

## Research article

## Predator protection dampens the landscape of fear

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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. Predation risk is variable in space and time creating a landscape of fear. In Australia, dingoes hunt red foxes and suppress their populations. As both predators are commonly subjected to eradication programs, the question arises whether humans alter the risk dingoes pose to foxes and in turn alter the foxes' avoidance behaviours. We studied the spatio-temporal activity patterns and wariness behaviours of foxes and dingoes at sites where they were protected (predator friendly), where they were persecuted (predator persecuted), and at sites where foxes were persecuted, and dingoes had been eradicated (dingo eradicated). The landscape of fear hypothesis predicts that foxes will be the most spatiotemporally restricted and most fearful at predator friendly sites, and least restricted and fearful at dingo eradicated sites. We found that fox occupancy was highest at dingo eradicated sites; and that they avoided times of heightened dingo activity at predator friendly sites more than at predator persecuted sites. Contrary to predictions, foxes were the least fearful (lowest frequency of cautious and vigilant behaviour) and most social (highest frequency of social interactions) 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). Where predators are protected, predator avoidance may be driven by knowledge rather than fear alone.

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). In addition to the direct effects that predators have on prey

populations, the fear of predation itself can drive ecosystem wide effects (Suraci et al. 2016). Fear of predation typically results in prey responding to risk by altering their behaviour to better detect and avoid predators (Gaynor et al. 2019). 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). Prey are expected to avoid peaks or, if unavoidable, access them with heightened vigilance (Lima and Dill 1990). The landscape of fear has provided important insights into understanding how predators influence prey behaviour (Brown et al. 1999, Lima and Bednekoff 1999) and how these fear effects cascade throughout ecosystems (Laundré et al. 2001, Kohl et al. 2018). However, recent studies have suggested that the non-consumptive effects apex predators have on mesopredators may not be entirely explained by fear alone (Swanson et al. 2016, Karanth et al. 2017, Mueller et al. 2018, Wooster et al. 2021).

For some apex predators, the manner in which they influence their prey depends on the functioning and structure of their social systems (Wallach et al. 2015). Predator social structures allow for cooperation, thus facilitating hunting of large and difficult prey and for defending territory. Many canids form family groups ('packs') composed 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. 2015). Persecution by humans fractures these social structures with implications for their ecological effects, including the regulation of smaller canid populations (Haber 1996, Ripple et al. 2014). Persecution tends to lead to demographic changes, including a higher proportion of juveniles and breeding pairs (Haber 1977), and can disrupt social knowledge pathways (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).

We examined how humans shape the responses of red foxes *Vulpes vulpes* to predation risk from dingoes *Canis dingo*. Dingoes are mainland Australia's only mammalian apex predator (Wallach et al. 2015). They structure ecosystems by suppressing populations of mesopredators and herbivores, a cascading ecological effect that is weakened when they are persecuted (Wallach et al. 2010). Similarly, red fox populations are persecuted by people but are also actively suppressed by dingoes (Letnic et al. 2011). If fear is the primary driver of these intraguild interactions foxes should be wariest where dingoes are protected, and fox avoidance of dingoes should be strongest where they are wariest (Laundré et al. 2009). However, in a previous study, at a single protected area, we observed that foxes avoid dingoes without heightening vigilance (Wooster et al. 2021). We therefore suggested 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 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 compared to predator friendly and predator persecuted sites; 2) that foxes would avoid dingoes in space and time, particularly at predator friendly sites; and 3) that foxes would be most fearful at predator friendly sites, where dingoes present the greatest threat. Our goal was to examine the extent to which intraguild relationships and behavioural responses were explained by the landscape of fear, and whether human treatment conditions could modulate these interactions.

## 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 2300 km<sup>2</sup> cattle station and Mount Willoughby a 5600 km<sup>2</sup> 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 and waterpoints that commonly feature very little vegetative cover (Supporting information). Mourachan is a 1180 km<sup>2</sup> 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, this understory provides good cover for foxes (Supporting information).

Capertee National Park is located within the Sydney basin bioregion and receives 677 mm of rain annually. The site is characterised by densely vegetated woodlands, dominated by eucalypt and angophora species. Given the dense vegetation and woodland, Capertee National Park provides good cover for foxes (Supporting information). Predators

have been subject to long term persecution within Capertee National Park through 1080 monofluoroacetate 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 267 mm 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 555 mm of rain annually. The region is subject to sustained and intensive predator shooting and poison-baiting. More site detail can be found in the Supporting information. It is worth noting that our sites occur across a large extent with a significant rainfall gradient. Regardless, previous work has highlighted that patterns of top-down suppression are consistent across large ranges that vary in habitat and rainfall (Brook et al. 2012).

We monitored foxes and dingoes using infrared motion sensing cameras (Bushnell MKII and Browning Dark Ops Pro) set between 2 and 10 km apart. As understanding how human management shaped the foxes landscape of fear was our primary objective, we established cameras at hotspots of predator activity, and thus peaks in the landscape of fear (Wooster et al. 2021) such as waterpoints, livestock carcasses and areas of high prey activity, as determined by prey movement pathways through vegetation and abundance of prey scats. While this approach is ad hoc, it allows for a more nuanced testing of the landscape of fear, as foxes, at least where the two species co-occur, accessing these areas should ultimately be fearful as they share these locations with dingoes. 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 804–5541 camera trap nights per site. All differences in sample effort were accounted for within each analysis. Across all sites, we collected 1974 fox and 3174 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 (17 km<sup>2</sup>) (Moseby et al. 2009) and dingoes (95 km<sup>2</sup>) (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 (ver. 3.6.3) package *wqid* (ver. 0.2) (<[www.r-project.org](http://www.r-project.org)>). 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 occupancy parameter from each of the 100 occupancy models generated for each site and ran generalised linear mixed

models (GLMM) with the *glmer* function in the R package *lme4* (ver. 1.1-26). We explored the relationships between fox and dingo detection as dependent variables and treatment by humans (predators persecuted, predators protected and dingo eradicated), amount of cover available for foxes (high or low) as determined by vegetative cover, and camera placement (resource point or prey hotspot) as successive predictor variables, with site as a random effect to account for inter-site difference in each model. As occupancy probabilities range between 0 and 1, we modelled occupancy data with a binomial distribution. Tukeys post hoc comparison between fixed effects were performed using the 'glht' function within R package *multcomp* (ver. 1.4).

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 *wqid* (ver. 0.2). As per the single species occupancy models, we interpreted the occupancy parameter ( $\psi$ ) as the probability of use given the 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* (ver. 0.3.3) and *circular* packages (ver. 0.4-93) 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 1000 bootstraps, sampling equally between each context and site. Following Lundgren et al. (2022), 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 (Supporting information).

We then scored the level of fear, or lack thereof, in foxes in each behavioural event. Fox detections were considered an independent behavioural event when foxes were detected more than five minutes apart. We confirmed their independence by testing for temporal autocorrelation between

events, using the *acf* function in R package *stats* (ver. 4.0.2). 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, with their neck held above horizontal. We aggregated cautious and vigilant behavioural states (defined as 'cautiousness'), to represent the state of fear (Laundre et al. 2009). 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 position well above the ground with legs extended. Within our study, confidence represents the absence of fear (Wooster et al. 2021). We then calculated the proportion of each behavioural event that was either confident or cautious, in an attempt to prevent single individual foxes having a disproportionate effect on the analysis. We did this by calculating the proportion each behaviour made up of the total captures within each behavioural event. 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 adult fox was observed at the same time (in the same capture). We did not detect any kits on camera traps during the sampling period. 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 (predators persecuted, predators protected and

dingoes eradicated), amount of vegetative cover available for foxes (high or low), and camera placement (resource point or prey hotspot) 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. As per other models, we included site as a random effect to account for inter-site variability. Models were run in succession to overcome convergence difficulties encountered when including all predictor variables. GLMMs of fox cautiousness and confidence were modelled using a binomial distribution, while social and scent-marking behaviours were modelled using a negative binomial distribution in the R package *lme4* (ver. 1.1-26).

## Results

Fox occupancy ( $\Psi \pm 95\% \text{ CI} = 0.65 \pm 0.061$ ) was highest at dingo eradicated sites compared to predator friendly ( $\Psi \pm 95\% \text{ CI} = 0.40 \pm 0.075$ ;  $z = -7.766$ ,  $df = 494$ ,  $p \leq 0.001$ , Fig. 1a) and predator persecuted sites ( $\Psi \pm 95\% \text{ CI} = 0.47 \pm 0.051$ ;  $z = -6.420$ ,  $df = 494$ ,  $p \leq 0.001$ ). Fox occupancy rates were similar at predator friendly and predator persecuted sites ( $z = 0.089$ ,  $df = 494$ ,  $p = 0.996$ ). Dingo occupancy was similar between predator friendly ( $\Psi \pm 95\% \text{ CI} = 0.59 \pm 0.068$ ) and predator persecuted sites ( $\Psi \pm 95\% \text{ CI} = 0.55 \pm 0.098$ ;  $z = 0.801$ ,  $df = 297$ ,  $p = 0.423$ , Fig. 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 ( $z = -0.154$ ,  $df = 494$ ,  $p = 0.878$ ). Camera location had no effect on the likelihood of fox ( $z = -0.664$ ,  $df = 494$ ,  $p = 0.142$ ) or dingo detection ( $z = 0.801$ ,  $df = 297$ ,  $p = 0.423$ ).

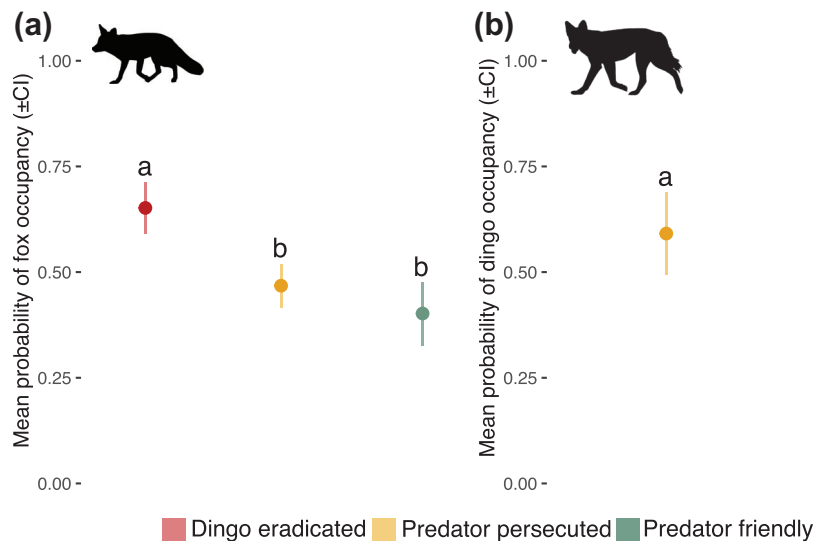


Figure 1. Comparison of fox and dingo weekly occupancy at sites with differing treatments of predators. The probability of (a) foxes and (b) dingoes being present at a camera station (occupancy) at sites of differing treatments of predators. Points and their error bars represent the mean probability 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 ( $z = -4.37$ ,  $df = 631$ ,  $p \leq 0.001$ ) and dingo eradicated sites ( $z = -4.43$ ,  $df = 631$ ,  $p \leq 0.001$ ) where cautiousness was observed twice as often (Fig. 2a, Supporting information). Confidence was observed more than twice as often at predator friendly sites compared to predator persecuted sites ( $z = 3.58$ ,  $df = 630$ ,  $p \leq 0.001$ ) and dingo eradicated sites ( $z = 3.78$ ,  $df = 630$ ,  $p \leq 0.001$ , Fig. 2b, Supporting information). Fox social interactions were observed more than three times as often at predator friendly sites than at predator persecuted ( $z = 2.507$ ,  $df = 72$ ,  $p = 0.03$ ) and dingo eradicated sites ( $z = 2.887$ ,  $df = 72$ ,  $p = 0.001$ , Fig. 2c). Fox scent-marking rates were similar between predator friendly and predator persecuted sites ( $z = 1.065$ ,  $df = 48$ ,  $p = 0.29$ , Fig. 2d); scent-marking was not observed at dingo eradicated sites. Foxes were more likely to scent mark at sites where vegetation cover

was low ( $z = 2.265$ ,  $df = 48$ ,  $p = 0.02$ ). Neither the amount of cover available nor camera location had any significant influence on the cautious (cover:  $z = -1.450$ ,  $df = 631$ ,  $p = 0.15$ ; camera:  $z = 0.961$ ,  $df = 631$ ,  $p = 0.336$ ) confident, (cover:  $z = 1.367$ ,  $df = 630$ ,  $p = 0.172$ ; camera:  $z = -1.003$ ,  $df = 630$ ,  $p = 0.316$ ) or social behaviour of foxes (cover:  $z = 0.694$ ,  $df = 83$ ,  $p = 0.49$ ; camera:  $z = 0.9667$ ,  $df = 83$ ,  $p = 0.053$ ).

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, Fig. 3). At predator friendly sites, dingoes were primarily active during the day while foxes were most active at night (Fig. 3a). At the predator persecuted site, fox activity peaked after sunset, near the peak of dingo activity (Fig. 3b). Foxes were most active around sunrise at dingo eradicated sites (Fig. 4).

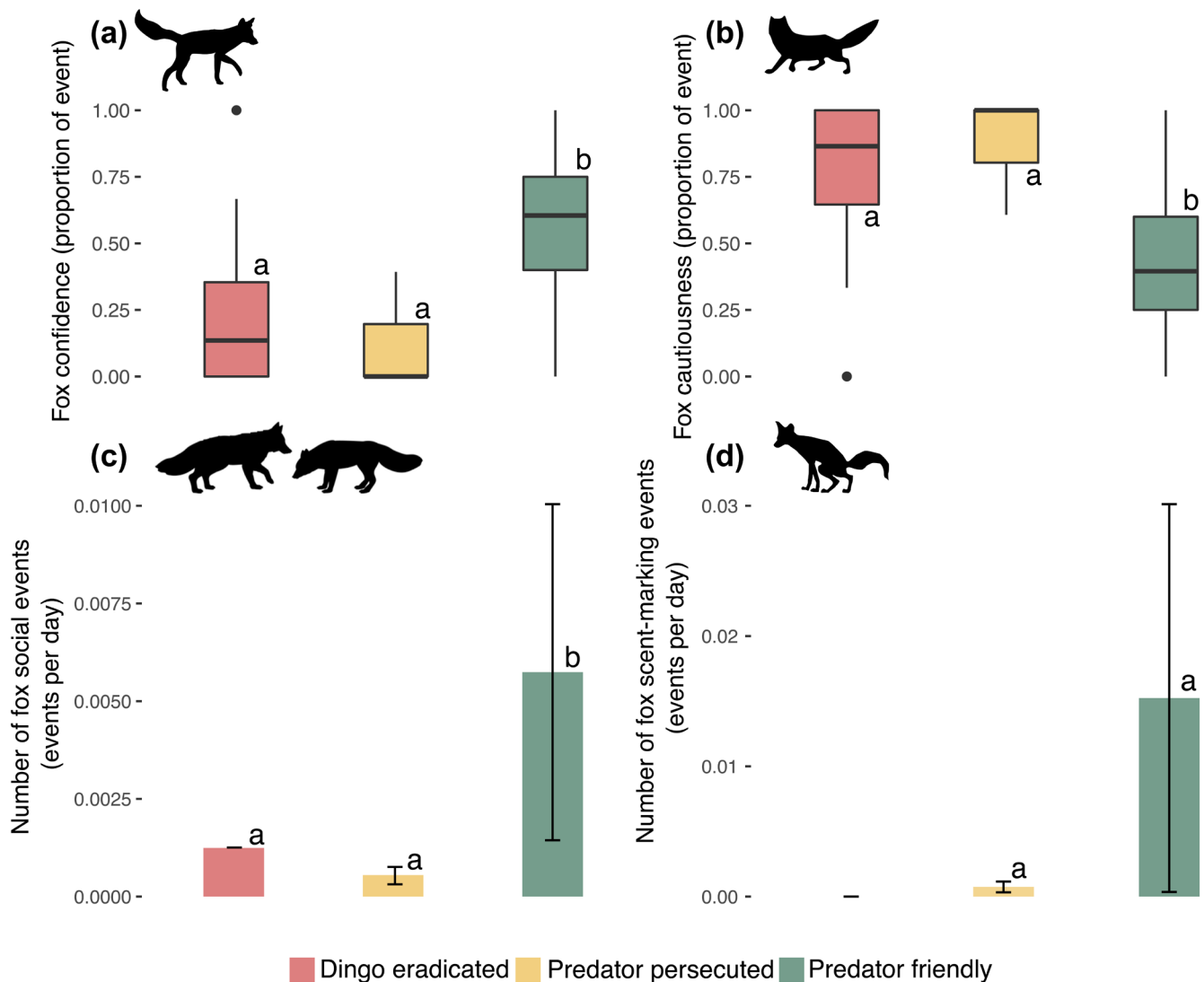


Figure 2. Comparisons of fox behaviour at sites with differing treatments of predators. The proportion of fox events classified as confident (a) and cautious (b). The frequency (events per day) of fox social (c) and scent-marking behaviour (d). Letters indicate significance groupings.

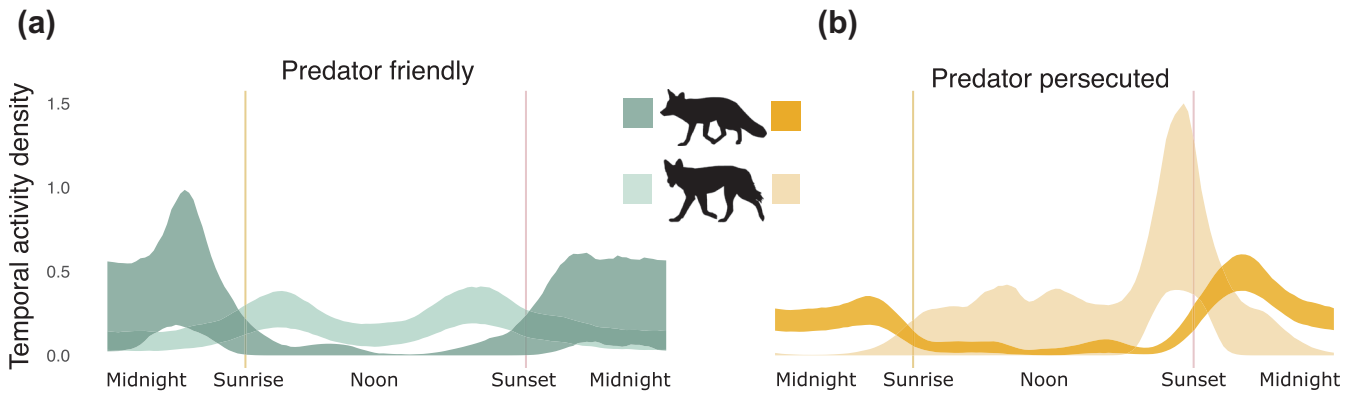


Figure 3. Fox and dingo temporal patterns at sites with differing treatments of predators. Overlap between the two predators at predator friendly sites (a) and predator persecuted sites (b). Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance. Fox temporal activity patterns are darker colours and dingoes lighter colours.

### Discussion

The landscape of fear predicts that mesopredators should increase avoidance and cautiousness where apex predators are protected. In line with predictions made under the landscape of fear, we found that foxes avoided dingoes in space and time, particularly at predator friendly sites. However, contrary to 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 protected areas enable for intraguild interactions among canids based on more than fear.

Dingo eradicated sites had the highest fox occupancy. Trophic cascades suggests that where apex predators are absent, mesopredators are freed from top to 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). It is also possible that both dingo and fox occupancy could be driven by unaccounted for bottom-up processes such as prey and resource availability. However, when testing this we could not identify any difference in occupancy based on site or cover alone, instead we found that the absence of dingoes best predicted fox site occupancy, aligning with other work in the field (Wallach et al. 2010, Letnic et al. 2011).

Human 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

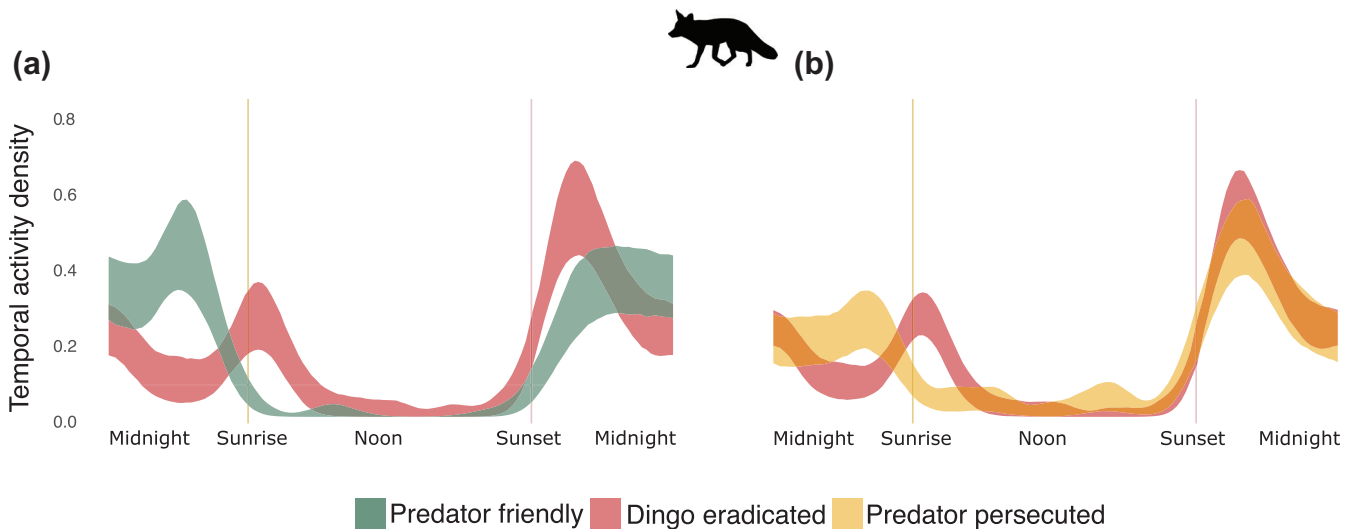


Figure 4. Fox temporal patterns at sites with differing treatments of predators. Fox temporal activity comparing dingo eradicated sites to predator friendly (a), and predator persecuted (b) sites. Ribbons are 95% confidence intervals from bootstrapped temporal activity. Non-overlapping of confidence intervals indicates significance. See the Supporting information for temporal patterns of all three fox activity patterns on the same plot.

regularly shifted their territories, while protected wolves did not. Similarly, we found that dingoes protected from and subject to human persecution 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 Brook et al. (2012), 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 change in activity pattern could be due to unmeasured site-specific differences, such as prey activity patterns and human shooting temporal activities. Other work has suggested that apex predators activity patterns are adaptable and can be fine-tuned to avoid context specific threats. For example, coyotes *Canis latrans* have been observed adjusting activity patterns to avoid hunters (Kitchen et al. 2000). Likewise, foxes responded to changes in dingo activity by altering their own to avoid times 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); the red deer *Cervus elaphus* doe 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). Future work could assess if foxes are less fearful 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 human hunters, other predators (e.g. raptors) and other foxes. Fear of humans as predators can also structure trophic cascades, inducing caution and avoidance (Kitchen et al. 2000) in both apex and mesopredators, cascading to alter both their interactions and free small mammals from top to down pressure (Suraci et al. 2019). Fear of humans can even surpass that of apex predators (Clinchy et al. 2016). Indeed, foxes were almost constantly cautious, when detected at sites where they experience both human persecution and dingo predation. 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, in addition to dingo predation. 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). Where mesopredators face the threat of both human 'super predators' (Darimont et al. 2015) and apex predators, our results suggest they may increase their caution to navigate complex landscapes of cryptic and unpredictable predation risk.

Persecution of predators can lead to the alteration of activity patterns, with cascading effects on prey (Bonsen et al. 2022). 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. 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 the suppressive effects by dingoes.

Our results are broadly supportive of mesopredator release theory, showing that fox occupancy is reduced in areas with dingoes. However, we acknowledge that without experimental manipulations the differences between treatments could be driven by other underlying factors. Future research, potentially employing experimental manipulations of predator cues across sites that vary in how predators are treated by humans would improve our mechanistic inferences of this interaction (Suraci et al. 2022). However, the broad spatial scale of this study, the integration of behavioural and spatiotemporal met, and the alignment found with other studies enhances the robustness of our conclusions.

While our results show that dingoes suppress fox occupancy and shape their temporal activity patterns as expected under the landscape of fear, it suggests a mechanism beyond fear alone: that protected foxes may utilise a wider set of cognitive abilities and forms 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). We suggest that accounting for the cognitive functions of predators and prey may nuance our understandings of predator-prey ecology. Overall, our study suggests that fear, while important in unpredictable environments, such as areas with predator persecution, is less important in stable environments (Swanson et al. 2016). After all, one of the most frightening things in life is uncertainty. We suggest that other forms of cognition and social learning may facilitate coexistence.

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## Author contributions

**Eamonn I. F. Wooster:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Daniel Ramp:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Visualization (equal); Writing – review and editing (equal). **Erick J. Lundgren:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal). **Adam J. O'Neill:** Investigation (equal); Methodology (equal). **Esty Yanco:** Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Gavin T. Bensen:** Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – review and editing (equal). **Arian D. Wallach:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.1rn8pk0x6>> (Wooster et al. 2022).

## Supporting information

The Supporting information associated with this article is available with the online version.

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