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Foraging behavior of three Tasmanian macropodid marsupials in response to present and historical predation threat

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It is often essential to understand historical selection regimes to explain current traits. We studied antipredator behavior of three Tasmanian macropodid marsupials – Forester kangaroos *Macropus giganteus*, Bennett's wallabies *M. rufogriseus*, and Tasmanian pademelons *Thylogale billardierii* – to understand how antipredator behavior functions in a relatively intact predator community. We also compared behavior of the kangaroos and wallabies on a predator-free island where they were translocated from mainland Tasmania 30 yr ago. Both species allowed humans to get closer to them on the predator-free island; a finding consistent with a reduced risk of predation on the island. Neither kangaroos, nor wallabies, exhibited group size effects – they did not modify time allocated to foraging or antipredator vigilance as a function of group size at either site. Nor did overall time allocation vary in any consistent way. In contrast, mainland Australian sibling-species of Forester kangaroos and Bennett's wallabies have both been reported to have group size effects. It is possible either that the extinction of the thylacine *Thylacinus cynocephalus* in the last century has led to an evolutionary loss of group size effects and other antipredator behavior, or that thylacines were never that important a predator on Tasmanian subspecies. In contrast, Tasmanian pademelons studied on the Tasmanian mainland modified time allocation as a function of group size suggesting that they perceived safety in numbers. Pademelons, because of their body size, are relatively more vulnerable than larger-bodied macropodids to the rich community of marsupial carnivores in Tasmania, and used a mix of social and individual strategies to manage predation risk.

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Islands, by their very nature, are isolated and isolation may offer the opportunity to study adaptations in the context within which they evolved. Tasmania, a 68 331 km^2 island 240 km off the Australian mainland (Berra 1998), offers the unique opportunity to study antipredator behavior of native mammals in a relatively intact predator community (Watts 1993). Tasmania was first occupied by humans ca 30 000 yr ago, and was last connected to mainland Australia ca 12 000 yr ago (Vandenbeld 1988, Kohen 1995). Native quolls (*Dasyurus* spp.) prey on the smaller mammals, and the Tasmanian devil (*Sarcophilus laniarius*) preys on mid-sized mammals (Jones 1997, pers. comm., Jones and Barmuta 1998). The thylacine (*Thylacinus cynocephalus*) was hunted to extinction only within the past century (Guiler 1985, Watts 1993, Paddle 2000). One recent hypothesis suggests that it was most likely to prey on 1–5 kg prey (Jones and Stoddart 1998), although both personal accounts (Paddle 2000) and subsequent analyses (Jones 2003, Wroe and Muirhead in press) suggest that larger-bodied prey may have also been taken. With respect to non-native predators, only the domestic cat *Felis catus* has been introduced to Tasmania where it has had a negligible impact on mammalian diversity

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(Watts 1993). Dingoes *Canis lupus dingo* have never been recorded in Tasmania, and Tasmania was entirely free of red foxes *Vulpes vulpes* until 1999 (Jones et al. 2003). It should therefore be possible to infer historical patterns of antipredator behavior (Byers 1997) before the widespread ecological changes and extinctions that accompanied European settlement in Australia (Flannery 1994, Kohen 1995, Burgman and Lindenmayer 1998).

As part of a series of studies designed to understand the evolution of antipredator behavior of macropodid marsupials, we focused on three Tasmanian species: the 25–50 kg Forester kangaroo *Macropus giganteus*, the 11–15 kg Bennett's wallaby *M. rufogriseus*, and the 4–7 kg Tasmanian pademelon *Thylogale billardierii* (body size estimates from Strahan 1995). Recent archaeological work suggests that humans preferentially hunted Bennett's wallabies for $>20\,000$ yr (Cosgrove and Allen 2001), although pademelons and kangaroos were hunted as well. Body size influences vulnerability to predators (Werner and Gilliam 1984) and, in macropodids, body size influences sociality and antipredator strategies (Croft 1989, Jarman and Coulson 1989). By studying species along a gradient of body sizes, we are in a better position to understand how different-sized macropodids manage predation risk.

Moreover, wildlife management has created further opportunities to study evolutionary processes of isolation from predators because prey species have been translocated to island reserves without native predators. One such location has been Maria Island, a 9672 ha island off the southeastern coast of Tasmania, where kangaroos, wallabies and pademelons were introduced in 1971 (Weidenhofer 1991). By comparing the behavior of "mainland" Tasmanian populations to those same species introduced to an offshore island, we can begin to understand the time course of relaxed selection for antipredator behavior. Developing such an understanding is important if we wish to predict the likely outcome of formerly isolated species encountering predators (Berger 1999, Blumstein 2000, 2002, Berger et al. 2001, Blumstein and Daniel 2002). Such processes happen both naturally during range expansions (Thomas et al. 2001), and intentionally, as an important strategy to help recover locally extinct populations (Kleiman 1989, Sarrazin and Barbault 1996). Most such translocations for conservation fail, and predation is often implicated as a factor contributing to failure (Wolf et al. 1996, Sinclair et al. 1998). Thus, by developing a fundamental understanding of the effects of relaxed selection, we can apply those findings to help increase the success of translocations for conservation.

To develop this understanding, we focus on antipredator behavior while foraging and examine four ways that animals may manage predation risk. A main aim is to document "group size effects" – the way in which time allocated to behavior is modified by group size (Bednekoff and Lima 1998). Three models of predation hazard assessment (dilution – Hamilton 1971; detection – Pulliam 1973; security – Dehn 1990) predict non-linear relationships between group size and time allocation. If animals directly translated the change in actual or perceived predation risk into increased foraging and reduced vigilance, then we would expect non-linear relationships in time allocation. It is important to understand if animals modify time as a function of group size because this may influence the likelihood that they will experience Allee effects (Stephens and Sutherland 1999) as population sizes decline. We also studied the overall amount of time allocated to vigilance and foraging, the distribution of behavior with respect to vegetative cover, and overall wariness of individuals at different locations inferred by quantifying the distance we could approach animals before they fled.

Methods

Subjects and study site

We studied kangaroos and wallabies at Maria Island National Park and at Mt. William National Park, Tasmania. We attempted to study pademelons at both Mt. William and Maria Island (where all three species co-occur), but had difficulties in differentiating them from small wallabies in the dark. Kangaroos and wallabies began to forage in the late afternoon, while most pademelons emerged from cover later in the evening. Most pademelons foraged in complete darkness. Thus, we focused on pademelons only in the Asbestos Range National Park (a park on mainland Tasmaina, where they co-occur with kangaroos but not large populations of wallabies). Observations were conducted throughout the month of January 2001; the height of the Austral summer.

General procedures

On days without rain we video-recorded 5 min focal samples of animals beginning either in the early morning or late afternoon, and affixed image intensifiers to our video cameras after dark. We stood or sat in locations where we did not detectably influence our focal subject's behavior.

Individuals were neither captured, nor marked, as part of this study. To avoid observing individuals more than once (i.e., to preserve statistical independence), we observed different aggregations of animals on different days and, while observing a single mob, attempted not to resample the same individual by systematically shifting our focus to different subjects. There were many more subjects at each of our study sites than our

sample sizes, and we are confident the majority of our observations come from different individuals.

At the beginning of each focal sample we noted the following variables: age (scored only when unambiguous as adult/sub-adult based on size and morphology); sex of the focal animal (scored only when positively identified); the distance the focal animal was from cover (all species rested by day in dense vegetation); and the number of other conspecifics within 10 and 50 m (solitary animals were scored as being in a group of 1).

A single person scored videotaped focal animal samples using JWatcher (Blumstein et al. 2000b), and noted the onset of each bout of foraging, 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), while rearing up (differentiated from quadrupedal crouching and bipedal standing by the upright – i.e., $> 50°$ – angle of the back). Other behaviors included: pentapedal walking (macropodids move their back legs forward while balancing on their forepaws and tail), hopping, grooming, affiliative behavior (e.g., sniffing and allogrooming), and aggressive behavior (displacement, chase, box). We also noted when animals went out of sight behind vegetation or conspecifics, and when they were back in sight.

From the video record we calculated the percent time allocated to each behavior out of the total time the animal was in sight. We combined our three measures of vigilance – crouching, standing, and rearing up – to generate one behavior, vigilance. Pentapedal walking and hopping were combined to form a new behavior – locomotion. These analyses focus on the three most common activities – foraging, vigilance, and locomotion.

At times other than when we were conducting focal samples, we walked at a constant pace of 0.5 m s^{-1} towards individuals to measure the flight initiation distance for each species and at each site. With calibrated paces, we measured the distance we began walking, the distance individuals first oriented to us, and the distance at which an individual hopped off. Humans are routinely used as a standardized surrogate of predation risk (e.g., Burger and Gochfeld 1990, Fernandez-Juricic et al. 2001, Blumstein 2002, Blumstein et al. 2003). Macropodids encountered humans at all locations where we studied them. On Maria Island and at the Asbestos Range National Park, most humans were likely encountered on foot, whereas at Mt. William National Park, most (but not all) humans were encountered in vehicles. We did not quantify human visitation objectively; our subjective impression was that animals on Maria Island encountered humans on foot daily, while subjects in Mt. William and Asbestos Range National Parks were less likely to encounter humans on foot daily. These experiences could have led to differential habituation, and we assume that any differences in our estimates of flight-initiation distance reflects differential exposure to predators. Previous work has shown that flight initiation distance varies as a function of exposure to predators with animals living with extant mammalian predators flushing at significantly greater distances than animals living on islands without mammalian predators (Blumstein 2002).

We estimated ground cover in locations where we observed animals foraging. Ground cover provides a rough estimate of available food, but it does not evaluate the abundance of specific foods that each species might prefer. At both Maria Island and Mt. William, we walked 16, 50 m line transects and recorded, every 5 m, the percent ground cover in 1.5 m diameter circular plots. This resulted in 176 locations/site. At Asbestos Range, we walked 8, 50 m line transects (i.e., 88 locations).

Statistical analysis

We used the individual as the unit of analysis. Statistical analyses were conducted using SPSS 10 (Anon. 2000). We report means and standard deviations for descriptive statistics.

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 the time allocations for all observations of individuals observed at a given group size, defining group size two ways; the total number of individuals within 10 and 50 m. For these aggregated analyses, we assumed that the model that explained the most variation reflected how macropodids assessed group size (see also Blumstein et al. 2001a, b).

We also conducted a series of un-aggregated analyses whereby each observation was a datum. We used parametric statistics to evaluate whether sex and the distance to cover influenced time allocated to the most common behaviors – foraging and vigilance. Sample sizes permitting, we also tested for the effects of the presence of young-at-feet on time allocation. While working at both Mt. William and Maria Island, we experienced periods of heavy wind. We noted when animals were observed foraging during heavy wind and tested for the effects of wind on time allocation. And, because we observed animals at different times of day (kangaroos and wallabies were observed in the morning and late afternoon until total darkness, while pademelons were observed both before and after sunset), we tested for time of day effects on time allocation.

Following bivariate analyses, we fitted fixed-factor ANCOVA models which included those factors that significantly explained variation in time allocation along with group size (defined as the number of conspecifics within 10 m) as a covariate and all possible interactions. We employed a backwards-stepping al-

gorithm 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.

Flight initiation distance was analyzed with ANCOVA where starting distance was entered as a covariate, and location was a fixed factor. We log transformed both starting distance and flight initiation distance to meet assumptions of parametric ANCOVA, and we tested for homogeneity of slopes by including the interaction between location and starting distance. The interaction was not significant and was removed before interpreting the final model. Percent ground cover of Maria Island National Park and Mt. William National Park was compared with a t-test.

Results

The number of individuals observed per site varied (Table 1). Overall time budgets varied by location, but not in any consistent way (Table 2). Forester kangaroos foraged more at Maria Island than at Mt. William ($p = 0.001$), although vigilance did not differ between the sites ($p = 0.102$). Wallabies foraged less ($p < 0.001$), and were more vigilant ($p < 0.001$) at Maria Island than at Mt. William.

Other measured factors had different effects on the species. There were no effects of sex on time allocation for kangaroos (all p-values > 0.60), wallabies (all p-values > 0.24), or pademelons ($p > 0.69$). Distance to cover explained variation in time allocation for kangaroos on Maria Island (foraging Adj. $R^2 = 0.08$, $p < 0.005$; vigilance Adj. $R^2 = 0.08$, $p < 0.005$) and pademelons (foraging Adj. $R^2 = 0.043$, $p < 0.018$; vigilance Adj. $R^2 = 0.028$, $p < 0.047$). Distance to cover did not explain significant variation in wallaby time allocation (p-values > 0.192), or variation for Mt. William kangaroos (p-values > 0.69). The presence of young-at-feet did not affect time allocation in kangaroos (p-values > 0.50). Wallabies on Maria Island were more vigilant when foraging during periods of high wind ($p = 0.035$), but time allocated to foraging was unaffected by wind ($p = 0.363$). There was no effect of wind for wallabies on at Mt. William (p-values > 0.165), or for kangaroos at either location (p-values > 0.206). Time of day explained significant variation for pademelons, kangaroos at Mt. William, but not for Maria Island kangaroos (p-values > 0.78) or wallabies at either location (p-values > 0.27). Specifically, pademelons foraged more ($p < 0.001$), and looked less ($p = 0.001$) at night than before dark. Kangaroos at Mt. William foraged more in the late afternoon compared to the morning ($p = 0.033$) and there was a tendency for them to be less vigilant in the late afternoon ($p = 0.087$).

When observations were aggregated, we found significant group size effects only for pademelons (Fig. 1). These results were further examined with a series of un-aggregated analyses.

For kangaroos, both aggregated and un-aggregated regressions explained more variation when group size was defined as the number of conspecifics within 10 m compared to a definition that included those conspecifics within 50 m, although none of these regressions were significant. Single factor models revealed that logarithmic regressions explained more variation than linear regressions in most cases. For un-aggregated analyses we included location as a fixed factor, and both distance to cover and the logarithm of the number of conspecifics within 10 m as continuous variables in the ANCOVA models fitted to explain time allocation. We focused on observations ($N = 312$) collected in the afternoon because observations in the morning were restricted in the range of observed group sizes. In the foraging model that explained the most variation, there were no significant terms. Non-significant terms included location ($p = 0.123$), group size ($p = 0.161$), distance to cover ($p = 0.170$), location × group size ($p = 0.177$), location × distance to cover ($p = 0.091$). In the vigilance model that explained the most variation, only location ($p = 0.016$) and the location × distance to cover interaction ($p = 0.003$) significantly explained variation, while the group size × location interaction was moderately significant ($p = 0.054$). Maria Island kangaroos were less vigilant, and tended to forage more than Mt. William kangaroos. Vigilance declined as

Table 1. Demographic composition of subjects observed foraging.

	Forester kangaroos Mt. William National Park N = 253	Forester kangaroos Maria Island National Park N = 222	Bennett's wallabies Mt. William National Park N = 125	Bennett's wallabies Maria Island National Park N = 82	Tasmanian pademelon Asbestos Range National Park N = 107
Adult females (with young-at-feet)	39 (20)	53 (24)	11 (0)	7 (2)	12 (11)
Adult males	34	34	9	5	6
Adult unknown sex	167	129	101	68	89
Subadults	13	6	4	2	0
Unknown sex					

Table 2. Average percent time engaged in behavior ($\pm$ SD) of three Tasmanian macropodid marsupials studied at three locations along with additional summary details about the focal observations (X $\pm$ SD).

	Foresters kangaroos Mt. William National Park N = 253	Foresters kangaroos Maria Island National Park N = 222	Bennett's wallabies Mt. William National Park N = 125	Bennett's wallabies Maria Island National Park N = 82	Tasmanian pademelon Asbestos Range National Park N = 107
Forage	73.8% ($\pm$ 20.6)	80.0% ($\pm$ 19.2)	85.1% ($\pm$ 17.3)	70.9% ($\pm$ 21.7)	80.4% ($\pm$ 22.5)
Vigilance	17.9% ($\pm$ 18.7)	15.2% ($\pm$ 17.7)	9.1% ($\pm$ 13.2)	20.8% ($\pm$ 19.2)	15.3% ($\pm$ 20.2)
Locomotion	4.1% ($\pm$ 5.0)	2.6% ($\pm$ 3.4)	2.4% ($\pm$ 2.2)	2.6% ($\pm$ 2.8)	2.1% ($\pm$ 1.8)
Groom	4.0% ($\pm$ 7.9)	2.1% ($\pm$ 5.1)	2.9% ($\pm$ 7.2)	5.0% ($\pm$ 11.1)	1.9% ($\pm$ 3.9)
Time in sight (300 s possible)	277 s ($\pm$ 46)	291 s ($\pm$ 28)	279 s ($\pm$ 40)	278 s ($\pm$ 44)	268 s ($\pm$ 49)
Distance to cover	68 m ($\pm$ 76)	189 m ($\pm$ 171)	32 m ($\pm$ 42)	42 m ($\pm$ 47)	18 m ($\pm$ 20)

Maria Island kangaroos moved from cover. Overall, these models explained limited variation (foraging Adj. $R^2 = 0.054$, model $p = 0.001$; vigilance Adj. $R^2 = 0.047$; model $p = 0.001$).

For wallabies, we defined group size as the number of conspecifics within 10 m. We included location and wind as fixed factors in ANCOVA models with group size as a continuous variable. Single factor models of un-aggregated data revealed that the log of the number of conspecifics within 10 m explained more variation than using the linear number of conspecifics within 10 m. Thus, we use the log of the number of conspecifics at 10 m as the definition of group size in these models. For vigilance, the three main effects were significant, but none of the interactions were significant in the final model that maximized explained variation. For foraging, only location was significant. Wallabies allocated more time to vigilance ($p = 0.007$) and less time to foraging ($p = 0.004$) at Maria Island than at Mt. William. Wind increased vigilance ($p = 0.016$), but had no effect on foraging ($p = 0.178$). Wallabies were less vigilant as group size increased ($p = 0.017$), but group size did not explain significant variation in time allocated to foraging ($p = 0.122$). Overall, these models explained significant variation in time allocation (foraging Adj. $R^2 = 0.137$, model $p < 0.001$; vigilance Adj. $R^2 = 0.172$, model $p < 0.001$).

For pademelons, we defined group size as the log of the number of conspecifics within 10 m. We aimed to include distance to cover and time of day in ANCOVA models. However, there were insufficient numbers of observations of pademelons > 10 m from cover before dark. After dark, there were insufficient numbers of observations of pademelons at small group sizes at distances > 10 m from cover. Thus, we focused on nocturnal observations of pademelons foraging ≤ 10 m from cover ($N = 26$) and found significant logarithmic relationships between group size and time allocated for vigilance (Adj. $R^2 = 0.186$, $p = 0.016$) and foraging (Adj. $R^2 = 0.148$, $p = 0.030$). In the entire un-aggregated data set ($N = 106$), logarithmic regressions explained significant (but not substantial) variation in time allocated to foraging (Adj. $R^2 = 0.11$, $p < 0.001$) and vigilance (Adj. $R^2 = 0.133$, $p < 0.001$).

Flight initiation distances varied by site (Maria Island wallaby = 21.3 m $\pm$ 14.4, Mt. William wallaby = 33.8 m $\pm$ 18.0; Maria Island kangaroo = 21.8 m $\pm$ 22.4, Mt. William kangaroo = 89.9 m $\pm$ 47.8). After accounting for significant variation explained by starting distance, wallabies ($p = 0.007$) and kangaroos ($p < 0.001$) allowed people to approach significantly closer before fleeing on Maria Island compared to Mt. William. By comparison, pademelons allowed a person to approach within 18.4 m ($\pm$ 7.4, $N = 92$) before taking flight.

Finally, there was significantly more ground cover ($p < 0.0001$) at the Maria Island site (X $\pm$ SD = 95.6% $\pm$ 12.2) compared to the Mt. William site (85.5% $\pm$ 17.8). Where pademelons were observed in Asbestos Range National Park, we estimated 97.1% ($\pm$ 7.2) ground cover.

Discussion

Taken together, these results suggest that group size consistently influenced time allocation only in Tasmanian pademelons; individuals in larger groups were less vigilant and allocated more time to foraging. In addition to this social strategy to manage predation risk, pademelons employed individual strategies. Specifically, they modified their time allocation as a function of distance to (presumably) protective cover, and they were sensitive to time of day. Such factors are likely to influence the likelihood of predation, and therefore should influence time allocation and space use (Brown 1999).

Isolation from all predators for 30 yr had no systematic influence on wallaby or kangaroo time allocation: wallabies were more vigilant on the island, while kangaroos were less vigilant. If we interpret the difference in flight initiation distance as a metric of perceived predation risk (e.g., Blumstein et al. 2003), then we might

infer that kangaroos felt proportionally safer on Maria Island than at Mt. William compared to wallabies. Regardless, we would not have predicted that wallabies would be more vigilant on Maria Island than at Mt. William because Bennett's wallabies presumably face some risk of predation at Mt. William. A previous study of tammar wallabies *M. eugenii* and western grey kangaroos *M. fuliginosus* on Kangaroo Island (south Australia) found a significant reduction in vigilance on islands compared to the predator-rich Australian mainland (Blumstein and Daniel 2002). For Forester kangaroos and Bennett's wallabies it is unlikely that the significant difference in food availability affected time allocation because there was no systematic response to different vegetation estimates: wallabies foraged less on the well-vegetated island, while kangaroos foraged more. We observed wallabies at distances where we did not obviously influence their foraging. These distances were significantly closer on Maria Island than at Mt. William ($p < 0.001$). However, within either site, there was no effect of the distance that wallabies were to us on the time they allocated to either vigilance or foraging (all p-values > 0.234). Thus, it is not likely that the different observation distances can account for our results.

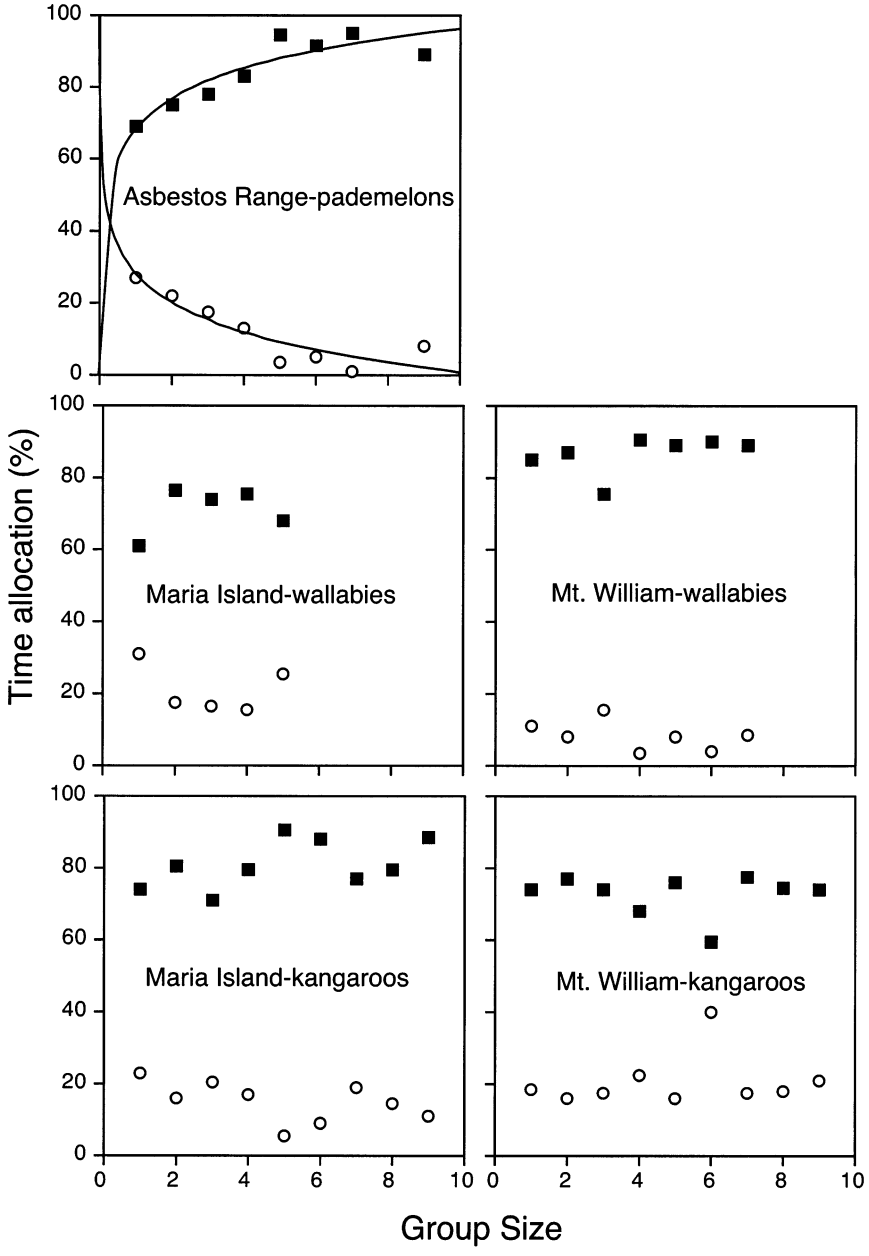

Fig. 1. Time allocated to foraging (■), vigilance (○) as a function of group size defined as the number of conspecifics within 10 m. Linear and logarithmic regressions were fitted to these aggregated (i.e., the average of individuals observed at each group size) results. In the case of pademelons, logarithmic regressions explained more variation than linear regressions. No other regressions were significant (see text).

Interestingly, Bennett's wallabies were sensitive to wind speed and were more vigilant when it was windy. Wind is likely to affect wallaby's ability to assess predation risk in two ways. First, there is an attentional cost (Dukas and Kamil 2000): by increasing movement in the surrounding vegetation, it would be more difficult to visually detect predator movement. Second, wind is noisy. Thus, it might be more difficult to acoustically assess predation risk. Controlled studies of predation hazard assessment in macropodid marsupials suggest that both visual and acoustic cues are important indicators of risk (Blumstein et al. 2000a). The effect of wind as a factor that modifies perceived (or real) predation risk requires further study.

Neither Bennett's wallabies, nor Forester kangaroos, had obvious group size effects or responded in a consistent manner to the presumed reduction of predation risk after their move to Maria Island 30 yr ago. Four hypotheses may explain the absence of group size effects.

First, modifying time allocation as a function of group size may not be an effective antipredator behavior against current or past predators. Aggregation and group size effects would seemingly be effective antipredator adaptations against nocturnally-active mammalian predators (like devils and thylacines) because hunting success declines precipitously once a predator has been detected (FitzGibbon 1989, FitzGibbon and Lazarus 1995), and animals would presumably benefit by being able to allocate more time to foraging (see below). Moreover, group size effects have been reported in a variety of birds and mammals (Quenette 1990, Bednekoff and Lima 1998), including congeners and sibling species (e.g., Coulson 1999, Wahungu et al. 2001, Blumstein and Daniel 2002). We therefore consider the first hypothesis unlikely, but note that much more work needs to focus on the behavior of predators to better understand the evolution of antipredator behavior (Lima 2002).

Second, it is possible that if humans are relatively effective predators, human hunting pressure on wallabies and kangaroos selected against group size effects because group size effects result from aggregation and aggregation may increase the likelihood of predation by human hunters. For instance, hunters could use the presence of one wallaby in a patch as a cue to indicate the presence of others (Cosgrove and Allen 2001). Cosgrove and Allen (2001) build a convincing case that wallabies were hunted selectively by humans in Tasmania for ca 20 000 yr. Part of their economic argument was that wallabies were more abundant than kangaroos and therefore provided a more predictable source of food. However, both wallabies and kangaroos provided sufficient food to make hunting them practical and it is possible that this consistent hunting pressure was sufficient to select against group size effects in Tasmanian populations. At this point we cannot refute this hypothesis, but point out that similar economic arguments will have to be made for mainland populations to understand why human hunting on the mainland did not select against group size effects. It is possible that hunters on the Australian mainland were generalist, rather than specialist, predators, and it is possible that human hunting pressure in Tasmania was a greater selective force against group size effects.

Third, it is possible that neither devils nor thylacines posed much risk to either wallabies or kangaroos. Jones and Stoddart (1998) suggested that thylacines hunted primarily small-bodied prey (i.e., smaller than adult Bennett's wallabies; but see Case 1985, Paddle 2000, Jones 2003, Wroe and Muirhead in press). Our results are consistent with Jones and Stoddart's reconstruction of thylacine behavior in Tasmania, and suggest that thylacines may not have been an important predator of adult kangaroos there. Nonetheless, we assumed that all but the largest Bennett's were vulnerable to some risk of predation from Tasmanian devils (Jones and Barmuta 1998, Jones pers. comm.) and that they would respond accordingly. It is possible that wallaby group size effects would have been detected if we studied animals in full darkness. We attempted to quantify time allocation at night, but we had difficulties distinguishing small wallabies from large pademelons. Rather than introducing error into our identification and group size counts, we excluded nocturnal observations of wallabies from further analysis. However, we know from the rich literature on group size effects in birds that avian predators may select for group size effects so that we do not believe that our twilight observations were insufficient to detect them if they were present.

Fourth, species may have lost antipredator behavior following the extinction of other historically-important predators. The lack of group size effects for the kangaroos also suggests that something other than predation by thylacines is responsible for the group size effects observed in Australian mainland populations of kangaroos (Heathcote 1987, Jarman 1987, Coulson 1999, Payne and Jarman 1999, Blumstein and Daniel 2002). Australia used to have a rich community of very large marsupial carnivores (Archer 1981, Wroe 1999, 2000, 2002). The thylacine – an intermediate-sized one – persisted on mainland Australia until ca 3000 yr ago. While the precise timing of Australian megafaunal extinctions is currently the subject of some controversy (e.g,. Field and Fullagar 2001, Wroe and Field 2001, Roberts et al. 2001a, b, Wroe et al. 2002), the marsupial lion *Thylacoleo carnifex*, and a much larger devil (*Sarcophilus harrisii laniarius*) went extinct at least an order of magnitude longer ago (20 000 yr ago – e.g., Kohen 1995 to 46 000 yr ago – Roberts et al. 2001a). If group size effects were an important adaptation against these marsupial carnivores, then group size effects may have been lost in Forester kangaroos in the tens of millennia following the extinction of mega-carnivores.

We need a hypothesis to explain the presence of group size effects in mainland animals and their absence in the Tasmanian subspecies. It is conceivable that dingoes and foxes have had a greater an effect on the evolution of antipredator behavior of macropodids than has been previously realized (sensu Short et al. 2002). The large body size, cooperative hunting, and relatively fast running speeds of dingoes could represent a novel selective pressure that indigenous marsupials had not previously experienced (Jones 2003, Jones et al. 2003). Both dingoes and foxes can affect kangaroo population biology (Banks et al. 2000, Pople et al. 2000), and behavior (Jarman and Wright 1993, Banks 2001). Group size effects may have evolved relatively recently in kangaroos on mainland Australia as an adaptation against predation by non-marsupial carnivores. The hypothesis of a recent origin of group size effects in kangaroos is consistent with our finding that western grey kangaroos isolated on Kangaroo Island for 9500 yr with no exposure to foxes or dingoes did not have group size effects while kangaroos on the Western Australian mainland did (Blumstein and Daniel 2002). In contrast, smaller body-sized macropodids may have evolved group size effects and related antipredator behavior in response to predation by the smaller marsupial carnivores. A recent origin of group size effects may also account for population-specific results where some studies have documented group size effects in a species (Heathcote 1987, Jarman 1987, Coulson 1999, Payne and Jarman 1999), while other studies have not (Johnson 1989, Colagross and Cockburn 1993).

We have previously suggested that antipredator behavior will persist as long as prey encounter some predators (Blumstein and Daniel 2002). Ultimately, we must better understand the costs to maintaining group size effects in the absence of predators, for it is this cost that will determine persistence or loss. When group size effects are present, individuals suppress foraging when alone. This suppression appears to have a fitness cost for some (e.g., kangaroos and wallabies in this study), but not all species (Blumstein and Daniel 2002). Body size may be one factor that influences cost. Large-bodied species are less selective foragers (Dawson 1989) and require absolutely more food. Thus, it might be particularly costly for large-bodied species to suppress foraging when alone if this limits intake. If so, we might expect kangaroos and Bennett's wallabies to lose group size effects when isolated from some but not all predators, while smaller body-sized quokkas *Setonix brachyurus* and tammar wallabies do not (Blumstein et al. 1999, Blumstein and Daniel 2002).

Finally, this study illustrates how knowledge of history is important to understand contemporary adaptations or lack of them (e.g., Byers 1997). It also emphasizes the importance of knowing about the history of a population's exposure to predators before animals from that population are placed into predator rich areas (Blumstein 2000, 2002, Griffin et al. 2000). In this case, even though Tasmania has a relatively intact predator community, the predators may have been insufficient to select for or maintain certain types of antipredator behavior.

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