, scent marking was also observed exclusively confidently. Descriptively, foxes were much more likely to be detected in a confident, rather than cautious, behavioural state. Confident states at carcasses were engaged in more frequently while investigating (23 times more often), sniffing (8.5 times), locomoting (7.5), and foraging (5.5 times), while confident foraging was engaged in more frequently than cautious foraging at water sources (6.6 times) (Table 4).

Scent marking was most common at carcasses with a rate of one scent mark every 88.5 s, followed by water points at one scent mark every 92.6 s. Scent marking was observed much less frequently at rabbit warrens, with only one scent mark every 9.3 min. Fox scent marking comprised of scat deposition and urination (n = 32), raking (n = 1), and rubbing (n = 1).

Foxes primarily accessed resource points between dusk and dawn (06:00 and 18:00), but they visited each at slightly different times throughout the night, overlapping at 56% (Figure 3). Fox activity at carcasses was concentrated at two peaks, in the early morning (00:00–03:00) and evening (18:00–22:00). Similarly, activity at water sources was most frequent between 03:00 and 06:00 as well as 20:00 and 23:00. Rabbit warren activity was concentrated into a single peak in the evening (19:00–22:00).

Fox social behaviour comprised of two pairs at two carcasses, lasting in total for 5–10 min. Fox pairs spent the highest average proportion of their time sniffing (43%), followed by locomotion (33%) and foraging (27%). During this time, they played (n = 6), greeted one another (n = 5), and scent marked (n = 4).

Figure 1. Behaviours observed in this study and used to classify fox behaviour: (A) confident sniffing and walking, (B) cautious sniffing and walking, (C) confident scavenging, (D) high vigilance, (E) cautious camera investigation, (F) social foraging. See supplementary material 1 for an example of behaviourally scored video.

Table 3. Descriptions of some red fox ethogram modifiers.

Behaviour	Modifiers	Description
Locomotion	A) Type	Walk: Slow quadrupedal movement Run: Fast quadrupedal movement Jump: Vertical or horizontal jump Perch: The lifting of two paws onto an object in order to investigate a resource or object of interest
	B) Attitudinal	Confident: Head not focused on anything in particular, head movements are relaxed, ears are relaxed and kept vertical (unless sound is heard, if so, ears will move directionally), little concern over movement. Tail held high, parallel to the ground, level with the back, may have a kink towards the end pointing upwards Cautious: Head moves erratically, ears pricked forward, cautious paw placement with back feet placed firmly with movement only occurring in front feet, stands with legs close together and bent. Tail positioned closer to the back legs, lower than level with the back, with no kink, shoulders are raised
Sniffing	Attitudinal	Confident: Sniffs are long and pronounced, little concern shown for anything apart from the object being sniffed. Head not focused on anything in particular, head movements are relaxed. Ears relaxed and kept vertical (unless sound is heard, if so, ears will move directionally), little concern over movement. Tail held high, parallel to the ground, level with the back, may have a kink towards the end pointing upwards Cautious: Sniffs are short. Head moves erratically, ears pricked forward, cautious paw placement with back feet placed firmly with movement only occurring in front feet stands with legs close together and bent. Tail positioned closer to the back legs, lower than level with the back, with no kink, shoulders are raised
Vigilance	Intensity	Low: Head is most commonly focused on a single location, can be represented by low to moderate speed head movements, neck is extended, stands with legs close together shoulders are raised. Can be performed standing or sitting quadrupedally. Tail is position is lower than the level the back High: Head raised and moves erratically and quickly, regularly change focal point, neck is heavily extended, ears are pricked forward, stands with legs close together and shoulders are raised. Can be performed standing or sitting quadrupedally. Tail positioned closer to the back legs, lower than level with the back, with no kink
Foraging	A) Type	Scavenging: The investigation of carrion resulting in an individual attempting to or successfully feeding Drinking: The act of utilising either an anthropogenic or natural water resource. Hunting: The act of actively searching for and/or consuming live prey
	B) Attitudinal	Confident: Individual attempting to consume resource makes slow movements, does not jump back after consuming the resource, consumes resource atop or very nearby resource. Ears perched vertical. Tail held high, parallel to the ground, level with the back, may have a kink towards the end pointing upwards Cautious: Individual attempting to consume resource is extremely jumpy, making erratic movements, ears perched forward, neck as elongated as possible to keep the majority of the body as far from resource as possible. Tail positioned closer to the back legs, lower than level with the back, with no kink, shoulders are raised. If possible, fox may take resource away from the resource to consume (most common during scavenging)
	C) Social	Social: The act of foraging with one or more conspecifics

Scent marking	Type	Defecation: The act of squatting or raising a hind leg in order to spray urine or deposit faeces in the environment Raking: The act of dragging or clawing the dirt with paws in order to transfer scent Rubbing: The act of rubbing facial or tail scent glands on objects of interest to transfer scent Social: Scent marking in a group with more than one conspecific
Flight	Type	Startled jump: Quick jump backwards, erratic and quick movement. Limbs move in unison, back is arched during the jump, fox will land behind the point it jumped from Startled flee: Commonly initiated through a quick turn in opposite direction the fox was previously facing, then engaging in very fast running away from a specific location. Foxes head and tail will move erratically during the behaviour
Investigating	Attitudinal	Confident: Body is relaxed, head movements are slow, ears are vertical, shoulders are lower, tail held high, parallel to the ground, level with the back, may have a kink towards the end pointing upwards Cautious: Head movements are slow, individual is not focused on a single point. Ears move directionally, shoulders are raised, tail is positioned towards the back legs
Greeting	Type	Facial: The act of sniffing the face and/or glands of the face of a conspecific Posterior: The act of sniffing the anus, anal glands or genitals of a conspecific Denial: The movement or jumping away from a conspecific after an attempted greeting
Play	Type	Jump: Leaping towards or away from a conspecific in a non-agonistic manner, with random and exaggerated movements Chase: The running or walking after or away from a conspecific in a non-agonistic manner, with random and exaggerated movements
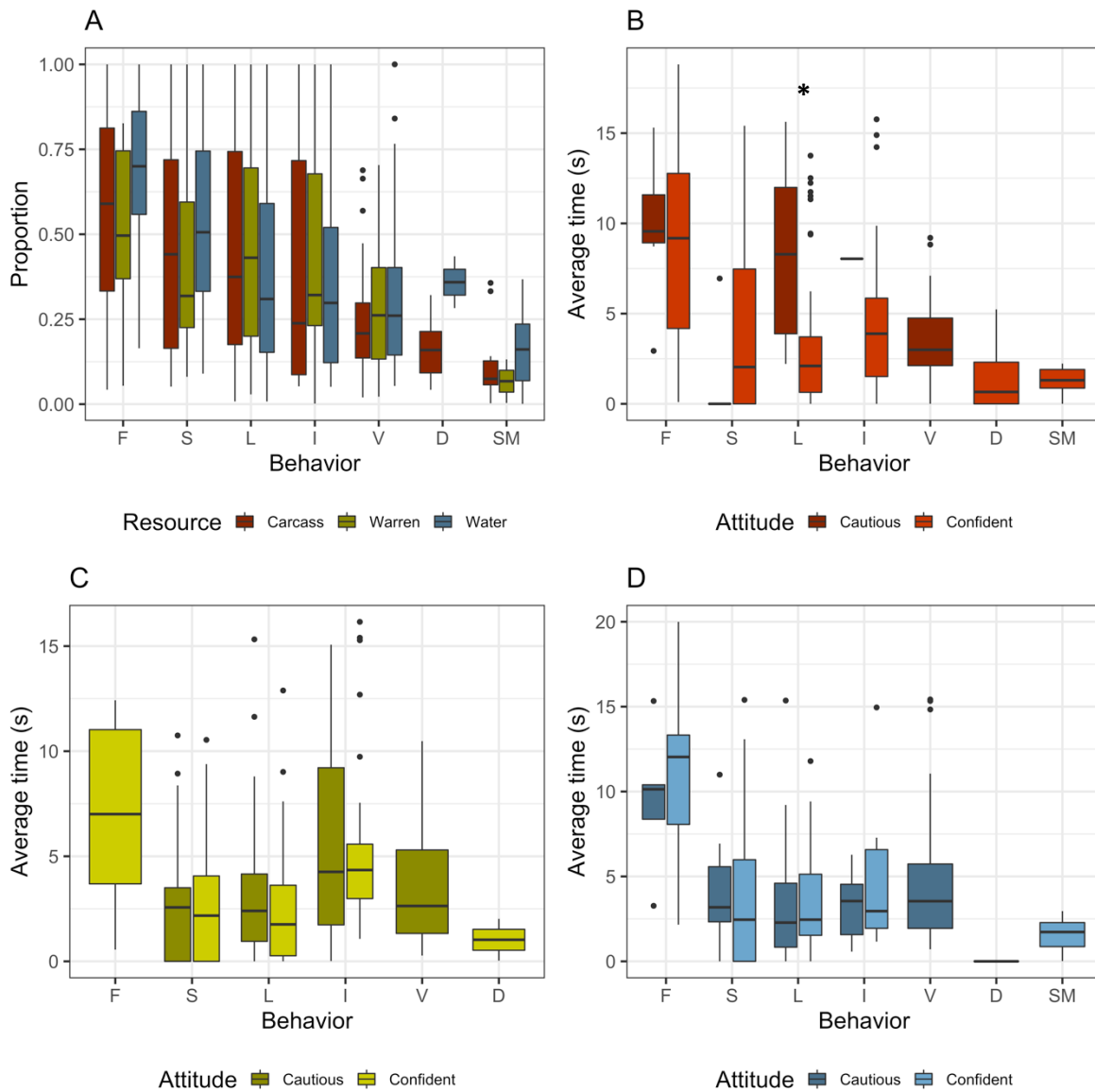
Figure 2. Confidence and cautiousness of red foxes at key resource points share with dingoes. Proportion of time allocated to each behaviour at each resource type (A). The average amount of time allocated to confident and cautious behaviours at carcasses (B), rabbit warrens (C), and water points (D). F = foraging, S = sniffing, L = locomotion, I = investigating, V = vigilance, D = digging, SM = scent marking). Significant difference indicated by an asterisk.
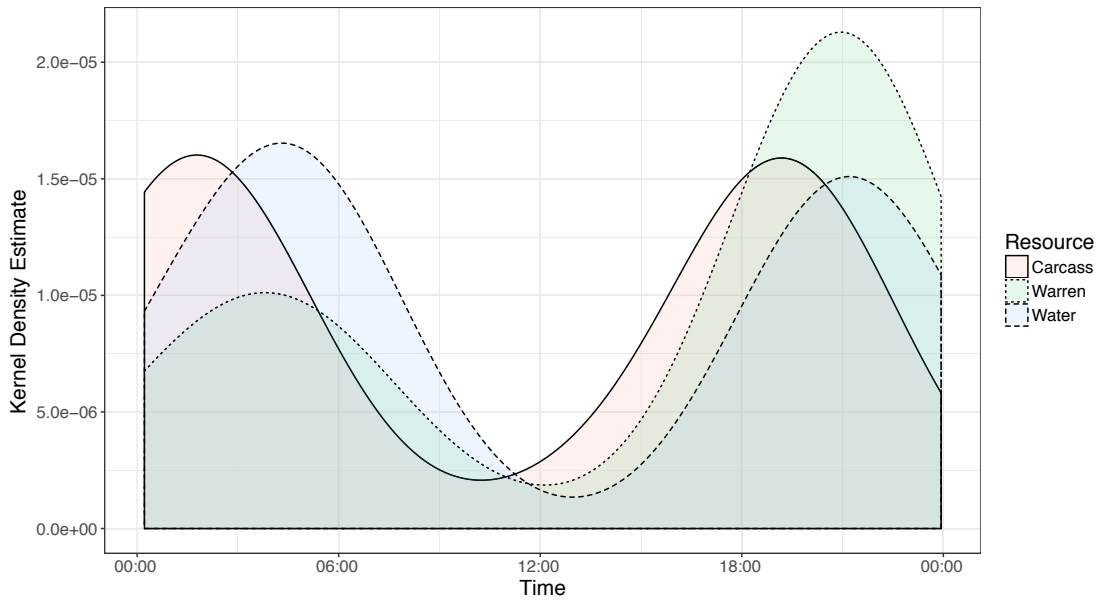
Figure 3. Fox temporal activity patterns at water points, rabbit warrens and carcasses gathered with camera traps in the Painted Desert, South Australia in the winters of 2016–2018. Solid line represents carcass temporal activity patterns, dashed line represents water points and dotted line represents rabbit warrens. Overlap coefficient between the three resource points is 0.56.

Table 4. Descriptive statistics of the time allocated to different behavioural states at the three resource points, depending upon whether the behaviours were expressed cautiously or confidently. Time is represented in seconds (s).

|		Cautious			Confident		
Resource	Behaviour	No.	Total time	Average time	No.	Total time	Average time
Carcass	Digging		0	N/A	7	10.5	1.5
	Foraging	8	80.3	10.0	44	386.6	8.8
	Investigating	1	8.0	8.0	23	112.7	4.9
	Locomotion	8	66.4	8.3	60	191.8	3.2
	Scent Marking		0	N/A	13	16.2	1.2
	Sniffing	6	7.0	1.2	51	218.0	4.3
	Vigilance	30	108.3	3.6		0	N/A
Warren	Foraging		0	N/A	9	65.2	7.2
	Investigating	18	98.2	5.4	34	183.7	5.4
	Locomotion	26	89.3	3.4	67	160.2	2.4
	Scent Marking		0	N/A	2	2.1	1.0
	Sniffing	18	54.7	3.0	32	93.2	2.9
	Vigilance	28	101.7	3.6		0	N/A
Water	Digging		0	N/A	2	0	0
	Foraging	5	47.5	9.5	33	362.3	11.0
	Investigating	15	48.6	3.2	10	46.5	4.7
	Locomotion	42	131.1	3.1	99	316.0	3.2
	Scent Marking		0	N/A	16	25.0	1.6
	Sniffing	15	59.3	4.0	41	145.0	3.5
	Vigilance	55	236.7	4.3		0	N/A
Grand Total		275	1137.1	4.1	543	2335.1	4.3

-

Discussion

Foxes were surprisingly confident at resource points shared with territorial dingo packs, when free from human persecution. We had hypothesised that the threat presented by socially stable dingoes would induce foxes, more often than not, to be "on their toes" when visiting these peaks in the landscape of fear. On the whole, we found that foxes were much more likely to express their behaviours in confident states while at resource points, suggesting that foxes are not living in a state of fear. However, the evidence of cautious

behaviours exhibited by foxes at resource points exemplifies the suppressive effects of apex predators within the landscape of fear, and mirrors behaviours observed in other fox populations coexisting with apex predators around the world (Haswell et al., 2018; Wikenros et al., 2014).

The behaviour of foxes may be influenced by both their own social stability and that of their predators. Social stability in apex predators is a key driver of ecosystem function and has significant ecological flow-on effects (Wallach et al., 2010). The protection of predators and the promotion of their social stability enables coexistence between predators (Wallach et al., 2015c). Cheetahs (*Acinonyx jubatus)* and Spotted hyenas (*Crocuta crocuta*) living in the protected areas of Serengeti National Park, Tanzania, coexist with lions (*Panthera leo*) through "moment-to-moment" temporal avoidance of the apex predator, suggesting that smaller predators have a developed understanding of the spatio-temporal activities of lions and how to behave in order to avoid them (Swanson et al., 2016). We propose the possibility that when a population of apex predators is socially stable, sympatric mesopredators may also be increasingly bold due to the territorial stability of apex predators, potentially reducing the risk involved with spatially avoiding predators.

Although foxes were much more likely to be confident at carcasses, when foxes were locomoting cautiously they did it significantly longer than when they did it confidently. This suggests that when foxes perceive increased risk at carcasses, they alter their behaviour to reduce the threat of encountering a dingo. Cattle carcasses are a valuable resource in

arid ecosystems and dingoes regularly feed upon them (Corbett and Newsome, 1987). The high value of carcasses to dingoes, and the increased caution that foxes exhibit on occasion, may suggest that dingoes are increasingly territorial and defensive of carcasses over other resource points.

Evidence for this is emphasised by dingoes' scent marking all of the carcasses surveyed, a behaviour that indicates ownership and territoriality in large canids (Wallach et al., 2009) . In apparent 'disregard' for dingo territoriality, foxes regularly scent-marked resource points, including on large carcasses and water sources heavily marked and visited by dingoes. Similar observations of foxes marking existing apex predator scats have been observed in Poland, where foxes were observed inspecting scats of lynx and scent-marked over them (Wikenros et al., 2017) . Likewise, grey foxes (*Urocyon cinereoargenteus*) have been observed remarking the scent marks of pumas (*Puma concolor*) (Allen et al., 2016) . The functional benefits of re-marking scats of apex predators can only be speculated on, but it may serve to communicate to both conspecifics and predators. Further research is required to develop a deeper understanding of the role of over marking in the behavioural interactions involving apex and mesopredators.

Observations of fox sociality in the wild are rare because foxes spend large amounts of time alone, however, we observed fox social behaviour at two carcasses. This may be attributed to our study being conducted in the winter, during their mating season (McIntosh, 1963). Pair interactions were comprised of amicable play and greeting,

suggesting the two were either already paired or kin. Play behaviour between pairs at carcasses commonly frequented by dingoes provides further evidence that these foxes were generally at ease in this landscape.

The foxes in this study were most commonly observed at resource points between dusk and dawn, which is consistent with observations that foxes are nocturnal in their native range (Cavallini, 1992; Lucherini et al., 1995). Temporal overlap between the three resource points was relatively low (56%), suggesting that foxes may engage in routines in which they access different resource points at different times of the day.

Considering that dingoes have been shown to have strong suppressive effects on foxes (Brawata and Neeman, 2011; Leo et al., 2015) , why where these foxes much more likely to be confident than cautious around these shared resources? One possibility is that socially stable apex predators are more predictable and therefore less frightening. Foxes may be able to identify, anticipate, and appropriately respond to the risk of dingo predation, therefore reducing the fear of unexpected attacks. Further research could help illuminate the role of social stability in shaping behavioural interactions between two of Australia's most prominent predators.

Acknowledgements

Supplementary material

Table S1. *Negative binomial model results of time spent in each behaviour at different resource points. The response variable was analyzed as proportion of time spent. We report omnibus test results using the function 'Anova' from the package "car" in R version 3.5.3. Post hoc results were calculated with the function 'cld' in the package "emmeans". Given that there was no significance difference between groups, we report only the upper and lower confidence intervals.*

	Omnibus test results			Post-hoc test results	
Behaviour	Chi-squared	df	p	Resource	95% CIs
Locomotion	0.8941	2	0.6395	Water	0.292 –0.550
				Warren	0.335 – 0.686
				Carcass	0.300 – 0.705
Foraging	0.6477	1	0.7234	Water	0.430 – 1.096
				Warren	0.371 – 0.889
				Carcass	0.163 – 1.543
Investigating	0.144	2	0.931	Water	0.179 – 0.833
				Warren	0.262 – 0.716
				Carcass	0.175 – 0.483
Sniffing	0.879	2	0.644	Water	0.351 – 0.835
				Warren	0.247 – 0.702
				Carcass	0.296 – 0.744
Digging	0.256	1	0.613	Water	0.026 – 5.03
				Carcass	0.019 – 1.32
Scent marking	0.209	2	0.900	Water	0.037 – 0.715
				Warren	0.0001 – 44.705
				Carcass	0.016 – 0.811
Vigilance	0.280	2	0.869	Water	0.174 – 0.553
				Warren	0.132 – 0.864
				Carcass	0.103 – 0.595

Chapter 4: Red foxes avoid apex predation without increasing fear

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Abstract

Apex predators structure ecosystems by hunting mesopredators and herbivores. These trophic cascades are driven not only by the number of animals they kill, but also by how prey alter their behaviours to reduce risk. The different levels of risk navigated by prey has been likened to a 'landscape of fear'. In Australia, dingoes are known to suppress red fox populations, driving a trophic cascade. However, most of what we know of this relationship comes from circumstances where predators are persecuted, which can affect their social and trophic interactions. Utilizing camera traps, we monitored fox behaviour when accessing key resource points used by territorial dingoes, in a region where both predators are protected. We predicted that foxes would avoid and be more cautious in

areas of high dingo activity. Indeed, foxes avoided directly encountering dingoes. However, contrary to our expectations, foxes were not more cautious or vigilant where dingo activity was high. In fact, fox activity and scent-marking rates increased where dingo scent-marking was concentrated. Further, foxes were increasingly confident with increasing levels of conspecific activity. Our results suggest that responses to the threat of predation are more complex than fear alone. In socially stable conditions, it is possible that prey may develop knowledge of their predators, facilitating avoidance, and reducing fear.

Introduction

"The fox knows many things"

Attributed to Archilochus (c.680-645 BC), translation

Apex predators affect ecosystems by hunting herbivores and mesopredators, which in turn influences the abundance, behaviour, and ecology of their prey (Ripple et al., 2014). These trophic cascades are understood to be driven not merely by mortality from predation, but by the strategies prey employ to avoid dangerous encounters with predators. This behavioural response has been analogized to a *landscape of fear*, which describes the levels of risk experienced by prey across a landscape (Laundre et al., 2009b). The variation in the spatial and temporal risk imposed by predators is likened to "*peaks*" where the risk of predation is high, and "*valleys*" where it is low. In arid ecosystems, key resources such as water points and large carcasses are often focal

points of apex predator activity (Wallach et al., 2009), and as such function as peaks to be avoided. Access to these resources can be denied by apex predators through harassment (Linnell and Strand, 2000), or through direct predation (Berger and Gese, 2007). However, sharing of resources may be unavoidable for mesopredators where no reasonable alternative exists. Given the risk of visiting resource points frequented by apex predators, mesopredators who need to access them should engage in risk-reduction strategies (Leo et al., 2015; Wikenros et al., 2017), such as reducing the amount of time spent at these sites, visiting at times of lower risk, and remaining vigilant and cautious.

In Australia, dingoes (*Canis dingo*) suppress red foxes (*Vulpes vulpes*) (Wallach et al. 2010). Fewer foxes exist where dingo activity is concentrated, both at large spatial scales (Letnic et al., 2011), and at localized resource points (Brawata and Neeman, 2011). Much of this evidence stems from landscapes where predators are regularly killed by humans (Wallach et al. 2010). Dingoes have been subjected to widespread eradication programs across Australia since European colonization (Philip, 2019), and foxes have been persecuted since their introduction in the 1830's (Rolls, 1923). Persecution disrupts predator ecology (Wallach et al., 2010), sociality and territoriality (Wallach et al., 2009), activity patterns and interactions (Brook et al., 2012), and cooperative behaviour and cultural learning (Greenberg and Holekamp, 2017; Haber, 1996). Destabilizing these trophic and social interactions can lead to increased predation pressure on small mammals from mesopredators and alter vegetation communities by releasing herbivore populations from top-down control (Gordon et al., 2017; Wallach et al., 2010).

Given the systemic and ubiquitous nature of predator persecution in Australia, there have been few opportunities to study the behavioural responses of foxes to dingoes where both predators occur and are socially-stable (Wooster et al., 2019). To address this knowledge gap, information on how foxes navigate resource sharing with dingoes in the absence of human persecution is required, particularly as calls to protect dingoes increase (Letnic et al., 2012; Wallach et al., 2015a). Here we studied the behavioural responses of foxes to dingoes in a unique rangeland environment, where both predators were protected (Wallach et al., 2017). We focused on key resource points used by both predators: water points, carcasses, and rabbit warrens, sites both predicted to be peaks in the landscape of fear and essential for survival for foxes (Brawata and Neeman, 2011; Wallach et al., 2009). Our objective was to understand how foxes navigate sharing vital resources in space and time with a potentially deadly predator and to comprehend how predation risk shapes the behaviour of foxes when populations were free from the destabilizing effects of persecution. We expected that (i) foxes would concentrate their activity at resources with lower dingo activity, that (ii) foxes would limit their visitations to these high-risk resource points to times when dingoes were absent, and that (iii) foxes would exhibit fear and increased vigilance to mitigate risk when doing so.

Methods

Our study was conducted at two conjoined properties in the Painted Desert, South Australia. Evelyn Downs, a 2,300 km2 cattle station, and Mount Willoughby, a 5,600 km2 Indigenous Protected Area, part of which is operated as a cattle station (Wallach et al., 2017) (Figure 1). Predators have been protected on both properties since 2012, however,

prior to the adoption of a wildlife friendly farming approach, predators were regularly and sporadically killed across both properties. The Painted Desert is arid, receiving 160mm annually, and characterised by chenopod shrublands, woodland areas predominated by Acacia species, and ephemeral creek lines supporting Eucalyptus species. Foxes have likely been present in the Painted Desert since the 1940s (Saunders et al., 1995).

In the winters of 2016, 2017, and 2018, we monitored dingoes and foxes visiting 21 water points, 4 cattle carcasses, and 25 rabbit warrens (Supplementary Table 1). At each resource point, we counted the number of dingo scent-marks as a metric of dingo territoriality. Scent-marking is a well-known form of communication for dingoes and other large canids, conferring messages such as territory boundaries, locations, and social and breeding status (Corbett, 1995). As scent-marks also convey information between species, we utilised dingo scent-mark frequency to infer the risk foxes would perceive when accessing each resource point, particularly as dingo scents have been shown to trigger a fear response in foxes (Leo et al., 2015). Scat surveys were conducted in the 20-metre radius surrounding the edge of each water point, carcass, and rabbit warren. Surveys took approximately an hour to complete.

Table 1. Number of resource points monitored across each year. Bracketed numbers represent number of new resource points monitored each year

	Waterpoint	Carcass	Rabbit Warren
2016	10	0	0
2017	18 (10)	2 (2)	17 (17)
2018	10 (1)	2 (2)	8 (8)

To document the activity and behaviour of foxes and dingoes at resources, we deployed Bushnell MKII and Browning Dark Ops Pro camera traps, randomly assigned to each resource point. Depending on the size of the resource point, between 1-3 cameras were deployed to ensure adequate coverage (e.g., 1 for a carcass, 3 for a large dam), and the data was aggregated for analysis. At water points, cameras were aimed at the dominant access points along the water's edge, as determined by trail and scat density, and also at the water. Rabbit warrens had a single camera focusing on what was deemed the main entrance point, this was determined by the size of the entrance hole and concentration of rabbit scats and trail dust emerging from the hole. All monitored warrens had evidence of rabbit activity (e.g., rabbits on camera, fresh scats and tracks). The monitored cattle carcasses had died on site at least a year before our study. Cameras were set to record 15-20 second videos when motion was detected, with a 1-second interval. Fox visitations separated by >5 minutes were considered independent events, which was confirmed by testing for temporal autocorrelation between events, using the 'acf' function in R package 'stats' (version 4.0.2). Over the 1,195 camera-trap nights we recorded 116 fox events (253 detections) and 260 dingo events (1,009 detections).
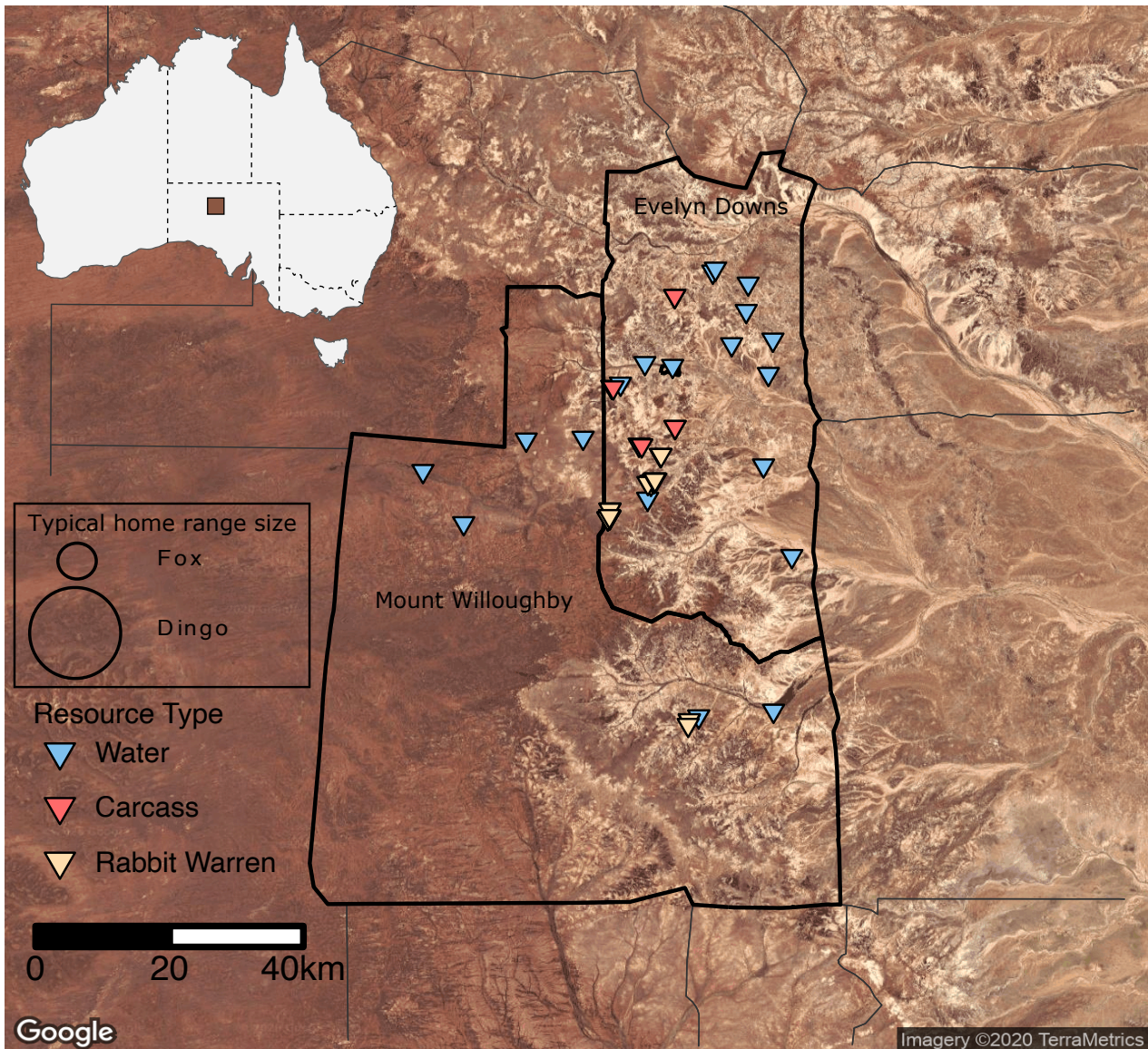
Figure 1. Predator-friendly study site in the Painted Desert, South Australia. Together, Evelyn Downs and Mount Willoughby cover 7,900 km2, which is large enough to contain several dingo territories. Typical home range sizes of dingoes and foxes in arid areas are shown for scale, based on average home ranges: 17 km2 for foxes (Moseby et al., 2009), and 95 km2 for dingoes (Thomson, 1992a). Resource points were a minimum of 5 km from poison baiting.

We calculated the overlap in temporal activity patterns of foxes and dingoes using the 'overlap' package (version 0.3.2) in R (version 3.6.3) (R Core Team, 2018). We estimated

kernel densities to describe the degree of temporal overlap between both species, quantified using the 'Dhat4' overlap statistic as it is considered reliable for estimating activity patterns of species with large sample sizes (>75 captures per species) (Ridout and Linkie, 2009). To calculate the Dhat4 overlap statistic and 95% confidence intervals, we generated 10,000 smoothed bootstrap samples for fox and dingo temporal activity patterns. The 2.5% and 97.5% percentile were adjusted to account for bootstrap bias using the 'basic0' approach. We examined overlap in space at resource points using two-species occupancy models with R package 'wiqid' (version 0.2) (MacKenzie et al., 2004). As foxes and dingoes have relatively large home range sizes (Moseby et al., 2009b), we interpreted the occupancy parameter (psi) as the probability of use to accommodate the lack of independence between our camera traps (MacKenzie et al., 2004). Data were combined where more than one camera was used at a resource point. We tested for spatial overlap between foxes and dingoes by calculating a species interaction factor (SIF) (Richmond et al., 2010) (Supplementary Table 2). Where SIF = 1, foxes and dingoes operate independently of one another; where SIF > 1, foxes aggregate with dingoes; and where SIF < 1 foxes avoid dingoes.

Fine-scale spatio-temporal patterns of overlap were then examined by creating a matrix of the number of camera trap events at each resource point, summarized by each hour excluding date. This matrix was then used to calculate the proportion of time both species were detected exclusively or where they co-occurred for any hourly period in space-time (Karanth et al., 2017). We used Chi-square goodness-of-fit tests to examine whether foxes avoided dingoes in space and time more than one would expect by chance.

To assess behavioural responses of foxes to dingoes, we measured their confidence and cautiousness, as well as their scent-marking and vigilance behaviour, in relation to dingo activity from camera trap videos and territoriality from field scat surveys. The proportion of time that foxes exhibited either confidence or cautiousness and vigilance was calculated for each event, determined by the fox's torso, leg and tail positioning and movement patterns. Following Wooster et al. (2019), confidence was primarily scored by a tail position above or level with the foxes back and their body positioned well above the ground with legs extended, while cautiousness was classified through a tail positioned below the back or between its legs and the fox in a crouched body position with its legs bent and stomach close to the ground. Vigilance was classified by the foxes eyes being directed away from the ground or focal point (i.e. resource point), the top of the head above the level of their shoulders and the neck being held above horizontal. Behaviour was scored using Behavioural Observation Research Interactive Software version 7.9.15 (Friard and Gamba, 2016). Average daily activity rates were calculated from the number of fox or dingo events recorded at each resource point divided by the number of trap nights. We estimated the temporal risk perceived by foxes when accessing resource points based on kernel density estimates used to calculate temporal overlap. We considered 7:00-10:00AM and 16:00-20:00PM high-risk hours for foxes (Figure 2).

We compared the influence of dingo activity and territoriality (scent-marks), as well as conspecific activity, on the confidence and cautiousness of foxes using generalized linear models (GLMs). We ran models for fox confidence, cautiousness, vigilance, activity rate, and scent-marking as the dependent variables, with the following as predictor variables:

number of dingo scent-marks counted in scat surveys, dingo activity rate, dingo temporal activity, and fox activity rate. The latter was excluded when used as a dependent variable. All predictor variables were standardized. GLMs of fox confidence, cautiousness and vigilance were modelled using a Quasibinomial distribution, fox scent-marking using a binomial distribution, and daily fox activity rate using a quasipoisson distribution. GLMs were constructed in R.

Results

Foxes concentrated their activity at resource points with the lowest dingo activity, creating spatial segregation between the two predators (2016 - SIF=0.12; 2017 - SIF=0.67; 2018 - SIF=0.83). Foxes also avoided dingoes temporally, creating low temporal overlap ($\Delta 4 \pm$ 95% CI = 0.43, ±0.39-0.47). As expected, foxes were primarily nocturnal and dingoes primarily diurnal (Figure 2). Temporal segregation was highest at carcasses ($\Delta 4 = 0.17$, ±0.13-0.23), followed by water points ($\Delta 4 = 0.51$, ±0.46-0.57), and rabbit warrens ($\Delta 4 = 0.59$, ±0.38-0.78). Foxes avoided dingoes in space and time (combined) at all resource points ($\chi^2 = 93.32$, $p =$ <0.001, df = 2). Spatiotemporal avoidance was clear at warrens and waterpoints ($\chi^2 = 37.44$, $p =$ <0.001, df = 2), but not at carcasses ($\chi^2 = 5.57$, $p = 0.061$, df = 2) (Figure 3).
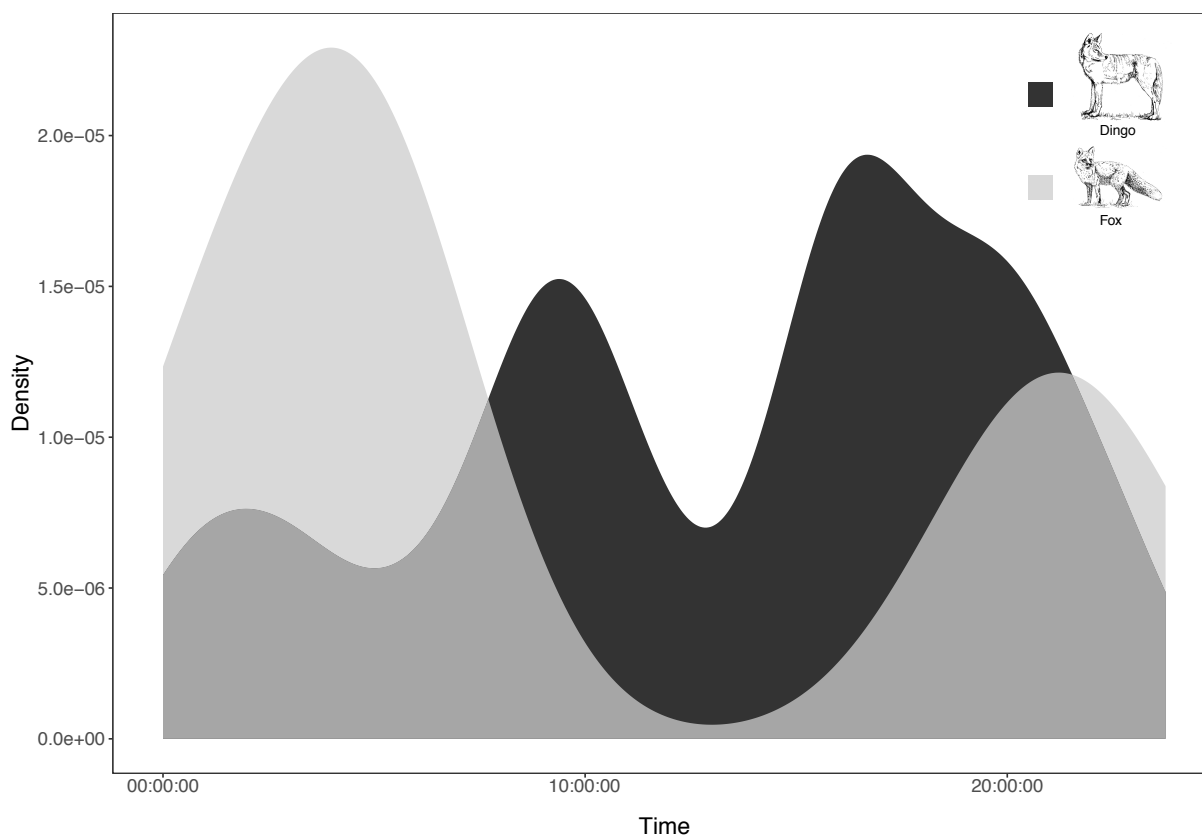
Figure 2. Fox and dingo temporal activity patterns at resource points. The Δ4 temporal overlap coefficient was 0.43 (±95% CI: 0.39-0.47).

Table 2. Output from generalized linear mixed effects model examining the effect of dingo and conspecific predictor variables on fox cautious behaviour. Model was constructed using the 'glmer' function within the R package 'lme4'. Asterisks denote significance (p < 0.05).

Parameter	Estimate	95% CI	SE	Test Statistic	p
Intercept	-0.585	-1.828 - 0.484	0.50098	-1.169	0.2422
Dingo scent-marking	1.463	-1.828 - 0.484	1.15923	1.262	0.2071
Time risk	-0.146	-1.89 - 1.040	0.66999	-0.219	0.8270
Dingo daily activity	0.0301	-1.565 - 1.558	0.66800	0.046	0.9631
Daily fox activity	-3.004	-7.408 -0.488	1.30729	-2.298	0.0216 *

In contrast with our expectations, foxes were not more cautious nor more vigilant where dingo activity was high. Neither dingo activity rates nor scent-marking influenced fox cautiousness (dingo activity: df = 92, p = 0.963, dingo scent-marking: df = 92 p = 0.207) (Figures 4a, 4b, Table 2) or vigilance (dingo activity: df = 92, p = 0.908, dingo scent-

marking: df = 92, p = 0.867) (Figures 4c, 4d, Supplementary table 2). Additionally, fox daily activity rates (df = 92, p = <0.001) increased at resource points with dingo scent-marking (Figure 5b), but not with dingo daily activity (df = 92, p = 0.983). Foxes were more likely to scent-mark where dingo scent-marking was concentrated (df = 19, p = <0.001, Supplementary table 3). Foxes were more confident at resource points where conspecific activity was highest (df = 92, p = 0.022) (Figure 5a).
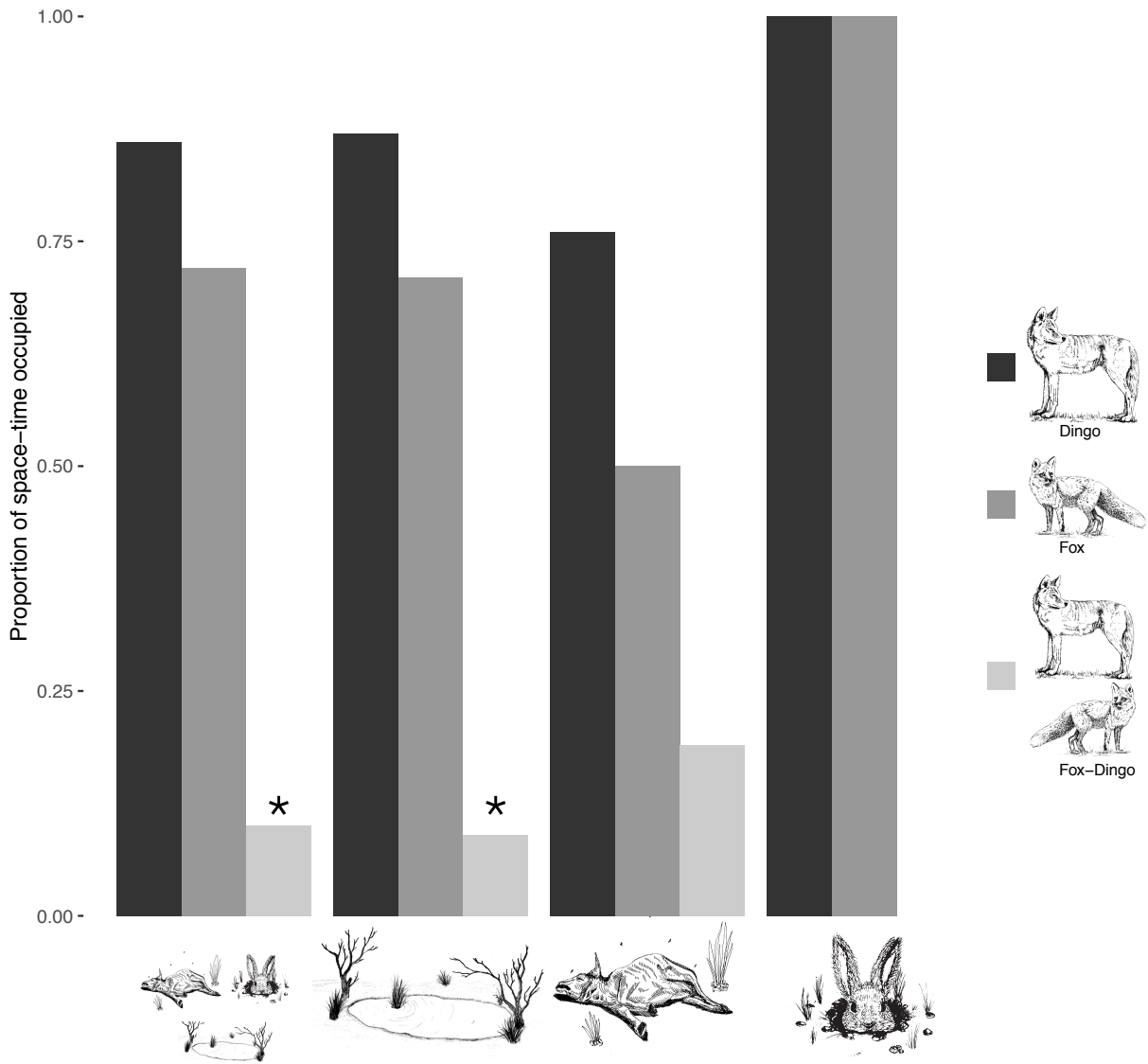
Figure 3. Proportions of space and time divided into hour-long bins, where predators were exclusively present at resource points or where they overlapped. X-axis indicates resource type: across all, water points, carcasses, and rabbit warrens. Asterisks denote significance (p < 0.05).

Figure 4. Predicted relationships from generalized linear mixed models comparing: **(a)** the proportion of time foxes were cautious to daily dingo activity rate at resource points; **(b)** the proportion of time foxes were cautious to number of dingo scent-marks counted in surveys across resource points; **(c)** the proportion of time foxes were vigilant to daily dingo activity rate at resource points; and **(d)** the proportion of time foxes were vigilant to number of dingo scent-marks counted in surveys across resource points. Grey bands represent 95% confidence intervals. All dingo and fox activity metrics were normalized to be between zero and one. Cautious models can be found in table 2, vigilance models can be found in Supplementary table 2.
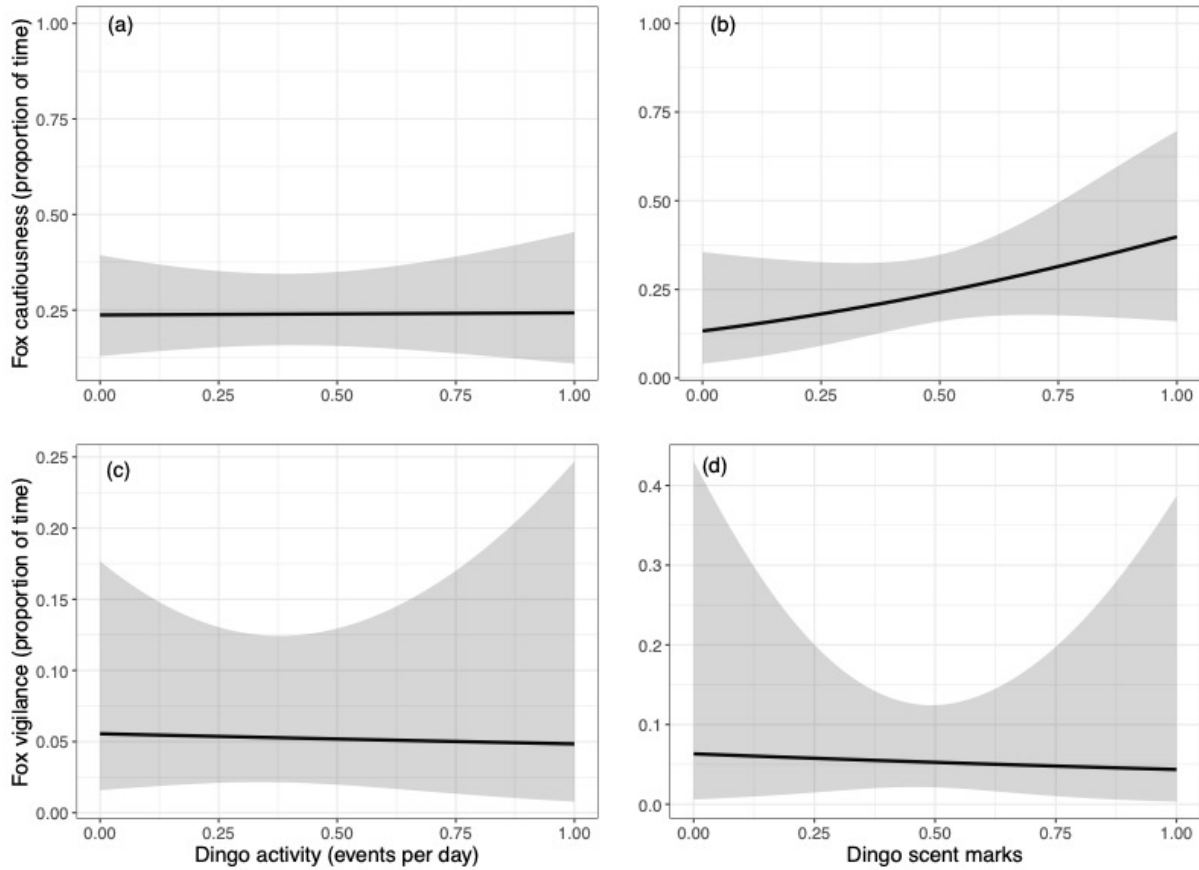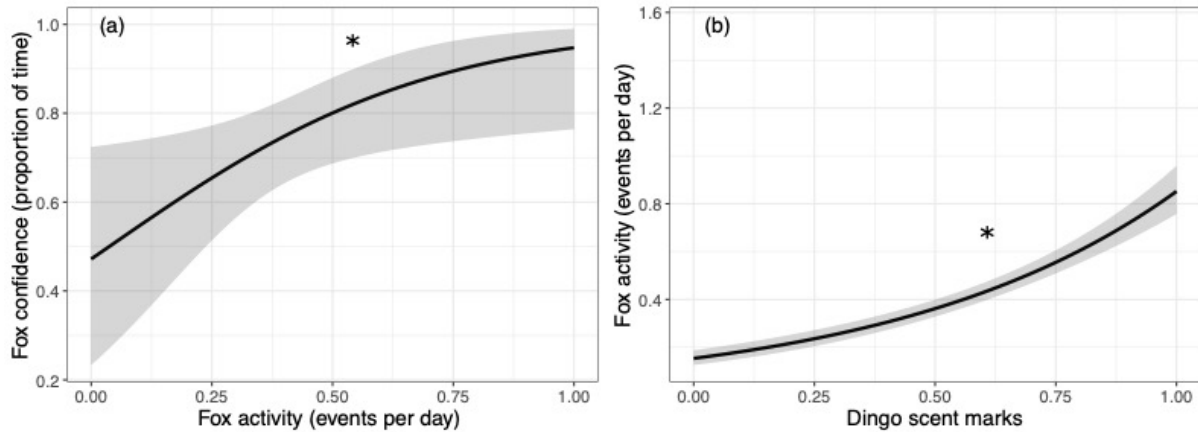
Figure 5. Predicted relationships from generalized linear mixed models comparing: **(a)** the proportion of time foxes were confident to the daily activity rate of foxes at resource points; and **(b)** daily activity rate of foxes to number of dingo scent-marks counted in surveys across resource points. Grey bands represent 95% confidence intervals. Asterisks denote significance ($p < 0.05$).

Discussion

The landscape of fear predicts that foxes should avoid areas and times where dingoes are most active (Laundre et al., 2009b; Letnic et al., 2011). Our results support this prediction, and align with observations of mesopredators avoiding apex predators in space and time (Karanth et al., 2017; Swanson et al., 2016). Foxes were also predicted to behave cautiously (fearfully) in places of higher risk. But we did not find evidence that foxes were fearful when visiting 'peaks' in the landscape of fear. While we did not directly manipulate predator cues (e.g. scent placement), we did not find evidence that foxes were fearful where dingo scent-marking or activity was highest. Instead, foxes were more active and more likely to scent-mark at resource points where dingo scent-marking was

concentrated. We do not dispute that foxes are fearful of encountering dingoes and wolves (Leo et al., 2015; Wikenros et al., 2017). Instead, a plausible explanation is that the activity patterns of socially-stable dingoes are more predictable (Brook et al., 2012; Wallach et al., 2009), and thus foxes can develop the necessary knowledge to reduce risky encounters and thus confidently avoid them in the heart of their territories.

Foxes were more confident at resource points with high levels of conspecific activity, suggesting a level of comfort at locations they frequent, or at least knowledge that resource points are safe during their visits. Our results align with observations of coyotes (*C. latrans*) and foxes coexisting with little fear or aggression, even during direct encounters (Mueller et al., 2018). While it is likely that fear may play a role in the interactions between socially stable predators, our results suggest that interactions are motivated by more complex mental states than fear alone.

There is good evidence for this. The decisions animals make are driven by more than singular impulses like fear and hunger (Gallagher et al., 2017). Many animals possess complex cognitive maps of terrain, food resources, their society, and of individuals of other species (Bshary et al., 2006; Couzin et al., 2005; Minta et al., 1992; Toledo et al., 2020). As sentient and sapient beings, they possess the capability to develop knowledge of their ecological communities. However, this knowledge has not yet been fully incorporated into mechanisms developed to explain emergent ecological processes, such as trophic cascades.

Accounting for the cognitive capacities of individuals has aided behavioural ecology research. For example, the study of predator social systems has uncovered the pivotal role social and cultural learning plays in raising young in gray wolves (*C. lupus*) (Haber, 1977); intraspecific cooperative hunting strategies of many carnivore species (Wallach et al., 2015b); interspecific cooperative hunting between coyotes and badgers (*Taxidea taxus*) (Minta, Minta & Lott 1992); and that human persecution alters the development of personalities in juvenile hyenas (*Crocuta crocuta*) (Greenberg and Holekamp, 2017). Incorporating key tenets of animal cognition research, like knowledge, cultural and social learning, memory, and innovation (Barrett et al., 2019), into ecological science may further elucidate ecological processes and help us better understand how predators and prey coexist.

Our results highlight the inherent complexity that comes with understanding ecological processes that involve highly cognitive beings. We found that where predators are protected from human persecution, foxes responded to the threat posed by socially-stable dingoes with spatiotemporal avoidance, rather than fear. While our research did not compare areas of protection to those of persecution, we suggest that where predators are protected and stable, interactions may be driven by knowledge, rather than just fear. Rather than a landscape of fear, perhaps, a *landscape of knowledge*.

Acknowledgements

Supplementary Material

Table S1. List of Parameters, equations and model run, and their descriptions used in two species occupancy modelling in this study

psiA–probability of occupancy of species A

psiBa–probability of occupancy of species B if A is absent

psiBA–probability of occupancy of B if A is present

pA–probability of detection of species A if B is absent

rA–probability of detection of species A if both are present

pB–probability of detection of species B if A is absent

rBa–probability of detection of species B if both are present but A was not detected

rBA–probability of detection of species B if both are present and A was detected

$$\varphi = \frac{\psi^A \psi^{BA}}{\psi^A \left(\psi^A \psi^{BA} + (1 - \psi^A) \psi^{Ba} \right)}$$

Richmond et al. 2010's equation for species interaction factor, describes the degree of spatio-temporal interaction between two species.

Supplementary Table 2. Output from generalized linear mixed effects model examining the effect of dingo and conspecific predictor variables on fox vigilance behaviour. Model was constructed using the 'glmer' function within the R package 'lme4'. Asterisks denote significance (p < 0.05).

Parameter	Estimate	SE	Test Statistic	p
Intercept	-3.040	0.9597	-3.171	0.00152*
Dingo scent-marking	-0.3937	2.3564	-0.167	0.86732
Time risk	-0.4815	1.0613	0.454	0.65004
Dingo daily activity	-0.1454	1.268	-0.115	0.90836
Daily fox activity	0.7068	2.5176	0.281	0.77890

Supplementary Table 3. Output from generalized linear mixed effects model examining the relationship between daily fox activity and dingo scent marks. Model was constructed using the 'glmer' function within the R package 'lme4'. Asterisks denote significance (p < 0.05).

Parameter	Estimate	SE	Test Statistic	p
Intercept	-1.8733	0.3727	-5.026	>0.0001 ***
Dingo scent-marking	1.7131	0.4897	3.498	0.000468 ***

Chapter 5: Predator protections dampens the landscape of fear

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Abstract

Apex predators structure ecosystems by hunting mesopredators and herbivores. Their ecological influence is determined not only by the number of animals they kill, but also by how prey alter their behaviours to reduce risk. The spatial and temporal risk predators create has been likened to a 'landscape of fear', which predicts that prey will be more wary under higher predation risk. In Australia, dingoes hunt red foxes and suppress their populations, but both predators are also subjected to intense eradication programs. It is, therefore, likely that the risk dingoes pose to foxes and the behaviours foxes adopt to avoid dingoes are influenced by human management programs. However, how human management shapes the interactions between these two predators remains unknown. In light of this, we studied the behaviour and spatio-temporal activity patterns of foxes from sites where both predators were either protected (predator friendly) or persecuted

(predator persecuted), and where dingoes were absent and foxes remained but were persecuted (dingo eradicated). According to the 'landscape of fear', foxes should be most cautious where dingo populations have the strongest ecological effects (predator friendly) and should be able to act unhindered where dingoes were absent (dingo eradicated). Fox occupancy was highest at dingo-eradicated sites. At predator-friendly sites, foxes avoided areas at times of heightened dingo activity, however, this avoidance was less evident at predator-persecuted sites. Contrary to predictions, foxes were least cautious at predator-friendly sites and were the most cautious at predator-persecuted sites. Likewise, the frequency of fox social interactions and their overall confidence were highest at predator-friendly sites. Our findings suggest that in the absence of persecution, mesopredators living with socially-stable apex predators can anticipate and avoid risk, reducing the need for constant vigilance (i.e., fear). Consistency of predator activity patterns may thus dampen landscapes of fear.

Keywords: behavioural ecology, introduced species, landscape of fear, predator interactions, trophic cascades.

Introduction

Apex predators drive trophic cascades by hunting herbivores and mesopredators (Ripple et al., 2014). Prey respond to predation risk by altering their behaviour to better detect and avoid predators (Suraci et al., 2016). Predation risk varies across space and time, creating a 'topography' of risk analogised as a *landscape of fear*, where 'peaks' are risky and 'valleys' are safe (Laundré et al., 2014). The landscape of fear has provided important insights into understanding how predators influence their prey (Brown et al., 1999; Lima and Bednekoff, 1999) and how these effects cascade throughout ecosystems (Kohl et al., 2018; Laundré et al., 2001). However, recent studies have suggested that the influence apex predators have on mesopredators may not be entirely explained solely by fear (Karanth et al., 2017; Lundgren et al., 2021; Mueller et al., 2018; Swanson et al., 2016; Wooster et al., 2021).

For many apex predators, the manner in which they influence their prey depends on the functioning and structure of their social systems (Wallach et al., 2015b). Predator social structures allow for cooperation, thus facilitating hunting of large and difficult prey and for defending territory. Many canids form family groups ('packs') comprised of a breeding pair and one or more generations of adult offspring, whom together cooperate to raise and educate young as well as cooperatively hunting prey (Wallach et al., 2015b). Persecution by humans fractures these social structures with implications for their ability to maintain ecological processes and regulation of subordinate canid species (Haber, 1996; Ripple et al., 2014). Persecuted predators tend to have a higher proportion of juveniles and breeding pairs (e.g., Haber 1977) while also disrupting knowledge pathways for learning

as the ability to cooperatively raise young and hunt are reduced (e.g., Haber 1996). The fracturing of predator social groups can dampen their suppressive effect on prey (Wallach et al., 2010), flattening the topography of the landscape of fear, with consequences for activity patterns, predation rates (Brook et al., 2012), and the vigilance and foraging of mesopredators and prey (Laundré et al., 2001). The outstanding question is whether fear alone is a sufficiently nuanced state to enable mesopredators to navigate predation risk in socially disrupted or socially stable environmental settings.

To address this, we examined the behaviour and responses of red foxes (*Vulpes vulpes*) to predation risk from dingoes (*Canis dingo*) at sites that varied in how predators were treated by humans. Dingoes are mainland Australia's only mammalian apex predator (Wallach et al., 2015b). They structure ecosystems by suppressing populations of mesopredators and herbivores, a cascading ecological effect that is weakened when they are persecuted and their social structures fragmented (Wallach et al., 2010). Similarly, red fox populations are also persecuted by people but are also actively suppressed by dingoes (Letnic et al., 2011). If fear is the primary driver of these intraguild interactions, the landscape of fear predicts that foxes should avoid interactions with dingoes and be more cautious where dingoes are present and their social structures stable (i.e., they are protected). There is evidence for this, as foxes have been observed to avoid dingoes where both are protected (Wooster *et al.* 2021) and to reduce their foraging in response to the scent of dingoes, even when they are persecuted (Leo et al., 2015). However, contrasting evidence suggests that foxes can achieve avoidance of dingoes at protected

sites without becoming fearful (Wooster *et al.* 2021), implying that foxes may be relying on a wider set of cognitive abilities to navigate predation risk.

Here we observed foxes and dingoes at sites where they were protected by humans (predator friendly), where they were both persecuted (predator persecuted), and at sites where foxes were persecuted, and dingoes had been eradicated (dingo eradicated). We tested the following predictions made under the landscape of fear hypothesis: (1) that foxes would be detected most often at dingo-eradicated sites; (2) that foxes would avoid dingoes in space and time, particularly at predator-friendly sites; and (3) that foxes would be most cautious at predator-friendly sites. Our goal was to examine the extent to which intraguild relationships and behavioural responses were explained by the landscape of fear, and whether deviances, if any, could be consistently related to human treatment conditions.

Methods

We recorded fox activity patterns and behaviours relative to dingo presence and activity across five sites in east and central Australia that differed in human treatment of predators and in environmental conditions. Two sites where foxes and dingoes were protected were defined as 'predator friendly' (Painted Desert, South Australia; and St. George, Queensland); one site where foxes and dingoes were persecuted was defined as 'predator persecuted' (Capertee National Park, New South Wales); and two sites where foxes were persecuted, but dingoes were absent, were defined as 'dingo eradicated' (Cobar and Bathurst, New South Wales). Dingo absence was determined by their

absence from camera trap images, however, it is possible they were still present in densities too low to be detected on the cameras. We were unable to locate a site where dingoes are absent, and foxes are protected.

The Painted Desert site consisted of two conjoined properties, Evelyn Downs, a 2,300 km^2 cattle station and Mount Willoughby a 5,600 km^2 indigenous protected site, part of which is a cattle station. The site is characterised by sparse chenopod shrublands, and acacia and eucalyptus woodlands. Predators have been protected on both properties since 2012. Prior to this, predators were regularly killed across both properties (Wallach et al., 2017). The site receives 160 mm of rainfall annually. The Painted Desert was considered to have low cover for foxes given its sparse vegetation.

Mourachan is a 1,180 km^2 privately-owned conservation property, located within the Brigalow Belt. The property is owned and managed by Australia Zoo and predators have been protected for over 20 years. The Brigalow Belt receives 590 mm of rain annually. The site is densely vegetated with a mix of eucalypt and corymbia woodland and a mixed shrub and grass understory. Capertee National Park is located within the Sydney basin bioregion and receives 677mm of rain annually. The site is characterised by densely vegetated woodlands, dominated by eucalypt and angophora species. Given the dense vegetation, Capertee National Park provides excellent cover for foxes. Predators have been subject to long term persecution within Capertee National Park through 1080 I baiting and shooting programs.

Cobar has a mix of sheep farming properties located in central New South Wales. The site is categorised by sparse poplar box woodlands, mulga communities, white cypress pine and an absence of a dense understory, providing low cover for foxes. The site receives 267mm of rain annually. Predators are regularly shot and poison-baited. Finally, our Bathurst site in south-eastern New South Wales consists of nature reserves and private agricultural properties. With diverse vegetation communities, including pasture and densely vegetated woodlands dominated by several eucalyptus and casuarina species, Bathurst provides good cover for foxes. Bathurst receives 555mm of rain annually. The region is subject to sustained and intensive predator shooting and poison-baiting. More site detail can be found in supplementary table 1.

We monitored foxes and dingoes using infrared motion sensing cameras (Bushnell MKII and Browning Dark Ops Pro) set between 2-10km apart. Cameras were established in hotspots of predator activity, and thus peaks in the landscape of fear (Wooster et al., 2021) such as waterpoints, livestock carcasses, and rabbit warrens. At two sites this proved ineffective at detecting predators, so cameras were set in areas of high prey activity as determined by prey movement pathways through vegetation and abundance of prey scats in addition to resource points. Data were collected in winter, except for Mourachan, where data were collected year-round due to low fox densities. We deployed 20-50 cameras at each site and gathered 804-5,541 camera trap nights per site. Fox visitations separated by >5 minutes were considered independent events. We confirmed their independence by testing for temporal autocorrelation between events, using the 'acf'

function in R package 'stats' (version 4.0.2). Across all sites, we collected 1,974 fox and 3,174 dingo records from 13,174 camera trap nights over five years.

We explored occupancy patterns of foxes and dingoes at each site by running single species occupancy models. Given the large home ranges of foxes (Moseby et al., 2009a) and dingoes (Thomson, 1992), we interpreted the occupancy parameter (psi) as the 'probability of use' to accommodate for the potential lack of independence between our camera traps (MacKenzie et al., 2004). All single species occupancy models were constructed with R (v3.6.3) package 'wiqid' (version 0.2). To correct for unequal sampling efforts across sites, which could bias occupancy estimates, we generated 100 weekly occupancy models for each site, across the entire study period. Start dates of weekly models were randomly selected. We then took the 100 occupancy models generated for each site and ran generalised linear mixed models (GLMM) with the "glmer" function in the R package "lme4" (Version 1.1-26). Tukeys post hoc comparison between fixed effects were performed using the 'glht' function within R package 'multcomp' (version 1.4). We explored the relationships between fox and dingo detection, treatment by humans, and amount of cover available for foxes (not explored for dingoes), as determined by vegetative cover. As occupancy probabilities range between 0-1, we modelled occupancy data with a binomial distribution.

We compared site differences in spatial overlap between foxes and dingoes using two species occupancy models (MacKenzie et al., 2004). All models were constructed using the R package "wiqid" (version 0.2). As per the single species occupancy models, we

interpreted the occupancy parameter (psi) as the probability of use given the large home range sizes of the two predators. After constructing the two species models, we tested the level of spatial overlap between foxes and dingoes by calculating the species interaction factor (SIF) (Richmond et al., 2010), where SIF = 1 infers foxes and dingoes occupy space independently of one another, SIF > 1 infers foxes are attracted to locations where dingoes activity is concentrated, while SIF < 1 infers that foxes are avoiding locations of dingo activity. We did not run occupancy models for dingoes, or two species models, at dingo-eradicated sites.

We then compared site differences in the temporal patterns of foxes and dingoes using the overlap (v0.3.3) and circular packages (v0.4-93) in R. Because the sites covered a wide longitudinal range, we converted clock time to sun time to relativise detection times to sunrise and sunset based on the date of the record and the geographic coordinates of each camera. We also corrected for potential bias in estimates pooled from sites with different sampling effort and fox detections by resampling our data over 1,000 bootstraps, sampling equally between each context and site. Following Lundgren et al. (2021), we then selected 25% of detections within our contextual categories (human treatment of predators or vegetative cover) with the least detections, using this quantity to sample equally from each category. Within these subsets, we calculated fox and dingo temporal activity patterns with a circular von Mises density distribution kernel (Ridout and Linkie, 2009) and calculated 95% confidence intervals (CIs), enabling significance testing of activity patterns of foxes between sites. Fox temporal activity patterns were compared to dingoes to explore temporal segregation between the two predators among sites, fox

activity patterns were compared across sites to explore changes in temporal activity. Cover availability did not significantly influence the temporal activity patterns of foxes (Figure S1).

We then scored the level of fear in foxes in each image or video. Cautious and vigilant behaviours were categorized following Wooster et al. (2019). Cautious behaviour was scored when foxes positioned their tail below their back or between their legs, and when they had a crouched body position with legs bent and stomach close to the ground (Fox, 1971; Way et al., 2006). Vigilance was identified by the fox's eyes being directed away from the ground or focal point (i.e., resource point), the top of their head above the level of their shoulders, and their neck being held above horizontal. We aggregated cautious and vigilant behavioural states (defined as 'cautiousness'), to represent the state of fear (Laundre et al., 2009b). We also scored fox confidence, again following Wooster et al. (2019). Confidence is a common behaviour metric that has been previously used to measure the level of comfort in canids (Fox, 1971; Way et al., 2006). Confidence was scored by a tail position above or level with the foxes back and a body positions well above the ground with legs extended. Within our study, confidence represents the absence of fear (Lundgren et al., 2021; Wooster et al., 2021). Furthermore, we used observations of foxes being social and scent marking to test whether these behaviours varied among sites. Social behaviour was recorded when more than one fox was observed at the same time, while scent-marking behaviour was defined as a fox defecating or urinating.

We modelled differences in the behaviour of foxes among sites using GLMMs. We analysed how the treatment of predators, cover availability, and camera location influenced fox behaviour, as measured by the proportion of cautious and confident behaviour per event and the number of social or scent-marking events observed. To account for inter-site variability, site was included as a random effect in all models. GLMMs of fox cautiousness and confidence were modelled using a binomial distribution, while social and scent-marking behaviours were modelled using a Poisson distribution in the R package "lme4" (Version 1.1-26).

Results

Fox occupancy ($\psi \pm 95$ % CI = 0.65 ± 0.061) was highest at dingo-eradicated sites compared to predator-friendly ($\psi \pm 95$ % CI = 0.40 ± 0.075; χ^2 = -7.766, df = 494, p = <0.001, Figure 1A) and predator-persecuted sites ($\psi \pm 95$ % CI = 0.47 ± 0.051; χ^2 = -6.420, df = 494, p = <0.001). Fox occupancy rates were similar at predator-friendly and predator-persecuted sites (χ^2 = 0.089, df = 494, p = 0.996). Dingo occupancy rates were similar between predator-friendly ($\psi \pm 95$ % CI = 0.59 ± 0.068) and predator-persecuted sites ($\psi \pm 95$ % CI = 0.55 ± 0.098; χ^2 = 0.801, df = 297, p = 0.423, Figure 1B). Foxes avoided locations of high dingo activity more strongly at predator-friendly sites (SIF = 0.45) than at the predator-persecuted site (SIF = 0.65). The availability of cover did not influence the likelihood of fox detection (χ^2 = -0.154, df = 494, p = 0.878). Camera location had no effect on the likelihood of fox (χ^2 = -0.664, df = 494 p = 0.142) or dingo detection (χ^2 = 0.801, df = 297, p = 0.423).
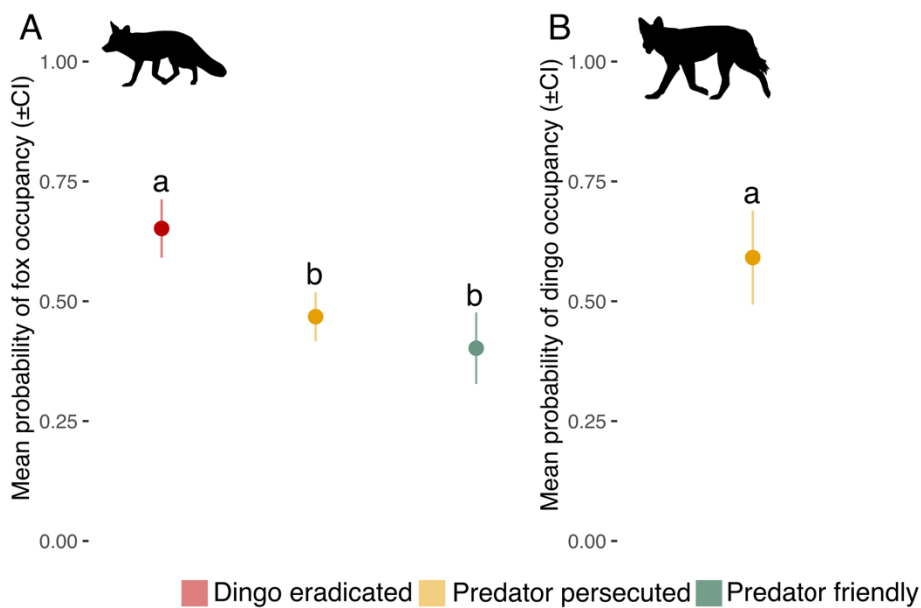
Figure 1. Comparison of fox and dingo weekly occupancy at sites with differing treatments of predators. The probability of (A) foxes and (B) dingoes being present at a camera station (occupancy) at sites of differing treatments of predators. Points and their error bars represent the mean probability of occupancy from weekly bootstrapped single species occupancy models and the 95% confidence intervals. Letters indicate significance groupings.

Fox cautiousness was lowest at predator-friendly sites compared to the predator-persecuted (χ^2 = -4.37, df = 631, p = <0.001) and dingo-eradicated sites (χ^2 = -4.43, df = 631, p = <0.001) where cautiousness was observed twice as often (Figure 2A, Table S2). Confidence was observed more than twice as often at predator-friendly sites compared to predator-persecuted sites (χ^2 = 3.58, df = 630, p = <0.001) and dingo-eradicated sites (χ^2 = 3.78, df = 630, p = <0.001, Figure 2B, Table S2). Fox social interactions were observed more than three times as often at predator-friendly sites than at predator-

persecuted (χ^2 = 2.719, df = 72, p = 0.02) and dingo-eradicated sites (χ^2 = 3.416, df= 72, p = 0.002, Figure 2C). Fox scent-marking rates were similar between predator-friendly and predator-persecuted sites (χ^2 = 2.109, df = 48, p = 0.055, Figure 2D); scent-marking was not observed at dingo-eradicated sites. Foxes were more likely to scent mark at sites where vegetative cover was low (χ^2 = 3.095, df = 48, p = 0.02). Neither the amount of cover available nor camera location had any significant influence on the cautious (cover: χ^2 = -1.450, df = 631, p = 0.15; camera: χ^2 = 0.961, df = 631, p = 0.336) confident, (cover: χ^2 = 1.367, df = 630, p = 0.172; camera: χ^2 = -1.003, df = 630, p = 0.316) or social behaviour of foxes (cover: χ^2 = 0.371, df = 83, p = 0.79; camera: χ^2 = 0.933, df = 83, p = 0.35).
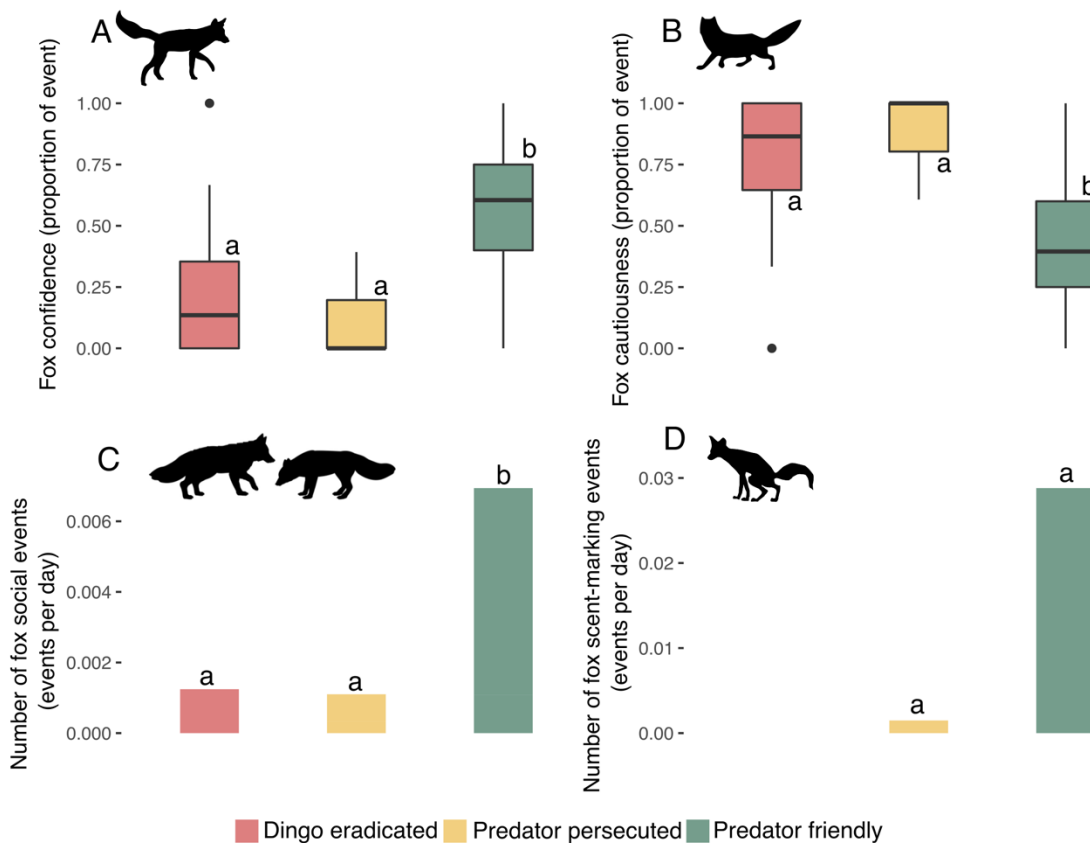
Figure 2. Comparisons of fox behaviour at sites with differing treatments of predators. The proportion of fox events classified as confident (A) and cautious (B). The frequency (events per day) of fox social (C) and scent-marking behaviour (D). Letters indicate significance groupings.

Fox-dingo temporal interactions differed between sites of varying predator protection status. Temporal overlap was lower at predator-friendly sites (95% CI overlap = 0.36) than at persecuted sites (95% CI overlap = 0.48, Figure 3). At predator-friendly sites, dingoes were primarily active during the day while foxes were most active at night (Figure 3A). At the predator-persecuted site, fox activity peaked after sunset, near the peak of dingo activity (Figure 3B). Fox activity at sunrise was highest at dingo-eradicated sites, and late evening (pre-midnight) activity was lowest at predator-friendly sites (Figure 4).
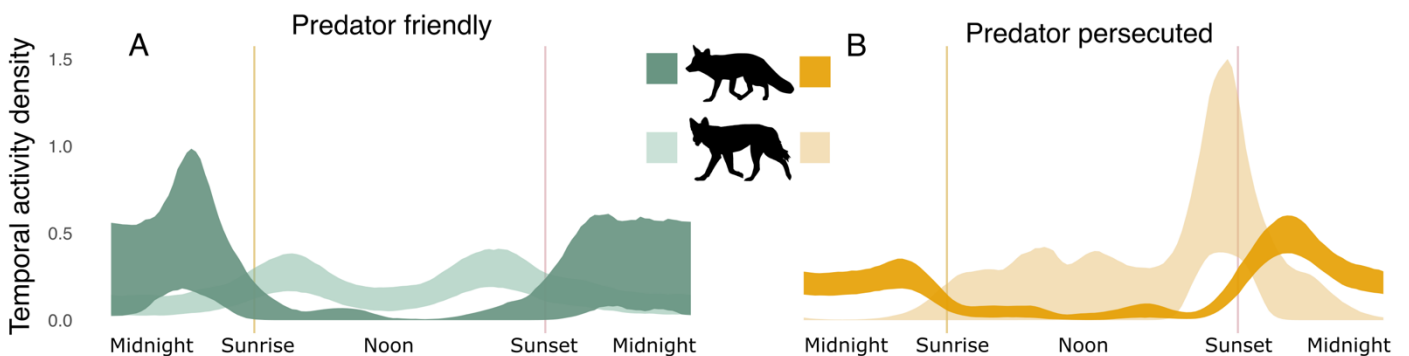

Figure 3. Fox and dingo temporal overlap at sites with differing treatments of predators. Overlap between the two predators at predator-friendly sites (A) and predator-persecuted sites (B). Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance.
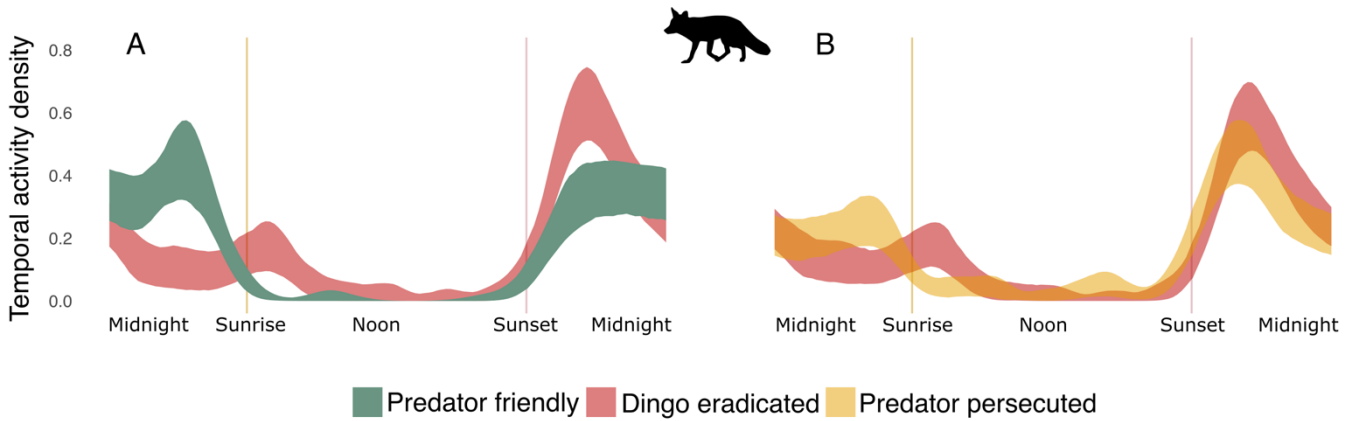
Figure 4. Fox temporal overlap between sites with differing treatments of predators. Fox temporal activity comparing dingo-eradicated sites to predator-friendly (A) and predator-persecuted (B) sites. Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance.

Discussion

The landscape of fear predicts that mesopredators should increase cautiousness where apex predators are protected. In line with predictions made under the landscape of fear and previous studies, we found that foxes avoided dingoes in space and time, particularly at predator-friendly sites (Karanth et al., 2017; Lundgren et al., 2021; Swanson et al., 2016; Wooster et al., 2021). However, contrary to our predictions, foxes were most cautious at predator persecuted sites regardless of the presence of dingoes, while foxes were least cautious, most confident, and most social at predator-friendly sites. These findings suggest that fear and risk sensitivity are heightened in persecuted landscapes, but that intraguild interactions among canids in protected landscapes may be more complex than can be explained by the landscape of fear alone.

Dingo-eradicated sites had the highest fox occupancy, as predicted by trophic cascade theory (Letnic et al., 2011; Wallach et al., 2010). Trophic cascades suggests that where apex predators are absent, mesopredators are freed from top-down pressure, resulting in increases in their densities and widening of their distributions (Prugh et al., 2009). Known as "mesopredator release", this phenomena has been documented across the globe, including between foxes and dingoes in Australia (Letnic et al., 2011). Both fox and dingo occupancy were similar between predator-friendly and predator-persecuted sites, aligning with studies that found that killing predators doesn't necessarily decrease their abundance or activity, primarily due to the loss of territoriality and increases in immigration and reproduction (Lazenby et al., 2015; Wallach et al., 2009). Instead, persecution alters fox activity patterns and behaviour, as has been documented in cats (*Felis catus*) in Australia (Brook et al., 2012).

Persecution of canids is known to fracture social structures (Haber, 1977; Wallach et al., 2009). Haber (1996) found that wolves (*Canis lupus*) subject to human killing regularly shifted their territories, while protected wolves did not. Similarly, we found that protected and persecuted dingoes exhibited different activity patterns. Both our results and those of Brook et al. (2012) show that protected dingoes have bimodal crepuscular peaks in activity. Persecuted dingoes in their study, however, shifted their activity to a peak prior to sunrise, while persecuted dingoes in our study concentrated their activity in a peak around sunset. This suggests that changes in activity patterns are adaptable and may be aimed at avoiding context specific threats. For example, coyotes (*Canis latrans*) have been observed to adjust activity patterns to avoid hunters (Kitchen et al., 2000). Likewise,

foxes responded to changes in dingo activity by altering their own to avoid times and locations of high risk. However, fox avoidance of dingoes was higher where the two predators were protected. This could be because dingoes kill and harass them more in protected landscapes (Wallach et al., 2010) or because foxes are better able to predict their movements. It is plausible that foxes develop more detailed knowledge of dingo activity where both predators are socially stable and where individuals live longer. Our observation that foxes are most confident under these conditions aligns with this reasoning.

Like larger canids, red foxes form multi-generational family groups (Macdonald, 1979). We found that social interactions between foxes were more common at the predator-friendly sites, suggesting that fox family groups may be more stable. A wide range of species, including red foxes, engage in cultural and social learning to avoid predation (Whiten, 2021). For example, meerkats (*Suricata suricatta*), are taught how to avoid scorpion stings by their parents and helper adults (Thornton and McAuliffe, 2006); red deer (*Cervus elaphus*) doe's teach their fawns to avoid areas where they have historically been hunted (Trouwborst et al., 2016); and predator recognition is culturally transmitted in several fish species (Mathis et al., 1996). Foxes may be more confident in protected landscapes because stable fox family groups are better able to transmit knowledge of how to avoid dingoes.

Fox cautiousness was most pronounced where foxes were subject to persecution, both with and without dingoes. It is, therefore, likely that caution is enhanced toward a range

of threats, including hunters, other predators (e.g. raptors), and other foxes. Fear of hunting and people can also shape the activity patterns and behaviour of predators (Kitchen et al., 2000; Suraci et al., 2019). Fox populations at predator-persecuted and dingo-eradicated sites have likely been subject to decades of eradication efforts (Philip, 2019), and given this, it is likely that foxes have developed behavioural strategies aimed at avoiding persecution. Alternatively, as canid territoriality breaks down where they are subject to persecution, increasing cautiousness could be due to the risk of encountering dispersing and potentially aggressive conspecifics (Cavallini, 1996).

Persecution of predators can lead to alteration of activity patterns, with cascading effects on prey. Dingoes were primarily diurnal at predator-friendly and predator-persecuted sites, and foxes avoided these times by being primarily nocturnal. As many of Australia's small mammals are also nocturnal (Linley et al., 2020), this shift may potentially result in increased predation pressure on their prey. Indeed, this has been argued by Brook et al. (2012), who found that the persecution of dingoes resulted in temporal shifts in both cats and dingoes, hypothetically increasing pressure on nocturnal prey. Although direct evidence of this is sparse, locations of predator persecution are also hotspots of small mammal decline (Wallach et al., 2010), and it is plausible that this could be driven, in part, by the temporal shift in mesopredator activity caused by the loss of suppressive effects by dingoes.

Taken together, our findings suggest that protected foxes utilise a wider set of cognitive abilities and states of knowledge to navigate avoidance of predators. Previously, we have

suggested that knowledge-based avoidance where predators are protected may be described as a *Landscape of Knowledge* (Wooster *et al.* 2021). Both predators and prey engage in social learning, cooperation, and innovation to exploit their environment and avoid predation and other threats, like hunting (Mathis et al., 1996; Whiten, 2021). Our findings highlight that foxes avoid their predators based on knowledge of their activity patterns at predator-friendly sites, an avoidance strategy that requires both high levels of learning and memory to function (Barrett et al., 2019). Accounting for the cognitive functions of predators and prey may drastically alter how we envision predator-prey ecology. Overall, our study suggests that fear is an important driver of behavioural states that helps navigate predation in risky and unpredictable environments. After all, one of the most frightening things in life is uncertainty. However, fear may not be a common state in stable environments, free from persecution, as other forms of cognition and social learning may assist species to establish predictable states of intraguild coexistence. The challenge is the development of research methods to fully capture and trace these rich behavioural patterns.

Acknowledgements

icons in Figure 2 A & D and E. Rogers for helpful discussions. This study was funded by

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Supplementary Material

Supplementary table 1. Descriptions of the name, the cover available for foxes as determined by vegetative cover and density, the treatment of both predators, camera trap days and number of cameras used in brackets, the camera placement (whether the camera was placed on a resource point or non-resource point hotspot of animal activity) and the size of the site surveyed.

Site	Cover	Dingoes	Foxes	Camera trap days	Camera placement	Size (km²)
<u>Predator friendly</u>						
The Painted Desert	Low	Protected	Protected	1,195 (50)	Resource	7,900
Mourachan	High	Protected	Protected	5,541 (43)	Resource	1180
<u>Predator persecuted</u>						
Capertee National Park	High	Persecuted	Persecuted	3,045 (30)	Hotspot & Resource	60
<u>Dingo eradicated</u> Bathurst	High	Absent	Persecuted	2,589 (20)	Hotspot & Resource	11
Cobar	Low	Absent	Persecuted	804 (16)	Resource	53

Supplementary table 2. Output from Tukeys post hoc tests of the generalized linear mixed effects models examining the effect of human treatment of predators on fox occupancy and behaviour. Model was constructed using the 'glmer' function in the R package 'lme4', post hoc test was performed using 'ghlt' in the R package 'multcomp'. Asterisks denote significance ($p < 0.05$).

Parameter	Estimate	SE	Test Statistic	p
Fox occupancy				
Predator persecuted – Predator friendly	0.0237	0.267	0.089	0.996
Dingo eradicated – Predator friendly	-1.694	0.2182	-7.766	<1e-07 ***
Dingo eradicated – Predator persecuted	-1.719	0.2677	-6.420	<1e-07 ***
Fox cautiousness				
Predator persecuted – Predator friendly	-1.93	0.44	-4.37	3.66e-05 ***
Dingo eradicated – Predator friendly	-1.76	0.40	-4.43	2.33e-05 ***
Dingo eradicated – Predator persecuted	0.17	0.47	0.36	0.929
Fox confidence				
Predator persecuted – Predator friendly	1.91	0.534	3.58	0.000985***
Dingo eradicated – Predator friendly	1.801	0.478	3.78	0.000472***
Dingo eradicated – Predator persecuted	-0.1041	0.5648	-0.184	0.98
Fox Sociality				
Predator persecuted – Predator friendly	2.8717	1.056	2.719	0.0168*
Dingo eradicated – Predator friendly	2.147	0.639	3.416	0.00152**
Dingo eradicated – Predator persecuted	-0.9708	1.155	-0.841	0.666
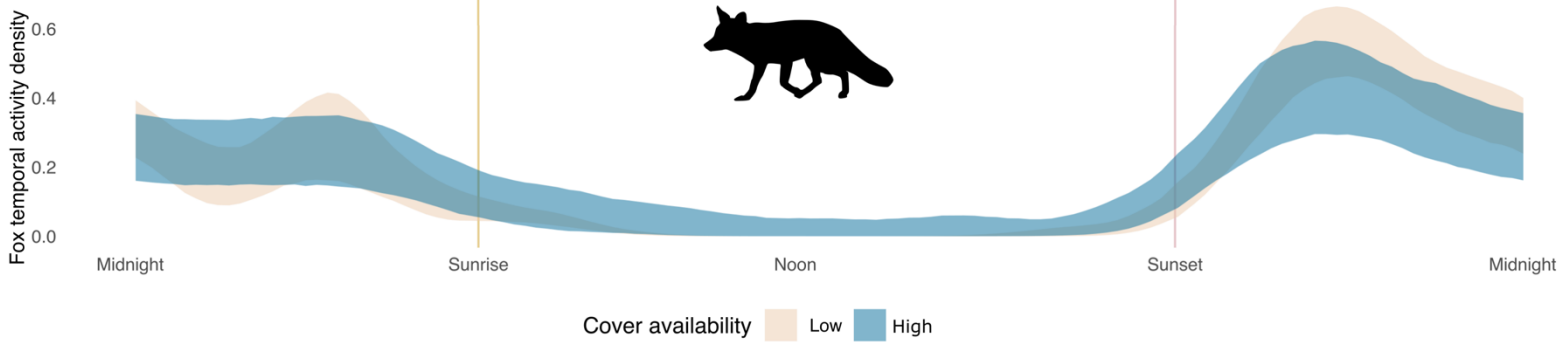
Supplementary figure 1. Fox and dingo temporal overlap at sites with differing cover for foxes. Overlap between the two predators at predator-friendly sites (A) and predator-persecuted sites (B). Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance.

Chapter 6: Animal cognition has cascading ecological effects

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Abstract

Predation and the threat of predation have cascading ecological effects, driving ecosystem-wide processes. Predator-prey interactions have been primarily understood through the landscape of fear, where fear of predation leads to behavioural avoidance of predators by prey. Recently, observations and empirical research have come to light that struggle to be explained by fear alone. We suggest that the field of animal cognition may offer insights into predator-prey ecology where fear cannot. We propose that the cognition of predators and prey have cascading ecological effects. We discuss the theoretical and methodological underpinnings of the ecological incorporation of animal cognition and provide case studies of how shifts in cognition can alter the ecological function of predators and thus, ecosystem wide processes. We propose the *landscape of knowledge*, a framework aimed at incorporating the

cognitive abilities of individual animals to better understand how predator and prey coexist.

The landscape of fear

Apex predators structure ecosystems from the top-down, limiting the densities of herbivores and mesopredators (Ripple et al., 2014). Consumptive effects of predation are driven through direct killing of smaller prey (Carbone and Gittleman, 2002), while the non-consumptive effects of predation drive alterations in prey behaviour, such as avoidance in space and time and increases in vigilance (Lima and Bednekoff, 1999; Sih, 1980). The net result of the predation risk exerted by predators and the behavioural changes made by prey and mesopredators are known as the *landscape of fear*.

The landscape of fear describes how the risk felt by prey varies throughout a landscape (Laundre et al., 2009a). The fear of predation influences prey physiology, behaviour, and life history, which can cascade to alter their ecology (Brown et al., 1999; Lima and Dill, 1990; Lundgren et al., 2021). The ecology of fear has become an increasingly important paradigm for describing interactions between predators and prey in ecosystems, particularly given the global ubiquity of large predator loss (Ripple et al., 2014). The paradigm proposes that prey species use of space and time in a landscape is driven by fear and that such effects can be observed throughout trophic levels. By accounting for the heterogeneity of landscape terrain and habitat and the ability of predators to hunt in those spaces, the landscape of fear aims to predict areas in which prey would avoid and thus observe ecosystem wide changes that occur based upon fear felt by prey species (Laundré et al., 2010).

The most pertinent example of a landscape of fear and its ensuing trophic cascade remains the wolves (*Canis lupus*) of Yellowstone national park. In 1995, wolves were reintroduced into the park, after their extirpation earlier in the century. The reintroduction of wolves to the park altered predator and herbivore assemblages (Ripple et al., 2001). The reappearance of wolves in the park had the most dramatic effect on their main prey species, elk (*Cervus canadensis*). The fear of predation altered their reproductive fitness, resulting in less deer in the park. Further, the risk of predation drove elk to occupy safer areas in the landscape known as "valleys", while areas of high wolf densities, "peaks" were avoided (Ripple et al., 2001). This resulted in changes in vegetation communities and natural landscapes, as cottonwood forests and aspen stands began to regenerate following the reduction in elk herbivory (Ripple and Beschta, 2003).

The landscape of more than fear

The landscape of fear plays and essential role in understanding the effects predators have throughout ecosystems, however, the paradigm has recently come into question, through both empirical studies that raise questions of fear as the primary driver of interactions and more conceptual work focusing on expanding our understanding of ecosystems (Doherty and Ruehle, 2020; Gallagher et al., 2017; Mueller et al., 2018; Swanson et al., 2016; Wikenros et al., 2017; Wooster et al., 2021). For example: In North America, red foxes (*Vulpes vulpes*) have been observed coexisting with coyotes (*Canis. latrans*), a deadly predator, in what appears to be the absence of fear. While foxes in the study generally avoided coyotes in space, direct encounters did not result in intraguild predations, rather coyotes displayed little aggression and foxes little fear (Mueller et al., 2018). The recent discovery of fine-scale spatio-temporal avoidance

patterns where subordinate predators avoid dominant ones at micro (hourly) rather than macro (complete spatial avoidance) scales, enables predator coexistence. It has been suggested that this type of coexistence may reduce fear in subordinate predators (Swanson et al., 2016). In Serengeti National Park, hyenas (*Crocuta crocuta*) and cheetahs (*Acinonyx jubatus*) suffer high rates of lion (*Panthera leo*) predation and yet are not spatially displaced by them. Rather, subordinate predators avoid lions on a moment-to-moment basis, this being less costly than long term spatial segregation, which restricts access to resources which lions frequent (Swanson et al., 2016). Similarly, in India, tigers (*Panthera tigris*) pose a substantial threat to both dholes (*Cuon alpinus*) and leopards (*Panthera pardus*). The two subordinate predators respond with fine-scale spatio-temporal avoidance, facilitating the co-occupancy of their shared functional niche. Further, the degree of avoidance engaged in by subordinate predators is dependent on resource availability (Karanth et al., 2017).

It is becoming increasingly apparent, as we learn more about the cognition and the lived experiences of non-human animals, that the decisions many prey and predator species make are driven by more complex mental and cognitive states than fear alone. The decisions made by these species, as highlighted by the trophic cascades framework, are not inconsequential (Wallach et al., 2015c). Just as elk choosing to avoid high wolf areas, foraging in low-risk meadows, drives cascading ecological effects, it is likely that the cooperation of predators alters spatial risk exerted onto their prey. For example; Coyotes and badgers (*Taxidea taxus*), two predators sharing a functional niche have been observed cooperating to hunt den dwelling prey (Thornton et al., 2018). When the two species cooperate they experience increased hunting success, making cooperation beneficial for both individuals (Minta et al., 1992). This

interspecific cooperative hunting behaviour, likely has cascading ecological effects, altering predation risk for prey species across landscapes where cooperation is common. Animal cognition has been poorly studied in the wild (Pritchard et al. 2016). However, incorporating tenets of animal cognition science such as memory, knowledge and learning, the capacity of individuals to form deep social bonds and to cooperate (inter- and intraspecifically) (Barrett et al., 2019) may assist ecology in better understanding how predator and prey come to coexist.

Box 1. Examples of cognitively complex interactions and their cascading or potential cascading ecological effects.

Coyotes and badgers (*Taxadea taxis*) cooperate to hunt uinta ground squirrels (*Spermophilus armatus*). The pair have increased hunting success when cooperating, likely altering landscapes of fear for the squirrels (Minta et al., 1992). Interspecific hunting mutualisms are relatively common (Anne and Rasa, 1983; Bshary et al., 2006), however, their ecological function and influence remains unexplored.

The ecological effect of dingoes is directly tied to their protection from humans (Wallach et al., 2010). Where They are killed by humans their social groups deteriorate (Wallach et al., 2009), resulting in reduction in their ability to pack hunt and raise young (Haber, 1996). The deterioration of dingo social groups alters the landscape of fear for mesopredators (Lundgren et al., 2021; Wooster et al., 2021) and thus their prey (Wallach and O'Neill, 2009a).

Fox species accompany brown bears (*Ursus arctos*) on hunting expeditions (Harris et al., 2008). The act of associating with a non-agonistic apex predator shields the mesopredator from predators (e.g. wolves) that avoid brown bears.

Juvenile meerkats are taught by adults how to safely consume scorpions by removing their stingers (Thornton and McAuliffe, 2006). Life history and demographic changes induced by climate change are predicted to result in the breakdown of meerkat social structures (Paniw et al., 2019). Without cultural teachings, the topography of risk may look different for scorpions and the other prey of meerkats.

Human killing drives the personality and risk-taking behaviour in hyenas. Hyenas experiencing persecution engaged in more exploratory behaviour (Greenberg and Holekamp, 2017). Recent advances highlight that personality can directly influence predator-prey dynamics, however, what this looks like for the prey and predators of hyenas remains unknown (Harris et al., 2020).

Black chinned hummingbirds (*Archilochus alexandri*) increase their breeding success by nesting in close proximity to hawks (*Accipiter* spp.), a genus that hunts their predators. This creates predation free nesting locations as their predators avoid hunting when hawks are nearby .

Red deer (*Cervus elephus*) teach their young about trauma experienced by past generations (Trouwborst et al., 2016), which drive their spatial patterns and thus their herbivory, with ecological consequences.

Animal cognition has unveiled the complex cognitive lives of wild animals. For example; barnacle geese (*Branta leucopsis*), a highly social, long-lived bird species develop lifelong bonds (Kurvers et al., 2020); and American crows (*Corvus brachyrhynchos*) distribute knowledge about which humans are safe or dangerous through social learning (Cornell et al., 2012). Only recently has animal cognition begun to be incorporated into ecological research. For example, Toledo et al. (2020) uncovered the complex cognitive maps Egyptian fruit bats (*Rousettus aegyptiacus*) utilize to maximize foraging efficiency. When foraging, bats engaged in goal-orientated missions where they flew straight to objectives, even engaging in shortcuts. The ecological effects of canid apex predator social groups have also received a significant amount of attention. For example, we understand that dingoes and wolves have deep social lives, live, hunt and raise young cooperatively and engage in social and cultural learning (Haber, 1977; Haber, 1996; Wallach et al., 2009) and that the ability to maintain these social groups distinctly influences not only their ecology, but the ecology of their prey (Wallach et al., 2010). These examples highlight that the cognitive capacities of animals can drive ecological processes. Complex cognitive interactions with ecological consequences can be found across the globe. For example predator

species display the ability to develop successful interspecies cooperative hunting arrangements (i.e coyotes and badgers (Minta et al., 1992), hornbills – *Tockus spp.* and mongooses - *Helogale parvula* (Anne and Rasa, 1983), groupers - *Plectropomus pessuliferus,* and the giant moray eel - *Gymnothorax javanicus (Bshary et al., 2006).* The ability for predators to cooperate, increasing their hunting success, likley has cascading behavioural and ecological effects throughout ecosystems, however, the reach and influence of this phonomena remain unknown.

The cascading ecological effects of animal cognition

The discoveries that non-human animals are indeed sentient, that they are able to feel, perceive and that they experience the world subjectively, have challenged the ecological sciences to account for and understand the inherent complexities of their subjects (Wallach et al., 2020a). Relatively recently researchers have discovered that non-human animals possess distinct and ecologically consequential *cultures*. Animal cultures, described as the inheritance of behavioural and social traditions from one generation to the next can be found across taxa all over the globe (Laland and Janik, 2006). These cultures govern prey preference, foraging techniques and spatio-temporal patterns (Whiten, 2021). For example, Meerkats (*Suricata suricatta*), teach their young how to handle and predate upon scorpions (from genera *Parabuthus* and *Opistophthalamus*) by providing them with live prey, with stinger removed. As the young grow, they are presented with prey with their stingers intact and are taught to remove them (Thornton and McAuliffe, 2006). As the climate warms, significant life history and demographic changes are predicted in this species, resulting in the breakdown of these complex social groups (Angulo et al., 2018; Paniw et al., 2019). In a climate altered future, topographies of risk may appear substantially different to

both meerkats, uneducated to the risk of their scorpion prey and to scorpions, who may have a greater chance of survival (Thornton and McAuliffe, 2006).

While culture can teach young to better avoid predation and forage, it can too, carry intergenerational trauma. Red deer (*Cervus elephus*) living on the border of Germany and the Czech Republic, carry such trauma. During the cold war, lethally patrolled fences stood along the border. Even 25 years after its removal, no deer approach the location the fence once stood. This is particularly striking with the realisation that no deer alive today ever saw the fence. Juvenile deer are taught the danger of the border by their mothers (Trouwborst et al., 2016). As highlighted by trophic cascades research within Yellowstone National Park, the movements and foraging patterns of deer are ecologically consequential, driving change in vegetation communities and herbivore assemblages (Beschta and Ripple, 2013; Ripple and Beschta, 2003).
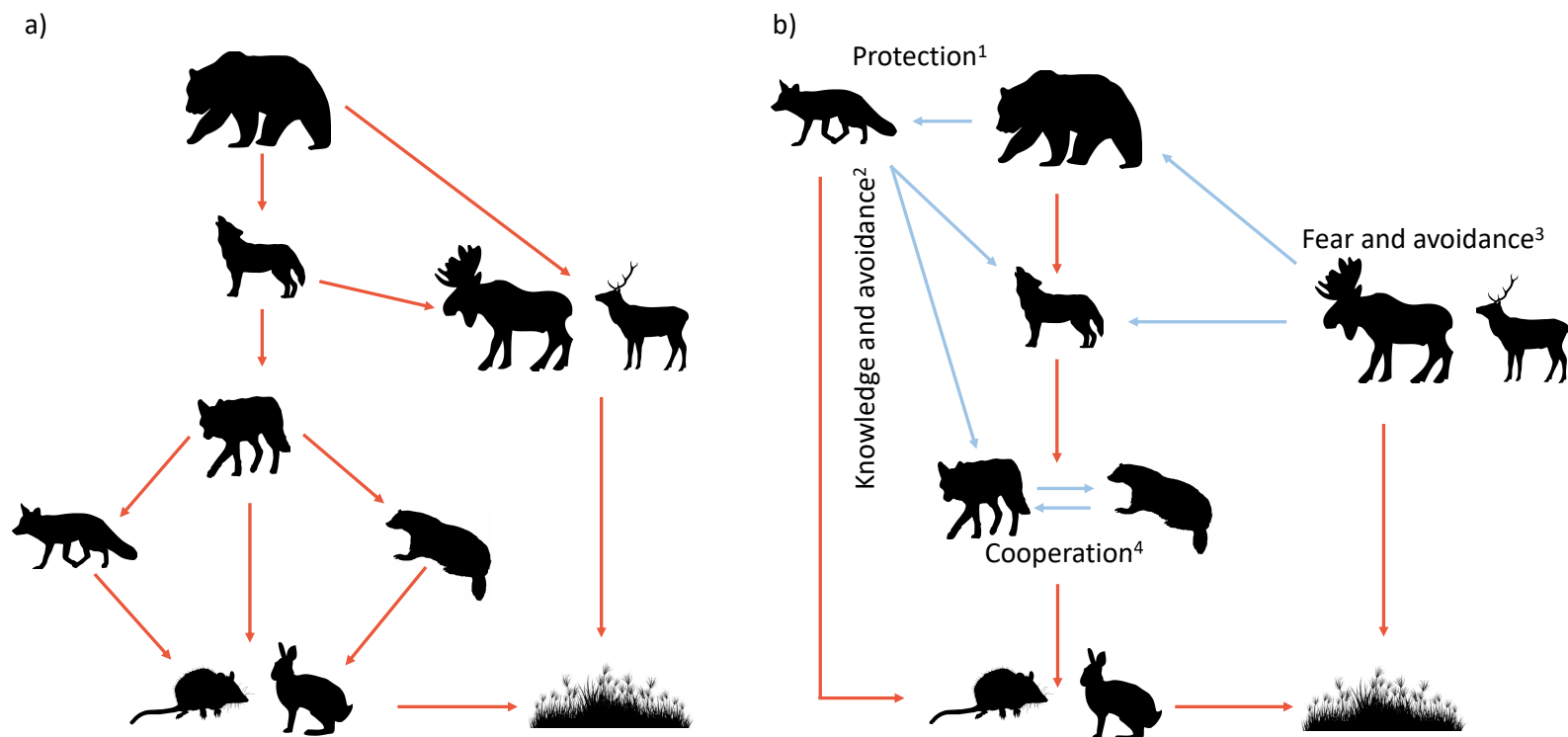
Figure 1. Trophic structures of a common mid-west North American ecosystems (i.e.,

Yellowstone National Park) visualised through two frameworks; a) the landscape of fear,

predators inspire fear in small prey and mesopredator species, both directly killing them and

altering their behaviour. b) A conceptual model describing the landscape of knowledge,

incorporating animal cognition. Brown bears tolerate fox presence while they hunt, serving to

protect foxes from wolf predation (1 - (Harris et al., 2008). Red foxes, when cohabitating with

apex predators develop detailed knowledge of their activity patterns and avoid them (2 -

(Wooster et al., 2021). Elk and other large herbivores increase their vigilance when wolves

are present, allowing them to avoid predation (3 - (Laundré et al., 2001). Coyotes and badgers

cooperate, instead of competing to hunt small mammals (4 - (Minta et al., 1992). Blue lines

represent cognitive trophic cascades. Red lines represent predation.

Cognition drives a landscape of knowledge

Here, we propose the *landscape of knowledge*, a framework describing how ecosystems are influenced by animal cognition. We theorise that interactions between predator and prey are mediated by more than just fear, warranting the expansion of behaviours and emotional states measured, examining how they influence predator-prey interactions. In Figure 1, we outline a classic example of a trophic cascade, taken from Yellowstone National Park. Figure 1a, describes trophic interactions under the landscape of fear, larger predators kill and inspire fear in smaller predators and prey, while this is factual, research has highlighted that these interactions may be more complicated. In figure 1b we present a theoretical model, describing interactions between predators and prey through the incorporation of animal cognition. Mesopredators may have their trophic status elevated when cohabiting with a tolerant apex predator, this interaction has been observed between fox species and brown bears (Harris et al., 2008). While, when apart from their bear protectors, they may peacefully coexist with coyotes (Mueller et al., 2018) or avoid wolves through knowledge based fine-scale avoidance (Wooster et al., 2021). The cooperation between mesopredators, badgers and coyotes, occupying the same functional niche, increases the predation pressure they exert on small mammal prey species (Minta et al., 1992). While the principles of the landscape of fear still apply, as large herbivores engage in increased vigilance and avoid both wolves and bears (Laundré et al., 2001). The landscape of knowledge, as outlined by figure 1b, aims to highlight that interactions between species are beyond just fear.

Integrating Animal Cognition and Ecology

To address the inability to account for the complexity of our subjects, the broadening of ecological fields to incorporate novel, interdisciplinary methods may be warranted. These being methods aimed at understanding the cognition of individuals, quantifying, for example, the learning, problem-solving and the cooperative capabilities of wild animals and their ecological effects.

Many of the examples we outline in Box 1, have explored the cognition of individuals, however, the link between cognition and ecology remains hypothesised. To explore this, we propose the melding of methods from animal cognition science into predator-prey ecology. For example, one might use puzzle box experiments, (Greenberg and Holekamp, 2017; Stanton et al., 2021), to quantify the ability of predators to solve problems, to then test, are individuals who are better at solving problems, better hunters? Or, one could conduct a series of learning tasks (Reichert et al., 2021) to then identify which cognitive traits enable prey to best avoid predation? Disentangling the link between cognition and ecology remains an important feet in the ecological sciences.

Box. 2 Outstanding questions

How would incorporating cognition reshape our knowledge of predator-prey interactions?

How do human management practices shape the cognition and thus ecological effects of wild animals?

How does the dissolution of sociality cascade ecologically?

How can we design 'cognition in the wild' experiments to better understand the cascading effects of cognition?

Concluding remarks

Throughout the last decade, behavioural ecology has become increasingly interested in the lived experiences of non-human animals (Fraser-Celin and Hovorka, 2019). While acknowledging the sentience and sapience of non-human animals is a step forward, the cascading ecological effects of animal cognition remains a significant knowledge gap. As we aim to understand the cognitive depth of wild non-human animals, we position them as "subjects" or "persons" enabling researchers to account for the lived experiences and agency of the species they are studying (Fraser-Celin and Hovorka, 2019; Wallach et al., 2020a). The simple theoretical model presented here outlines how predator-prey relationships can be modulated by accounting for cognition. We believe that the integration of animal cognition into the ecological sciences, in particular predator-prey ecology, offers exciting new perspectives for understanding how predators and prey coexist and shape their environments. By aiming to understand the complex nature of the species we study we open ourselves

to a range of possibilities, that the lives of non-human animals may be more human

that we realise.

Thesis reference

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