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Dichotomies in perceived predation risk of drinking wallabies in response to predatory crocodiles

David Steer[a,1], J. Sean Doody[b,*]

[a] Institute for Applied Ecology, University of Canberra
[b] School of Botany and Zoology, Australian National University

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Most advances in our understanding of predation risk involve foraging animals, yet animals also trade off predation risk with other essential activities. Drinking under the risk of predation may elicit similar prey behaviours to those in foraging animals, but has been little studied. Agile wallabies, *Macropus agilis*, manipulate their environment by excavating drinking holes just out of reach of predatory saltwater crocodiles. Paradoxically, however, some wallabies drink from the river's edge despite the immediate availability of the lower-risk drinking holes. We studied the behaviour of wallabies with multiple drinking options to test a series of predictions for animals drinking under the risk of predation. More wallabies drank during the day than at night, regardless of drinking site. However, night-drinking wallabies were much more likely to use the excavated holes than the 'riskier' river. This spatiotemporal dichotomy in perceived predation risk may reflect a mismatch in nocturnal sensory capabilities between predator and prey, and would provide sufficient motivation for wallabies to create low-risk drinking holes. Drinking duration, our surrogate for harvest, was not influenced by drinking site type (hole versus river), drinking time or social context (solitary versus group), suggesting that some animals may not forego drinking during high-risk periods, as predicted and observed for some foraging animals. Compared to wallabies in groups, solitary wallabies were less likely to drink from the river, especially at night, and were more vigilant. Although evidence is limited, our research suggests that vigilance may be ineffective for nocturnally drinking wallabies in the face of this concealed, ambush predator.

Predation risk can alter the behaviour of prey, and can vary spatially and temporally in ways that are not always intuitive (Cowlishaw 1997; Lima & Bednekoff 1999). Although predation pressure is notoriously difficult to measure, it is generally assumed that spatial and temporal variation in antipredator behaviour reflects similar variation in actual risk, although prey may underestimate or overestimate the risk of predation (Abrams 1994, 1995; Bouskila et al. 1995). Nevertheless, the links among predation risk, activity times, habitat use and social factors are often poorly understood and require further study (Cowlishaw 1997; Lima & Bednekoff 1999; Sih et al. 2004; Jackson et al. 2006).

Most recent theoretical and empirical treatments of predation risk focus on foraging animals. For example, the 'risk allocation hypothesis' predicts that if periods of high risk are brief, an animal might shift its foraging to low-risk periods (Lima & Bednekoff 1999; Hamilton & Heithaus 2001). Despite the focus on foraging, however, animals also trade off predation risk with other essential activities such as mating and courtship displays, nest site choice, thermoregulation, sleeping and drinking (Huey & Slatkin 1976; Hamilton 1982; Ryan 1985; Burger & Gochfield 1992; Koga et al. 1998; Campbell et al. 2005; Lima et al. 2005; Eggers et al. 2006).

Although theoretical models of predation risk constructed for foraging animals may apply to drinking animals, few studies have quantified antipredator behaviour at drinking sites (Burger 2001). Many animals require regular access to surface water and drinking bouts are particularly conspicuous during the dry season or in dry environments (Redfern et al. 2003; Campbell et al. 2005). Predators exploit this habit by ambushing prey at drinking sites (Altmann & Altmann 1970; Skinner & Smithers 1990; Marlowe 2003; Joubert 2006).

Ambush predators often rely on the element of surprise to capture prey, and when this surprise is lost their capture success is diminished (e.g. Curio 1978; Kenward 1978). In a classic example, crocodiles use the element of surprise when hunting terrestrial prey, although the details of this strategy are little known (Cott 1961; Webb & Manolis 1989). Australian saltwater crocodiles,

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* Correspondence: J. S. Doody, School of Botany and Zoology, Australian National University, ACT 0200, Australia.

E-mail address: sean.doody@anu.edu.au (J.S. Doody).

[1] D. Steer is at the institute for applied Ecology, University Canberra, ACT 2601, Australia.

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Crocodylus porosus, prey upon drinking agile wallabies, *Macropus agilis*, in this way (Doody et al. 2007). Wallabies drink both during the day and at night, and are visibly apprehensive when approaching drinking sites. In response to this risk, however, the wallabies exhibit a novel antipredator behaviour: they excavate drinking holes near the river's edge (Doody et al. 2007). Many of these holes are out of reach of lunging crocodiles, while other holes are likely to be safer than the 'high-risk' river's edge, despite being potentially within striking range.

Paradoxically, however, some wallabies drink from the river despite the immediate availability of excavated holes (Fig. 1; Steer 2007). Why do some individuals drink from the 'higher-risk' river? One hypothesis is that drinking behaviour is state dependent, whereby thirstier wallabies have more to gain from drinking than quenched wallabies and thus are more likely to take a risk by drinking from the river. This hypothesis assumes an inverse relationship between risk and energetic state, an assumption broadly supported by theory and some empirical data (Lima 1988; Clark 1994; Kotler et al. 2004). A second hypothesis is that individual variation in apprehension exists because of experience, or behaviours learned from parents or conspecifics (Curio 1993; Brown et al. 1997). A third possibility is that more dominant wallabies exclude less dominant individuals from drinking at the excavated holes (Freese 1978). Agile wallabies form a pecking order when drinking in groups (males, then females, then juveniles), although less dominant individuals eventually drink from the holes (Doody et al. 2007). A fourth hypothesis is that some wallabies perceive holes as risky because the drinking wallaby's field of vision may be compromised (Fig. 1). An obstructed field of view is known to increase vigilance of foraging and drinking animals (Lazarus & Symonds 1992; Burger 2001). A fifth hypothesis suggests that temporal variation in predation risk explains the wallabies' drinking site choice. Whether an animal is diurnal or nocturnal should depend on the relative costs and benefits of being active at those times (Clark & Levy 1988; Metcalfe et al. 1998). Because benefits (water uptake) should be similar between day and night for drinking wallabies, temporal variation in costs (predation risk) might best explain the paradox.

We used remote video at a drinking site with multiple drinking options to test a series of predictions for animals drinking under the risk of predation. First, we hypothesized that drinking time influenced drinking site choice, and thus explained the drinking site paradox. Thus, we predicted that diurnally drinking wallabies would use both excavated holes and the river because stalking crocodiles would generally be visible in the shallow approaches (Fig. 1). In contrast, we predicted that nocturnally drinking wallabies would prefer using the lower-risk holes because the river's edge is relatively unsafe. Accordingly, we predicted that river-drinking wallabies would be more vigilant than hole-drinkers. Second, our focal data also allowed us to test the alternative hypothesis that river-drinking wallabies were competitively excluded from the holes. Third, because water is an inflexible resource we predicted that (drinking) harvest would not differ between day and night. For this we used drinking duration as a surrogate for harvest. Finally, we tested the hypothesis that wallabies in groups would be less vigilant than solitary wallabies at drinking sites. A reduction in individual vigilance with an increase in group size (Pulliam 1973; Caro 2005) is a common trend in foraging animals including macropods (Heathcote 1987; Jarman & Coulson 1989; Roberts 1996; Banks 2001; but see Colagrass & Cockburn 1993). However, if the primary adaptive mechanism for the 'group vigilance effect' is early detection (Roberts 1996; Bednekoff & Lima 1998), then a reduction in apprehension in groups may be detrimental to drinking wallabies facing a concealed ambush predator within strike range, because the advantage of early detection in groups may not be possible (Cowlishaw 1997).

Figure 1. Drinking site 'paradox': multiple agile wallabies drinking simultaneously from the 'safer' excavated holes and from the 'riskier' river.

METHODS

Study Area and Study Species

We conducted the study in a remote location along the Daly River, Northern Territory, Australia, near Oolloo Crossing (14°00′18″ S, 131°14′25″ E) during the dry season of 2007 (May–October). The area is wet–dry tropics, and is dominated by open savannah woodland, but with a narrow, closed riparian zone. During this time water clarity is generally high, and river levels continue to fall slowly until the onset of the next wet season (November). Also during this time most nearby river swamps (billabongs) dry completely, restricting free water to the river and riverbank springs (Doody et al. 2007).

The agile wallaby is a medium-sized macropod widely distributed across northern, tropical Australia and Papua New Guinea (Flannery 1995; Strahan 1995). It is primarily associated with riparian habitats (Strahan 1995), and is particularly abundant in areas with agricultural development such as the middle to upper reaches of the Daly River (Doody et al. 2007). Agile wallabies drink both during the day and at night, but show peak drinking times at around 0900 and 1700 hours (Doody et al. 2007). The saltwater crocodile is a large crocodile 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). Adults capture large mammals such as wallabies, pigs, cattle, buffalo and horses (Webb & Manolis 1989; Doody et al. 2007). These crocodiles hunt mainly at night, but are active at dusk, and known to feed opportunistically during the day (Webb & Manolis 1989). The linear density of saltwater crocodiles in the present study area was about one per 10 km (Doody et al. 2007).

Experimental Design, Apparatus and Data Collection

Because our main goal was to compare the behaviours of wallabies drinking from excavated holes and the river's edge, we chose a drinking site with multiple excavated holes. The chosen site was a relatively flat beach protruding from the river bank (approximately 20 m long × 20 m wide) and was accessible by motorboat. Up to six excavated drinking holes were used on the