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GROUP SIZE BUT NOT DISTANCE TO COVER INFLUENCES AGILE WALLABY (*MACROPUS AGILIS*) TIME ALLOCATION

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Despite their widespread distribution and relative abundance, little is known about the antipredator behavior of agile wallabies (*Macropus agilis*). The ability to modify time allocation as a function of group size is an antipredator behavior that has been reported in some, but not all, previous studies of members of the genus *Macropus*. We studied group-size effects and space use for agile wallabies foraging in the open to develop a better understanding of behavior of mid-sized macropods. We found that agile wallabies modified time allocated to foraging and vigilance as a function of group size but were insensitive to distance from cover. We contrast the group size results from agile wallabies with those from other macropodids and speculate that predation by saltwater crocodiles (*Crocodylus porosus*) may have a profound effect on how agile wallabies perceive and manage predation risk.

Key words: agile wallaby, group-size effects, habitat selection, *Macropus agilis*, predation risk, time allocation

Australia has the world's worst record of recent mammalian extinctions (Burgman and Lindenmayer 1998). Unlike many other macropodid marsupials (Maxwell et al. 1996), however, agile wallabies (*Macropus agilis*) have not been negatively affected by European settlement (Bell 1973; Merchant 1995), and they are both widespread and abundant throughout tropical Australia (Merchant 1995). Surprisingly, there have been relatively few studies of their behavior (Croft 1987; Dressen 1993; Johnson 1980; Stirrat and Fuller 1997), and none of these studies have focused specifically on antipredator behavior. Macropods and other marsupials evolved with a variety of predators (Archer 1981; Robertshaw and Harden 1989; Wroe 1999). In response to this, they have a complex repertoire of antipredator behavior (Coulson 1996), which includes some degree of ''innate'' predator recognition (Blumstein et al. 2000), the ability to quickly learn to increase responsiveness to predators (Griffin et al. 2001; McLean et al. 2000), and a variety of behaviors that ''manage'' (Lima and Dill 1990) or reduce the risk of predation while foraging (Blumstein 2000; Blumstein et al. 2001a, 2001b; Jarman and Wright 1993; Wahungu et al. 2001).

Of these strategies to manage predation risk, the ability to modify time allocation as a function of group size (Bednekoff and Lima 1998) has been reported in some, but not all, previous studies of members of the genus *Macropus* (Table 1). Such effects of group size are commonly reported in mammals (Quenette 1990), and individuals may receive a number of antipredator benefits by aggregation (Alexander 1974; Hamilton

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TABLE 1.—Published reports of the presence or absence of group-size effects in the genus *Macropus*.

Species	Body size[a]	Present	Absent
Macropus agiliis	15 kg, females; 27 kg, males	No previous reports	No previous reports
Macropus eugenii	6 kg, females; 10 kg, males	Blumstein et al. (1999), Blumstein and Daniel (2002)	Blumstein et al. (in litt.)
Macropus fuliginosus	27.5 kg, females; 53.5 kg, males	Coulson (1999), Blumstein and Daniel (2002)	Blumstein and Daniel (2002)
Macropus giganteus	32 kg, females; 66 kg, males	Heathcote (1987), Jarman (1987), Coulson (1999), Payne and Jarman (1999)	Colagross and Cockburn (1993)
Macropus rufogriseus	15.5 kg, females; 23.7 kg, males	Coulson (1999)	Johnson (1989)

[a] Maximum body size from Strahan (1995).

1971; Kenward 1978; Powell 1974; Pulliam 1973; Vine 1971). These benefits, however, must be traded-off with the costs of increased competition (Beauchamp 1998; Blumstein et al. 2001a; Clark and Mangel 1986), and thus, group-size effects may not always be detected (Blumstein et al. 2001a).

Variation in the presence of group-size effects in the genus *Macropus* could reflect several factors. First, different researchers have used different definitions to define groups (variously defined as the number of conspecifics within 10–50 m). Second, ecological factors may vary at different sites. For instance, Blumstein and Daniel (2002) found group-size effects in a predator-rich mainland population of western grey kangaroos (*M. fuliginosus*) but not on a predator-free insular population. And, tammar wallabies (*M. eugenii*) translocated to (from the wallaby's perspective) predator-free New Zealand 130 years before lost group-size effects that were hypothesized to be present before their movement (D. T. Blumstein et al., in litt.). The importance of competition may also vary among different sites, which can influence the trade-offs between benefits of aggregation and ability to acquire sufficient food (Blumstein et al. 2001a). Finally, body size may be an important factor influencing occurrence of group-size effects because body size influences vulnerability to predators (Jarman 1991) and therefore benefits individuals could obtain by aggregating with others. Small body–sized (maximum mass about 10 kg) members of the genus *Macropus* seemingly benefit from aggregation, whereas there is more variation in midsized (maximum mass 10–25 kg) and larger animals (maximum mass >25 kg; Table 1).

Studies of group-size effects in midsized species living with predators could be revealing. Thus, the midsized agile wallaby is an optimal study subject to develop a deeper understanding of group-size effects and management of predation risk in the genus *Macropus*. Theory predicts that agile wallabies found on the predator-rich mainland will have group-size effects because they are vulnerable to predation by both aerial predators such as wedge-tailed eagles (*Aquila audax*) and terrestrial predators, which include dingoes (*Canis lupus dingo*), and saltwater crocodiles (*Crocodylus porosus*). We tested this prediction by studying group-size effects and space use in free-living agile wallabies.

MATERIALS AND METHODS

We studied free-ranging agile wallabies at the 200-ha East Point Reserve, Darwin, Australia from 28 May to 4 June and from 2 to 11 July

2001. The study site has been used by previous researchers (Stirrat and Fuller 1997) and has high population densities of agile wallabies that are easy to observe. At the time of our study, there were about 600 wallabies living on the reserve (D. Perry, pers. comm.). Dingo–dog hybrids as well as feral dogs have been observed hunting wallabies in the reserve, and people picnic and visit the reserve (D. Perry, pers. comm.). Like other macropodids, agile wallabies rest by day in cover and emerge to forage in open cleared areas at night (Bell 1973). At the study site we focused on 58 ha in the northwest corner of the reserve, which was prime wallaby habitat where wallabies foraged on grassy areas adjacent to patches of dense monsoon vine forest.

General procedures.—We video-recorded 5-min observations of focal animals within 3 h of sunrise (0650–0939 h) and sunset (1730–1921 h) when the wallabies foraged on the open sward. Animals were observed on days without rain or heavy wind. We recorded from locations where we did not detectably influence behavior of our focal subject. Most observations were conducted from inside an automobile. We video-recorded 109 independent wallabies (26 adult females, 26 adult males, 16 unsexed adults, 3 subadult males, 2 males of unknown age, 3 females of unknown age, 33 of unknown age or sex). On average, we observed wallabies from 80 m (±34.4 *SD*).

Individuals were neither captured nor marked as part of this study. To avoid observing individuals more than once and thereby to preserve statistical independence, we took care to choose different individuals based on location, size, sex, and reproductive status when sampling within each area of the reserve. We are confident that most of the observations came from different individuals.

At the beginning of each focal sample, we noted the following variables: sex of focal animal (scored only when positively identified); distance of focal animal from protective cover (agile wallabies returned to dense vegetation when alarmed); and number of conspecifics within 10 m and within 50 m (with solitary animals scored as being in a group of 1).

Parts of the study area were mowed between the first sampling period in May–June and the second sampling period in July, and we also noted whether the observation was conducted in May–June or July. Vegetation height was not measured directly but was estimated using the wallaby as a reference. Our general impression was that there was vegetation of varying height during observation periods. There were more extensive areas with $>$20 cm tall vegetation in May–June compared with July. In July, the majority of observations were of animals foraging in areas with $<$10 cm tall vegetation (which included patches of bare earth as well as locations that had been grazed to 1–2 cm). A wallaby with its head in 20 cm tall vegetation would have its vision obstructed more than one foraging on vegetation $<$10 cm tall.

One observer (JCD) scored all videotaped focal animal samples using the software JWatcher (www.jwatcher.ucla.edu) and noted the onset of each bout of foraging (included foraging on the sward and digging in the ground), vigilance, and several other behaviors. Vigilance was divided into several categories: while crouching or standing (the onset of a bout was scored each time an individual moved its head and fixated) and while rearing up (differentiated from quadrupedal crouching and bipedal standing by upright angle—$>$50°—of the back). Other behaviors included walking, hopping, grooming, affiliative behavior (sniffing and allogrooming), and aggressive behavior (displacement, chasing, boxing). We also noted when animals went out of our sight and when they were back in sight.

From the video record we calculated the percentage of time allocated to each behavior out of total time the animal was in sight. On average, wallabies were in sight for 278.8 s (±41.4 *SD*) during our focal samples. We combined our 3 measures of vigilance—crouching, standing, and rearing up—to generate 1 behavior, vigilance. Walking and hopping were combined to form a new behavior—locomotion. These analyses focus on the 3 most common agile behaviors: foraging, vigilance, and locomotion.

Statistical analysis.—We used the individual as the unit of analysis. Statistical analyses were conducted using the software package SPSS 10 (SPSS 2000). To study group-size effects, we fitted linear and logarithmic regression models to the proportion of time in sight allocated to vigilance, foraging, and locomotion. We averaged time allocations for all observations of agile wallabies observed at a given group size, defining group size in 2 ways: total number of wallabies within 10 m and number within 50 m. We examined residuals from the linear and logarithmic models to test for goodness of fit. We then assumed that the model that explained the most variation reflected how wallabies assessed group size (Blumstein et al. 2001a, 2001b).

We used parametric statistics to evaluate whether distance to nearest conspecific, vegetation depth (mowed or unmowed), distance to cover, and distance to observer influenced time allocated to foraging, vigilance, and locomotion. The time males and females allocated to foraging, vigilance, and locomotion did not have homogeneous variances, so we used a Mann–Whitney *U*-test to test for sex effects on time allocation.

Following bivariate analyses, we fitted fixed-factor models of analysis of covariance (ANCOVA) that included those variables that significantly explained variation in time allocation (distance to conspecific, vegetation depth) along with group size (defined as number of conspecifics within 10 m) as a covariate as well as all 2-way and 3-way interactions. We employed a backward-stepping algorithm in which we removed the term with the largest *P*-value until the model's adjusted R^2 was maximized. We then interpreted these models. Values are given as mean ± *SD.*

RESULTS

On average, wallabies foraged 73.3% (±15.1) of the time, were vigilant 22.6% (±15.0) of the time, moved around 2.6% (±3.3) of the time, and groomed 1.1% (±2.2) of the time. Wallabies were recorded at an average of 58.0 m (±34.5, $n = 109$) from cover, and at an average of 10.5 m (±12.7, $n = 98$) from their nearest conspecific.

Group size influenced the time agile wallabies allocated to foraging (10 m linear, adjusted $R^2 = 0.65$, $P = 0.032$; 10 m log, adjusted $R^2 = 0.70$, $P = 0.024$; 50 m linear, adjusted $R^2 = 0.38$, $P = 0.019$; 50 m log, adjusted $R^2 = 0.71$, $P < 0.0001$). Group size also influenced the time wallabies allocated to vigilance (10 m linear, adjusted $R^2 = 0.76$, $P = 0.014$; 10 m log, adjusted $R^2 = 0.84$, $P = 0.006$; 50 m linear, adjusted $R^2 = 0.56$, $P = 0.003$; 50 m log, adjusted $R^2 = 0.83$, $P < 0.0001$). However, group size did not influence the time allocated to locomotion (all adjusted R^2 values = 0; all P values < 0.381). In all cases, more variation was explained by logarithmic regressions than by linear regressions (Fig. 1). When comparing linear regression functions, more variation in time allocation was explained when group size was defined as the number of conspecifics within 10 m than when it was defined as within 50 m. For logarithmic models, slightly more variation in time allocated to vigilance was explained by defining group size at 10 m rather than 50 m, but the reverse was true for foraging.

Wallabies significantly increased vigilance (adjusted $R^2 = 0.108$, $P = 0.0006$, $n = 98$) and decreased foraging (adjusted $R^2 = 0.116$, $P = 0.0004$, $n = 98$) when far from the nearest conspecific. Time allocated to locomotion was not influenced by distance to the nearest conspecific (adjusted $R^2 = 0$, $P = 0.691$).

While being observed, agile wallabies foraged significantly more and were less vigilant in low vegetation than in high vegetation (foraging in tall grass, 71.4 ± 15.4%, $n = 89$; low grass, 81.9 ± 10.7%, $P = 0.005$, $n = 20$; vigilance in tall grass, 24.4 ± 15.3%; low grass, 14.7 ± 10.6%, $P = 0.009$). Vegetation height did not significantly affect time allocated to locomotion (tall grass, 2.6 ± 3.5%, low grass, 2.4 ± 2.3%; $P = 0.753$).

Sex, distance to cover, or distance to observer did not influence time allocation. There was no effect of sex on time allocation (vigilance $P = 0.119$, $n = 60$, foraging $P = 0.220$, locomotion $P = 0.468$). There was no significant effect of distance to cover on time allocation (vigilance adjusted $R^2 = 0.012$, $P = 0.127$, $n = 109$; foraging adjusted $R^2 = 0.019$, $P = 0.081$; locomotion adjusted $R^2 = 0$, $P = 0.815$). There was no significant effect of distance to observer on time allocation (vigilance adjusted $R^2 = 0$, $P = 0.675$, $n = 109$; foraging adjusted $R^2 = 0$, $P = 0.838$; locomotion adjusted $R^2 = 0.01$, $P = 0.164$).

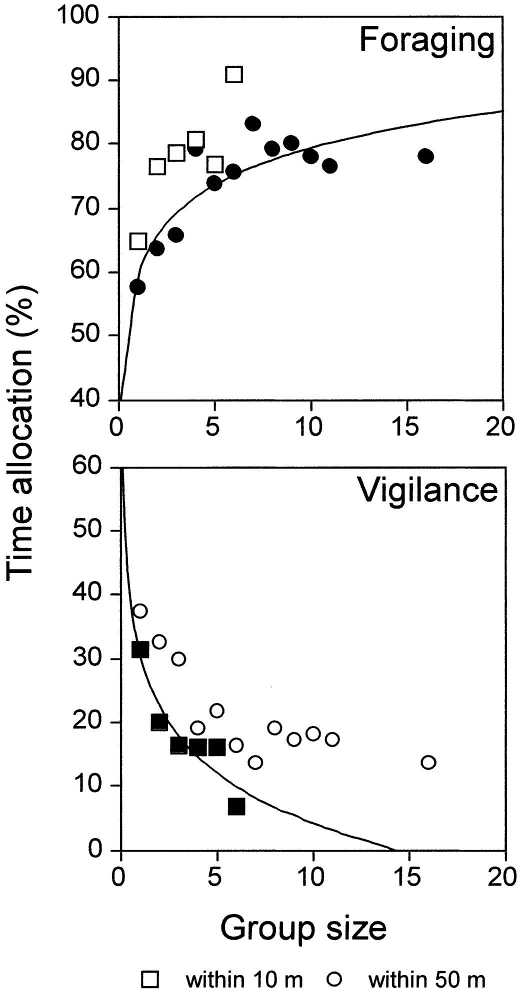

FIG. 1.—Time that agile wallabies allocated to foraging and vigilance as a function of number of conspecifics within 10 and 50 m. For both behaviors, logarithmic regression models explained more variation than linear models. For log models, slightly more variation in vigilance was explained when group size was defined as including those conspecifics within 10 m (filled squares), whereas more variation in foraging was explained when group size was defined as the number of conspecifics within 50 m (filled circles). Symbols indicate mean percentage of time for each behavior. The equation for foraging is $Y = 19.4 \times \log(x) + 59.9$. The equation for vigilance is $Y = -26.1 \times \log(x) + 30.2$.

Group size was defined as the number of conspecifics within 10 m for ANCOVA models and significantly explained variation allocated to foraging and vigilance after accounting for potentially confounding or obscuring factors (Table 2). The only other factor that explained variation in the models that maximized explained variation was a 3-way interaction of group size by distance to conspecific by vegetation depth.

DISCUSSION

Nonlinear models fit the data better based on examination of residuals, and explained more variation in time allocation than did linear models. Based on these nonlinear models, we infer that agile wallabies treated those conspecifics within 10 m as "group mates" when modifying their time allocated to vigilance, whereas conspecifics within 50 m influenced time allocated to foraging. That these relationships were nonlinear suggests that agile wallabies benefit from aggregation (Blumstein et al. 2001a). Similar findings have been reported in the congeneric tammar wallaby (Blumstein et al. 1999; Blumstein and Daniel 2002). Linear relationships, which suggest an important role of intraspecific competition for food mediating any beneficial effects of aggregation (Blumstein et al. 2001a), have been reported in western grey kangaroos living with predators (Blumstein and Daniel 2002), in quokkas (*Setonix brachyurus*) living on a densely-packed predator-free island (Blumstein et al. 2001b), and in a captive population of yellow-footed rock wallabies (*Petrogale xanthopus*—Blumstein et al. 2001a).

At this point, it seems that body size is associated with the distance within which kangaroos and wallabies perceive conspecifics as group mates; small body-sized animals are more sensitive to the presence of relatively close conspecifics, whereas larger body–sized animals are influenced by individuals distributed over a greater distance. Agile wallabies have an intermediate

TABLE 2.—Final models for explaining variation in time allocated to foraging and vigilance after employing a backward-stepping algorithm designed to maximize adjusted R^2 (ANCOVA). Group size was defined as the number of conspecifics within 10 m for both analyses ($n = 98$).

Factor	Foraging	Vigilance
Model	$P < 0.0001$	$P < 0.0001$
Group size	$P = 0.046$	$P = 0.006$
Group size × vegetation depth × distance to conspecific	$P = 0.002$	$P = 0.007$
Adjusted R^2	0.156	0.167

body size and are seemingly sensitive to both close and more distant animals.

Agile wallabies are also sensitive to height of the vegetation; they foraged more and looked about less when the area was recently mowed and visibility was presumably greater. A similar effect of sward height was found in the congeneric Bennett's wallaby (*M. rufogriseus rufogriseus*) studied in paddocks in the United Kingdom. The bite rate of Bennett's wallabies (and therefore time allocated to foraging) decreased with increasing vegetation height, although the authors interpret this by saying that search time increased with vegetation depth.

Interestingly, distance to cover had no significant effect on time allocation. Agile wallabies have been reported to seek refuge in cover (Merchant 1995) and also did so when alarmed by us (initiation of flight occurred at a mean of 37.1 ± 19.1 m; 50 of 61 wallabies fled to cover when approached). Species may perceive cover as being either obstructive or protective (Blumstein and Daniel 2002; Caraco et al. 1980; Lima 1990). For instance, western grey kangaroos foraging on the predator-rich mainland leave cover quickly and forage more in the center of meadows, whereas when on a predator-free island they forage closer to cover (Blumstein and Daniel 2002). When alarmed in the higher-risk location, they hop off, remaining in the open where, presumably, they can identify and monitor distant predators. In contrast, tammar wallabies studied at the same locations forage closer to cover at the higher-risk site and retreat to cover when alarmed. From these observations, Blumstein and Daniel (2002) infer that kangaroos perceive safety in the center of meadows, whereas wallabies perceive safety in cover. Studies of some other macropodids report distance effects (Blumstein et al. 2001b; Colagross and Cockburn 1993), while studies on other species have not found distance effects (Wahungu et al. 2001).

One possible explanation for insensitivity of agile wallabies to distance to cover is that they are preyed on by multiple types of predators. Recent theory suggests that it is important to think critically about the different risks posed by different types of predators (Krams 2000; Lima 1992; Sih et al. 1998). The same antipredator behaviors that work well when helping a small rodent avoid a raptor might not be very effective against a snake (Bouskila 1995). It is possible that the general insensitivity of agile wallabies to distance from cover is because the risks their predators create vary differently as a function of distance from cover. For instance, although wallabies drinking by a river's edge are either in riparian vegetation or relatively close to cover, when sympatric with crocodiles they are still exposed to a potential risk of predation. In contrast, raptors may have the greatest successes hunting wallabies in the open. Thus wallabies may seek safety in cover but do not necessarily perceive safety in their proximity to cover. The presence of a diversity of predators may have a profound influence on how animals perceive risk.

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