



Original Article

Red foxes avoid apex predation without increasing fear

Eamonn I.F. Wooster,^{a,*,} Daniel Ramp,^a Erick J. Lundgren,^{a,b,c} Adam J. O'Neill,^d and Arian D. Wallach^a

^aCentre for Compassionate Conservation, University of Technology Sydney, Ultimo, New South Wales 2007, Australia, ^bCentre for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus, Denmark, ^cSection for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark, and ^dDingo for Biodiversity Project, PO Box 156, Mount Perry, Queensland 4671, Australia

Received 22 October 2020; revised 30 April 2021; editorial decision 7 May 2021; accepted 7 May 2021.

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 behaviors 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 behavior 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.

Key words: behavioral ecology, introduced species, landscape of fear, predator interactions, trophic cascades.

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, behavior, 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. These behavioral responses have been attributed to a “landscape of fear.” 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 (Laundre et al. 2009). 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 are thus expected to be avoided by mesopredators and other prey (Lima and Dill 1990). Access to

these resources can be denied by apex predators through harassment (Linnell and Strand 2000) or direct predation (Berger and Gese 2007). Sometimes, however, accessing these resources is unavoidable. In these cases, prey would need to employ 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.

It is well understood that predators shape the activity patterns and behavior of prey. For example, on the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park, elk (*Cervus elaphus*) responded with increases in vigilance in areas of high wolf density (Laundre et al. 2009). Further, individuals of many small mammal species have been shown to reduce their time spent at locations of high risk (Brown et al. 1999) and engage in spatio-temporal avoidance of their predators (Lima and Bednekoff 1999). Although fear is a well-established mediator of the relationship between predator and prey, trophic interactions between apex and mesopredators appear more nuanced. Recent studies have shown that apex and mesopredators can coexist without aggression, even during direct encounters

Address correspondence to E.I.F. Wooster. E-mail: eamonn.wooster@uts.edu.au.

(Mueller et al. 2018), that spatiotemporal avoidance of apex predators may facilitate co-occurrence (Swanson et al. 2016), and that mesopredators are attracted to the scent marks of their predators (Allen et al. 2016). Although increased vigilance in mesopredators has been detected experimentally (Haswell et al. 2018), it remains unclear how mesopredators utilize caution and vigilance, in conjunction with avoidance, to navigate coexistence with apex predators. In light of this, we set out to understand how mesopredators utilize time, space and antipredator behaviors such as vigilance and caution to reduce the risk of predation from an apex predator.

Dingoes (*Canis dingo*), as Australia's apex predator suppress red foxes (*Vulpes vulpes*) (Wallach et al. 2010). Fox densities are lower 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 both 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 establishment (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 behavior and cultural learning (Haber 1996; Greenberg and Holekamp 2017).

Given the systemic and ubiquitous nature of predator persecution in Australia and globally (Ripple et al. 2014), there have been few opportunities to study the behavioral responses of mesopredators to apex predators where both predators are socially-stable (Wooster et al. 2019). As such, information on how mesopredators coexist with apex predators in the absence of human persecution is

required, particularly as calls to protect apex predators globally increase (Letnic et al. 2012; Wallach et al. 2015a).

To find out how mesopredators respond to apex predators under socially stable conditions, we studied the behavioral responses of foxes to dingoes in a rangeland environment where both predators were protected (Wallach et al. 2017). We focused on key resource points used by both predators, sites predicted to be peaks in the landscape of fear that are also essential for survival. We expected that: 1) foxes would concentrate their activity at resource points with lower dingo activity; 2) foxes would limit their visitations to times when dingoes were less active; and 3) foxes would be more cautious and vigilant when visiting sites with high dingo activity.

METHODS

Our study was conducted at two conjoined properties in the Painted Desert, South Australia: Evelyn Downs, a 2300 km² cattle station; and Mount Willoughby, a 5600 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. Given the size of both properties, the low human density, and the large home range of predators, human-predator encounters were uncommon. Whereas our study site is large enough to contain multiple dingo family groups, it is possible that both dingoes and foxes may venture onto neighboring persecuted properties. The Painted Desert is arid, receiving 160 mm of rainfall annually, and characterized by chenopod shrublands, Acacia woodlands, and ephemeral creek lines supporting Eucalyptus species. Foxes have likely been present at the study site since the 1940s (Saunders et al. 1995).

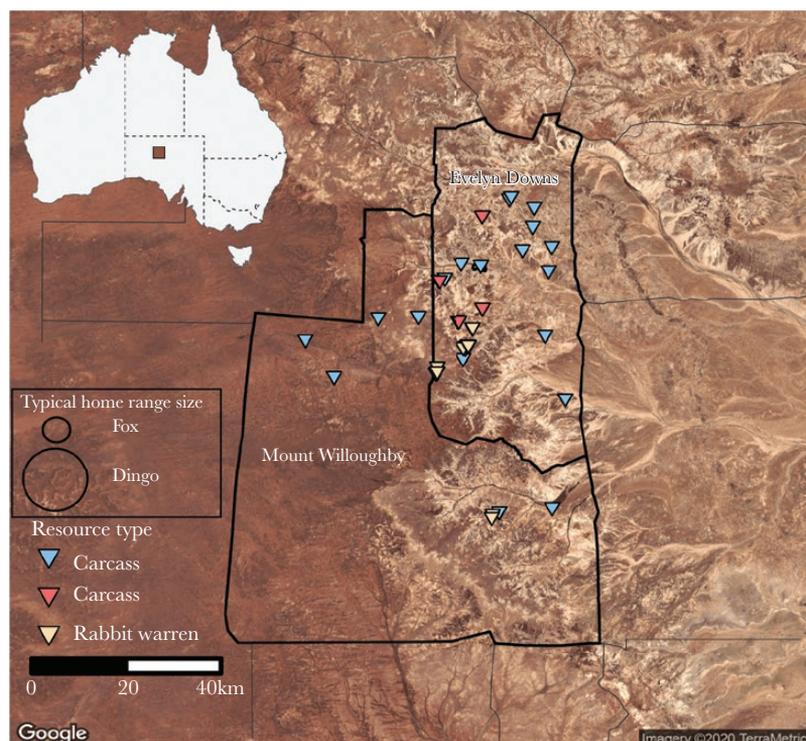


Figure 1 Predator-friendly study site in the Painted Desert, South Australia. Together, Evelyn Downs and Mount Willoughby cover 7900 km², which is large enough to contain several dingo territories. Typical home range sizes of dingoes and foxes in arid areas are shown for scale, based on average home 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.

In the winters of 2016, 2017, and 2018, we monitored foxes and dingoes at 21 water points (a mix of natural and artificial waters), 4 cattle carcasses, and 25 rabbit warrens (Table 1). After Wallach et al. (2009), we surveyed dingo scent-marks at each resource point as a metric of dingo territoriality. Scent-marking is a well-known form of communication for dingoes and other canids, conferring messages such as territory boundaries, locations, and social and breeding status (Corbett 1995). As scent-marks also convey information between species, we utilized dingo scent-mark frequency to infer the risk foxes would perceive when accessing each resource point, particularly as dingo scents have been shown to alter the behavior of foraging foxes (Leo et al. 2015). Dingoes often scent mark at focal points such as resource points or road junctions (Thomson 1992b; Wallach et al. 2009). Scat surveys were conducted in the 20 m radius surrounding the edge of each water point, carcass, and rabbit warren. Surveys took approximately an hour to complete and were conducted at the beginning or end of study period (Wallach et al. 2009).

To document the activity and behavior 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 were 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 s videos when motion was detected, with a 1-s interval. Fox visitations separated by >5 min 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). With more than 1195 camera-trap nights we recorded 116 fox events (253 detections) and 260 dingo events (1009 detections).

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 the two species, quantified using the Δ_4 overlap statistic as it is considered reliable for estimating activity patterns of species with sufficiently large sample sizes (>75 captures per species) (Ridout and Linkie 2009). To calculate the Δ_4 overlap statistic and 95% confidence intervals, we generated 10000 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”

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)

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 (Thomson 1992a; Moseby et al. 2009), we interpreted the occupancy parameter (psi) as the probability of use (likelihood of a species occurring at a resource point) to accommodate the lack of independence between our camera traps (MacKenzie et al. 2004). Error introduced by camera traps prematurely ending before the end of the sampling period was corrected for when generating detection histories using the R package “camtrapR” (version 2.0.3). We tested for spatial overlap between foxes and dingoes by calculating a species interaction factor (SIF) (Richmond et al. 2010) (Supplementary Table 1). Where SIF = 1, foxes and dingoes are considered to operate independently of one another; where SIF > 1, foxes are considered to aggregate with dingoes; and where SIF < 1 foxes avoid dingoes.

Fine-scale spatiotemporal 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.

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. Dingo activity was highest during 7:00 AM–13:00 PM and 16:00 PM–22:00 PM, indicating high-risk time periods for foxes (Figure 2).

To assess behavioral responses of foxes to dingoes, we conducted behavioral ethogram analysis from camera trap videos, which we compiled with evidence of dingo territoriality from field scat surveys. We focused on 4 behavioral metrics: confidence, cautiousness, vigilance, and scent-marking. Confidence has been used as a metric to describe the behavior of canids across contexts and individuals across species. Measures of confidence have described the tendency for foxes to increase their level of comfort in urban areas (Gil-Fernández et al. 2020), categorize the behaviors of captive fox kits (Fox 1971) and coyotes (Way et al. 2006). Confidence serves primarily as a metric to measure the absence of fear, within our study.

Behaviors were scored using Behavioral Observation Research Interactive Software version 7.9.15 (Friard and Gamba 2016). After 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, whereas cautiousness was classified by 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 (Fox 1971; Way et al. 2006). 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. All behaviors were summarized by their total duration per event, with the exclusion of scent-marking, which was measured as the number of discrete occurrences.

We compared the influence of dingo activity and territoriality (scent-marks), as well as conspecific activity (fox daily activity rate), on the confidence, cautiousness and vigilance of foxes using generalized linear mixed models (GLMMs). We ran successive models treating fox confidence, cautiousness, vigilance, activity rate, and

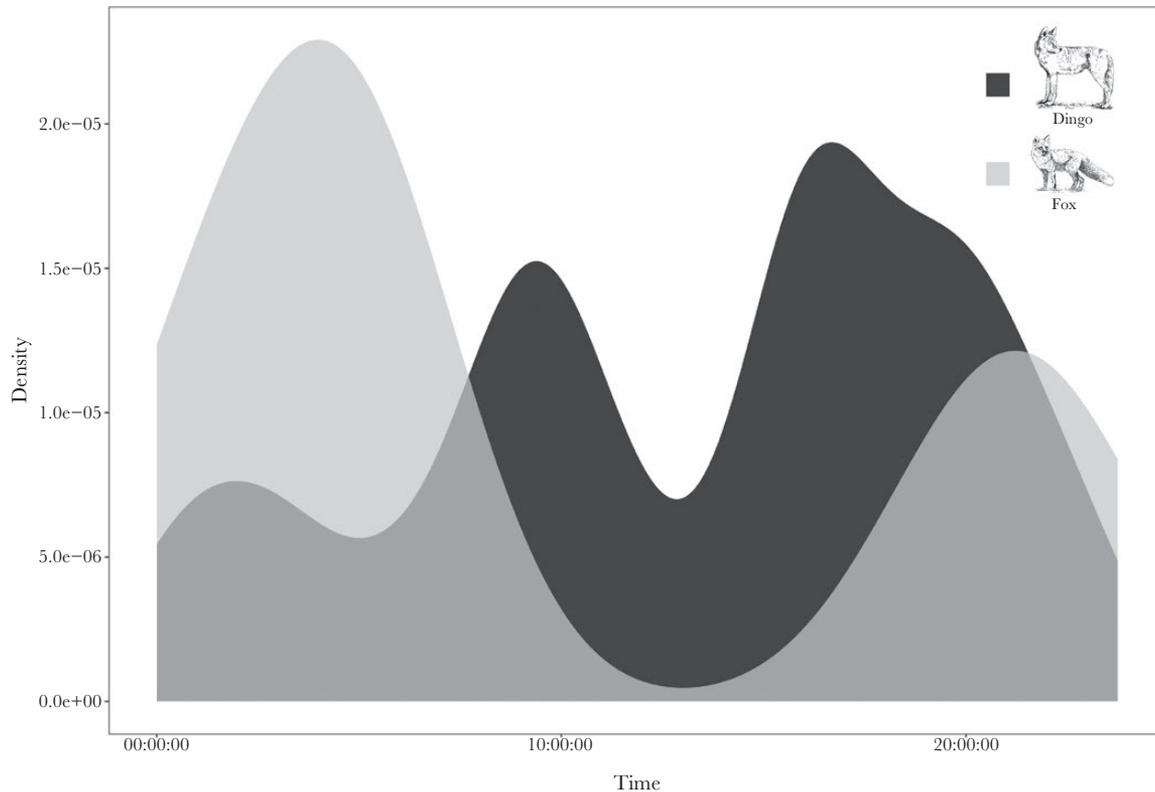


Figure 2

Fox and dingo temporal activity patterns at resource points. The Δ_4 temporal overlap coefficient was 0.43 ($\pm 95\%$ CI: 0.39–0.47).

scent-marking as 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. To account for the repeat sampling of resource points we included resource point nested in year as a random effect within our models. All predictor variables were standardized. GLMMs of fox cautiousness were modeled using a binomial distribution, vigilance with a negative binomial distribution, as previous models were heavily zero inflated, fox scent-marking using a binomial distribution and daily fox activity rate using a Poisson distribution. Zero inflation and overdispersion were tested for using the R package “DHARMA” (version 0.3.3.0). GLMMs were constructed using the “glmer” function in the R package “lme4” (Version 1.1–26). Partial dependence plots were constructed to highlight the relationships between predictor and dependent variables. They were constructed using the “effect_plot” function within the R package “jtools” (version 2.1.2).

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 ($\chi^2 = 93.32$, $P \leq 0.001$, $df = 2$).

Spatiotemporal avoidance was clear at warrens and waterpoints ($\chi^2 = 37.44$, $P \leq 0.001$, $df = 2$), but not at carcasses ($\chi^2 = 5.57$, $P = 0.061$, $df = 2$) (Figure 3).

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: $df = 92$, $P = 0.207$) (Figure 4a,b, Table 2) or vigilance (dingo activity: $df = 92$, $P = 0.908$, dingo scent-marking: $df = 92$, $P = 0.867$) (Figure 4c,d, Supplementary Table 2). Additionally, fox daily activity rates ($df = 92$, $P \leq 0.001$) 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 ($df = 19$, $P \leq 0.001$, Supplementary Table 3). Foxes were more confident at resource points where conspecific activity was highest ($df = 92$, $P = 0.022$) (Figure 5a).

DISCUSSION

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

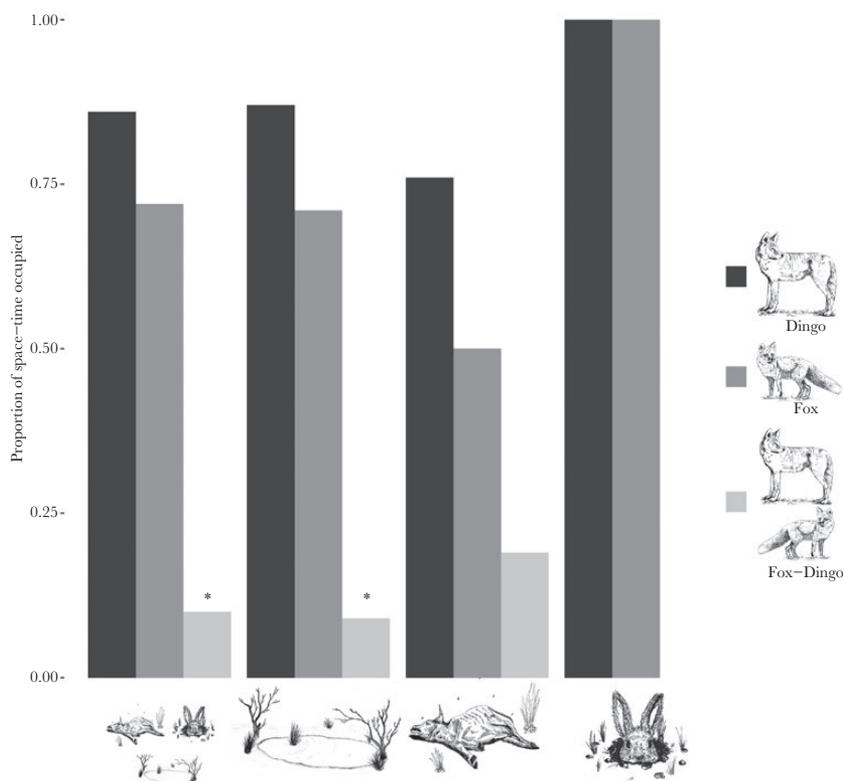


Figure 3 Proportions of space and time divided into hour-long bins, where predators were exclusively present at resource points or where they overlapped. X axis indicates resource type: across all, water points, carcasses, and rabbit warrens. Asterisks denote significance ($P < 0.05$).

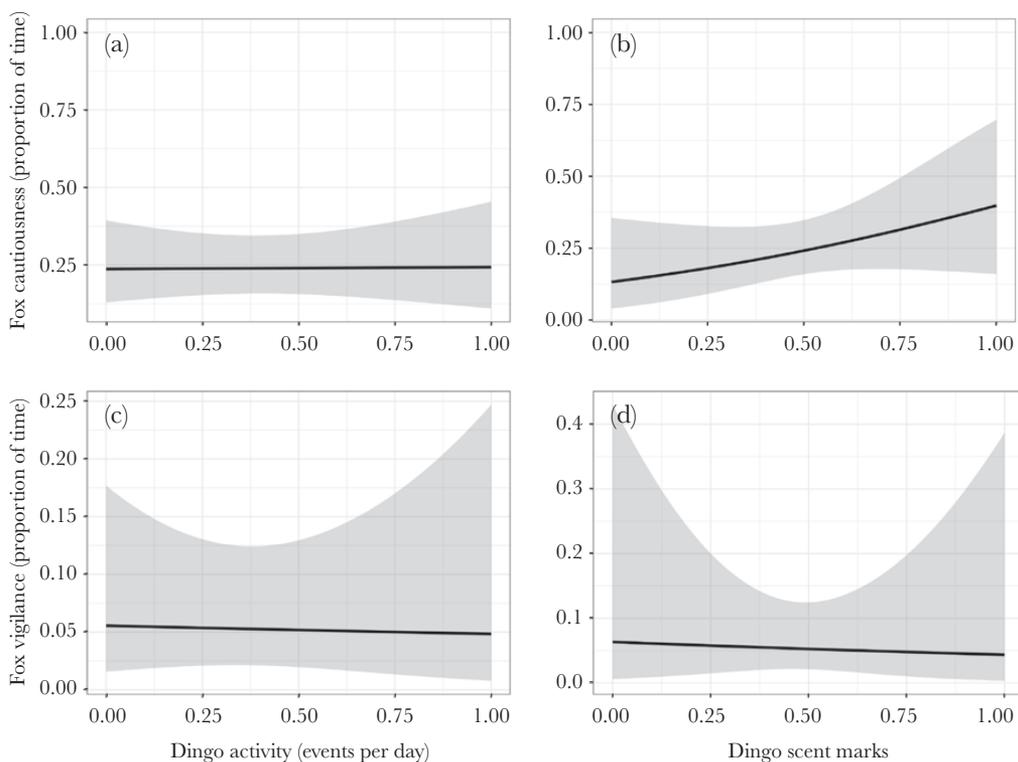
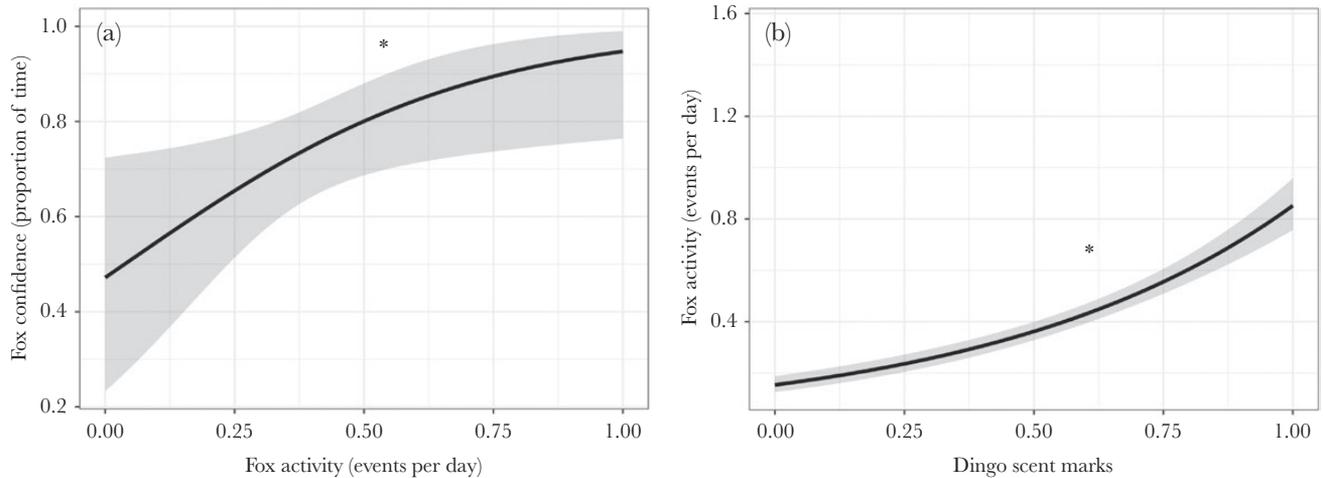


Figure 4 Predicted relationships from generalized linear mixed models comparing: (a) the proportion of time foxes were cautious to daily dingo activity rate at resource points; (b) the proportion of time foxes were cautious to number of dingo scent-marks counted in surveys across resource points; (c) 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.

Table 2

Output from generalized linear mixed effects model examining the effect of dingo and conspecific predictor variables on fox cautious behavior. 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	<i>P</i>
Intercept	-0.585	-1.828 to 0.484	0.50098	-1.169	0.2422
Dingo scent-marking	1.463	-1.828 to 0.484	1.15923	1.262	0.2071
Time risk	-0.146	-1.89 to 1.040	0.66999	-0.219	0.8270
Dingo daily activity	0.0301	-1.565 to 1.558	0.66800	0.046	0.9631
Daily fox activity	-3.004	-7.408 to 0.488	1.30729	-2.298	0.0216 *

**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 ($P < 0.05$).

that foxes avoided dingoes in space and time yet increased their activity at resource points where scent-marks were concentrated, scent-marks are likely not to deter foxes or inspire fear as foxes access resource points when dingoes are absent. Similarly, various species of fox (red and gray foxes – *Urocyon cinereoargenteus*) display attraction to the scents of their predators, increasing both activity and scent marking rates where the scent-marks of their predators are concentrated (Allen et al. 2016; Wikenros et al. 2017). We do not dispute that foxes are fearful of encountering dingoes (Leo et al. 2015). Instead, a plausible explanation is that the activity patterns of socially-stable dingoes are more predictable (Wallach et al. 2009; Brook et al. 2012), and thus foxes may develop the necessary knowledge to reduce risky encounters and thus confidently avoid them in the heart of their territories.

Around the globe, protected populations of predators have been observed coexisting through the use of similar fine-scale avoidance strategies. In Serengeti National Park, where predators are protected, hyenas (*Crocuta crocuta*) and cheetahs (*Acinonyx jubatus*) experience high rates of lion predation (*Panthera leo*) yet are not spatially displaced by them. Rather, subordinate predators avoid lions on a “moment-to-moment” basis, which is much less costly than long-term spatial segregation, restricting access to space that lions frequent (Swanson et al. 2016). Similarly, in protected reserves in India, tigers (*Panthera tigris*) pose a substantial threat to dholes (*Cuon alpinus*) and leopards (*Panthera pardus*). Subordinate predators respond with fine-scale spatiotemporal avoidance, facilitating the co-occupancy of space (Karanth et al. 2017). Foxes in our study

site mirror the fine-scale avoidance strategies utilized by other mesopredator species to prevent direct encounters with potentially deadly predators.

In addition to this finding, however, we found that foxes were more confident at resource points with high levels of conspecific activity, suggesting a level of comfort at resource points they and other conspecifics frequent. Our results align with observations of coyotes (*Canis latrans*) and foxes coexisting with little fear or aggression (Mueller et al. 2018). Whereas 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 substantial 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 (Minta et al. 1992; Couzin et al. 2005; Bshary et al. 2006; Toledo et al. 2020). As sentient, sapient and social beings, they possess the capability to develop knowledge of their ecological communities. However, this knowledge has not yet been fully incorporated into theories developed to explain emergent ecological processes, such as trophic cascades.

Accounting for the cognitive capacities of individuals has aided behavioral 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 carnivores (coyotes and badgers – *Taxidea taxus*) (Minta et al. 1992); and that human persecution alters the development of personalities in juvenile hyenas (*C. 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 and shape their environments.

Our results highlight the inherent complexity that comes with understanding ecological processes involving 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 increases in fear. Although 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. Future work may benefit from exploring predator–prey interactions beyond the landscape of fear, perhaps, venturing into a *landscape of knowledge*.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This study was funded by Australian Research Council grant number DP180100272.

We are grateful to Caroline Thomas and John Knight, Evelyn Downs, and the Lennon family, traditional custodians of Mount Willoughby, for site access and hospitality. We thank L. Juillard for assistance with video analysis; J. Parkhurst for dingo and fox illustrations; L. Toke for resource point figure illustrations; and E. Rogers, E. Yanco, C. Hasselerharm, and G. Bensen for helpful discussions. We thank Dr Snell-Rood and three anonymous reviewers for comments on the manuscript.

AUTHOR CONTRIBUTIONS

E.W., D.R., A.J.O., and A.D.W. conceived and designed the project. E.W., E.J.L., A.J.O., and A.D.W. collected the data. E.W., D.R., E.J.L., and A.D.W. performed the analysis. E.W. lead the writing and all authors contributed to the editing.

Data availability: Analyses reported in this article can be reproduced using the data provided by (Wooster et al. 2021).

Handling editor: Emilie Snell-Rood

REFERENCES

- Allen ML, Gunther MS, Wilmers CC, 2016. The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore. *J Ethol.* 35:13–19.
- Barrett LP, Stanton LA, Benson-Amram S, 2019. The cognition of “nuisance” species. *Anim Behav.* 147:167–177.
- Berger KM, Gese EM. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *J Anim Ecol.* 76:1075–1085.
- Brawata RL, Neeman T, 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. *Wildl Res.* 38:426–436.
- Brook LA, Johnson CN, Ritchie EG, 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *J Appl Ecol.* 49:1278–1286.
- Brown JS, Laundré JW, Gurung M, 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J Mammal.* 80:385–399.
- Bshary R, Hohner A, Ait-el-Djoudi K, Fricke H. 2006. Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biol.* 4:e431.
- Corbett LK, 1995. *The Dingo in Australia and Asia.* Ithaca, NY: Comstock/Cornell.
- Couzin ID, Krause J, Franks NR, Levin SA. 2005. Effective leadership and decision-making in animal groups on the move. *Nature.* 433:513–516.
- Fox M, 1971. *Behaviour of wolves, dogs and related canids.* Wenatchee (WA): Dogwise Publishing.
- Friard O, Gamba M, 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol.* 7:1325–1330.
- Gallagher AJ, Creel S, Wilson RP, Cooke SJ. 2017. Energy landscapes and the landscape of fear. *Trends Ecol Evol.* 32:88–96.
- Gil-Fernández M, Harcourt R, Newsome T, Towerton A, Carthey A, 2020. Adaptations of the red fox (*Vulpes vulpes*) to urban environments in Sydney, Australia. *J Urban Ecol.* 6:juaa009.
- Greenberg JR, Holekamp KE, 2017. Human disturbance affects personality development in a wild carnivore. *Anim Behav.* 132:303–312.
- Haber GC, 1977. *Socio-ecological dynamics of wolves and prey in a sub-arctic ecosystem.* Vancouver: University of British Columbia.
- Haber GC, 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. *Conserv Biol.* 10:1068–1081.
- Haswell PM, Jones KA, Kusak J, Hayward MW. 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia.* 187:573–583.
- Karanth KU, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, Kumar NS, 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proc R Soc B Biol Sci.* 284:20161860.
- Laundré JW, Hernandez L, Ripple WJ, 2009. The landscape of fear: ecological implications of being afraid. *Open J Ecol.* 3:1–7.
- Leo V, Reading RP, Letnic M. 2015. Interference competition: odours of an apex predator and conspecifics influence resource acquisition by red foxes. *Oecologia.* 179:1033–1040.
- Letnic M, Greenville A, Denny E, Dickman CR, Tischler M, Gordon C, Koch F, 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Glob Ecol Biogeogr.* 20:343–353.
- Letnic M, Ritchie EG, Dickman CR. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biol Rev Camb Philos Soc.* 87:390–413.
- Lima SL, Bednekoff PA. 1999. Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Anim Behav.* 58:537–543.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool.* 68:619–640.
- Linnell JD, Strand O, 2000. Interference interactions, co-existence and conservation of mammalian carnivores. *Divers Distrib.* 6:169–176.
- MacKenzie DI, Bailey LL, Nichols JD, 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *J Anim Ecol.* 73:546–555.
- Minta SC, Minta KA, Lott DF, 1992. Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). *J Mammal.* 73:814–820.
- Moseby KE, Stott J, Crisp H, 2009. Movement patterns of feral predators in an arid environment implications for control through poison baiting. *Wildl Res.* 36:422–435.
- Mueller MA, Drake D, Allen ML. 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. *PLoS One.* 13:e0190971.
- Philip J, 2019. The institutionalisation of poison: a historical review of vertebrate pest control in Australia, 1814 to 2018. *Aust Zool.* 40:129–139.
- R Core Team. 2018. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Richmond OM, Hines JE, Beissinger SR. 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecol Appl.* 20:2036–2046.
- Ridout MS, Linkie M, 2009. Estimating overlap of daily activity patterns from camera trap data. *J Agr Biol Envir St.* 14:322–337.
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science.* 343:1241484.
- Rolls EC, 1923. *They all ran wild: the story of pests on the land in Australia.* Sydney: Angus and Robertson.

- Saunders G, Coman B, Kinnear J, Braysher M, 1995. Managing vertebrate pests: foxes. Canberra: Australian Government Publishing Service.
- Swanson A, Arnold T, Kosmala M, Forester J, Packer C. 2016. In the absence of a “landscape of fear”: how lions, hyenas, and cheetahs coexist. *Ecol Evol.* 6:8534–8545.
- Thomson P, 1992a. The behavioural ecology of dingoes in north-western Australia. IV. Social and spatial organization, and movements. *Wildl Res.* 19:543–563.
- Thomson PC, 1992b. The behavioural ecology of dingoes in north-western Australia. II. Activity patterns, breeding season and pup rearing. *Wildl Res.* 19:519–529.
- Toledo S, Shohami D, Schiffner I, Lourie E, Orchan Y, Bartan Y, Nathan R. 2020. Cognitive map-based navigation in wild bats revealed by a new high-throughput tracking system. *Science.* 369:188–193.
- Wallach AD, Bekoff M, Nelson MP, Ramp D. 2015a. Promoting predators and compassionate conservation. *Conserv Biol.* 29:1481–1484.
- Wallach AD, Izhaki I, Toms JD, Ripple WJ, Shanas U. 2015b. What is an apex predator? *Oikos.* 124:1453–1461.
- Wallach AD, Johnson CN, Ritchie EG, O’Neill AJ. 2010. Predator control promotes invasive dominated ecological states. *Ecol Lett.* 13:1008–1018.
- Wallach AD, Ramp D, O’Neill AJ. 2017. Cattle mortality on a predator-friendly station in central Australia. *J Mammal.* 98:45–52.
- Wallach AD, Ritchie EG, Read J, O’Neill AJ. 2009. More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLoS One.* 4:e6861.
- Way JG, Szumylo D-LM, Strauss EG. 2006. An ethogram developed on captive eastern coyotes *Canis latrans*. *Can Field-Nat.* 120:263–288.
- Wikenros C, Jarnemo A, Frisén M, Kuijper DPJ, Schmidt K. 2017. Mesopredator behavioral response to olfactory signals of an apex predator. *J Ethol.* 35:161–168.
- Wooster EIF, Ramp D, Lundgren EJJ, O’Neill AJ, Wallach AD. 2021. Red foxes avoid apex predation without increases in fear. *Behav Ecol.* <https://data.dryad.org/stash/dataset/doi:10.5061/dryad.ghx3fbbnv>
- Wooster E, Wallach AD, Ramp D. 2019. The wily and courageous red fox: behavioural analysis of a mesopredator at resource points shared by an apex predator. *Animals.* 9:907.