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An experimental study of behavioural group size effects in tammar wallabies, *Macropus eugenii*

DANIEL T. BLUMSTEIN*†‡, CHRISTOPHER S. EVANS† & JANICE C. DANIEL†
*Department of Biology, Macquarie University
†Department of Psychology, Macquarie University
‡The Cooperative Research Centre for Conservation and Management of Marsupials, Macquarie University

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As animals aggregate with others, the time they allot to social and nonsocial activities changes. Antipredator models of vigilance and foraging group size effects both predict a nonlinear relationship between group size and the time allocated to behaviour. Group size effects were experimentally studied in captive adult female tammar wallabies, a small macropodid marsupial, by increasing group size from 1 to 10. Tammars foraged more, looked less, groomed more, engaged in more aggressive interactions and moved about less as group size increased. Nonlinear regression models explained more variation in the time allocated to foraging, looking, locomotion and affiliative behaviour than linear models. Variation in self-grooming and aggression was better explained by linear models. Wallabies lay down significantly more, and walked significantly less, as group size increased: these relationships were significantly nonlinear. Thus, changes in perceived predation risk, which are characterized by nonlinear relationships, explain tammar wallaby group size effects for most activities. These results support the assertion that predation has played an important role in macropodid social evolution. Moreover, the findings suggest that conservation biologists should pay particular attention to group size when translocating or reintroducing endangered macropodids.

Sociality has costs and benefits. A commonly cited benefit of aggregating with others is a decrease in the probability that a given individual will be killed by a predator (Hamilton 1971; Alexander 1974; Pulliam & Caraco 1984). This per capita reduction in predation risk can result from the presence of alternative prey (the dilution effect: Hamilton 1971; Vine 1971), or from having more individuals to locate predators (the detection effect: Pulliam 1973; Kenward 1978). Regardless of the mechanism, group size effects are reported in many species (Elgar 1989; Quenette 1990; Bednekoff & Lima 1998). Individuals characteristically reduce their vigilance and devote more time to foraging and other activities as group size increases.

Because animals must trade off the benefits from engaging in a particular activity with the predation costs of compromised vigilance while in that activity (Lima & Dill 1990; Blumstein 1998; Dukas 1998), perceived predation risk should influence the time animals allocate to different activities. Models and studies of vigilance group size effects have suggested that both detection and dilution effects should generate nonlinear and asymptotic relationships between group size and the time allocated to vigilance and/or foraging (e.g. Pulliam 1973; Jarman 1987; Dehn 1990). For instance, dilution models assume that a solitary individual's risk of predation decreases by 50% with the addition of one other individual (i.e. $N=2$), by 67% with the addition of two others (i.e. $N=3$), by 75% with the addition of three others (i.e. $N=4$), etc. Thus, time allocation of behaviours sensitive to predation risk should vary nonlinearly with group size. Less is known about how time devoted to activities other than vigilance or foraging change systematically as a function of group size (but see Caraco 1979a, b; Watts 1985), or specifically whether predation risk or social factors influence possible group size effects. However, the logic developed for studying vigilance and foraging group size effects should be generalizable to other activities. Thus, if perceived predation risk is responsible for group size effects, theory predicts a nonlinear relationship between group size and the amount of time animals allocate to other activities as well. There is a need for a more comprehensive understanding of how predation risk influences trade-offs in time allocation for different activities to understand how predation risk and social factors influence time allocation

Correspondence: D. T. Blumstein, Department of Biology, Macquarie University, Sydney, NSW 2109, Australia (email: dan@galliform.bhs.mq.edu.au).

as a function of group size. We studied how group size influences the time allocated to several activities in tammar wallabies, a macropodid marsupial.

Although there are some exceptions (e.g. Powell 1974; Lazarus 1979; Kildaw 1995; Beauchamp & Livoreil 1997), most studies reporting vigilance and foraging group size effects have been correlational (Elgar 1989). The results obtained may consequently be influenced by a variety of ecological factors, such as the distribution of food and cover, which either covaried with group size or were responsible for the group size effect. Moreover, because many vigilance studies are conducted in the field on unknown subjects (e.g. Bertram 1980; Heathcote 1987; Hunter & Skinner 1998), it is often impossible to control for potentially confounding social factors such as age, individual identity, or dominance rank, which can also influence how animals allocate their time. Experimental manipulations of group size, which can be designed to control for any of the above factors, are a more powerful way to quantify group size effects. Manipulating group size experimentally to study group size effects is therefore important (Elgar 1989). In this study, we manipulated group sizes to study their effect on how tammars allocated their time to vigilance, foraging, maintenance behaviour and social activities. We studied tammar wallabies for several reasons.

First, body size and gregariousness are reported to covary in macropodids: kangaroos, wallabies and rat-kangaroos (Kaufmann 1974; Russell 1984). Tammar wallabies are a small (4–10 kg), moderately social macropodid (Croft 1989; Smith & Hinds 1995) that spend their days alone in dense scrub, but may aggregate on foraging grounds at night. Group size effects for vigilance and foraging have been reported in the larger and more social congeneric eastern grey kangaroo, *M. giganteus* (Heathcote 1987; Jarman 1987; Jarman & Wright 1993; Coulson 1999; but see Colagross & Cockburn 1993) and western grey kangaroo, *M. fuliginosus* (Coulson 1999). Group size effects were found in one study of the medium-sized and less-social red-necked wallaby, *M. rufogriseus* (Coulson, 1999), but not another (Johnson 1989). Nevertheless, theory predicts that based on the asymptotic shape of detection and dilution effects, the greatest effect of group size will be found when a solitary individual joins a conspecific. While not normally studied, we should expect group size effects in moderately social animals. Tammars are thus an excellent species in which to document the effects of group size on time allocation.

Second, predation has been an important selective factor in marsupial evolution (Coulson 1996). Group size effects could be related to the evolution of macropodid sociality. If relatively larger group size effects are found in more social species, then group size effects may contribute towards the evolution of sociality in less-social macropodids as well. Our systematic group size manipulations tested for the presence of any effect, measured its magnitude, and determined whether the effect extends to larger associations in the moderately social tammar.

Third, for applied reasons, it is important to understand how time budgets change as a function of group size. The majority of Australia's small and medium-sized macropodids are either extinct on the mainland or live in threatened populations (Johnson et al. 1989). Predation by introduced predators is one of several factors responsible for the decline of mainland macropodids, including tammars. Translocation from surviving insular populations, or reintroduction from captive populations, is a management option for tammars and other species (Serena & Williams 1995). However, the majority of translocations and reintroductions for conservation purposes are unsuccessful (McCallum et al. 1995). Knowledge of how group size influences time allocation may increase translocation success for vulnerable species.

In this study we had two main aims: to determine (1) whether group size influenced the time individuals allocated to several social and nonsocial activities and (2) the shape of the relationship between group size and time allocation. Nonlinear group size effects would suggest that perceived predation risk influenced how tammars allocated their time to particular activities. In contrast, linear group size effects would be incompatible with perceived predation risk being primarily responsible for variation in time allocation and would suggest that other factors (i.e. social) were important determinants of time allocation.

METHODS

Housing and Husbandry

We studied adult female tammar wallabies at the Macquarie University Fauna Park, Sydney, Australia, from 7 September to 18 November 1998. Full details of capturing and handling wallabies can be found elsewhere (Cooper 1998). When not participating in the experiment, the wallabies lived in mixed-sex aggregations. For this study, we temporarily placed the experimental females into a fenced yard measuring 10 × 24 m which was divided into 21 quadrants measuring 3.2 × 3.4 m. The yard was encased with a band of 90% shade-cloth 2 m tall to prevent subjects seeing wallabies in three adjacent yards, although they could hear and smell them. Occasionally, lighting conditions meant they could see shadows of animals in adjacent yards next to the fence. The wallabies noticeably 'relaxed' within a day of being introduced to the experimental yard; they stopped exploring the perimeter of the enclosure, they began to groom, they generally looked less tense, and they behaved similarly to individuals in other yards. They were given kangaroo pellets (Gordon's stock feed) and water ad libitum and also grazed on natural vegetation. The experimental yard contained both natural shade (tree shadows and piles of sticks) and artificial cover (concrete tubes and aluminium sheets arranged to form a lean-to). The cover, designed both to provide protection against the elements (wind, rain), and to facilitate viewing, was distributed throughout the enclosure and was constant for all treatments. The wallabies did not monopolize or obviously defend cover or other resources.

Subjects and Ethical Concerns

For this study, we randomly selected five females with pouch young and five females without pouch young (one female's joey subsequently died) from four different breeding yards and assigned them to the experiment. Tammars come from a number of genetically distinct populations (Cooper & McKenzie 1997). Our subjects were either wild-caught from Kangaroo Island, South Australia, for the Fauna Park breeding colony, or the first-generation offspring from wild-caught individuals. Wild-caught subjects had lived in the Fauna Park for over 2 years.

We fitted the females with cat collars 1 cm wide and attached a coloured plastic key-chain, measuring 2.2 × 5.0 cm, to the cat collar. Unique patterns of coloured reflective tape on the collars and key-chains permitted identification of animals during the day and night. Collars have no obvious adverse effects on wallabies and have been used to identify individuals in other studies (e.g. Ord et al., in press). The wallabies appeared to habituate quickly to the collars, which caused no obvious chafing or irritation.

We ear biopsied the females to collect a tissue sample for genetic analysis, and to make a small hole in which to affix a numbered eartag for permanent identification. A small piece of tissue (a circle 2–3 mm in diameter) was removed from one ear without anaesthetic. This procedure caused no obvious distress and only slight bleeding. This is a standard method used at zoos and fauna parks to identify macropods and to collect tissue for genetic material because it minimizes handling time and avoids any adverse effects of anaesthetics.

This experiment involved moving animals to create social groups of a fixed size (see below). Animals are moved between enclosures in the fauna park as part of routine management generating no adverse effects. Nevertheless, we were particularly sensitive to the potential effect of social group manipulations on aggressive behaviour. For our experiment, we focused on female tammar wallabies because female–female aggression is largely limited to displacement and the occasional chase. The wallabies were moved in the cool early mornings to reduce the likelihood of potentially fatal hyperthermia. Heat stress was a far greater danger to the health and well-being of our animals than social factors. After moving females between groups, we checked them later in the day for signs of high-level aggression and never found any. They 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 the females were no longer required for the experiment, they were replaced in the social group from which they originated. Here too, newly replaced animals did not engage in high-level aggression, but nevertheless they were routinely monitored for signs of aggression. Ultimately, we have no evidence suggesting that the social group manipulations caused undue stress: the females maintained condition and behaved and ate normally while involved in the experiment.

Experimental Design

We planned to use a within-subject 'staircase' design in which group size was first increased and then decreased over 12 weeks, with each group size treatment lasting 1 week. Group size treatments were N=1, 2, 4, 6, 8, 10, 10, 8, 6, 4, 2 and 1 subject. We refer to the increasing group size treatments as 1a, 2a, 4a . . . 10a, and the decreasing group size treatments as 10b, 8b, 6b . . . 1b. The same individuals were used in a and b treatments. Statistical analyses are based upon the average response of each subject to the two treatments of each type. By counterbalancing the order in which group size was experienced and averaging the two group size treatments, we hoped to isolate the effect of number of conspecifics present and to separate this from any change caused by the direction in which group size was being manipulated.

We used the smallest possible sample of animals to answer our question. The staircase design we selected is optimal to detect effects of interest (in this case group size effects) using a small sample size (10 animals). In choosing this approach, we realize that the group size estimate of 1a and 1b is based on a single subject. By selecting animals from the breeding colony at random, testing them in seminatural conditions, and during a variety of weather conditions, we believe results should be generalizable to other tammars. Because estimates of smaller group sizes are necessarily based on smaller sample sizes than larger group sizes, it may be valuable for future studies to concentrate on studying how time allocation changes during the transition between groups sizes of one and two.

Each Thursday we added or subtracted either one or two females to the experimental group in a predetermined order. We allowed them to habituate to their new physical and social surroundings over the weekend and then observed their behaviour on the following Monday and Tuesday.

The experiment was initially designed to last 12 weeks, but an unidentified pathogen that killed quickly and at epidemic proportions struck tammar wallabies at Macquarie and in at least five other fauna parks in New South Wales and the Australian Capital Territory. Consequently, we shortened the experiment to 11 weeks. It is important to note that animals were healthy and vigorous one day and were dead the next. One female who was to be in the 4b manipulation died the day we were to remove two others to create the 4b group. Another female looked lethargic in the morning and died between observation periods during the 2b manipulation.

To complete the experiment, we included one female from the 6b group in the 4b group. We did not include the data from the female that died during the 2b treatment, but we did use the 3 h of scan samples (see below) and two focal animal samples collected from its healthy companion for the 2b treatment. The next 2 days we observed the behaviour of the remaining solitary female for the 1b treatment.

Behavioural Observations

Tammar wallabies are predominantly nocturnal (Kinloch 1973; Inns 1980; Smith & Hinds 1995). However, preliminary data collected during all hours suggested that the transitional periods around dawn and dusk were ideal for observing the full repertoire of behaviour. Thus, we observed the tammars both in the early morning (from sunrise to 3 h after sunrise) and in the early evening (2 h before sunset and ca. 1 h after sunset). All observations were conducted from a hide adjacent to one wall of the experimental enclosure.

We used 10 × 40 binoculars and a video camera with a zoom lens (Panasonic VX77A) to assist observations in the day. To observe animals in the dark, we attached an image intensifier (ITT Nightcam 300) with a zoom camera lens (Nikkor 80–200 mm) to the video camera and supported this assembly with a custom-built frame. We illuminated the observational yard with red-filtered, 4-W garden lights (ARLEC, Mooroolbark, Australia) mounted on the fence and angled away from the hide. We used an infrared spotlight, and occasionally an unfiltered flashlight, to illuminate the reflective marks on the collar and key-chain to identify distant animals. The wallabies did not obviously respond to any of the supplemental light sources.

During the 10 h of daylight observations for each group size treatment, we used instantaneous scan sampling (Martin & Bateson 1986), noting the subject female's location in the experimental yard, together with its posture and activity every 10 min. We identified six behaviours: looking (head elevated, eyes fixed), foraging (head either down on ground during food ingestion or investigation, or head up and ingesting food directly from a plant), self-grooming (included scratching and oral manipulation of fur), aggression (included all aggressive behaviour where one individual was ultimately displaced), affiliative social behaviour (included allogrooming, nose-to-nose greeting and sniffing, where an animal was not obviously displaced) and locomotion (included hopping and pentapedal walking). We identified seven postures: lie down (legs on side), crouch (quadrupedal, back curved), stand (bipedal, back curved), rear (bipedal, back erect), pentapedal walk and bipedal hop. In addition to these behaviours and postures, we also scored subjects as out of sight if vegetation obstructed them from our view during the rapid scan. The two observers (D.T.B. and J.C.D.) trained by conducting simultaneous observations from the hide until scans were scored identically.

Affiliative social behaviour and aggression were relatively rare. To quantify their frequency, we recorded two 5-min focal animal samples in the morning and one after sunset each day, leading to a total of 30 min of focal observations per individual at each group size treatment. The order of focal samples was randomized among individuals on the first observation day and reversed on the second. The six behaviours (looking, foraging, self-grooming, aggression, affiliative social and locomotion), but not the postures, were scored from the videotapes. After training to a high degree of intraobserver reliability (>95% agreement: Bakeman & Gottman 1986), one observer (J.C.D.) scored all the videotaped focals using Observe 2.1 event recording software (Deni 1996). We calculated the proportion of time allocated to each behaviour out of the total time an animal was in sight, and the average duration of each bout of behaviour.

Statistical Analyses

We used the individual, the individual in a group size treatment and the scan sample as units of analysis. Statistical analyses were conducted using StatView 5.0 (SAS Institute 1998).

We used both focal results and scan sample results to study time allocation as a function of group size. To estimate the time allocated to the relatively uncommon affiliative and aggressive behaviours, we averaged the results of the six 5-min focal samples for each subject during each treatment to generate a mean subject time budget for a given treatment. We then averaged the individual time budgets to obtain a treatment mean. The mean of the two treatments was the overall group size mean. We calculated overall group size means for the proportion of time engaged in behaviour and for the mean bout length of each behaviour. Scan sample data were similarly analysed to calculate the proportion of scans in which an individual was engaged in looking, foraging, self-grooming and locomotion at each group size.

To determine whether predation risk trade-offs influenced wallaby behaviour, we fitted both linear regressions and nonlinear logarithmic regressions to examine group size relationships and report the model that had the greater adjusted R^2. Specifically, we examined the form of the relationships between group size and looking, foraging, self-grooming, aggression, affiliative social behaviour and locomotion.

In addition to overall time budgets, we examined how postures varied as a function of group size. We fitted both linear regressions and nonlinear logarithmic regressions to the scan sample data to look for group size relationships for postures.

Confounding Variables

We aimed, whenever possible, to control experimentally for factors that could influence group size effects by testing only potentially reproductive females, and by observing them at the same relative time of day (3 h after sunrise, 2 h before sunset, and 1 h after sunset). Food, water and availability of cover were identical in all treatments.

Reproductive status

Reproductive status may influence vigilance behaviour (Sullivan 1988; Byers 1997; Hunter & Skinner 1998). Because we wished to obtain results that could be generalized to all female tammars, we elected not to standardize this factor. We thus included both reproductive and nonreproductive females.

Kinship

Kinship may also influence social behaviour (Emlen 1997). While tammars are not reported to associate in kin-structured groups (Kinloch 1973; Inns 1980; Smith & Hinds 1995), we wanted to be certain that the experimental animals were unrelated. We selected subjects from different breeding groups to minimize both familiarity and kinship.

To verify that animals were unrelated, we calculated the coefficient of relationship for each group size treatment. To estimate relationships, we used eight highly variable microsatellite loci (Me1, Me14, Me15, Me17, Me28, Pa 297, Pa595 and Yf148: Taylor & Cooper 1998; K. Zenger, unpublished data). Details of DNA extraction and microsatellite amplification can be found in Taylor & Cooper (1998, 1999). We used the allele frequencies of animals on Kangaroo Island (Taylor & Cooper 1999; K. Zenger, unpublished data), the source of experimental subjects, as the background population frequency from which we calculated the coefficient of relationship (Queller & Goodnight 1989) using the computer program Relatedness 5.0.4 (Goodnight 1998).

Dominance

Dominance may influence how animals allocate their time as a function of group size (e.g. Ekman 1987; Waite 1987; Waite & Grubb 1987; Rasa 1989) and may change after group composition changes. We used all-occurrence sampling (Martin & Bateson 1986) and recorded dyadic displacements over the 2 days of observations. At group sizes less than or equal to six, we were confident that we recorded virtually all displacements. For groups of eight and 10 subjects, we recorded the majority of displacements; however, the wallabies were often found throughout the yard and it was impossible to observe all simultaneously.

We used the computer program PeckOrder 1.03 (Hailman 1994) to calculate dominance hierarchies. In five of the group size treatments (6a, 10a, 10b, 8b, 6b), there was no single unique, linear hierarchy. In these cases we used PeckOrder's single hierarchy as the estimated dominance relationship for that group size. Despite unresolved hierarchies, the relative dominance of the majority of females remained the same: there were clearly high-ranking, mid-ranking and low-ranking individuals. We calculated the relative dominance rank for each group size manipulation. To do this we divided a given female's rank by the total group size; the smaller the number, the higher the relative rank.

To determine whether variation in the time individuals allocated to different activities was influenced by dominance, we regressed relative dominance rank against the proportion of time allocated to each behaviour. For this analysis, we used the time budgets calculated from the focal animal samples, and we treated each individual in each treatment as an independent data point.

Location of other conspecifics

Because the location of other conspecifics can influence vigilance and foraging (Barash 1973; Holmes 1984), but could not be controlled, we tested for the effect of proximity to conspecifics. Using each scan sample as an independent observation, we noted whether there was at least one other wallaby in the same grid of 3.2 × 3.4 m. Using chi-square tests, we examined the independence of the performance of each behaviour during a scan (scored as foraging/not, looking/not, grooming/not, etc.) with the presence of at least one other wallaby in the quadrant.

RESULTS

Time Allocation and Group Size

The amount of time tammar wallabies allocated to all studied behaviours was substantially influenced by group size (Fig. 1). This factor alone accounted for as much as 96% of the variation in time allocation. Wallabies foraged more, looked less, groomed more, moved less, engaged in more affiliative behaviour and engaged in more aggressive interactions as group size increased. In addition to activities, some postures were significantly influenced by group size (Fig. 2). Wallabies lay down on their side significantly more, and walked significantly less as group size increased.

Most group size effects were better explained by nonlinear regression models. Variation in foraging, looking, locomotion, affiliative social behaviour and all postures was better explained by nonlinear models than by linear ones. Only variation in self-grooming and aggression as a function of group size were better explained by a linear model.

Confounding Variables

Group size effects were unlikely to be confounded by most of the uncontrolled variables.

Microsatellite analyses suggested that the females were unrelated and that kinship was unlikely to have confounded group size effects. In all the treatment groups average relationship was not significantly different from 0 ($R \pm 95\%$ CI for the groups were: 2a/b=0.2254 ± 0.3306; 4a=0.1023 ± 0.2246; 4b=0.0290 ± 0.1207; 6a/b=0.0210 ± 0.1109; 8a/b=0.0356 ± 0.0970; 10a/b=0.0473 ± 0.0925).

Dominance did not appear to confound group size effects. Only 7% of the variation in affiliative social behaviour was significantly explained by relative dominance (linear regression: adjusted R^2=0.074, P=0.021), and this factor explained no significant variation in the proportion of time allocated to any other activity (all adjusted R^2s<0.01, all Ps>0.2).

While aggression and affiliative social behaviour were, by definition, likely to occur when a wallaby was in a quadrant with at least one other companion, two other behaviours were also influenced by the location of conspecifics (Table 1). Wallabies foraged more when they were in a quadrant with at least one other wallaby. Locomotion and the presence of at least one other wallaby were also significantly associated. When sharing a quadrant, wallabies were significantly less likely to

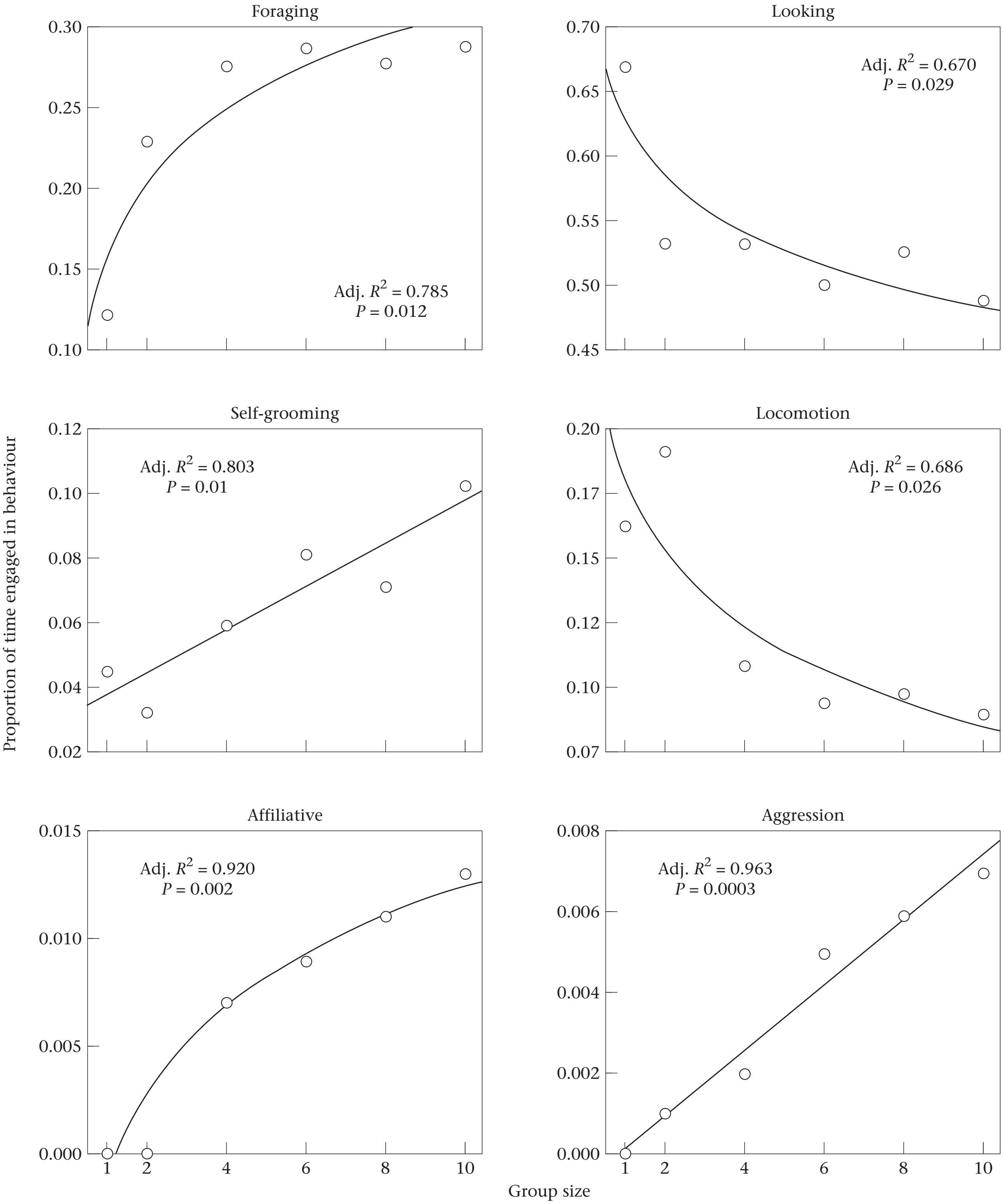

Figure 1. The average proportion of time tammar wallabies allocated to different behaviours as a function of group size. Foraging, looking, self-grooming and locomotion results were calculated from scan samples. The time allocated to the relatively infrequent affiliative social behaviour and aggressive behaviour was calculated from more detailed focal animal samples. Linear and nonlinear logarithmic regression models were fitted to these results; adjusted R^2 and P values are for the illustrated (better-fitting) curve.

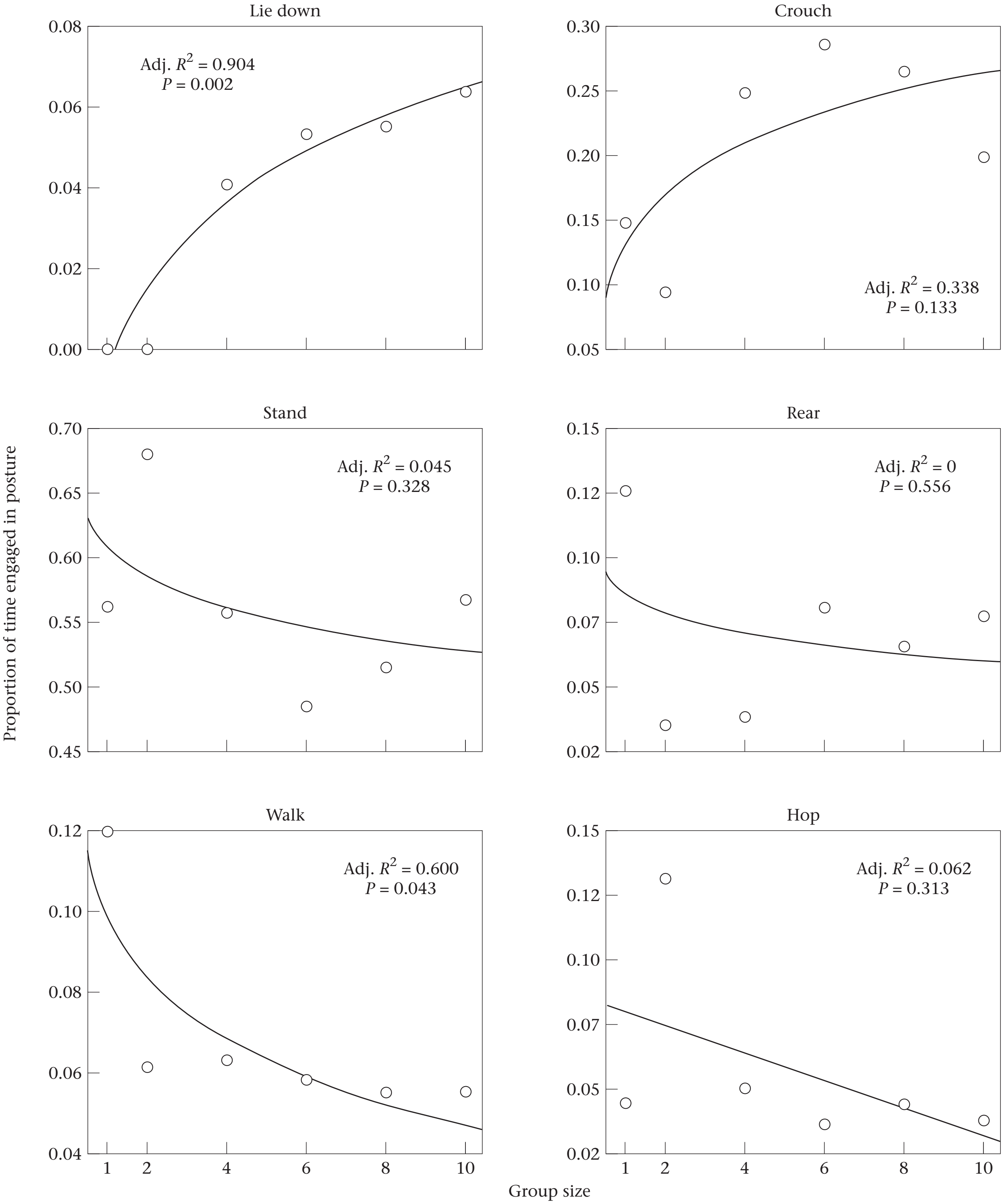

Figure 2. The average proportion of time tammar wallabies allocated to different postures as a function of group size calculated from scan samples. Linear and nonlinear logarithmic regression models were fitted to these results; adjusted R^2 and P values are for the illustrated (better-fitting) curve.

Table 1. The relationship between frequency of behaviour (measured from scan samples) and whether at least one other conspecific was in the focal subject's quadrant

	Alone	Others in quadrant	χ^2_1	P
Foraging	1151	381		
Not foraging	1660	686	8.882	0.003
Looking	1181	810		
Not looking	1165	722	2.276	0.131
Self-grooming	1399	133		
Not self-grooming	2164	182	0.939	0.307
Locomoting	1427	105		
Not locomoting	2061	285	28.139	<0.0001
Affiliative social	7	31		
Not affiliative social	2399	1501	26.676	<0.0001
Aggressive	5	72		
Not aggressive	2341	1460	93.570	<0.0001

In some cases, animals were close to each other, but in adjacent quadrants. Thus seven observations of affiliative social behaviour and five observations of aggressive behaviour were scored as being in different quadrants.

locomote (cell: χ^2_1=15.628, P<0.001) than expected by chance. When alone in a quadrant, they were significantly more likely to locomote (cell: χ^2_1=10.205, P<0.005). Neither looking nor self-grooming was influenced by having a conspecific in the same quadrant.

DISCUSSION

Group size influenced how female tammar wallabies allocated their time among various activities. For the majority of activities, and postures, nonlinear logarithmic regression models explained significantly more variation than linear regression models, suggesting that tammar wallabies were potentially sensitive to predation risk when allocating their time to different activities.

Wallabies foraged more in larger groups (Fig. 1). Results suggest a strong, nonlinear relationship between group size and the time allocated to foraging. Another way to gain an appreciation of group size effects is to examine the difference in time allocation when alone versus when in a group of 10. Wallabies in groups of 10 allocated 16.5% more time to foraging than solitary animals. Both natural and artificial food was available 24 h/day and there was no indication that wallabies foraged more as a result of increased feeding competition at larger group sizes (Watts 1985; Clark & Mangel 1986; Elgar 1987).

Looking behaviour decreased as a function of group size. Wallabies in groups of 10 allocated 18% less time to looking than did solitary wallabies. This was most likely a function of a decline in perceived predation risk. As we scored it, looking behaviour included antipredator vigilance, social vigilance and resting (when resting, wallabies' heads remained upright and their eyes fixated). Our measure of looking was designed to be scored without error both during the day and night, but it did not allow us to draw inferences about function. As group size increased, the duration of a bout of looking tended to increase. When vigilant, wallabies' ears move constantly and their heads turn frequently. Thus, long bouts of looking suggest relaxation, rather than acute vigilance. Consistent with this is the observation that wallabies in groups of 10 allocated 5.6% more time to self-grooming than solitary wallabies. There was no indication that the increase in grooming as a function of group size was a stereotypy or an obvious displacement activity, suggesting that the wallabies were able to allocate time to grooming because other important activities or 'drives' had been satisfied (Woolridge 1987). Nor was there any indication of excessive thermoregulatory grooming as a function of increased group size; macropodids, when thermally stressed, lick their capillary-rich forearms to increase evaporative cooling. More importantly, as group size increased, wallabies lay down on their sides more and moved about less (Fig. 2). Taken together, these results suggest that wallabies perceived less risk of predation as group size increased.

As group size increased, however, wallabies engaged in significantly more aggressive behaviour, although the absolute frequency of aggressive behaviour remained relatively small. Wallabies in groups of 10 allocated 0.6% more time to aggressive interactions than did the pair of wallabies. Aggressive behaviour may contribute to predation risk if animals engaged in aggressive interactions pay less attention to their surroundings (Blumstein 1998). The strong linear relationship between group size and the frequency of aggressive behaviour suggests that the decision to engage in aggressive behaviour is not influenced by perceived predation risk. Presumably, the benefits of engaging in potentially risky aggressive behaviour outweigh predation costs, a pattern seen in other species. Caraco (1979b) found a linear relationship between group size and aggressive interference in yellow-eyed juncos, *Junco phaeonotus*. We reanalysed Watts' (Figure 2 in Watts 1985) data on aggressive behaviour in mountain gorillas, *Gorilla gorilla beringei*, and found a strong linear relationship between group size and the number of displacements/h (linear adjusted R^2=0.734, P=0.018).

As group size increased, tammar wallabies tended to engage in more affiliative behaviour. Like aggression, affiliative behaviour was rare in smaller group sizes and increased only a little; wallabies in groups of 10 allocated 1.3% more time to affiliative behaviour than did the pair of wallabies. The curvilinear function suggests that wallabies were sensitive to the risk of predation and allocated more time to affiliative behaviour because they perceived a lower predation risk at larger group sizes.

Together, these results illustrate that wallabies perceive a significant and substantial net antipredator benefit from living with others. These antipredator benefits reach their inflection point at the relatively small group sizes of N=2–4, and may reach an asymptote by N=6 (Figs 1, 2).

Tammar wallabies, while potentially benefiting from living socially, have not evolved the complex social behaviour seen in some larger macropodids (Kaufmann 1974; Russell 1984; Croft 1989). Social interactions, both affiliative and agonistic, were relatively rare. Nevertheless, our results suggest that in tammars, affiliative social behaviour is influenced by the perception of predation risk.

Tammars and other small and mid-sized macropodids are more vulnerable to predation than larger macropodids and this vulnerability may have consequences for social evolution. Jarman & Coulson (1989) noted that selection would favour aggregation only in larger animals which could potentially escape from predators, while smaller species would best manage predation risk by living alone and hiding from predators. However, some macropodids may be less social because they lack social 'predispositions'. Johnson (1989) noted that the red-necked wallaby had relatively sophisticated social skills, yet the species is viewed as being only moderately social (Croft 1989). Our results also suggest that tammar wallaby behaviour is sensitive to the perceived risk of predation. Thus, predation pressure may have influenced the ability of tammars to express their social tendencies which may be quite sophisticated. Ultimately, the release in predation pressure obtained by evolving larger body size, rather than substantially different social predispositions, may have allowed the larger macropodids to evolve and/or express more complex social behaviour.

What are the implications of nonlinear group size effects for the conservation and management of tammars and potentially other macropodids? Tammars appear to perceive and achieve benefits from aggregation: they forage more, look less and adopt more relaxed postures. To maximize these benefits, the minimum group size for translocations and reintroductions should be above the inflection point of the relationship between group size and time allocated to beneficial activities. Our captive results suggest that animals should be introduced in groups of at least four to six animals. However, as individuals allocate time to activities other than antipredatory vigilance, they may make themselves more vulnerable to predation. For instance, increased predation risk has been seen in animals engaged in a variety of social activities such as play (Harcourt 1991), fighting (Jakobsson et al. 1995) and allogrooming (Maestripieri 1993). Ultimately, experimental translocations/introductions to areas with predators are required to see if the benefits wallabies receive while aggregating with others actually increase survival.

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