

RISK SENSITIVE FORAGING: AN EXPERIMENTAL STUDY OF A SOLITARY MARSUPIAL

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DETECTION and avoidance of predators are the principle strategies employed by prey to evade attack; by scanning their environment, prey individuals can reduce the likelihood of a predator approaching to within striking distance (Elgar 1989; Lima and Dill 1990). However, vigilance is often incompatible with foraging behaviours, and thus animals may be forced to trade-off the risk of predation against acquiring food. Consequently, the quality of a particular resource patch and its associated predation risk may influence the foraging decisions of animals (Werner *et al.* 1983; Newman and Caraco 1987; Heithaus and Dill 2002). Cover is an important feature of a foraging site because it can provide a hiding place to escape potential predators (Lazarus and Symonds 1992). Thus, animals may prefer foraging sites that are close to cover, or adjust their level of vigilance at different distances from cover in order to compensate for changes in the chance of early detection and escape (Elgar 1989; Lima and Dill 1990; Lima *et al.* 1985; Kramer and Bonenfant 1997).

Empirical studies that investigate trade-offs between predation risk and food acquisition in mammals are rare relative to the literature on other taxa; see Lima (1990) and Elgar (1989) for reviews. There are some experimental studies of captive populations (e.g., Blumstein *et al.* 1999, Ramp *et al.* 2005), but correlational studies of individuals in their natural environment are more typical (Risenhoover and Bailey 1985; Heithaus and Dill 2002, Blumstein and Daniel 2003; Carter and Goldizen 2003; Cowlshaw *et al.* 2004), with gregarious mammals often the focus (e.g., Underwood 1982; LaGory 1986; Coulson 1999; Blumstein *et al.* 2001). However, grouping behaviour also increases competition for resources (Elgar 1986; Beauchamp and Livoreil 1997; Abramsky *et al.* 1998; Blumstein *et al.* 2001), and so the observed behaviour may be a

response to competition and/or predation risk (e.g., McDonald-Madden *et al.* 2000). Solitary species may be a more appropriate model as the influence of competition is minimised. Our understanding of the foraging behaviour of solitary free-living mammals derives primarily from studies of rodents (Lima *et al.* 1985; Newman and Caraco 1987; Brown 1988; Dill and Houtman 1989; Kramer and Bonenfant 1997). Studies of solitary foraging marsupials are comparatively rare (Carter and Goldizen 2003) and there are none involving field experiments (but see McDonald-Madden *et al.* 2000, 2004).

We investigated experimentally the foraging trade-offs of free-ranging swamp wallabies (*Wallabia bicolor*) in response to a perceived risk of predation when foraging away from cover. *W. bicolor* is a solitary macropod that inhabits thick undergrowth in forests and woodlands along the east of Australia from Cape York to Western Victoria (Maynes 1989). They are generalist browsing herbivores that feed mainly on forbs, ferns and shrubs (Hollis *et al.* 1986). *W. bicolor* generally spend the day foraging and resting in the forest understorey but may venture out into grasslands in the late afternoon and evening (Troy *et al.* 1992).

This study was conducted at Boho South in the Strathbogie Ranges, North-East Victoria (-36.48 S, 145.45 E) between December 2002 and February 2003. The dominant vegetation is wet sclerophyll forest, which has been fragmented by clearing for agriculture, resulting in a mosaic of remnant forest patches. The overstorey comprises *Eucalyptus* spp., and the understorey mostly silver wattle (*Acacia dealbata*) and austral bracken (*Pteridium esculentum*). The study site was located on private land at the edge of a 150 ha forest block surrounded by pasture.

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We collected data from 14 *W. bicolor* that regularly use the forest edge at the study site. The animals inhabit different areas along the forest edge and in order to collect data from all of the individuals in the study area, six identical feeding stations (wooden trays placed on the ground holding 1/8 pieces of an apple) were used. We positioned these at different locations, of similar floristic composition, along the forest edge. For each observation, we noted the sex and size of the focal animal and, if possible, identified the individual by scars and other natural markings. We restricted our observations to periods around the new moon to avoid the possible confounding effect of moonlight (Biebouw and Blumstein 2003). All data were collected in relatively calm weather conditions, beginning approximately 3 hrs before sunset and finishing on last light.

At each of the six feeding stations, we randomly designated a tray to one of four distances from the forest edge (5, 10, 20 or 30 m). These distances were later categorised into 'near' (≤ 10 m) and 'far' (≥ 20 m) for analysis. We observed *W. bicolor* from a stationary position no closer than 50 m, using binoculars when necessary. While an animal was at the feeding tray, we recorded the time spent at the feeder and the level and duration of vigilance behaviour. Vigilance behaviour was categorised into four levels: *None* — no vigilance behaviour observed (head down, feeding); *Low* — animal feeding but head is slightly raised and animal is listening; *Medium* — animal stops feeding and sits semi-upright with head raised; *High* — animal stops feeding, sits completely upright with head up, chest out and ears forward. These behaviours are similar to those observed in eastern grey kangaroos (*Macropus giganteus*) (Colagross and Cockburn 1993) and mountain brushtail possums (*Trichosurus cunninghami*) (McDonald-Madden *et al.* 2004). We recorded the duration of time spent at each level of vigilance while at the feeder.

To examine the effect of distance from cover on food-handling time, we placed one medium-sized apple cut into 1/8 pieces in the tray. For each individual, we timed and recorded food handling. Handling time was recorded from when the piece of apple was first picked up to when the remaining portion was put in the mouth. These data were analysed using ANOVA to investigate the effect of distance from cover on handling time. Handling-time data were then grouped into near (≤ 10 m) and far (≥ 20 m) and analysed using a two-tailed *t*-test (95%).

Wallabia bicolor emerged from the forest in late afternoon and began feeding on forbs. They foraged with their heads down, searching for and then breaking off plant material for consumption. Once a

feeding station was encountered, the animals would pick up a piece of apple in their mouth and then pass it to their forepaws, gripping the apple while they consumed it. *W. bicolor* remained in a semi-upright posture while feeding on the apple. When animals feeding away from cover were disturbed they fled back toward or into the forest.

Wallabia bicolor were significantly less likely to approach and feed at an artificial feeder that was placed further from the forest edge (Wald chisq = 4.08, $df = 1$, $p = 0.04$). Once the animals were at a feeder they spent a similar amount of time there, regardless of their distance from cover ($t_{12} = -0.185$, $p = 0.85$, Cohen's $d = -0.08$). The total time animals allocated to vigilant behaviour did not change with distance from the forest edge ($t_{15} = 1.69$, $p = 0.11$, Cohen's $d = -0.07$) and there was also no influence of distance on any of the three vigilance levels recorded (Low, Medium or High) with low vigilance remaining the predominate state (Fig. 1). There was a marginally significant decrease ($t_{30} = 2.02$, $p = 0.052$, Cohen's $d = 0.65$) in the mean handling time for animals feeding on apple pieces far (≥ 20 m) from cover compared with those feeding near (≤ 10 m).

The observed behaviour of *W. bicolor* in this study is not entirely consistent with that predicted by theory. In particular, there was no significant increase in vigilance level or in the time allocated to vigilance with increasing distance from the forest edge (cover). This contrasts with evidence from numerous species that individuals devote a greater proportion of time to vigilance when foraging further from cover (for reviews see Elgar 1989; Lima and Dill 1990). There are several explanations for this result. First, the *W. bicolor* in this study may not have perceived a greater risk of predation when foraging at the feeders placed further from cover. If the time taken to reach cover does not differ significantly between 5 and 30 m, then we would predict a similar level of vigilance at these distances. Further, vigilance and feeding may not necessarily be incompatible in *W. bicolor* feeding on apples because they can consume the apples while standing upright. However, the reduction in food handling time when further from cover, and their perception of the forest as a refuge (flight was always toward the forest) suggests that they do perceive greater risk when further out. The apparent reluctance of animals to approach feeders placed further from cover is also consistent with this view, although it may also be the result of feeders being more difficult for animals to locate. Finally, the relationship between risk of predation and distance from cover may not be linear; for example, foraging close to the forest may offer closer proximity to protective cover, but may potentially harbour predators (see also Lazarus and Symonds 1992, Blumstein and Daniel

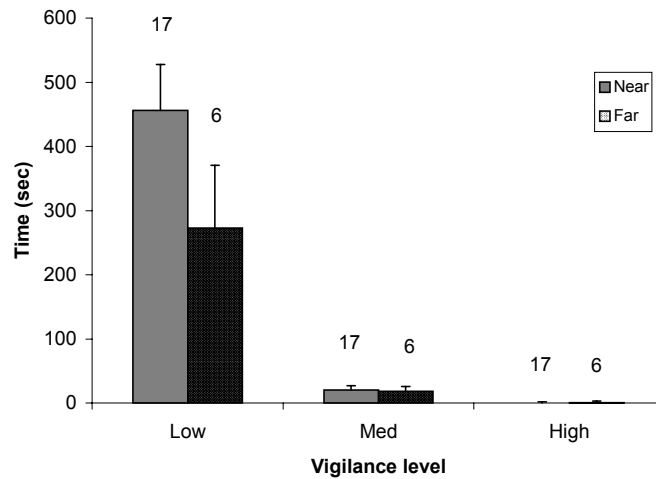


Fig. 1. The mean time that *W. bicolor* spent at each vigilance level (Low, Medium, High) while foraging near (≤ 10 m) or far (≥ 20 m) from a forest edge. Vertical bars indicate one standard error, numbers above bars show the number of observations.

2002). Accurate data on the natural foraging patterns of *W. bicolor* with respect to distance from cover was not collected but may help to clarify our findings and the wallabies' perception of cover.

Our results highlight the complexity of animals' decision-making under the risk of predation and the importance of considering both biological and ecological aspects of the model species in order to avoid ambiguity when testing behavioural theory in the field. The choice of food items is particularly important, since certain items may not constrain vigilance behaviour. Our data may have been different if the animals were forced to keep their heads down while consuming the food.

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