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Yellow-footed Rock-Wallaby Group Size Effects Reflect A Trade-Off

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Abstract

As group size increases, individuals of many species modify the time allocated to anti-predator vigilance and foraging. Group size effects can result from a reduction in predation risk or from an increase in competition as a function of aggregation. Anti-predator models of vigilance and foraging group size effects both predict a non-linear relationship between group size and time allocation. Linear relationships between group size and time allocation may reflect the modification of such relationships by intraspecific interference competition for limited resources, which would reveal a fundamental cost of sociality. We studied the degree to which group size effects in the yellow-footed rock-wallaby (*Petrogale xanthopus*, a macropodid marsupial) were non-linear. Like several other macropods, yellow-footed rock-wallabies foraged more and looked less as group size increased. Variation in vigilance was best explained by the number of conspecifics within 10 m—a distance substantially less than the 30–50 m often used to quantify group size in macropodids. Linear regressions explained more variation than non-linear ones, suggesting that wallabies traded-off the benefits of aggregation with the costs of competition. Moreover, dominant yellow-foots looked less and tended to forage more than subordinate animals. We hypothesize that competition may be relatively more important in the life-histories of yellow-footed rock-wallabies than those of other macropodid marsupials.

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Introduction

The large amount of literature on the relationship between anti-predator vigilance and group size illustrates that many animals are able to forage more efficiently by aggregating with others (Quenette 1990; Roberts 1996; Bednekoff & Lima 1998). However, the underlying cause of the relationship between group size and time allocation is not self-evident. Two popular hypotheses suggest that the per capita risk of predation decreases as group size increases, either because there are alternative prey (Vine 1971; Alexander 1974), or because there are more individuals to detect predators (Pulliam 1973; Powell 1974; Kenward 1978). In both of these cases, variation in predation risk is responsible for group size effects and aggregation is truly beneficial. Such benefits are likely to have been an important factor in the evolution of sociality (Hoogland 1995). However, scramble competition for scarce resources (Clark & Mangel 1986; Elgar 1989; Lima et al. 1999) could also generate similarly shaped curves if individuals forage more and look less when surrounded by conspecifics. In this case, increased competition would be a cost of aggregation and sociality. This example illustrates the more general principle that intraspecific competition can be an important alternative explanation for group size effects (Beauchamp & Livoreil 1997; Beauchamp 1998).

We developed a simple model to assess the importance of interference competition. An observational study of group size effects in a captive breeding colony of yellow-footed rock-wallabies (*Petrogale xanthopus*) was then conducted to determine whether the beneficial group size effects that have been described in other wallabies (Blumstein et al. 1999; Coulson 1999) and kangaroos (Heathcote 1987; Jarman 1987; Jarman & Wright 1993; Coulson 1999) are also found in this species.

Consider the anti-predator benefits of aggregation. Theory predicts a non-linear relationship between group size and time allocated for looking and foraging (Fig. 1). It is easiest to envision this by considering the risk to a solitary individual joined by at first one, then two other conspecifics. Assuming that a predator only takes one prey, the solitary individual's risk of predation is halved by associating with one other individual. The probability of getting killed is reduced to one third that of when alone, when an individual associates with two other conspecifics. Other models also predict similar non-linear relationships between group size and predation risk, and therefore between group size and time allocated to looking and/or foraging (e.g. Pulliam 1973; Dehn 1990).

Aggregation may also have costs. Interference competition (Fig. 1) should reduce an individual's ability to allocate time to foraging as group size increases (Clark & Mangel 1986; Beauchamp 1998), although the specific shape of the resulting function may vary.

Observed group size effects are likely to reflect the integration of such costs and benefits. Assuming that predation risk influences time allocation, generating a positively curvilinear relationship as described above for foraging, then the addition of interference competition will drive the curve away from its initial form (Fig. 1). The final shape of the relationship will be determined by the relative

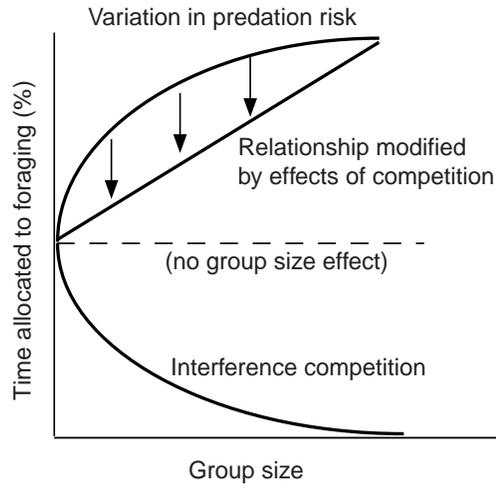


Fig. 1. Predicted relationships between group size and time allocated to foraging. A positive curvilinear function could result from variation in predation risk alone. Interference competition alone would result in a negative relationship between time allocated to foraging and group size; one possible function (Clark & Mangel 1986) is illustrated. A positively linear relationship would therefore result from an interaction between variation in predation risk and the effects of competition

strengths of these effects, but any departure from a positively non-linear relationship (i.e. linear or negative) between group size and foraging will imply that interference competition also influences group size effects and that individuals trade-off the benefits and costs of aggregation.

We quantified time allocation and dominance relationships to study how competition influenced the shape of the group size function in captive yellow-footed rock-wallabies. Yellow-footed rock-wallabies, a 6–12 kg macropodid marsupial (Sharman et al. 1995), are now found in two genetically isolated populations: one centered on the Flinders Ranges of South Australia, and the other in the Adavale Basin of Queensland (Lim et al. 1987; Eldridge 1997). They live in colonies of up to 100 individuals and spend their days on rocky outcrops (Lim 1987), descending at dusk onto the areas below the cliff bands and rocky outcrops to forage. Our experimental set-up was designed to mimic such foraging aggregations.

Methods

Subjects and Observations

We observed 10 adult female rock-wallabies housed with one adult male wallaby in a 1300-m² enclosure with natural vegetation, artificial rock mounds and tunnels, and ad libitum supplemental food and water (provided at a single feeder) at the Macquarie University Fauna Park. Our captive-born subjects are descendants from the South Australian population, and had been housed together

in the enclosure for the previous 5 months. Wallabies were fitted with 1 cm-wide cat collars to which we affixed colored tape and a 2.2×5.0 cm colored plastic key chain to permit the identification of individuals at a distance. Wallabies were observed from a 2-m-tall elevated tower at the edge of the colony at distances of 3–39 m. Twenty-seven hours of observations were conducted on 15 d between 16 Mar. and 17 Apr. 1999. Dusk has been reported as a period of peak activity (Lim et al. 1987), so we elected to begin observations 1 or 2 h before sunset, continuing until it became too dark to score behavior.

We video-recorded individual foraging wallabies for up to 5 min. Because group size and composition varied, we were unable to do a full 5 min focal on each animal. The final data set contains focals that were 2–5 min long, during which group size and composition remained constant.

At the beginning of a foraging bout, we noted the number of other wallabies within 5, 10, 15, and 20 m of the focal animal. Distances were estimated with respect to mapped features in the enclosure and using a marked grid. Group sizes calculated at different distances were not fully independent because the same individuals could be simultaneously represented in different group size counts. Group size is variously defined in macropodids to include the number of conspecifics within 10–50 m (e.g. Jarman 1987; Heathcote 1987; Johnson 1989; Coulson 1999). A previous field study on tammar wallabies (Blumstein & Daniel, unpubl. data) suggested that they might perceive conspecifics within 10 m as group-mates (i.e. the number of animals at this distance explained the most variation in behavior). Our aims in quantifying the effect of group size variation using a range of distance criteria were to establish whether observed changes in behavior were robust and also to obtain insights into how the yellow-footed rock-wallabies perceived group size.

One observer (JCD) scored videotapes using the event recorder Observe (Deni 1996), and noted the onset of all incidences of foraging (nose to ground ingesting food, or holding food items in paws while ingesting food), looking (head elevated, eyes fixated), affiliative and aggressive social interactions (determined by the nature and direction of displacement), and auto-grooming behavior. Behaviors were all mutually exclusive. For each focal, we then calculated the total time allocated to foraging and looking.

There are many factors that can influence the expression of group size effects (Elgar 1989; Blumstein et al. 1999). By studying wallabies in captivity, we were able to control for several of these. All wallabies were adult females with no young-at-foot. The male had recently been introduced into the social group and pouch-young, if present, were less than 1 mo old during our observation period. We elected not to catch females to check for pouch-young to avoid unnecessary capture-related stress. Our observations were restricted to the 2 h preceding sunset to reduce the effects of diel variation on activity. Food and water were provided ad libitum at a fixed location, in addition to naturally available vegetation. The location and type of protective cover remained fixed. Finally, we focused on animals only once they began foraging within 5 m of the single supplemental feeder (whether or not they used the supplemental food); by doing

so, we aimed to control for variation in motivational state as well as distance to the observer and protective cover. Animals did not forage exclusively at the feeder; they also foraged on natural vegetation throughout their enclosure.

We focused specifically on the effects of dominance on time allocation. We never observed high-level aggression, but displacements from perches and from feeding spots—whether natural or artificial—were common. Displacements were scored whenever the arrival of one individual to within 1 m of another caused the other individual to move away, or when two wallabies interacted and one moved away quickly. Some displacements were preceded by one individual swatting another with her forepaws. During our 27 h of observations we noted the identity and outcome of all observed displacements. Approximately 60% of the yard was visible from the elevated tower. It was thus impossible for us to quantify all displacements, but there is no reason to suspect that the patterns observed would not be representative. We used the program Peck Order (Hailman 1994) to analyze displacements and to estimate a dominance hierarchy for the female wallabies.

Statistical Analyses and the Final Data Set

To test for group size effects, we aggregated our set of focal observations. For each individual observed at each group size, we first calculated the average time allocated to foraging and vigilance and then averaged these mean values to obtain a single score for each group size. An unavoidable consequence of this process was that the same individuals contributed to multiple group size estimates. We find this dependence acceptable because multiple observations of the same individual make the overall analysis more conservative (i.e. they would be more likely to eliminate a group size effect than to create a spurious one). Moreover, this aggregation reduced our degrees of freedom by using one average value for each group size. We regressed this aggregated group size against time allocation and fitted two models to these data: a logarithmic model and a linear model.

To test for dominance effects, we averaged each individual's values for percentage time spent in foraging and vigilance across all group sizes and then linearly regressed dominance against each of these time allocations. We also used unaggregated data and fitted a two-variable multiple regression (independent variables were group size and dominance) to the percentage time allocated to looking and foraging. Because the number of individuals within 10 m explained the most variation in time allocation, we restricted this analysis to group size defined this way. Following Sokal & Rohlf (1981), we angularly transformed these unaggregated data. In neither case was there a significant interaction between group size and dominance rank (p -values > 0.5). To increase our power to study the main effects, we report the results of a model without the interaction term.

All statistical analyses were conducted using Statview 5.0 (SAS Institute 1998) and SuperAnova (Abacus Concepts 1991). We report adjusted R^2 values to interpret the goodness of fit of the regression models. Significant effects are those with two-tailed p -values < 0.05 .

We collected a total of 110 focal animal samples on nine of the 10 adult female yellow-footed rock-wallabies. The lowest-ranking adult female was never observed foraging in the designated area adjacent to the supplemental feeder. Each individual was observed an average of 12.2 times (± 6.4 SD, $n = 110$ focals). The average focal duration was 4.3 ± 0.94 min ($n = 110$ focals). An average of 5.0 ± 2.1 individuals ($n = 10$, group sizes averaged across all four group size estimates) contributed to each estimate of time allocation. Each subject was not observed at every group size; subjects were observed an average of 2.6 ± 0.18 times ($n = 4$ group size estimates) per group size estimate.

Results

Yellow-footed rock-wallabies modified their time allocation as a function of the number of relatively close conspecifics; the number of individuals within 10 m explained the most variation in time allocation (Table 1, Fig. 2). For most of the distance criteria used, linear regression models explained more variation in the time wallabies allocated to foraging and looking, as a function of group size, than logarithmic models (Table 1).

There was a significant relationship between dominance rank and the time wallabies allocated to looking. Higher-ranking wallabies looked less than lower-ranking individuals; 46% of the variation in the percentage of time allocated to looking was explained by dominance ($R = 0.73$; $p = 0.026$). There was also a non-significant tendency for higher-ranking wallabies to forage more than lower-ranking wallabies; 33% percent of the variation in the percentage of time allocated to foraging was explained by dominance ($R = 0.64$, $p = 0.062$). Two-factor analyses on unaggregated data emphasize the joint importance of dominance (looking, $p = 0.005$; foraging, $p = 0.002$) and group size (looking,

Table 1: Comparison of linear and logarithmic regression models in explaining variation (adjusted R^2) in the percentage time allocated to looking and foraging explained by group size (n conspecifics within 5, 10, 15, 20 m) yellow-footed rock-wallabies

Distance (m)	Linear		Log	
	p-values	Adjusted R^2	p-values	Adjusted R^2
Looking				
5	0.054	0.56	0.091	0.44
10	0.018	0.65	0.053	0.47
15	0.012	0.63	0.047	0.43
20	0.098	0.22	0.043	0.35
Foraging				
5	0.052	0.56	0.135	0.33
10	0.011	0.71	0.053	0.47
15	0.020	0.56	0.061	0.38
20	0.108	0.20	0.093	0.23

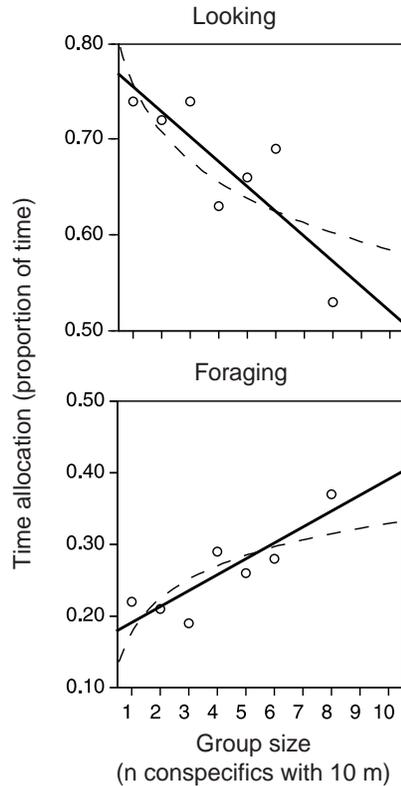


Fig. 2: The relationship between group size and time allocated to looking and foraging in yellow-footed rock-wallabies. Group size was sequentially defined as the number of conspecifics within different distance annuli. The number of conspecifics within 10 m explained the most variation, suggesting that yellow-footed rock-wallabies count conspecifics within 10 m as 'group mates'. Linear and logarithmic regressions are illustrated; the linear relationship explained more variation and is highlighted (statistics in Table 1)

$p = 0.001$; foraging, $p = 0.004$) in explaining yellow-footed rock-wallaby time allocation (looking model, $p = 0.0001$, adjusted $R^2 = 0.31$; foraging model, $p = 0.0002$, adjusted $R^2 = 0.30$).

Discussion

Our results demonstrate that yellow-footed rock-wallaby time allocation is influenced by group size. Wallabies foraged more and looked less as group size increased. Separate analyses examining the group size effect at a range of distances found that the number of companions within 10 m explained the most variation, and that there was an abrupt decrease in the amount of variation explained when individuals as distant as 20 m were included in the analysis. Both

results suggest that the number of relatively close conspecifics (see also Treves 1998) best approximates the way in which rock-wallabies perceive group size.

In most cases (Table 1), linear regressions explained more variation in time allocation than non-linear, logarithmic ones (Fig. 2). If predation risk were sufficient to account for the response to variation in group size, then we should find non-linear relationships among the relatively small group sizes, because this is the range over which the greatest change will occur. The linear relationships that were actually obtained suggest that a second factor interacts with reduction in predation risk to define the group size function (Fig. 1). We infer that yellow-footed rock-wallabies trade-off the anti-predator benefits of aggregation with the costs of intraspecific interference competition.

This inference is supported by the effect of social dominance. We found that dominant yellow-foots devoted significantly less time to looking and tended to forage more than subordinate animals. In contrast, a captive study of tamar wallaby (*Macropus eugenii*) group size effects revealed no such effect of dominance on time allocation (Blumstein et al. 1999).

It seems likely that these differences in the relative importance of dominance reflect fundamental differences between the natural history of *Petrogale* and *Macropus*. Compared with other macropodids (Dawson 1995), rock-wallabies exhibit extreme site fidelity and return to specific rock cavities in which they spend their days and may leave their young (Hornsby 1978; Lim et al. 1987). Species within the genus *Macropus* may maintain home ranges and shelter by day in the same general area, but most do not rely on a specific habitat feature to the degree that rock-wallabies do (Dawson 1995). Perhaps this requirement to defend a cavity has ramifications for other behaviors and sets the stage for interference competition.

In conclusion, we suggest that foraging and vigilance-related group size effects in yellow-footed rock-wallabies reflect the integration of perceived predation risk and intraspecific interference competition. The importance of competition in a rock-wallaby, and not in at least one other macropod of the genus *Macropus*, similarly highlights the potential importance of life-history and natural history in the evolution of mammalian group size effects. While future studies will be required to determine the degree to which such variation influences group size effects in other taxa, the model developed here can be used to identify the influence of interference competition on group size effects. Beauchamp (1998) has made the analogous point that variation in diet has influenced the form of the group size function in birds.

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