



## Differential behavioural flexibility in response to predation risk in native and introduced tropical savannah rodents



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Differential predation risk between habitats, or 'the landscape of fear', can have profound impacts on foraging strategies of prey. Few studies, however, have described the landscape of fear in the wild, in relation to predator densities. Using giving-up density experiments, and vertebrate surveys, we described the landscape of fear for two rodent species in relation to actual predator abundances in a tropical savannah. We offered native eastern chestnut mice, *Pseudomys gracilicaudatus*, and introduced house mice, *Mus musculus domesticus*, food in the open, and under the cover of grass. When eastern brown snakes, *Pseudonaja textilis*, were absent, both eastern chestnut and house mice consumed more food items under grass. In habitats where snakes were abundant, however, eastern chestnut mice changed their foraging behaviour, and consumed more food items in the open than under grass. In contrast, non-native house mice reduced their foraging activity under cover, but showed no increase in foraging in the open in the presence of snakes. Thus, native eastern chestnut mice have the ability to change their foraging tactics to adjust their antipredator behaviour to remain successful in the presence of native eastern brown snakes, whereas introduced house mice did not exhibit this behaviour.

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Predation is a strong force influencing most aspects of life for prey animals (Lima & Dill, 1990). Time of day, season, moon radiance, habitat structure and vegetation height, distance to shelter, predator odours and predator abundance may all influence activity because of their influence on the perceived risk of predation (Abramsky, Rosenzweig, & Subach, 2002; Bouskila, 1995; Jacob, 2008; Jacob & Brown, 2000; Kotler, Ayal, & Subach, 1994; Lima & O'Keefe, 2013; Orrock, Danielson, & Brinkerhoff, 2004; Sih, 2013; Ylönen, Jacob, Davies, & Singleton, 2002). Because predation risk has such a profound influence on activity, avoiding predation can be costly. Time spent avoiding predators may influence fitness because foraging or mating success is reduced (Lima & Dill, 1990), so there should be selection for prey to temper their responses according to the real level of risk posed by different predators. Predator-specific responses have been observed in many groups (reptiles: Lloyd, Alford, & Schwarzkopf, 2009; mammals: Cremona, Crowther, & Webb, 2014; Phillips & Waterman, 2013; amphibians Bulbert, Page, & Bernal, 2015). Thus, although animals alter their

behaviour to avoid predators, they are often adept at minimizing the costs of predator avoidance.

Many rodent species avoid open microhabitats, which are perceived as areas with higher predation risk, and therefore they forage under and around structures to reduce detection (e.g. Abu Baker & Brown, 2010; Dickman, 1992; Dickman, Greenville, Beh, Tamayo, & Wardle, 2010; Fanson, Fanson, & Brown, 2010; Jacob, 2008; Jacob & Brown, 2000; Mandelik, Jones, & Dayan, 2003; Pastro & Banks, 2006; Powell & Banks, 2004; Strauss, Solmsdorff, Pech, & Jacob, 2008). Rodents threatened by snakes may, however, avoid cover (Abramsky et al., 2002; Bouskila, 1995; Embar, Raveh, Hoffmann, & Kotler, 2014; Kotler, Blaustein, & Brown, 1992), and others do not change their foraging habits between open and more sheltered locations (Roschlau & Scheibler, 2015). In any case, we expect that long-term evolution in a particular environment with predators is likely to shape the landscape of fear, and therefore determine the antipredator behaviour of many species. Appropriate antipredator behaviour may influence the success of introduced species (Dickman, 1992); inappropriate responses to novel predators in the predator-filled natural environment may reduce their success (e.g. Cisterne, Vanderduys, Pike, & Schwarzkopf, 2014). Comparing antipredator behaviour in native and introduced fauna can reveal differences in responses to

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predators that may, in turn, influence introduced species' success (e.g. Cisterne et al., 2014; Zozaya, Alford, & Schwarzkopf, 2015).

Perceived risk of predation is often measured using giving-up densities, which quantify the amount of risk a foraging animal will tolerate before leaving a productive foraging patch, by determining the amount of food left in the patch when the animal 'gives up' (Brown, 1988). Many studies assume that giving-up densities are a measure of the level of predation, or make assumptions about the kind of habitats that are likely to cause fear (e.g. open or closed habitats depending on the prey species; Bouskila, 1995; Dickman, 1992; Kotler et al., 1994). Some studies use experimental enclosures, stocked with a known numbers of predators, such as reptilian ambush hunters or trained predatory birds, or both, to create a landscape of fear in which to conduct giving-up density experiments (Abramsky et al., 2002; Embar et al., 2014; Kotler et al., 1992). Such experiments allow control over the landscape of fear, but may not transfer well to natural situations, in which the risk of predation is less predictable for the researcher.

In the wild, predation risk is difficult to assess, depending on both the types of predator present and their densities (Menezes, Kotler, & Mourão, 2014). Few studies have directly examined predator and prey densities in natural habitats (Laundre et al., 2014), or conducted giving-up density experiments in the field with a known predator community, although this is probably the best method for describing the real landscape of fear. By quantifying the predator assemblage in locations in which giving-up density experiments are conducted, we can describe the landscape of fear (Laundre et al., 2014; Orrock et al., 2004).

To investigate the landscape of fear in a native tropical savannah system and evaluate the antipredator response of two rodent species, we quantified predator and prey richness and abundance (Abom, Parsons, & Schwarzkopf, 2016; Abom & Schwarzkopf, 2016; Abom, Vogler, & Schwarzkopf, 2015). Based on the fauna surveys, we selected the study organisms on which we focused, but had information on other predators and prey. We selected the two most common small tropical savannah mammals, the native eastern chestnut mouse, *Pseudomys gracilicaudatus*, and the non-native house mouse, *Mus musculus domesticus*, and the most common predator of mammals in our system, the eastern brown snake, *Pseudonaja textilis*, to investigate the landscape of fear in a tropical savannah in northern Australia. Eastern brown snakes actively pursue prey in dense vegetation (Shine, 1989), whereas other predators, such as birds of prey and feral cats, prefer open foraging habitat (McGregor, Legge, Jones, & Johnson, 2014). We hypothesized that antipredator responses of the two species of rodents would differ due to their different evolutionary backgrounds. We predicted that eastern chestnut mice, which have evolved with eastern brown snakes, would forage less under cover and more in the open when snake abundance was high. In contrast, we predicted that house mice may not have the behavioural flexibility to switch to foraging in the open, even if it was a better strategy in the presence of snakes. To test these predictions, we established a series of giving-up density experiments based on abundances of free-ranging eastern brown snakes.

## METHODS

### Study Area and Sampling Period

The study was conducted in open savannah woodland at Undara Volcanic National Park (18°19'29.92"S, 144°36'28.31"E), approximately 420 km northwest of Townsville, Queensland, Australia.

We trapped rodents and snakes and conducted visual surveys for raptors (Appendix Fig. A1, Table A1) at 24 sampling sites over

eight trapping periods between October 2008 and July 2010 (described in more detail in Abom et al., 2016; Abom & Schwarzkopf, 2016; Abom et al., 2015). Each sampling site was 50 × 50 m with a 30 × 30 m trapping grid in the centre of the sampling site (Appendix Fig. A1). We used pitfall and baited Elliott traps to measure small mammal abundance and funnel traps to capture snakes and we conducted visual surveys (day and night) for birds using binoculars. Each trapping grid had five pitfall traps (20 l straight-sided buckets) buried with the lip flush with the ground, in a cross shape with one trap in the centre and four at the ends of 'arms'; pitfall traps were spaced 10 m apart, and were connected with a 50-cm high cyclone drift fence (Appendix Fig. A1). Each site included eight funnel traps (180 × 730 mm and 170 mm high), one placed on each side of the drift fence on each arm of the trapping grid, and 12 baited Elliott (100 × 325 mm and 100 mm high) traps 10 m apart and positioned around the outer 30 × 30 m perimeter of the trapping grid (Appendix Fig. A1). To prevent overheating, thirst or hunger for animals in traps, pitfall and funnel traps were equipped with shade and moistened sponges and checked and cleared twice daily, in the early morning (0530–0830 hours) and in the late afternoon (1600–1800 hours), while Elliott traps were baited with a honey, oats and peanut butter mixture, and checked, cleared and closed in the early mornings, and opened and rebaited in the late afternoon. To prevent exposure of trapped animals, Elliott traps were placed in shaded locations, contained cotton wool for bedding and were housed in plastic bags if it was raining. We batch-marked rodents by trimming 5 mm of the tip of the tail to differentiate between new captures and recaptures and to collect the tissue for use in another study. We sterilized scissors with an open flame between individuals to avoid transfer of infection. All captured rodents and eastern brown snakes were released at their point of capture, raptors were surveyed by using binoculars, and we did not capture the rodents in our foraging experiments. We maintained the same visual surveyor for the entire project (R.A.), and used the *Field Guide to the Birds of Australia* to identify birds (Pizzey & Knight, 2007). We identified mammals using Menkhorst and Knight (2004). Rodent and snake trapping and visual raptor surveys were concluded before the rodent foraging experiments, which were performed over two 10-day periods in the dry season (8–28 July 2011). The two previous years of trapping (eight trapping sessions) indicated that abundances of snakes and mammals were stable and repeatable over time in the different sites.

### Ethical Note

We followed the ethical guidelines set down by the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th edition, 2007 and the Queensland Animal Care and Protection Act 2001 (JCU Animal Ethics approval number A1354), and conducted our work in accordance with the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching. We also obtained a permit to work with wildlife issued by the Department of Environment and Resource Management, Permit number WITK05527908, which included a review of our activities relevant to animal ethics.

### Study Species

The two abundant rodent species at our study sites were introduced non-native house mice, *M. musculus domesticus*, and native eastern chestnut mice, *P. gracilicaudatus* (Menkhorst & Knight, 2004; Van Dyck & Strahan, 2008). Both species feed on a variety of seeds, fungi, plant material and invertebrates (Luo, Fox, &

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