DEVELOPING PREDICTIVE MODELS OF BEHAVIOUR: DO ROCK-WALLABIES RECEIVE AN ANTIPREDATOR BENEFIT FROM AGGREGATION?

DANIEL T. BLUMSTEIN AND JANICE C. DANIEL

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Many species receive an antipredator benefit from aggregation such that animals in larger groups are able to allocate more time to foraging and less to antipredator vigilance. These beneficial 'group size effects' must be traded-off against the costs of increased competition for limited resources that may result from aggregation. Certain species, or species living in certain habitats, may be predisposed to receive greater benefits from aggregation than others. Based on the results of a study of captive yellow-footed rock-wallabies (*Petrogale xanthopus*; a 'Vulnerable' macropodid marsupial), we predicted that because rock-wallabies must defend vital resources (the locations where they shelter by day), there are costs which reduce the overall antipredator benefits obtained from aggregation while foraging. We tested this prediction by observing three different species of free-living rock-wallabies as they foraged in aggregations of different sizes. Allied (*P. assimilis*) and unadorned (*P. inornata*) rock-wallabies received no obvious antipredator benefits from aggregation since there was no effect of group size on time spent vigilant by individuals. Mareeba rock-wallabies (*P. mareeba*) may receive antipredator benefits, since animals tended to forage more and looked less as group size increased. However, this result was influenced by two observations that had substantial leverage. Additionally, even if present, the specific shape of this group-size function suggests that intraspecific competition in *P. mareeba* increases with group size. As a clade, rock-wallabies appear to have costs which reduce or eliminate antipredator benefits associated with aggregation. Conservation efforts to recover populations should consider the likely importance of intraspecific competition for these species, and generalizations about introducing or translocating social animals socially should rest upon their being demonstrable benefits from aggregation.

Key words: antipredator behaviour, conservation behaviour, group-size effects, rock-wallaby.

D.T. Blumstein and J.C. Daniel, Department of Organismic Biology, Ecology and Evolution, 621 Charles E. Young Drive South, University of California, Los Angeles, CA 90095-1606, U.S.A. E-mail: marmots@ucla.edu. *Manuscript received 28 April 2003; accepted 23 July 2003.*

MANY species aggregate, and many birds and mammals have been reported to allocate more time to foraging and less to antipredator vigilance as group size increases (Bednekoff and Lima 1998). These 'group size effects' may reflect a benefit from aggregation, but animals must trade-off any benefits with costs (Beauchamp and Livoreil 1997; Grand and Dill 1999; Blumstein *et al.* 2001a). Species are likely to differ in how they make this trade-off. For instance, species living in certain habitats may be predisposed to receive benefits from aggregation while others may not. Contrast a muskox (*Ovibos moschatus*) with a tree squirrel (*Sciurus carolinensis*). Social species in open habitats (like *O. moschatus*) may have to rely on their conspecifics to reduce predation risk (Heard 1992; Blumstein and Daniel 2003). In contrast, less social species living near cover (like squirrels) may be able to independently manage risk by remaining close to cover (Kotler and Blaustein 1995), maximising the attention they allocate to detecting predators while away from cover (Blumstein 1998), or by foraging more efficiently when they are away from cover (Lima and Valone 1986; Newman *et al.* 1988; Brown 1999). But how do we predict which species or types of species will benefit by aggregating, and how should this knowledge be applied?

Resources differ in their defensibility and importance. For non-divisible critical resources, the benefits of acquiring those resources may counter any benefits from cooperation. For instance, rock-wallabies (*Petrogale* spp.) — mid-sized macropodid marsupials — avoid the hot summer days by sheltering in rocky outcrops and when wallabies live in sufficient densities, they emerge to feed in aggregations in the surrounding area in the evening (Batchelor 1980; Lim *et al.* 1987; Jarman and Capararo 1997). Their rocky outcrops are defensible, crucial resources providing both shelter from the environment, protection from predators, and nursery sites for juveniles (Lim *et al.* 1987; Sharp 1997; Jarman and Coulson 1989). Rock-wallabies have been demonstrated to have well-developed dominance relationships (Barker 1990; Horsup 1986, 1994; Blumstein *et al.* 2001a) which may have evolved to help ensure access to this key resource (Batchelor, 1980; Bulinski *et al.*, 1997). Interestingly, these dominance relationships seemingly influence time allocation while foraging away from their caves.

A previous study of captive yellow-footed rock-wallabies (*Petrogale xanthopus*) found that higher-ranking animals foraged more and were less vigilant than lower ranking individuals (Blumstein *et al.* 2001a). Moreover, linear models explained more variation than non-linear models in time allocated to these behaviours. This was notable because 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 (which changes non-linearly) into increased foraging and reduced vigilance, then we would have expected non-linear relationships in time allocation. The fact that *P. xanthopus* had linear group size effects suggested that something prevented the animals from receiving the full antipredator benefits from aggregation. Blumstein *et al.* (2001a) hypothesised that this linear relationship was the result of intra-specific competition, which decreased the benefits to the wallabies from aggregation.

In contrast to rock-wallabies, the similarly-sized tammar wallaby (*Macropus eugenii*) has non-linear relationships between group size and time allocated to vigilance and foraging (Blumstein *et al.* 1999; Blumstein and Daniel 2002). Compared to *Petrogale*, *M. eugenii* day-shelters are neither obviously limited (they shelter in dense vegetation), nor obviously indivisible. Consistent with the reduced importance of competition in *M. eugenii*, dominance rank explained no significant variation in time allocation (Blumstein *et al.* 1999). From these findings, we inferred that while individual *M. eugenii* receive an antipredator benefit from aggregation, individual *P. xanthopus* may not (Blumstein *et al.* 2001a).

Translocations and reintroductions are important tools for macropod management (Short *et al.* 1992; Pople *et al.* 2001), but many of these fail and predation is implicated in their failure (Short *et al.* 1992; McCallum *et al.* 1995). It follows that designing strategies to increase translocation/reintroduction success would be valuable. Translocations and reintroductions are currently being conducted with some rock-wallabies, and more are planned (Maxwell *et al.* 1996; McCallum 1997; Lapidge 2003).

Understanding whether animals are likely to receive an antipredator benefit from being in groups is not merely an academic exercise. Typically, macropods are introduced alone or without regard to group size (K. Morris, pers. comm.; P. Copley, pers. comm.; but see Pople *et al.* 2001). We have previously suggested that tammar wallabies may benefit from being introduced socially because they have non-linear group size effects (Blumstein *et al.* 1999). In contrast, we predicted that *P. xanthopus* may not benefit from aggregation because of the previously described effects of competition (Blumstein *et al.* 2001a). Here, we focus on the generalisability of this suggestion. We predicted that rock-wallabies, as a clade, may not benefit from aggregation. We tested this by studying three additional species of rock-wallabies in their native north-east Queensland habitat. The three species were closely-related, but were distantly related to *P. xanthopus* (Campeau-Peloquin *et al.* 2001).

MATERIALS AND METHODS

Subjects and study site

We studied free-ranging Mareeba rock-wallabies (*Petrogale mareeba*) at Granite Gorge, Mareeba, Queensland (17°S, 145°E). The Granite Gorge wallabies were very habituated to humans. The wallabies lived around a campground, and the site was a local ecotourism destination where visitors fed wallabies grain and wandered throughout their habitat. Wallabies also foraged on natural vegetation. Allied rock-wallabies (*P. assimilis*) were studied at the Arcadia ferry landing on Magnetic Island, Queensland (19°S, 146°E). These wallabies were very habituated to humans, and local residents provisioned the wallabies with large quantities of fresh fruit and vegetables. Wallabies also foraged on natural vegetation around the ferry terminal. A smaller data set collected from non-provisioned and non-habituated rock-wallabies on Magnetic Island generated identical results. Here, we report only those data collected at the ferry landing. In contrast, the unadorned rock-wallabies (*P. inornata*) studied on Mt. Inkerman, Queensland (19°S, 147°E) did not live at an ecotourism destination; they lived beneath a microwave transmission tower. Both technicians and local residents visited Mt. Inkerman, but wallaby feeding was not a well-developed pastime. All observations were conducted in November and December 2000 to control for possible seasonal effects on time allocation.

Overall time budgets and habitat selection are likely to be influenced by predation risk, food ability (e.g., Brown 1999), and degree of habituation to humans (Frid and Dill 2002). However, there is no reason to expect that habituation, per se, will influence our ability to determine whether group size effects are present and if present, whether they are non-linear (implying that a species translates reduction of predation risk into changes in time allocation), or linear (implying that something other than predation risk alone is responsible for this effect). Similarly, high densities of rock-wallabies may be found in areas without artificial provisioning (Horsup 1994; Hornsby 1997), so studying provisioned locations does not necessarily create biologically unrealistic densities. Finally, predators (wedge-tailed eagles *Aquila audax*, and/or dingoes *Canis lupus dingo*, dogs—*Canis (lupus) familiaris*, cats *Felis catus*) were present in all locations, and the presence of predators has been implicated in maintaining group-size effects in other macropodid marsupials (Blumstein and Daniel 2002).

General procedures

We focused on foraging animals and video-recorded 5 min focal samples beginning in the late afternoon until we could no longer observe the animals on days without rain or heavy wind. We stood or sat in locations where we did not detectably influence our focal subject's behaviour (i.e., animals foraged and did not spend their time looking directly at us). On average we observed *P. mareeba* from 14.1 m (± 9.2, *n* = 88), *P. assimilis* from 23.1 m (± 8.6, *n* = 20) and *P. inornata* from 28.3 m (± 21.0, *n* = 24). We videotaped 106 samples of independent (i.e., individuals that were not young-at-foot) *P. mareeba* foraging: 42 adult females (five with young-at-foot), 17 adult males, 19 adults of unknown sex, one sub-adult male, two females of unknown age, and 25 non-juveniles of unknown age or sex. We videotaped 159 samples of independent *P. assimilis* foraging: 46 adult females (one with young-at-foot), 17 adult males, 35 adults of unknown sex, two sub-adults of unknown sex, four females of unknown age, and 55 non-juveniles of unknown age or sex. We videotaped 24 samples of independent *P. inornata* foraging: seven adult females, four adult males, six adults of unknown sex, seven non-juveniles of unknown age or sex.

Individuals were not captured or marked as part of this study. Rock-wallabies are restricted to certain rocky-outcrops and the methods we have successfully used to avoid re-sampling individuals in other studies (e.g., Blumstein *et al.* 2001b; Blumstein and Daniel 2002) did not work. We acknowledge that some individuals were re-sampled in this study. However, we did aim to avoid re-sampling the same individual during the same observation session by shifting our focus to different individuals. The dependency introduced by re-sampling individuals is unlikely to influence our analyses where we average the results of all individuals observed at a single group size, because we are not increasing our degrees of freedom by potentially re-sampling subjects. In contrast, the results from general linear models, where each observation is a unit of analysis, should be interpreted with caution because results may be inadvertently biased if all individuals were not re-sampled an identical number of times.

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) and sex of the focal animal (scored only when positively identified); whether they had young-at-foot, the distance the focal animal was from us; the distance subjects were from the rocky outcrop (their refuge), and the number of other conspecifics within 10 m (solitary animals were scored as being in a group of one). Previous studies have demonstrated that small and mid-sized macropodid marsupials seemingly count those conspecifics within 10 m as 'group mates' (Blumstein *et al.* 2001a,b, 2003; Blumstein and Daniel 2002; unpubl. obs.).

A single person scored videotaped focal animal samples using JWatcher (Blumstein *et al.* 2000b), and noted the onset of each bout of foraging (defined as nose to the substrate — some subjects foraged on food provisioned on either natural rocky substrate or a ferry terminal bench), vigilance, and several other behaviours. 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 behaviours included: pentapedal walking (rock-wallabies move their back legs forward while balancing on their forepaws and tail), hopping, grooming, affiliative behaviour (e.g., sniffing and allogrooming), and aggressive behaviour (displacement, chase, box). We also noted when animals went out of sight and when they were back in sight.

From the video record we calculated the percent time allocated to each behaviour out of the total time the animal was in sight (time in sight: X_{Mareeba} = 255 s ± 53.4, X_{allied} = 238 s ± 59.9, $X_{\text{unadorned}}$ = 212 s ± 97.8). We combined our three measures of vigilance

— crouching, standing and rearing up — to generate one behaviour, vigilance. Pentapedal walking and hopping were combined to form a new behaviour–locomotion. These analyses focus on the three most common rock-wallaby activities —foraging, vigilance, and locomotion.

Statistical analysis

We used the individual observation as the unit of analysis. Statistical analyses were conducted using SPSS 10 (SPSS Inc. 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 rock-wallabies observed at a given group size.

With the un-aggregated data, we used parametric statistics to evaluate whether sex, the distance to the nearest rocky outcrop (i.e., refuge), the distance to nearest conspecific, and the distance to observer influenced time allocated to foraging, vigilance and locomotion. Variable sample sizes reflect the different number of accurate measurements available for each analysis. Upon finding no significant effects, we fitted linear and logarithmic regressions to model group size effects on time allocation with the un-aggregated data.

Petrogale inornata were studied at a location where they lived in low densities and thus were only observed foraging alone or with one other individual. Theory predicts that predation risk declines proportionally less as more individuals are in a group. Thus, the largest change antipredator benefit will result from associating with one other individual. We used *t*-tests to determine if this led to a significant change in time allocated to foraging and vigilance for this species.

RESULTS

Mareeba rock-wallabies (*P. mareeba*)

During general bouts of foraging, individual *P. mareeba* foraged 57.5% (± 17.9, $n = 106$) of the time, allocated 35.5% (± 16.0) of their time to vigilance, locomoted 2.6% (± 2.3) of their time and groomed 3.3% (± 6.9) of their time. On average, they were 5.9 m (± 5.8, $n = 78$) from their nearest conspecific and 6.2 m (± 4.7, $n = 86$) from the rocky outcrop.

When the observations of group size were aggregated, there was a tendency for group size to influence time allocation in *P. mareeba* (Fig. 1). This result was not present when we removed the observations of wallabies foraging in a group of 8 (only two wallabies were observed foraging in a group of 8 and this data point had substantial leverage). When significant, linear models explained more variation than logarithmic models (foraging: linear adjusted $R^2 = 0.65$, $P = 0.018$, log adjusted $R^2 = 0.55$, $P = 0.034$; vigilance: linear adjusted $R^2 = 0.60$, $P = 0.024$, log adjusted $R^2 = 0.51$, $P = 0.043$; locomotion: adjusted $R^2 = 0$, P-values ≥ 0.81). When the group size of 8 was removed, and all values had $\geq$ 4 observations, there were no significant group size effects (foraging: linear adjusted $R^2 = 0.45$, $P = 0.089$, log adjusted $R^2 = 0.36$, $P = 0.121$; vigilance: linear adjusted $R^2 = 0.42$, $P = 0.097$, log adjusted $R^2 = 0.33$, $P = 0.137$; locomotion: adjusted $R^2 = 0$, P-values ≥ 0.77).

When un-aggregated data were analysed, there was a tendency for group size to explain variation in time allocated to foraging and vigilance, but not locomotion (foraging: linear adjusted $R^2 = 0.03$, $P = 0.058$, log adjusted $R^2 = 0.02$, $P = 0.073$; vigilance: linear adjusted $R^2 = 0.03$, $P = 0.056$, log adjusted $R^2 = 0.02$, $P = 0.063$; locomotion: adjusted $R^2 = 0$, P-values ≥ 0.85). Again, when the two observations of individuals foraging in a group of 8 were removed, this tendency disappeared (foraging: linear adjusted $R^2 = 0.02$, $P = 0.113$, log adjusted $R^2 = 0.01$, $P = 0.121$; vigilance: linear adjusted $R^2 = 0.02$, $P = 0.113$, log adjusted $R^2 = 0.02$, $P = 0.107$; locomotion: adjusted $R^2 = 0$, P-values ≥ 0.75).

No other examined factors explained significant variation in time allocation. Distance to rocky outcrop explained no significant variation in foraging ($P = 0.216$, $n = 86$), vigilance ($P = 0.190$), or locomotion ($P = 0.081$). Distance to observer explained no significant variation in time allocated to foraging ($P = 0.319$, $n = 88$), vigilance ($P = 0.205$), or locomotion ($P = 0.271$). The distance to the nearest conspecific did not explain significant variation in time allocated to foraging ($P = 0.208$, $n = 78$), vigilance ($P = 0.295$), or locomotion ($P = 0.493$). There was no effect of sex on time allocation (foraging $P = 0.995$, $n = 18$ males, $n = 44$ females; vigilance $P = 0.774$, locomotion $P = 0.478$).

Allied rock-wallabies (*P. assimilis*)

During general bouts of foraging, individual *P. assimilis* foraged 62.6% (± 20.3, $n = 159$) of the time, allocated 32.4% (± 20.0) of their time to vigilance, locomoted 3.3% (± 2.6) of their time and groomed 0.8% (± 2.1) of their time. On average, they were 3.0 m (± 3.2, $n = 18$) from their nearest conspecific and 5.3 m (± 10.4, $n = 27$) from the rocky outcrop.

Any way examined, we found no effect of group size on time allocation (Fig. 1). When data were aggregated, and we removed group size estimates based on fewer than 4 observations, there was no effect of group size on time allocation (all adjusted R^2 values = 0; foraging P-values > 0.83, vigilance P-

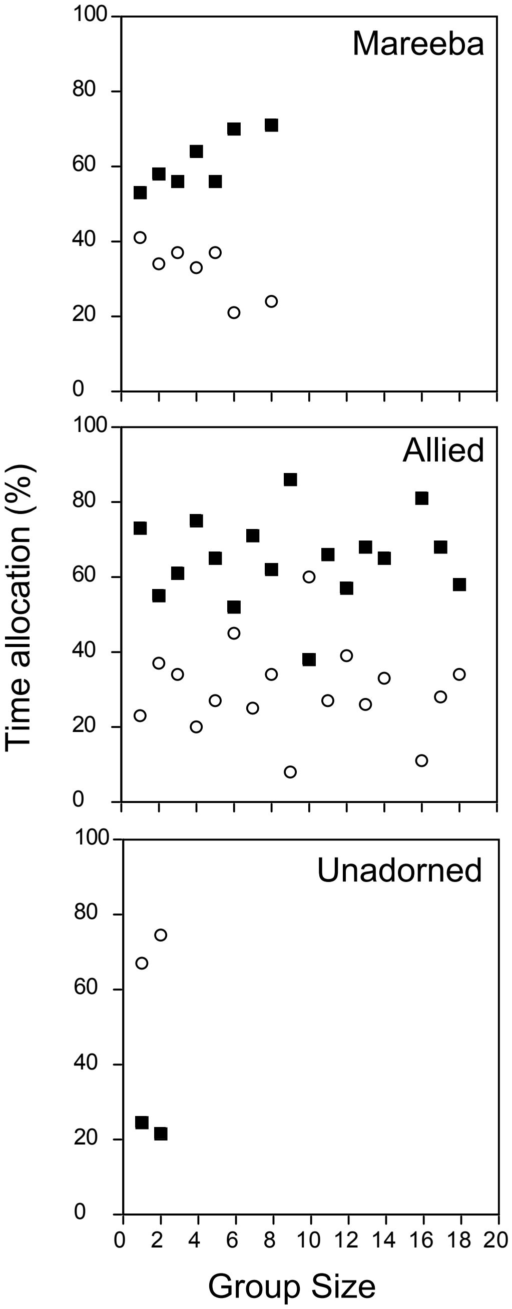

Fig. 1. The relationships between group size and time allocated to foraging (■) and vigilance (○) for *P. mareeba*, *P. assimilis* and *P. inornata*. Estimates of time allocation at a given group size are calculated from all observations of subjects foraging at a given group size (range 2 – 31 observations per group size). Analyses were conducted on the entire data set and on subsets with ≥ 4 observations per group size (see text for details).

values > 0.82, locomotion *P*-values > 0.64). Similarly, when data were not aggregated, and group sizes based on fewer than 4 observations were removed, there was no effect of group size on time allocation (all adjusted R^2 values = 0; foraging *P*-values > 0.77, vigilance *P*-values > 0.77, locomotion *P*-values > 0.12).

Because the animals foraged on supplemental food in a ferry shelter, and the distance to the rocky outcrop and the observer was relatively constant, we only examined sex effects and found no effect of sex on time allocation (foraging *P* = 0.698, *n* males = 17, *n* females = 50; vigilance *P* = 0.522; locomotion *P* = 0.382).

Unadorned rock-wallabies (*P. inornata*)

During general bouts of foraging, individual *P. inornata* foraged 23.4% (± 20.1, *n* = 24) of the time, allocated 69.1% (± 20.1) of their time to vigilance, locomoted 2.5% (± 2.1) of their time and groomed 4.6% (± 7.8) of their time. On average, they were 2.1 m (± 3.0, *n* = 21) from the rocky outcrop; there were only observed foraging in groups of 1 and 2 on the low-density Mt. Inkerman study site.

Petrogale inornata were much more vigilant than their congeners (Fig. 1). However, no measured parameter influenced time allocation in unadorned rock-wallabies. There was no effect of foraging with a companion on time allocation (foraging *P* = 0.752, vigilance *P* = 0.409, locomotion *P* = 0.603; *n* = 16 singletons and *n* = 8 pairs). Nor was there an effect of distance to rocky outcrop (foraging *P* = 0.906, *n* = 21; vigilance *P* = 0.933; locomotion *P* = 0.968), or distance to observer on time allocation (foraging *P* = 0.211, *n* = 24; vigilance *P* = 0.398; locomotion *P* = 0.150).

DISCUSSION

There were two consistent patterns. Rock-wallabies seemingly foraged independently of other individuals. Moreover, no measured parameters that have been shown to influence time allocation in other species (e.g., Elgar 1989), or in macropodid marsupials (e.g., Blumstein *et al.* 2001a,b, 2003; Blumstein and Daniel 2002, 2003; Colagross and Cockburn 1993; Wahungu *et al.* 2001), explained significant variation in time allocation in any of these three species. Group size effects in *P. mareeba*, if present, are linear; a finding that suggests that aggregation is not entirely beneficial. Thus, as a clade, rock-wallabies may have costs which reduce or eliminate antipredator benefits associated with aggregation. These findings are consistent with field studies that reported dominance hierarchies (Barker 1990; Horsup 1994), as well as the results of a captive study of rock-wallaby behaviour (Blumstein *et al.* 2001a) that suggested that intraspecific competition is an important facet of rock-wallaby life which reduces the benefits of aggregation.

This is a remarkable finding because at Granite Gorge, at the ferry landing on Magnetic Island, and particularly in captivity, wallabies were provisioned with abundant, non-monopolisable and, in the case of captivity, non-depletable food. Thus, competition for food should not be an important factor influencing time allocation. If supplemental feeding increased group sizes to abnormally high levels, it has provided an opportunity to determine whether animals have the potential to experience group-size effects should they find themselves aggregated. Rock-wallabies appeared not to receive an antipredator benefit from aggregation while foraging. Based on these and previous findings (Blumstein *et al.* 2001a), we speculate that the need to compete for caves influences competition in other aspects of rock-wallaby life (e.g., while foraging).

The finding that no other measured factors influenced rock-wallaby time allocation requires discussion. Our sample sizes for both *P. mareeba* and *P. assimilis* are similar to those in our previous studies that found significant effects of distance to cover, age, sex, etc. (Blumstein *et al.* 2001a, b; Blumstein and Daniel 2002), so we do not believe that this reflects a relative lack of statistical power. We do believe that the finding is consistent with the hypothesis that wallabies independently assessed predation risk (Blumstein 1996) and maintained a 'suitable' level of vigilance regardless of their location. We tested this directly with *P. assimilis* by providing food at a location 10 m from their rock outcrop and comparing this to those foraging within 2 m of the rocks and found no effect on time allocation (unpubl. data). Theory predicts that refuging species should reduce their overall exposure (Blumstein 1998) by foraging faster and allocating less time to vigilance when far from a refuge (Brown 1999). While we did not measure intake rate per se, we found no effect of distance on overall time allocated to vigilance, or to foraging (unpubl. data).

Other un-measured factors, such as predator density, might influence time allocation. We did not assess predator density and are not in a position to evaluate this formally (e.g., Banks 2001). However, in other species studied using similar methods, we found that the presence of predators maintained detectable group-size effects (Blumstein and Daniel 2002), and other antipredator behaviour (Blumstein *et al.* 2000a). We do not believe that differential habituation to humans at the different sites systematically biased our results. Habituation might be predicted to create ceiling effects, whereby animals would be expected to allocate all their time to foraging and none to antipredator vigilance. We did not see this; neither *P. assimilis*, nor *P. mareeba* eliminated vigilance. Because we aimed to avoid sampling each individual more than once (admittedly a goal not entirely achieved with *P. mareeba* and *P. assimilis* for which there were fewer than 100 individuals and more than 100 observations), we concentrated our observations to one season — early summer. Thus, we cannot comment on seasonal variation in antipredator behaviour. It is known that rock-wallabies spend more time out during the day during the cool winter months (Lim *et al.* 1987) and that forage availability varies seasonally (Lim *et al.* 1987). However, it is not known how this influences antipredator behaviour.

Of the 22 recognised species and sub-species of rock-wallabies (Maxwell *et al.* 1996), one is 'Endangered', seven are 'Vulnerable', and six are 'Near Threatened'. Conservation efforts include ranslocation and reintroduction (Lim *et al.* 1987; Lim and Giles 1987; McCallum 1997) to repopulate former ranges and to maintain genetic diversity of genetically isolated and unique populations (Eldridge *et al.* 1999). Predation of newly-introduced macropodids is a factor contributing to the failure of many previous translocations and reintroductions (Short *et al.* 1992, 2002; Lapidge 2003).

Managers deciding whether and how to introduce animals have to decide whether to introduce them socially or alone. Most translocations of Australian macropodid marsupials, by design, disperse individuals throughout their new habitat (P. Copley, pers. comm.; K. Morris, pers. comm.), and by doing so, introduce animals alone. A potential cost of solitary introductions is that species that may receive an antipredator benefit will not. In contrast, a potential cost of social introduction of a species that does not receive an antipredator benefit is that clumped animals may be vulnerable to surplus killing by red-foxes (*Vulpes vulpes*) (Short *et al.* 2002). We have suggested previously that by studying the occurrence and type of group size effects, it should be possible to determine whether animals will receive a net antipredator benefit by being introduced socially. Rock-wallabies, as a clade, are expected not to receive an antipredator benefit from such a social introduction policy; experimental re-introductions can be used to test this hypothesis.

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