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RESEARCH NOTE

The red fox (*Vulpes vulpes*) is the dominant predator of lizard models in a semi-arid landscape, and predation risk is reduced by vegetation cover

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Abstract

Vegetation structure affects predation risk in ecosystems around the world. Spinifex (*Triodia* spp.) is a foundation species in fire-prone grasslands and woodlands that cover more than a third of Australia's land surface. Spinifex habitats are known for their high reptile diversity, and it has long been hypothesized that the spiky structure of spinifex dissuades predators, thereby providing a haven for prey. We investigated predation risk to small lizards in semi-arid Australia by identifying teeth marks on replica model plasticine lizards, in combination with remote camera surveillance, to quantify and verify predation risk across several microhabitats, including spinifex. The introduced red fox (*Vulpes vulpes*) was identified as the main predator of lizard models, constituting 43.9% of all predation attempts. Lizard models placed at the base of spinifex plants (*Triodia scariosa*) were significantly less likely to be attacked than all other microhabitat types (bare ground, leaf litter, burrows), confirming the hypothesis that spinifex reduces predation risk. Our results support recent work that has highlighted foxes as a significant predator of Australian reptiles. Given that fire is a driver of spinifex cover in arid ecosystems, our findings have implications for interactions between fire and invasive predators in Australian ecosystems.

KEYWORDS
hunting, mammalian predators, microhabitat, squamate, vegetation cover, wildfire

INTRODUCTION

Vegetation structures play a critical role in mediating predation risk in ecosystems worldwide (Janssen et al., 2007). Spinifex grass (*Triodia* sp.), characterized by its tough, spiky texture, dominates more than a third of Australia's immense arid and semi-arid interior. Spinifex is an essential habitat for various small vertebrates due to its comparatively cooler microclimate, rich invertebrate composition, and spiky structure that provides protection from predators (Bell et al., 2021; Pianka, 1989). However, spinifex is highly flammable, rendering the associated vegetation communities susceptible to fire. As such, the abundance and cover of spinifex in a given location often reflects the area's fire history (Haslem et al., 2011), which in turn influences animal species whose abundance varies in response to changes in spinifex structure, such as cover or height (Verdon et al., 2020).

Invasive predators are a major driver of global biodiversity loss (Doherty et al., 2016). Often, native species are naïve to the risks posed by invasive predators, leading to increased mortality rates (Sih et al., 2010). As a result, invasive predators tend to exert a stronger suppressive effect on native prey compared with native predators (Salo et al., 2007). Recent studies have emphasized the predatory pressure exerted by invasive predators on Australian reptiles. For instance, red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) are known to prey on 263 and 108 reptile species, respectively, including 15 and 20 threatened species (Stobo-Wilson et al., 2021). However, beyond their dietary habits, little is known about the fine-scale behaviours of foxes and cats when hunting reptiles, including what triggers their detection of prey and decisions on whether or not to launch an attack.

We conducted a field experiment using model plasticine lizards to assess which predators most frequently attack lizards, and to test the influence of spinifex on attack rates. Plasticine models provide a surrogate measure of predation pressure on stationary prey in instances where studying real animals is not feasible or ethically permissible. Their use allows for an approximation of predation risk, but does not incorporate some important elements of real predator–prey encounters; namely, prey in real encounters have the option to flee an approaching predator. Nonetheless, plasticine models have been successfully used to study lizard predation in a variety of contexts, including drivers of niche divergence (Daly et al., 2008), the influence of colour on predation risk (Stuart-Fox et al., 2003), and the impact of vegetation structure on predation rates (Bradley et al., 2022; Sato et al., 2014). We were particularly interested in predation pressure exerted by the red fox (*Vulpes vulpes*), after a previous study revealed it to be the most widespread invasive predator within the study region (Payne et al., 2014). We conducted this study in the semi-arid mallee region of Victoria, Australia, which is home to many reptile species closely associated with spinifex grass (Bell et al., 2021; Cogger, 1989). We hypothesized that red foxes would be frequent predators of the model lizards. Additionally, we predicted that the model lizards situated in areas with simpler vegetation structures would be more susceptible to predation compared with those positioned within densely vegetated areas, like those containing spinifex grass.

MATERIALS AND METHODS

Study area

We conducted this study in Murray-Sunset National Park in the semi-arid northwest region of Victoria, Australia (coordinates: 34.81° S, 141.64° E). The research focused on the predominant vegetation type in the park, known as 'triodia mallee'. This vegetation is characterized by a canopy of multi-stemmed *Eucalyptus dumosa* and *E. socialis*, underlain by spinifex grass (*Triodia scariosa*) and interspersed with shrubs (Haslem et al., 2010). The area is vulnerable to wildfires, which typically result in the consumption of most vegetation biomass at a site, including the vast majority of spinifex. As the time elapsed since the last fire increases, vegetation, including spinifex, progressively regenerates (Haslem et al., 2011).

Study design

Replica lizard models

We hand-crafted 280 plasticine lizards (Rainbow modelling clay, S & S Wholesale Pty Ltd, Thornleigh, New South Wales, Australia; see Daly et al., 2008). Each model had an approximate 80 mm snout-vent length, a tail of equal length, and weighed around 90 g. They were painted to match the mallee dragon's (*Ctenophorus fordi*) colour—an agamid lizard (i.e., Family Agamidae) that is locally abundant and influenced by fire and vegetation structure (Nimmo et al., 2012)— using colour-matching scanners (Bunnings Warehouse Pty Ltd, Thomastown, Victoria, Australia) from a photograph of a mallee dragon. To simulate movement and attract predators, we attached each model to a platform connected to a spring, allowing them to sway in the wind.

Experimental design

The lizard replicas were spread across 40 sites that were 20 ×20 m in size and separated by at least 300 m. Within each plot, seven plasticine lizard models were arranged (280 models total). In each of the 40 sites, six lizard models were placed in the three dominant microhabitats: (1) bare ground, (2) leaf litter, and (3) spinifex, with allocation to each microhabitat being relative to proportional coverage, which was visually estimated by SB using a Braun-Blanquet cover scale. Additionally, a seventh lizard model was situated within a small hole in the sandy substrate, simulating a lizard emerging from its burrow. Models set in spinifex were positioned so that they were partially emerging from the base of the spinifex clump, which imitates the behaviour of spinifex specialist lizards that use this anti-predator tactic during the initial stages of basking (Cogger, 1974). At each site, a motion-sensing camera (ScoutGuard 550) was installed 1 m in front of one of the lizard models placed on bare ground at a height of 50 cm to monitor for any predation events.

Monitoring predation events

Models were deployed for 47 days in summer (December 2012 to January 2013) when reptile activity in the region is at its highest. Following retrieval, models were inspected for bite marks to identify instances of predation and the likely predator involved (e.g., fox, varanid lizard, other lizards, bird, cat, or unknown). This approach has been successfully employed in previous studies to both recognize predators and to measure predation rates (Bateman et al., 2017; Daly et al., 2008). To ensure the accuracy of predator identification based on bite marks, the data were corroborated using known predation events captured by the remote cameras. The relatively long period between deployment and retrieval means that predators may have learned that lizard models were not real prey during the deployment period, but we are unable to verify this with our data.

Statistical analysis

We employed generalized linear mixed models (GLMMs) with a binomial error distribution using the lme4 package in R (Bates et al., 2015). We included 'site' as a random effect because the models were spatially clustered within sites. The response variable in our analysis was a binary variable with 0 indicating no predation on a model and 1 indicating any predation. Total predation was chosen over predation by specific predators due to the relatively low sample size of predation events for each group.

To evaluate whether the cameras' presence influenced the likelihood of predation, we first constructed a GLMM to compare the lizard models that were positioned in front of cameras with those situated in the same microhabitat (i.e., bare ground) but not in front of cameras. Next, we modelled the probability of predation in relation to the type of microhabitat, which was treated as a single predictor variable with four categories. 'Spinifex' was designated as the reference category, and it was compared against 'bare ground', 'leaf litter', and 'burrow'. GLMMs were used to calculate odds ratios which measure the odds that a predation event will occur under one treatment in relation to the reference category.

RESULTS

During the 47-day sampling period, attacks were recorded on 57 of the 280 lizard models (20.4% of all models). Foxes were the primary predators, accounting for the largest number of predation attempts (25 instances, or 43.9% of the attacks) (Figure 1). They were followed by birds (12 instances; 21.1%), other reptiles (10 instances; 17.5%), unidentified predators (9 instances; 15.7%), and lastly, a single predation event by a feral cat (1 instance; 1.8%). The footage from the motion-sensing cameras captured foxes exhibiting strong behavioural responses indicative of predation attempts. They were seen carefully approaching the models and then chewing and pulling at them for several seconds, leaving behind characteristic stretching on the devices and chew marks on the models (Figure 2). In most cases, the evidence for identifying the predators was clear, as distinguishable teeth marks were left on the models. Moreover, tracks and scat found near the models often aided in predator identification. Out of the 25 instances involving foxes, cameras recorded 28%, with each recording confirming the correct field identification of fox predation. The placement of models in front of cameras did not have an impact on the overall predation rates (GLMM coefficient = −0.50, S.E. = ±0.86).

The microhabitat where a lizard model was positioned significantly impacted the likelihood of predation overall (Figure 3, Table 1). In terms of total predation, models placed on bare ground, in leaf litter, and in burrows were 3.58, 3.44, and 6.03 times respectively more likely to be preyed upon compared with those placed in spinifex (Figure 3, Table 1). Microhabitat accounted for ~10% of the variation in the data (Table 1).

DISCUSSION

Our study has demonstrated that foxes are a dominant predator of lizards in the study region, accounting for more than 40% of all recorded attacks. It is increasingly evident that red foxes play a significant role as predators of reptiles, particularly lizards, in Australian ecosystems. Stobo-Wilson et al. (2022) estimated that foxes are responsible for the predation of ~88 million reptiles annually across Australia, including 95 squamate (i.e., lizards and snakes) species. Fleming et al. (2021) noted that reptiles are frequently found in the scats and stomachs of foxes, especially in arid and semi-arid regions. Our study corroborates this by demonstrating that foxes were the dominant predator of lizards during the summer months in a semi-arid region. More generally, our findings are consistent with previous

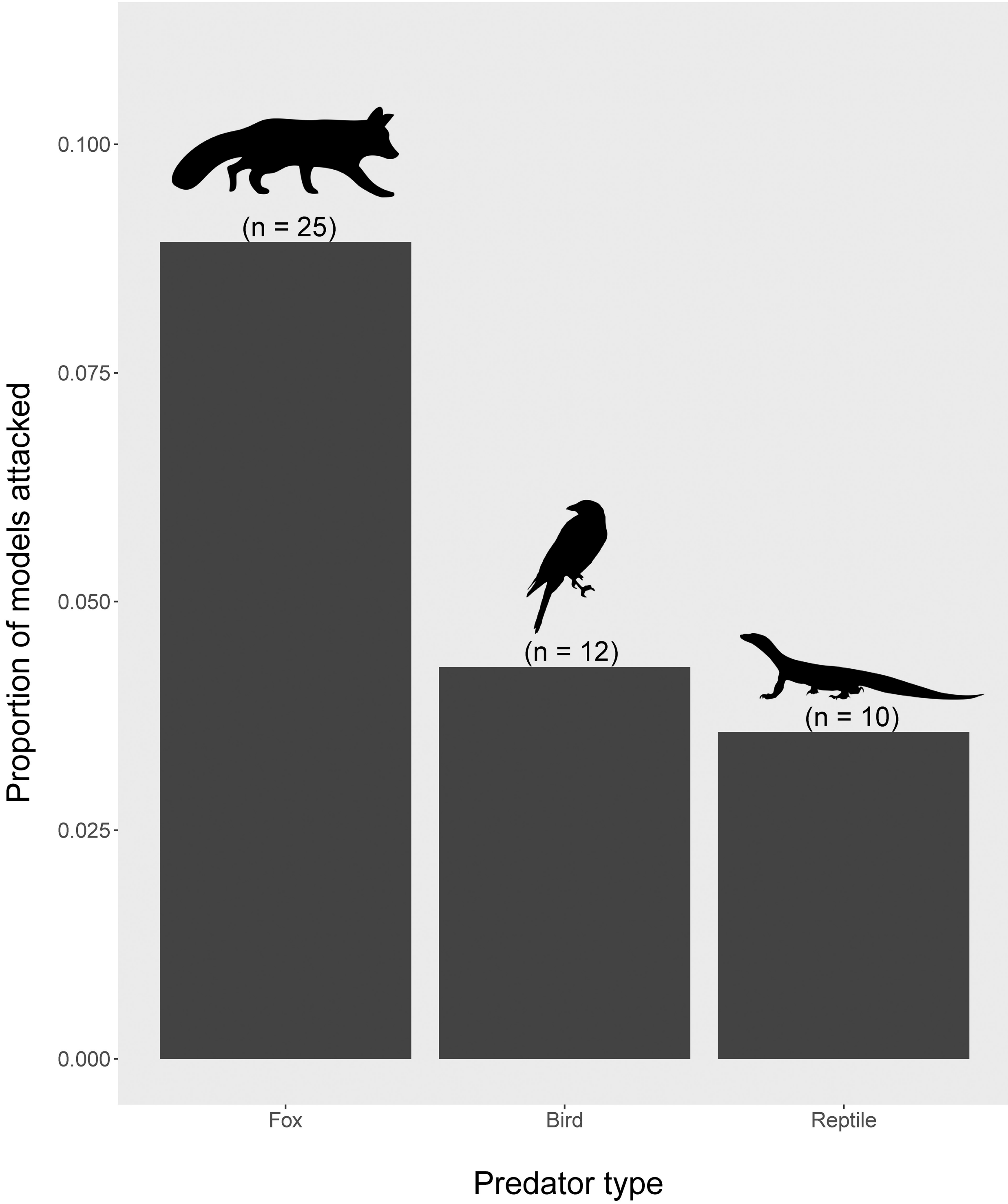

FIGURE 1 The proportion of predator attacks made by foxes, birds, and reptiles out of 280 lizard models placed throughout mallee habitats in south-eastern Australia. The total number of attacks by each predator type is provided in parenthesis.

studies of plasticine model reptiles that have found mammals to be dominant predators (Duchesne et al., 2022; Purger et al., 2017).

Stobo-Wilson et al. (2022) observed that reptiles are more frequently found in the diets of foxes in areas with sparse vegetation and higher temperatures. This finding is complemented by other research underscoring the role of vegetation structure in moderating reptile predation risk (Duchesne et al., 2022; Hansen et al., 2019; Sato et al. 2014). Our research

FIGURE 2 Screen shots of predation attempts on lizard models. Top row: red foxes (*Vulpes vulpes*); bottom row: red fox, white winged chough (*Corcorax melanorphamphos*) and central bearded dragon (*Pogona vitticeps*).

contributes to this discussion, revealing that lizards placed near the base of spinifex clumps are less likely to fall prey, indicating that denser vegetation like spinifex serves as a refuge for small vertebrates. The protective role of spinifex can be attributed to two primary factors: its physical protection and its impact on prey detection by predators. Spinifex's dense and spiky nature provides a physical barrier that would likely be uncomfortable for predators to penetrate during hunting (Cogger, 1974; Pianka, 1989). This deterrent may discourage predators from pursuing prey within spinifex clumps. Additionally, our positioning of lizard models—designed to imitate lizards partially covered by spinifex while basking at the base of the clump—could obscure predators' visual detection from behind or above. Therefore, the lower predation rates on lizard models under spinifex may also be due to reduced prey visibility to predators. We believe that these two factors, protection and reduced detection, jointly contribute to the observed decrease in predation rates on our lizard models, and real lizards.

Spinifex is a crucial resource for numerous lizards throughout much of arid and semi-arid Australia, and its cover and structure significantly influence the presence of spinifex specialist species (Nimmo et al., 2014; Verdon et al., 2020). Besides offering refuge from predators, spinifex also provides shelter from temperature extremes by moderating the microclimate (Bell et al., 2021; Cogger, 1974) and supports termite populations, which are essential prey for many spinifex specialists (Morton & James, 1988). Our study suggests that protection from predation is likely to account for at least part of the association between reptiles and spinifex (Pianka, 1989).

The pace of spinifex recovery after a fire is closely tied to the rate at which fauna dependent on spinifex can re-colonize burnt landscapes. In our study system, spinifex is very rare in the years after fire, comprising about 2% of ground cover immediately after fire, and taking ~30 years to reach peak cover of ~20% (Haslem et al., 2011). Fire regimes that result in large amounts of recently burnt vegetation are likely to heighten predation risk for a variety of spinifex-dependent species by removing the protection from predation that is afforded by spinifex. This predation pressure could be

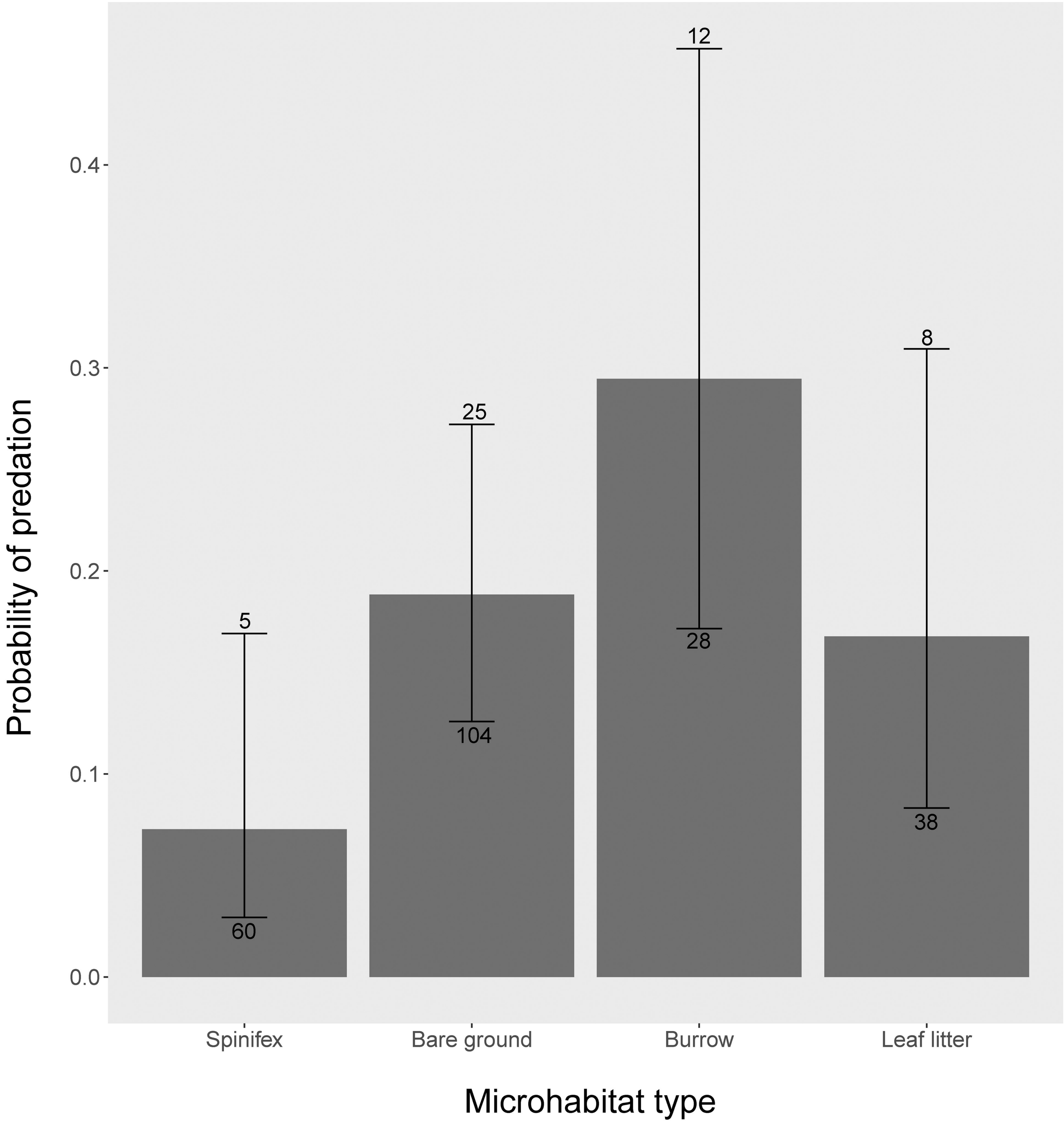

FIGURE 3 Predictions from generalized linear mixed models of the probability of a model being attacked by any predator over the 47 days deployment period according to the microhabitat within which the lizard model was placed. Error bars represent 95% confidence intervals. The number above each error bar represents the total count of models attacked, while the number below indicates the count of models not attacked, within each microhabitat type.

magnified if red foxes and cats are drawn into recently burnt areas, which has recently been demonstrated in the Murray mallee (Senior et al., 2023). Retaining patches of unburnt spinifex within the fire boundary could be one way of maintaining reptile species diversity during prescribed burning. In support of this, Senior et al. (2023) found three species of reptile and reptile richness was higher in areas near large unburnt refuges following a prescribed fire in the mallee.

Our study does have limitations. First, employing a more realistic model, perhaps created from 3D prints of scanned lizards and equipped with life-like movements, might yield more ecologically meaningful predation rates

TABLE 1 Generalized linear mixed model results depicting the odds of replica lizard models being attacked in different microhabitats, with 'Spinifex' as the reference category.

Predictors	Odds ratios	CI	*p*
Intercept (Spinifex)	0.08	0.03–0.20	<0.001
Bare ground	3.58	1.30–9.85	0.013
Burrow	6.03	1.92–18.95	0.002
Leaf Litter	3.44	1.07–11.03	0.038
Observations	280		
Marginal R^2/conditional R^2	0.096/0.137		

Note: The table presents the odds ratios, confidence intervals (CI), and *p*-values for each predictor (Bare ground, Burrow, Leaf Litter). Random effects, Intraclass Correlation Coefficient (ICC), and *R*-squared values (Marginal R^2 and Conditional R^2) are also displayed.

compared with what was observed in the current study. Second, introducing novel objects into the environment, even if they are designed to resemble real animals, might prompt predators to investigate the objects for reasons other than predation. Some studies have employed control models constructed from the same materials as the animal replicas but without mimicking the shape of an animal (e.g., Bell et al., 2021). Although relatively few studies deploy such controls, this approach can be instrumental in distinguishing genuine predation from other behaviours that might be misconstrued as predation events (e.g., predators investigating or attempting to remove the unfamiliar object). It can also help differentiate the cues that predators rely on to locate prey (i.e., visual versus olfactory) (Bateman et al., 2017). It would be beneficial for future studies to compare predation rates in other types of low vegetation, such as small shrubs that lack spiky features, to better differentiate between the protection and detection factors mentioned earlier. Future research could also examine how varying environmental conditions affect predation rates. Our study was conducted after 2 years of very high rainfall (2010–2011) relative to the long-term average, which likely inflated predator populations through increased prey abundance. In contrast, Bell et al. (2021) conducted a similar experiment during a drought, but recorded almost no predator attacks on their lizard models.

Our study has confirmed that spinifex protects prey animals from predation by an invasive predator, the red fox. Fire management should seek to maintain unburnt patches of spinifex during prescribed burning to create predator refuges that facilitate the persistence and recovery of prey animals following fire.

AUTHOR CONTRIBUTIONS

Shannon Braun: Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal). **Euan G. Ritchie:** Conceptualization (lead); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); writing – review and editing (equal). **Tim S. Doherty:** Formal analysis (equal); writing – review and editing (equal). **Dale G. Nimmo:** Conceptualization (lead); formal analysis (lead); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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