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Does Feeding Competition Influence Tammar Wallaby Time Allocation?

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Abstract

Animals may aggregate to reduce predation risk, but this potentially incurs the cost of increased competition. We studied the degree to which competition for food influenced the time tammar wallabies (*Macropus eugenii*) allocate to foraging and vigilance by experimentally manipulating access to food, while holding other factors constant. Groups of six wallabies were observed when they had access to either one or six non-depleting bins of supplemental food. Food availability had no effect on the time allocated to foraging, looking or affiliative interactions, and this was true whether individuals or groups were treated as the unit of analysis. However, wallabies engaged in substantially more aggressive acts in the high-competition treatment. These results, when combined with other findings, suggest that the moderately social tammar wallaby receives an antipredator benefit by aggregating with conspecifics which is not reduced significantly by foraging competition.

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Introduction

Predation risk and feeding competition both have an important influence on the foraging decisions that animals make. As group size increases, the per-capita risk of predation declines, and individuals often allocate more time to foraging and less to vigilance (Lima and Dill 1990). Such 'group size effects' are typically attributed to the decline in individual risk of predation with increasing group size

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(Quenette 1990; Roberts 1996; Bednekoff and Lima 1998). However, several studies suggest that competition for scarce resources increases with aggregation (Clark and Mangel 1986; Beauchamp 1998; Grand and Dill 1999), leading some to suggest that observed group size effects may instead result from this, or other, confounding factors (Elgar 1989).

The mechanism(s) responsible for group size effects are of theoretical interest because they directly influence the benefits that individuals obtain from aggregation and may therefore determine the costs and benefits of sociality (e.g., Caraco 1979a,b; Pulliam and Caraco 1984; Lee 1994). A fundamental understanding of group size effects is also important for conservation. Translocation and reintroduction – where extinct wild populations are recovered by moving animals either from other existing populations or from captivity (Kleiman 1989) – are increasingly important conservation tools (Griffith et al. 1989). However, most of these interventions fail (Wolf et al. 1996), and predation is often implicated as a major cause (Beck et al. 1991; Short et al. 1992). Knowledge about a species' natural antipredator behaviour has the potential to increase translocation success (Curio 1996; Anthony and Blumstein 2000; Blumstein 2000). Introducing animals in groups may be beneficial (Blumstein et al. 1999), but such social introductions or translocations should only be attempted when a net benefit of aggregation has been demonstrated.

Here, we focused on female tammar wallabies (*Macropus eugenii*), a 4–10-kg moderately social macropodid marsupial (Kinloch 1973; Inns, 1980; Smith and Hinds 1995). In nature, tammars spend their days resting in dense vegetative cover and forage by night in loose mixed-sex aggregations that may contain >20 individuals (Inns 1980; D. T. Blumstein, unpubl. data). Adults have well-developed dominance relationships (Blumstein et al. 1999).

Previous results suggest that tammars modify their behaviour as a function of the number of surrounding conspecifics, both in captivity and in the field. They increase the time allocated to foraging, and decrease that allocated to vigilance, as a function of group size (Blumstein et al. 1999; Blumstein and Daniel 2002). Such group size effects are thought to reflect reduced predation risk. However, competition may also be a factor that influences group size effects. For instance, scramble competition may increase foraging and decrease vigilance as a function of group size (Clark and Mangel 1986), whereas interference competition may decrease foraging and increase vigilance as a function of group size (Blumstein et al. 2001a). Studies of macropodids (Blumstein et al. 2001a,b) and other species (e.g., Caraco 1979a,b; Dill and Fraser 1984; Monaghan and Metcalfe 1985; Beauchamp and Livoreil 1997; Grand and Dill 1999) have suggested that individuals may trade-off the benefits of aggregation against the costs of intraspecific competition.

Our previous experiment (Blumstein et al. 1999), which manipulated group size systematically, did not keep per-capita food availability constant. Thus, observed group size effects could have resulted from variation in foraging competition. In the present study, we assessed directly the importance of competition for food in determining time allocation by tammar wallabies. We held group size constant, experimentally manipulated the distribution of food, and measured the effect on time allocated to foraging, vigilance and both affiliative and aggressive social behaviour. By studying feeding competition in captivity, we were able to control both confounding factors (e.g., group size) and potential obscuring variables (e.g., the distribution of cover). Our key assumption was that the effects of varying food availability, while holding group size constant, would be similar to those obtained by keeping food constant and varying group size. We thus aimed to draw conclusions about the relative importance of these factors on time allocation.

Methods

Housing and Husbandry

We studied adult female tammar wallabies at the Macquarie University Fauna Park, Sydney, Australia. Full details of capture and handling techniques for this species can be found elsewhere (Cooper 1998). While not participating in the experiment, subjects lived in mixed-sex aggregations of 6–12 animals. For our study, we moved subjects temporarily into a 10 × 24 m enclosure in which the fence was covered with a 2-m tall band of 90% shade-cloth to provide visual isolation from conspecifics in three adjacent pens. Wallabies noticeably ‘relaxed’ within 24 h of being introduced to the experimental enclosure; they stopped exploring the perimeter, began to groom, and behaved similarly to individuals in other groups. Subjects had access to kangaroo pellets (Gordon’s stock feed) for 5 h/d, and ad libitum access to water and natural vegetation. This feeding regime was sufficient to maintain normal body condition. The experimental enclosure contained both natural shade (tree shadows and a patch of dense brush) and artificial cover (concrete tubes), which was designed to provide protection against the elements and arranged to facilitate observation. All of these environmental factors were constant throughout the study.

Subjects

We randomly selected 36 females from six different breeding enclosures. Tammars come from a number of genetically distinct populations (Cooper and McKenzie 1997). Our subjects were either wild-caught from Kangaroo Island, South Australia, or were the offspring of wild-caught individuals. Wild-caught subjects had lived in the Fauna Park for over 4 yr.

Each subject was fitted with a 1-cm wide cat collar with a 2.2 × 5.0 cm coloured plastic key chain attached. Uniquely coloured key chains permitted individual identification. Collars have no adverse effects on wallabies and have been used to identify individuals in other studies (e.g., Ord et al. 1999; Blumstein et al. 1999, 2001a; D. T. Blumstein, unpubl. data). Subjects habituated quickly to the collars, and we could detect no sign of chafing or irritation.

Creation of experimental social groups required us to move animals between enclosures, which is part of routine Fauna Park management. Nevertheless, we were sensitive to the possibility that social group manipulations might increase the rate of aggressive interactions. We selected female tammar wallabies as subjects because female–female aggression is limited largely to displacement and the occasional chase; female wallabies have never been observed to injure each other. We minimized the number of unfamiliar individuals by maintaining, whenever possible, pre-existing social group composition. This was a conservative strategy because a previous study found no significant effect of familiarity on the rate of aggressive behaviour (Blumstein et al. 2002). Animals were moved in the cool early mornings to reduce the likelihood of hyperthermia. After moving animals between groups, we checked them later in the day for signs of serious aggression or stress and never found any. Animals were subsequently checked at least once per day. Moved animals seemed quickly to integrate into the new social setting and none of our subjects engaged in high-level aggressive interactions with others. When subjects were no longer required for the experiment, they were replaced in the social group from which they originated.

Experimental Design

We created six social groups of six subjects each, and allowed the wallabies to habituate to their new enclosure for 2.5 d. We used groups of six subjects for two reasons. First, groups of this size should have received most of the antipredator benefits from aggregation because the non-linear group size effect function begins to asymptote at group sizes greater than six (Blumstein et al. 1999). Moreover, we might expect competition for food to become relatively more important as the marginal benefits of aggregation declines. Secondly, planned introductions to recover a locally extinct population will involve moving animals in groups of five or six. Pragmatically, we wished to understand whether competition for food could be an important factor influencing time allocation under these conditions.

One feeder (covered feeders measured 30 × 30 × 60 cm with a 25.5 × 14 cm access 'window' on one side) containing a non-depleting supply of supplementary feed was left open for the first 2 d of the habituation procedure. Wallabies were then observed during eight 2.5-h sessions on each of four successive mornings and evenings, generating a total of 20 h of observations per group. At the beginning of each observation session, we opened either one feeder (the 'high-competition' treatment) or six (the 'low-competition' treatment). Treatment order was randomized. At the end of the session, all bins were closed. Normally, wallaby enclosures have a single bin containing supplemental food, so by providing one bin per subject we reduced feeding competition. Bins were lined up together in a central location in the enclosure and were equidistant from protective cover and water. By the end of the 4-d observation session, each group had been observed for 10 h in the 'high-competition' treatment and 10 h in the 'low-competition' treatment. Data from one subject was excluded because she became lethargic during the study and was returned to her home group.

Behavioural Observations

Tammar wallabies are predominantly nocturnal (Kinloch 1973; Inns 1980; Smith and Hinds 1995), but the periods after sunrise and before sunset are active times where the full behavioural repertoire is seen (Blumstein et al. 1999, unpubl. data). We thus observed tammars both in the early morning (from sunrise to 2.5 h after sunrise) and in the early evening (2.5 h before it became too dark to identify subjects). All observations were conducted from a centrally located hide adjacent to one wall of the experimental enclosure, directly opposite the feeding bins.

We estimated the time each subject allocated to vigilance (scored when a subject's head was elevated and immobile), foraging (scored when subjects were acquiring food either with their head down in the vegetation, or by placing their head into a feeder), affiliative social behaviour (scored when subjects allogroomed or sniffed each other) and aggression (scored when one subject displaced another including aggressive displacements and simple displacements where one individual moved away immediately following the approach of another individual; full ethogram in Blumstein et al. 1999). Time allocation for the common behavioural activities (vigilance and foraging) was quantified by noting the activity of the focal subject every 5 min during the 10 h of observation. The rate of the remaining rare behaviours was estimated by noting each occurrence.

Statistical Analyses

Analyses were conducted using both individual scores and averages from social groups. Pairwise Wilcoxon Signed Rank tests were used to avoid the distributional assumptions of parametric statistics. Statistical analyses were conducted using StatView 5.0 (SAS Institute 1998).

Results

Experimental manipulation of feeding competition had no effect on the time tammar wallabies spent foraging, looking, or in affiliative encounters (Fig. 1). This is true whether individuals or groups were used as the unit of analysis. Time allocated to foraging did not differ significantly in the high- and low-feeding competition treatment (Fig. 1; group $p = 0.46$; individual $p = 0.61$). Similarly, time allocated to looking was unaffected by feeding competition (Fig. 1; group $p = 0.46$; individual $p = 0.80$). Finally, the average number of affiliative interactions did not differ significantly in the high and low feeding competition treatments (Fig. 1; group $p = 0.34$; individual $p = 0.39$).

Aggressive behaviour was uniquely influenced by the number of open food bins (Fig. 1), and many displacements occurred around the feeding bins. The average number of aggressive interactions in the high-competition treatment was 1.4 times that in the low-competition treatment ($p = 0.03$). This effect was also present when the individual was treated as the unit of analysis ($p = 0.0001$).

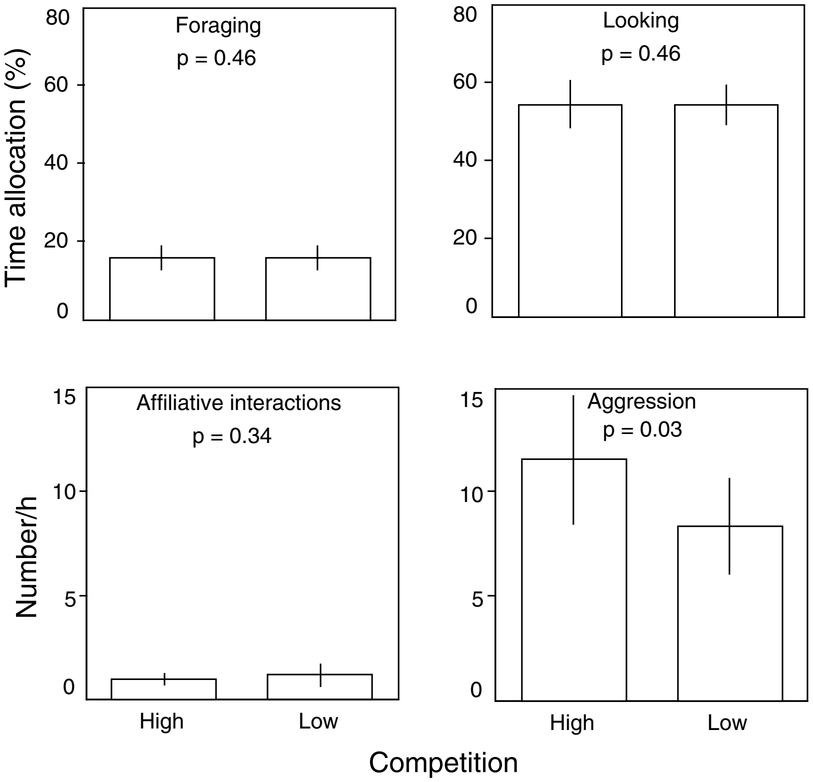

Fig. 1: The effect of competition (high = 1 supplemental feed bin open; low = 6 supplemental feed bins open) on the average (±1 SD) time allocated to foraging, looking, affiliative social behaviour and aggressive interactions. Foraging and looking were estimated from 5-min scan samples over the 10 h of observations for each competition treatment, while affiliative and aggressive behaviour reflect the number of observed interactions per hour of observation for each treatment. The p-values are from Wilcoxon signed rank tests conducted on group means (n = 6 subjects in each of six groups)

Discussion

Our manipulation of foraging competition influenced the rate at which tammar wallabies engaged in aggressive encounters, but it did not otherwise alter their overall time budgets. The frequency of aggressive interactions was significantly higher when only one feeder was available. Interestingly, wallabies did not forage more under these conditions than when food was more readily available (six feeders open). Results thus suggest that foraging competition does not directly influence the foraging vs. vigilance trade-off in tammar wallabies. This finding is consistent with those of a recent study that evaluated the relative importance of competition costs vs. antipredator benefits of aggregation (Lima et al. 1999).

More generally, these results suggest that group size (Blumstein et al. 1999) affects time allocation qualitatively more than the other factors considered (kinship – Blumstein et al. 2002; feeding competition – this study). One interpretation of this finding is that, for some species, competition and kinship are unlikely to either obscure or confound studies of group size effects in the field, as has been suggested by Elgar (1989) (but see Beauchamp 1998). In fact, results from our studies of tammar wallaby group size effects in the field (Blumstein and Daniel 2002) largely match those obtained in captivity, suggesting that observational studies of group size effects may also be useful in understanding mechanisms.

Engaging in aggression or other social behaviour that require animals to attend to each other may indirectly increase risk by making individuals less able to identify predators or cues that predict increased predation threat (Blumstein 1998). Despite its low frequency, aggression may thus still incur a substantial predation cost. Such effects would be relevant for planning conservation interventions.

In summary, these results have both a theoretical and an applied message. For some species, group size may have a relatively large effect on time allocation. Given the large number of reports of group size effects in vertebrates (Quenette 1990), but some controversy over their validity (Elgar 1989), we suspect that group size may in fact be a very important variable that influences time allocation in many species. However, other factors also affect time allocation and predation risk. Competition and kinship influence both the rate of aggressive behaviour and the cost of aggregation. For tammars, there seems to be a net benefit of aggregating, but it would be desirable to identify the exact costs of increased aggression. The applied message is simple: the moderately social tammar wallaby should benefit by being introduced socially. Planned re-introductions to recover a now-extinct mainland South Australian population (Maxwell et al. 1996) will test this hypothesis.

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