RESEARCH PAPER

Environmental Manipulation to Avoid a Unique Predator: Drinking Hole Excavation in the Agile Wallaby, *Macropus agilis*

J. Sean Doody*, Rachel A. Sims† & Mike Letnic‡

* Applied Ecology Research Group, University of Canberra, Australia
† School of Botany and Zoology, Australian National University, Australia
‡ Parks and Wildlife Service of the Northern Territory, Palmerston, Australia

Abstract

The simplest way of avoiding an ambush predator is to entirely avoid the habitat in which it hunts. However, this strategy requires that the prey species find alternative, risk-free sources of essential resources. Herein we describe a novel strategy used by agile wallabies (*Macropus agilis*) to avoid saltwater crocodile (*Crocodylus porosus*) predation: the creation of risk-free sites to obtain water. We studied the anti-predator behaviour of agile wallabies for 3 yr during the dry season along the Daly River, Northern Territory, Australia. Wallabies excavated holes in the sand 0.5–18.0 m from the water's edge, and preferred to drink from these holes over drinking from the river. We determined a hierarchy of preferred drinking-site options for the wallabies: non-river sites: springs, puddles, excavated holes; and river sites: sites with cover, shallow water sites and deep water sites. Drinking holes were twice as far from the water's edge in a river stretch with high crocodile density (2/km) than those in a stretch with low crocodile density (0.08/km). However, site differences could also be explained by river bank morphology. Collectively, our findings indicate that agile wallabies excavate drinking holes to avoid crocodile predation. We contend that this behaviour represents environmental manipulation specifically to alter the risk associated with obtaining a key resource.

Introduction

Predation risk has a profound effect on the behaviour of prey species (reviewed in Lima & Dill 1990; Blumstein 1998). Perhaps the most fundamental effect is modulation of the way individuals capture resources in order to minimize the exposure to predation risk (Werner & Anholt 1993). For example, well-documented trade-offs occur between foraging and predator avoidance in a wide variety of taxa (e.g. insects: McBean et al. 2005; reptiles: Cooper 2000; birds: Yasue et al. 2003). Prey species have been found to forage at times when predators are least active (e.g. Helfman 1986; Caldwell 1986; Jacob & Brown 2000), or in places where predators are less likely to be hunting or are more easily thwarted

(e.g. Milinski 1986; Fergusson et al. 1988; Walker et al. 2000). In many cases these predator avoidance strategies incur costs in foraging time and food intake (e.g. Abramsky et al. 2002; Fortin et al. 2004). Less commonly, individuals may manipulate the environment in which they wish to gather resources to reduce the chance of a successful attack by a predator (e.g. Schroder 1979).

Members of the Australian Macropodoidea employ a complex suite of behaviours to reduce the risk of predation (reviewed in Coulson 1996). In general, most species rely heavily on vigilance, often teamed with grouping, as a primary predator defence strategy. Upon detection of a threat, many species transmit alarm signals (foot thumps) before taking rapid flight. These behaviours appear well adapted to combat

the active search and pursuit strategies employed by Australia's primary predators of macropods: terrestrial mammals [dingoes (*Canis lupis dingo*), and historically, the thylacine (*Thylacinus cynocephalus*)] and large birds of prey (e.g. wedgetailed eagles, *Aquila audax*) (Croft 1987; Robertshaw & Harden 1989).

Agile wallabies (*Macropus agilis*) of tropical Australia face an additional predator with an alternative tactic, the ambushing saltwater crocodile (*Crocodylus porosus*). The two species are highly sympatric, with agile wallabies occurring in greatest densities along watercourses. No other macropod species has such range overlap with saltwater crocodiles. Observations suggest that wallabies prefer to drink free water when it is available (Bell 1973), bringing them into contact with the habitat of predatory crocodiles. Crocodiles are true ambush predators, preferentially feeding on terrestrial prey at the water's edge, where the crocodile can remain concealed until the attack has commenced (Webb & Manolis 1989). The prey of adults include a variety of large mammals including agile wallabies (Pye 1976; Webb & Manolis 1989; S. Doody & M. Letnic pers. obs.). Agile wallabies must therefore contend with a predator unlikely to be avoided by the typical strategies employed by a macropod of medium size: namely high vigilance and swift escape. To gain access to free water, agile wallabies must either face the risk of an ambush attack or employ alternative strategies suited to avoidance of an ambush predator.

Clearly, the simplest way of avoiding an ambush predator is to entirely avoid the habitat in which it hunts. However, this strategy requires that the prey species find alternative, risk-free sources of essential resources. Herein we describe a novel strategy used by agile wallabies to avoid crocodile predation: the creation of risk-free sites to obtain water. We contend that these 'drinking holes' represent environmental manipulation specifically to alter the risk associated with obtaining a key resource. We describe the nature of wallaby drinking holes and the evidence for this behaviour as a key to avoiding crocodile predation. We then explore other drinking-site options for agile wallabies and determine a hierarchy of drinking-site preferences. Finally, we test the hypothesis that the distance of drinking holes from the river will vary with risk of attack by predatory crocodiles.

Methods

Study animals

The agile wallaby (*M. agilis*) is a medium-sized macropod of northern Australia and Papua New Guinea

that is primarily associated with riparian habitats (Strahan 1998). Their diet consists of grasses, sedges, leaves and fruits, and they are capable of digging up to 30 cm to access grass roots (Strahan 1998). The saltwater crocodile (*C. porosus*) is a large crocodilian species inhabiting rivers, estuaries, billabongs and swamps from northern Australia through to southeast Asia and eastern India (Webb & Manolis 1989). Saltwater crocodiles have a wide prey spectrum that includes crustaceans, fish, frogs, reptiles, birds and mammals (Taylor 1979). Large crocodiles are known to capture large mammals such as wallabies, pigs, cattle, buffalo and horses (Webb & Manolis 1989). The species has increased in abundance in Australia since it was afforded protection in the NT in 1971 (Stirrat et al. 2001; Read et al. 2004).

Study sites

We studied agile wallaby behaviour along two stretches of the Daly River, Northern Territory, Australia between 2000 and 2004. Specifically, we studied the water access habits of agile wallabies along a 11-km stretch of the middle Daly River near Oolloo Crossing (14°04′40″S, 131°15′00″E, elevation 40 m) (hereafter OR site) during the dry seasons of 2000–2001 and 2004. Specific drinking-site choice data were gathered only in 2001. This site is approximately 125 km upstream of any tidal influences and has low densities of saltwater crocodiles (Letnic & Connors 2006).

To provide a contrasting site with higher predation risk we studied the placement of drinking holes along a 15-km stretch of the lower Daly River near the Daly River Township (hereafter DRT site), where tidal influences prevail and crocodile densities are much higher (Webb et al. 1983; Letnic & Connors 2006).

The riverbanks of the Daly are characterized by sandy banks, variably covered with trees (dominated by *Melaleuca* sp.), ferns and grasses but with bare sand and gravel bars scattered along the river. The river is in flood during much of the wet season (November to March), while dry-season water levels are low and relatively stable (slowly receding). During this time natural non-river water sources (e.g. seepage springs, puddles) change in distribution, and sand bars become more common. During the dry season the OR stretch of river is relatively shallow (approx. 1.5 m) with high visibility (>1 m), while the DRT site is deeper (up to several metres). Agile wallabies are extremely abundant along the river at both sites, as evidenced by their tracks along virtually every linear metre of riverbank (J. S. Doody, per. obs.).

Drinking hole surveys

Low-lying sandy banks were accessed by motor boat and then examined on foot for disturbances indicative of drinking holes. Drinking holes were defined as holes dug in sand or fine gravel free from vegetation that were apparent attempts to reach the water table (most successfully reached water). All surveys for drinking holes were conducted during periods when river levels were slowly receding during the dry season, so wallabies were forced to continually reassess their drinking options.

To confirm that drinking holes were specifically the result of agile wallaby activity we employed Trailmaster® remote camera systems (Goodson & Associates, Inc., Lenaxa, Kansas, USA) on the holes. These systems utilized an infra-red beam that was broken as animals approached the drinking holes, triggering the automatic camera, which was mounted on a metal stake 1.5 m above ground. The resulting photographs provided a record of the identity of visitors and times of visits to drinking holes.

When new drinking holes were discovered we recorded the date of excavation, distance from water, depth, slope of the square metre surrounding the hole, slope of the square metre up the bank from the hole, minimum and maximum diameters, substrate type, and whether the hole had successfully reached water. Slopes were used to obtain contours of areas containing drinking holes. In some cases slope was measured directly using a clinometer, while in other cases we estimated slope using distance from water and depth to water of the drinking holes, and the formula $\sin(\theta) = \text{depth/distance}$ (because distance was measured along the ground, it was approximately equivalent to the hypotenuse).

Distribution of drinking holes

To examine the broader context of water access by agile wallabies we conducted detailed drinking-site surveys at the main study site (OR). Specifically, we were interested in the relative preference for each type of drinking site (e.g. excavated holes vs. springs vs. river edge). To examine the wallabies' relative preference of springs vs. drinking holes, we conducted a survey of the linear distribution of springs, drinking holes, and sites available for excavation of drinking holes, for 8.8 km of river. Sites were considered available for excavation when gentle slopes (<20°) allowed a hole to be excavated at a depth of 20 cm at a distance of 2 m from water. This reflected the maximum slope found for holes in the main

(OR) study stretch. We hypothesized that springs would be preferred to holes because of the effort involved in drinking hole excavation. Thus, we made the prediction that drinking holes would not be excavated in areas where there were springs. We tested this prediction by examining the spatial association between excavated holes and springs. We used a chi-squared goodness-of-fit test on the presence or absence of springs, holes, and sites available for excavation, within 50 m length of river bank (351 50-m stretches).

Surveys for river-edge drinking sites

To determine the choices wallabies were making relative to the naturally occurring drinking sites that were available to them, we conducted a survey of a 1145 m stretch of river bank at OR with sandy substrates where drinking hole excavation had not occurred. A footprint pattern indicative of a resting posture with all four feet on the ground in close proximity to a water source was considered as evidence that the site was used by wallabies for access to free water. We then compared the proportion of used drinking sites to the proportion of total river frontage categories in each of three types of drinking sites: shallow water sites, deep water sites and sites with cover. Shallow water sites were those in which water depth was <0.3 m at a distance of 2 m from the river bank, while the remainder of sites were recorded as deep water sites. Sites with cover were those in which logs, sticks, trees or pandanus bushes in shallow water provided an obstruction to attack from deeper water.

Crocodile surveys

To confirm that crocodile densities were different at the two sites, we conducted surveys for saltwater crocodiles near each wallaby study stretch in early September 2004. Crocodile surveys were not conducted in the exact present study stretches because the former were a part of regular monitoring by the Parks and Wildlife Service of the Northern Territory. The OR crocodile survey spanned a 12-km stretch between the Douglas River and Beeboom Crossing (approx. 15 km downstream of the main study stretch), while the DRT crocodile survey covered a 13.5-km river stretch between the DRT and Wooliana (adjacent to the study stretch and downstream). One survey was conducted in each stretch by boat at night using a spotlight (following the methodology of Messell et al. 1979). There was one observer, a data recorder and a driver, and the observer was

experienced at identifying crocodiles in this manner. Crocodiles were located by their reflective eyeshine, and were approached closely to allow for species identification (freshwater crocodiles, *Crocodylus johnstoni*, are also common at the site) and an estimation of the total length (TL) of each individual. Total length estimates were made in 0.3 m intervals, and were arbitrarily split into four size classes. The density of crocodiles was calculated as the number of individuals per kilometre.

Results

Wallaby drinking holes, and seasonal and diel use

Descriptive characteristics of drinking holes is given in Table 1. Distance of holes from water ranged from 0.5 to 18.0 m. Most holes were excavated in soft sand, but substrate type varied from loamy sand to gravel. Muddy sites were generally avoided but were utilized when no other substrate was available. Tracks and claw marks in and around the holes suggested that the holes were excavated by agile wallabies, the only common macropod along the river, and remote camera systems and focal observations (J. S. Doody, unpubl. data) confirmed that the wallabies both excavated and drank from the holes (Fig. 1). Drinking holes were often isolated, but we observed up to seven holes per site (within a few metres of one another, Fig. 2). Wallaby tracks were more numerous at sites with multiple holes. Over 99% of animals recorded using the drinking holes were *M. agilis*, but other species observed included one antilopine wallaroo (*Macropus antilopinus*), one northern quoll (*Dasyurus hallucatus*), several barred-shouldered doves (*Geopelia humeralis*) and peaceful doves (*Geopelia placida*), two Torresian crows (*Corvus orru*), and one whistling kite (*Haliastur sphenurus*).

The number of holes increased as the dry season progressed (Fig. 3). During the mid-dry season water

Fig. 1: An agile wallaby drinking from a hole excavated approx. 1.5 m from the river's edge (background)

Fig. 2: Drinking holes excavated by agile wallabies along the Daly River, viewed from above. Note the similar distance (approx. 3 m) of each hole from the river's edge (top)

levels gradually dropped, exposing more gently sloped areas close to water that could be readily excavated. Prior to this there was little or no opportunity for the wallabies to excavate drinking holes because of the steepness of the riverbanks adjacent

Table 1: Characteristics of *M. agilis* drinking holes at two sites differing in predatory crocodile density, with statistical comparisons between sites

attribute	Oolloo Road (OR) site	Daly River Township (DRT) site	differences b/n sites (ANOVA)
distance (m)	2.2 ± 0.20 (67)	5.9 ± 0.68 (47)	$F_{1,113} = 35.21$, $p < 0.0001$***
depth (cm)	12.7 ± 1.00 (67)	17.8 ± 1.31 (47)	$F_{1,113} = 9.90$, $p = 0.002$**
slope (°)	4.6 ± 0.49 (67)	2.7 ± 0.32 (47)	$F_{1,113} = 8.32$, $p = 0.004$**
max dia (cm)	29.1 ± 3.90 (34)	39.8 ± 7.02 (17)	$F_{1,50} = 2.07$, $p = 0.156$
min dia (cm)	15.2 ± 0.99 (33)	20.4 ± 4.19 (17)	$F_{1,49} = 2.51$, $p = 0.120$

The Oolloo Road site has low densities of saltwater crocodile sites (0.08/km), while the Daly River Township site has considerably higher crocodile densities (2.88/km).
Data are mean ± 1SD. Sample sizes are in parentheses.
Distance = from the water's edge; dia = diameter.
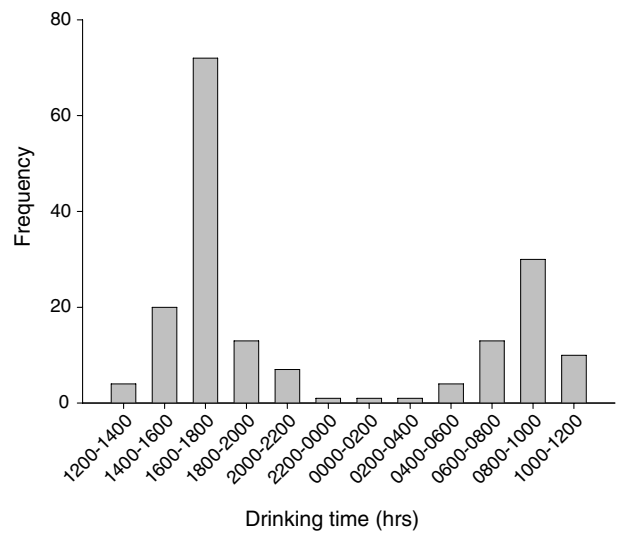*p < 0.05, **p < 0.01, ***p < 0.001.
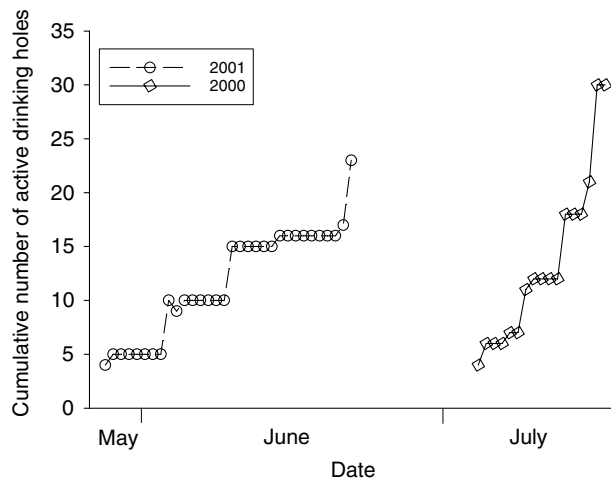
Fig. 3: Annual and seasonal variation in the number of excavated drinking holes at the study site, because of variation in the magnitude of the previous wet season and the contour of river banks

Fig. 4: Temporal distribution of drinking times in *M. agilis* recorded by remote cameras at drinking holes and river edges

Fig. 5: Comparison of drinking-site availability and use by *M. agilis* along a 1145-m stretch of riverbank at a low crocodile density site (Oolloo Road site). Cover sites had a natural obstacle hindering attack from the water; shallow water sites had a water depth <0.3 m at 2 m distance from the river bank; all other sites were classified as deep water. Numbers above columns are sample sizes

to water while the river is receding from the previous wet season. The difference in timing of hole excavation between years is attributable to annual variation in water levels associated with the magnitude of the previous wet season. The resulting density of holes peaked at 2.1–2.7/km, depending on the year (Fig. 3). However, this density may increase during the late dry season, because river levels continue to fall throughout the dry season.
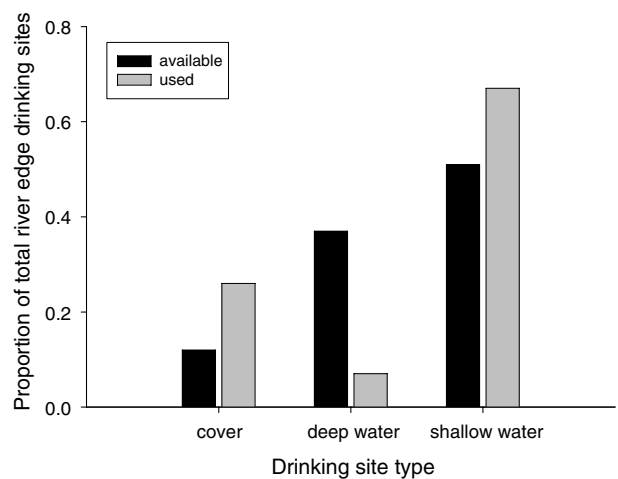
Wallaby drinking times peaked in the evening at around 17:00 hours, and peaked again to a lesser extent in the early morning at around 08:30 hours, based on remote camera data for 14 drinking holes and seven river-edge sites during 2000–2001 (Fig. 4). Almost no drinking occurred between 22:00 and 04:00 hours (Fig. 4). Focal observations (>30 h of video footage; J. S. Doody, unpubl. data), and sequential photographs from remote camera systems indicated that a wallaby drinking bout spans 5–20 min.

Drinking-site choice

Drinking holes were not excavated along stretches of river with springs emanating from the river banks. No 50-m stretch of river bank contained both a spring and an excavated drinking hole, and the two were significantly dissociated ($\chi_1^2 = 4.38$, p = 0.036). As expected, drinking holes were not independent of sites available for excavation ($\chi_1^2 = 22.93$, p < 0.0001). Moreover, as expected, the distribution of springs was independent of the distribution of sites available for excavation ($\chi_1^2 = 2.39$, p = 0.122). Of 351 50-km stretches, 108 (31%) contained sites available for excavation, 68 (19%) contained springs and 10 (3%) contained excavated holes.

Our intensive survey of 42 river-edge drinking sites vs. available sites over a 1145-m stretch demonstrated that the proportion of each drinking site used differed significantly from the availability of those sites (Fig. 5; $\chi_2^2 = 19.96$, p < 0.0001). Wallabies used shallow water sites and sites with cover preferentially over deeper water sites (Fig. 5).

Relative crocodile densities between sites

Crocodile density differed markedly at the sites. Crocodile density at the DRT site was 2.88 individuals/km compared with 0.08 individuals/km at the OR site (Table 2). Only crocodiles >2 m TL are likely to prey upon wallabies (Taylor 1979). The density of crocodiles >2 m TL was 2 individuals/km at the DRT site and 0.08 individuals/km at the OR site (25:1 ratio).

Site differences in drinking hole characteristics and crocodile density

Distance of drinking holes from the water's edge did not differ among years at the OR site ($F_{2,66} = 1.46$, p = 0.241) or the DRT site ($F_{1,46} = 3.55$, p = 0.066), and so these data were pooled for analysis of site on drinking hole distance from water. Drinking holes at

Table 2: Saltwater crocodile survey counts for a 12-km stretch near the Oolloo Road (OR) site and a 13.5 km stretch near Daly River Township (DRT) site

Size category	Oolloo Road (OR) site counts	Daly River Township (DRT) site counts
<1.2 m	0 (0)	4 (0.30)
1.2–2.0 m	0 (0)	8 (0.59)
2.1–3.3 m	1 (0.08)	17 (1.26)
>3.3 m	0 (0)	10 (0.74)
Total number	1	39
Density	0.08	2.88

Counts are based on night surveys with spotlights from a boat. Densities (in parentheses) are numbers of crocodiles sighted per river kilometre.
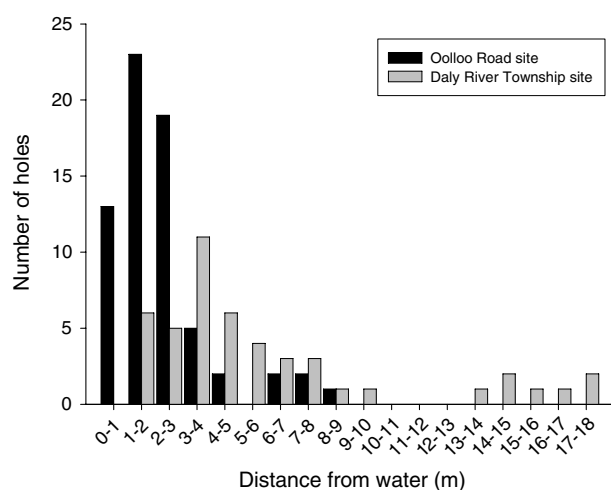
Fig. 6: Distance of excavated drinking holes from the river's edge at a site with low crocodile density (Oolloo Road site) and a site with high crocodile density (Daly River Township)

the DRT site were significantly farther from water than those at the OR site (Fig. 6; Table 1).

Depth of holes also did not differ among years at either site (OR: $F_{2,66} = 1.69$, p = 0.343; DRT: $F_{1,46} = 2.61$, p = 0.103), and so data were pooled for further analysis of site differences in depths of drinking holes. Drinking holes at the DRT site were significantly deeper than those at the OR site (Table 1). Slope at the drinking hole, calculated from depth and distance data, was significantly steeper at the DRT site than at the OR site (Table 1).

Discussion

A fundamental way in which predation influences prey behaviour is the modulation of how individuals capture the resources required for survival and reproduction in order to minimize the exposure to predation risk (Werner & Anholt 1993; Brown & Kotler 2004). We demonstrated that agile wallabies use a novel strategy to avoid saltwater crocodile predation: the creation of risk-free sites to obtain water (Fig. 1; Fig. 2). The naturalist Serventy (1966) recalled observing the behaviour at the Fitzroy River, Western Australia: 'Many wallabies were drinking at that early hour. I noticed that some would not approach the river but dug a hole in the sand near the water. More likely this is a safeguard against being caught with one's nose in the water, so to speak, as this is a favourite opportunity for crocodiles to grasp their prey'. We contend that this behaviour represents the first reported case of environmental manipulation by a macropod to specifically alter the risk associated with obtaining a key resource.

It is probable that saltwater crocodiles are important predators of agile wallabies along the Daly River (Pye 1976). Although there have been no quantitative studies of their diet, large (>2 m) saltwater crocodiles are known to prey on large terrestrial mammals including wallabies, pigs, cattle and horses (Webb & Manolis 1989). At our study site, we observed several crocodiles towing and attending dead wallabies, and crocodiles attacked experimental model wallabies (J. S. Doody, unpubl. data). Finally, the distance of excavated drinking holes was generally greater than the lunging distance of saltwater crocodiles ambushing terrestrial prey (half their body length; Webb & Manolis 1989).

A complex predator avoidance strategy

Reduction of predation risk often involves both reducing the probability of an encounter with a

predator and reducing the probability of any attack being successful. Our data suggest that agile wallabies use spatial avoidance as a first line of defence against crocodile attacks. Wallabies exhibited a distinct hierarchical preference for different drinking-site options, preferring the effort-free low-risk water provided by natural springs and puddles as a first option to avoiding encounters with crocodiles. When these options were not available, wallabies would then create high-effort low-risk drinking holes. Holes provide an intermediate step between natural risk-free sites and high-risk river-edge sites. At drinking holes, wallabies trade digging effort for risk in order to obtain an essential resource.

When all low-risk sites were unavailable, wallabies drank from the river, enabling the possibility of an encounter with a crocodile, but preferred drinking sites with attributes that reduced the risk of a successful attack. Wallabies selected drinking sites behind cover (logs, bushes, etc.) more often than expected by chance (Fig. 5). Such cover may prevent a clear approach from a crocodile, and may also serve to provide some concealment. If detected behind cover, the obstacle may slow the approach of the crocodile, enabling the wallaby to escape (see below). Finally, when cover was not available, wallabies showed a strong preference for shallow water sites over deep water sites (Fig. 5). Shallow water sites may force a hunting crocodile to break its own concealment at a greater distance from the terrestrial target than deep water sites, allowing the prey greater time to react and attempt an escape.

The probability of an encounter between predator and prey is also influenced by how their times of peak activity overlap. Wallaby drinking times were bimodal, with a large peak in the evening (around 17:00 hours) and a smaller peak in the morning (around 08:30 hours) (Fig. 4). Most crocodilians hunt between dusk and dawn (approx. 18:30 to 07:00 hours during the dry season), but prey are frequently taken opportunistically during the day (Webb & Manolis 1989). Therefore, although wallabies drink infrequently during peak hunting times, they are still likely to be at sufficient risk of predation to avoid direct contact with watercourses.

Site differences in expression of a predator avoidance trait

The probable encounter rate between predator and prey is an important component of overall predation risk, influencing the selective forces on anti-predator

behavioural strategies (Lima & Dill 1990). The observed 25-fold difference in crocodile density suggests that the risk of predation posed by crocodiles was markedly greater at the DRT site than at the OR site. Consequently, we hypothesized that wallabies at the DRT site would reduce the encounter with a crocodile by investing more into hole excavation behaviour than individuals at the OR site. This was supported by our observations that drinking holes at the DRT site were deeper and further from the water's edge than those at the OR site (Table 1). At DRT wallabies expend an extra 40% more effort (depth 40% greater) to obtain drinking sites removed from crocodiles by an extra 3.7 m (119% greater distance). This additional expenditure and associated removal from risk may reflect the higher risk (both actual and perceived) faced by wallabies at DRT. These observations beg questions. Was the digging behaviour learned through experience or the product of selection pressure?

An alternative explanation for site differences in the depth and distance of drinking holes from water may be differences in bank morphology. Many of the holes at the OR site occurred on beaches where slope increased considerably behind the hole (up to 20–40°). Therefore, at this site, holes dug farther from water might have been prohibitively deep. This is in contrast to many holes at the DRT site, which occurred on wide beaches with low and consistent slope. It is possible that wallabies at DRT have more scope for digging farther from water. Unfortunately, our data are not sufficient to determine the relative importance of crocodile density and bank morphology on the placement of drinking holes. However, observations of holes close to the water at the high-density crocodile site (DRT) suggest that bank morphology does play a role. Further research in areas where crocodile density and bank morphology do not covary would be necessary to determine the ultimate reason for the site differences in the distance of drinking holes from water.

Conclusions

Agile wallabies utilize a complex suite of antipredator behaviours to avoid fatal encounters with saltwater crocodiles. Although the primary defence strategies of spatial (and possibly temporal) avoidance teamed with high vigilance corroborates Coulson's (1996) review of marsupial anti-predator behaviour, we report a new feature: environmental manipulation to alter risk. The creation of risk-free sites for resource acquisition is a hitherto unrecognized and exciting

addition to our knowledge of predator avoidance in marsupials.

Acknowledgements

Literature Cited

Abramsky, Z., Rosenzweig, M. L. & Subach, A. 2002: The costs of apprehensive foraging. Ecology **83**, 1330—1340.

Bell, H. M. 1973: The ecology of three macropod marsupial species in an area of open forest and savannah woodland in north Queensland, Australia. Mammalia **37**, 527—544.

Blumstein, D. T. 1998: Quantifying predation risk for refuging animals: a case study with golden marmots. Ethology **104**, 501—516.

Brown, J.S., & Kotler, B.P. 2004: Hazardous duty pay and the foraging cost of predation. Ecol. Lett. **7**, 999—1014.

Caldwell, G. S. 1986: Predation as a selective force on foraging herons: effects of plumage color and flocking. Auk **103**, 494—505.

Cooper, W. E. Jr. 2000: Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (*Eumeces laticeps*). Behaviour **137**, 1175—1189.

Coulson, G. 1996: Anti-predator behaviour in marsupials. In: Comparison of Marsupial and Placental Behaviour (Croft, D. B. & Ganslosser, U., eds). Filander Press, Fürth, Germany, pp. 158—186.

Croft, D. B. 1987: Socio-ecology of the antilopine wallaroo, *Macropus antilopinus*, in the Nothern Territory, with observations on sympatric *M. robustus woodwardii* and *M. agilis*. Wildl. Res. **14**, 243—255.

Fergusson, S. H., Bergerud, A. T. & Ferguson, R. 1988: Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia **76**, 236—249.

Fortin, D., Boyce, M. S., Merrill, E. H. & Fryxell, J. M. 2004: Foraging costs of vigilance in large mammalian herbivores. Oikos **107**, 172—180.

Helfman, G. S. 1986: Behavioral responses of prey fishes during predator-prey interactions. In: Predator–Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates (Feder, M. E. & Lauder, G. V., eds). Univ. Chicago Press, Chicago, IL, pp. 135—156.

Jacob, J. & Brown, J. S. 2000: Microhabitat use, giving up densities and temporal activity as short- and long-term anti-predator behaviours in common voles. Oikos **91**, 131—138.

Letnic, M. & Connors, G. 2006: Changes in the distribution and abundance of saltwater crocodiles (*Crocodylus porosus*) in the upstream, freshwater reaches of rivers in the Northern Territory, Australia. Wildlife Research **33**, 1—10.

Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**, 619—640.

McBean, M. C., White, S. A. & MacGregor, J. 2005: Foraging behaviour of the damselfly larva *Pyrrhosoma nymphula* (Sulzer) in response to predator presence (Zygoptera: Coenagrionidae). Odonatologica **34**, 155—164.

Milinski, M. 1986: Constraints placed by predators on feeding behaviour. In: The Behaviour of Teleost Fishes (Pitcher, T., ed). Croom Helm Ltd., London, pp. 236—252.

Pye, J. 1976: The Daly River Story: A River Unconquered. Colemans Printing Pty. Ltd., Darwin.

Read, M. A., Miller, J. D., Bell, I. P. & Felton, A. 2004. The distribution and abundance of the estuarine crocodile, *Crocodylus porosus*, in Queensland. Wildl. Res. **31**, 527—534.

Robertshaw, J. D. & Harden, R. H. 1989: Predation on Macropodoidea: a review. In: Kangaroos, Wallabies and Rat Kangaroos (Grigg, G., Jarman, P. & Hume, I., eds). Surrey Beatty and Sons, Sydney, pp. 735—753.

Schroder, G. D. 1979: Foraging behavior and home range utilisation of the bannertail kangaroo rat (*Dipodomys spectabilis*). Ecology **61**, 657—665.

Serventy, V. 1966: A Continent in Danger. The Trinity Press, London.

Stirrat, S. C. & Fuller, M. 1997: The repertoire of social behaviours of agile wallabies, *Macropus agilis*. Aust. Mammal. **20**, 71—78.

Stirrat, S. C., Lawson, D., Freeland, W. J. & Morton, R. 2001. Monitoring *Crocodylus porosus* populations in the Northern Territory of Australia: a retrospective power analysis. Wildl. Res. **28**, 547—554.

Strahan, R. 1998: The Mammals of Australia. Reed, Sydney.

Taylor, J. A. 1979: The foods and feeding habits of subadult *Crocodylus porosus* Schneider in northern Australia. Aust. Wildl. Res. **6**, 347—359.

Walker, R. S., Ackermann, G., Schachter-Briode, J., Pancotto, V. & Novaro, A. J. 2000: Habitat use by

mountain viscachas (*Lagidium viscacia* Moli 1782) in the Patagonian steppe. Zeit. Fur Saug. – Int. J. Mamm. Biol. **65**, 293—300.

Webb, G. J. W., Manolis, S. C. & Sack, G. 1983: *Crocodylus johnstoni* and *C. porosus* coexisting in a tidal river. Aust. Wildl. Res. **10**, 639—650.

Webb, G. J. W., & Manolis, C. 1989: Crocodiles of Australia. Reed, Sydney.

Werner, E. E. & Anholt, B. R. 1993: Ecological consequences of the trade-offbetween growth and mortality rates mediated by foraging activity. Am. Nat. **142**, 242—272.

Yasue, M., Quinn, J. L. & Cresswell, W. 2003: Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. Funct. Ecol. **17**, 727—736.