acta ethol (2003) 5:95–99
DOI 10.1007/s10211-002-0070-5

ORIGINAL ARTICLE

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Red kangaroos (*Macropus rufus*) receive an antipredator benefit from aggregation

Received: 2 April 2002 / Revised: 3 July 2002 / Accepted: 17 September 2002 / Published online: 22 January 2003
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Abstract For species that cannot seek cover to escape predators, aggregation becomes an important strategy to reduce predation risk. However, aggregation may not be entirely beneficial because aggregated animals may compete for access to limited resources and might even attract predators. Available evidence suggests that foraging competition influences time allocation in large-bodied macropodid marsupials, but previous studies have focused primarily on species in areas with protective cover. We studied red kangaroos, a species often found in open country without noticeable cover, to determine whether they experienced a net benefit by aggregation. Red kangaroos varied their time allocation as a function of group size and, importantly, more variation in time allocation to vigilance and foraging was explained by non-linear models than by linear models. This suggests red kangaroos directly translated the reduction of predation risk brought about by aggregation into greater time foraging and less time engaged in vigilance. We infer that red kangaroos received a net benefit by aggregation. Social species living in the open may be generally expected to rely on others to help manage predation risk.

Keywords Antipredator behavior · Benefits and costs of sociality · Group-size effects · Red kangaroo

Introduction

Animals have evolved a remarkable variety of antipredator behaviors (Lima and Dill 1990) that broadly can be defined to include predator recognition and 'management' strategies to reduce the probability of predation. Habitat selection is often an important antipredator strategy that reduces the risk of predation (e.g., Kotler 1984; Suhonen 1993; Sharpe and Van Horne 1998). Many species spend non-foraging time in cover locations that provide safety from predators. To forage, however, they must leave the safety of cover to forage in more profitable areas. For such refuging species (e.g., Hamilton and Watt 1970; Blumstein 1998), distance to cover is often associated with an increased risk of predation (e.g., Caraco et al. 1980; Dill 1990). Other species live in areas without substantial cover and cannot retreat to refugia to escape predation risk. For non-refuging species, habitat selection to reduce predation risk may be less important and a combination of wariness, crypsis, and/or social strategies must be used to reduce predation risk. One such social strategy is grouping, and individuals may receive a number of antipredator benefits by aggregation (Vine 1971; Alexander 1974; Pulliam 1973; Powell 1974; Kenward 1978; Lazarus 1979). Many birds and mammals aggregate while foraging and, by doing so, are able to allocate less time to antipredator vigilance and more time to foraging as a function of group size (Quenette 1990; Bednekoff and Lima 1998). However, these antipredator benefits must be traded off with the costs of increased competition (Clark and Mangel 1986; Beauchamp 1998; Grand and Dill 1999; Blumstein et al. 2001a). Thus, a net increase in foraging and a net reduction in antipredator vigilance may not always be seen (Blumstein et al. 2001a). Moreover, it is possible that phylogenetic constraints (Beauchamp 1998) or historical experience (e.g., Caterall et al. 1992; Blumstein and Daniel 2002) prevent or eliminate beneficial group-size effects in some species or populations.

Macropod marsupials – kangaroos and wallabies – make an excellent comparative system to study group-

Communicated by K. Kotrschal

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size effects. Many species spend their days resting in cover and, at dusk, leave cover to forage in more exposed habitat. Species (and in some cases populations) are found living with a variety of predators and in a variety of habitat types (e.g., Dawson 1995). These factors have been shown to influence foraging behavior and antipredator vigilance in other taxa (Lima and Dill 1990). That there are changes in group sizes as a function of available forage suggests that macropods may be sensitive to intraspecific foraging competition (Jarman and Coulson 1989). Finally, available evidence suggests that ecological factors, such as the presence of predators (Blumstein and Daniel 2002) and competitors (Payne and Jarman 1999), may influence the occurrence of time allocation and group-size effects.

If ethological theory is to be useful, however, it must be predictive. Red kangaroos live in the Australian arid zone (Newsome 1995). Although they apparently seek cover when available (Low 1979), in much of the arid zone there is not substantial cover and they must therefore employ other methods to manage predation risk. We predicted that in a relatively open area without cover, red kangaroos (like other open country species, Bertram 1980) would modify their time allocation as a function of group size. We studied this by observing red kangaroo foraging behavior in the Australian arid zone.

Methods

Subjects and study site

We studied free-ranging red kangaroos on and around the University of New South Wales, Fowlers Gap Research Station (31°S, 142°E) from 30 June to 7 July 2000. Red kangaroos are protected on the 38,888-ha field station and foraged freely throughout the lower elevation sheep paddocks. The station is south of the dingo fence (Pople et al. 2000), thus dingoes (*Canis lupus dingo*) currently do not represent an important risk of predation. Other potential predators (red foxes, *Vulpes vulpes*, and wedge-tailed eagles, *Aquila audax*) are locally common.

General procedures

We video-recorded 5-min focal samples of animals either in the morning (07:30–09:10), or in the late afternoon (15:00–18:05) on days without rain or heavy wind. We stood or sat in the open at distances where we did not obviously influence our focal subjects' behavior, but later we tested this assumption. We videotaped 152 independent kangaroos (i.e., individuals that were not young-at-foot): 57 adult females (20 with young at foot), 22 adult males, 55 adults of unknown sex, 2 sub-adult males, 1 sub-adult female, 3 sub-adults of unknown sex, and 12 non-juveniles of unknown age or sex.

Individuals were not captured or marked as part of this study. To avoid observing individuals more than once (i.e., to preserve statistical independence), we observed different aggregations of kangaroos on different days and, while observing a single mob, attempted not to resample the same individual by systematically shifting our focus to different subjects. There were many more kangaroos at Fowlers Gap than our sample size, and we are confident the majority of our observations come from different individuals.

At the beginning of each focal sample we noted the following variables: age (scored only when unambiguous as adult/sub-adult based on size and morphology) and sex (scored only when positively identified) of the focal animal; the distance the focal animal was from us; whether the focal subject was in 'grassy' habitat, or slightly more 'shrubby' habitat; and the number of other conspecifics within 10 m and 50 m (solitary animals were scored as being in a group of 1).

A single person scored videotaped focal animal samples using JWatcher (Blumstein et al. 2000), an event-recording program that logs keystrokes and calculates time budgets. We noted the onset of each bout of foraging, vigilance, and several other behaviors. Vigilance comprised three behaviors: crouching (all four feet were planted on the ground), standing (the hind feet were on the ground and front feet were elevated slightly above the ground), and rearing up (differentiated from quadrupedal crouching and bipedal standing by the upright angle – that is, >50° – of the back). Locomotion included pentapedal walking (kangaroos and wallabies move their back legs forward while balancing on their forepaws and tail), and hopping. Other behaviors included: grooming, affiliative behavior (e.g., sniffing and allogrooming), and aggressive behavior (displacement, chase, box). We also noted when animals went out of sight (by moving into a depression, behind another individual, or behind vegetation) and when they were back in sight.

From the video record we calculated the percentage of time allocated to each behavior out of the total time the animal was in sight (mean=289 s±25.8 SD, *n*=152). These analyses focus on the three most common kangaroo activities – foraging, vigilance, and locomotion.

Statistical analysis

We used the individual as the unit of analysis. Statistical analyses were conducted using SPSS 10 (SPSS Inc. 2000).

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 kangaroos observed at a given group size, defining group size two ways: the total number of individuals within 10 m and 50 m. We excluded those estimates based on fewer than five observations per group size and thus the final analyses of group-size effects focus on groups of one to five (when group size was defined as the number of conspecifics within 10 m) and one to eight (when group size was defined as the number of conspecifics within 50 m). We assumed that the model that explained the most variation reflected how kangaroos assessed group size (see also Blumstein et al. 2001a, 2001b).

We used parametric statistics (*t*-tests and regression) to evaluate whether sex, the presence of young-at-foot, the distance to nearest conspecific, microhabitat type (grassy/scrubby), and the distance to observer influenced time allocated to foraging, vigilance, and locomotion. Because animals were observed over a wide range of distances, we used the median distance (300 m) to divide the data into two categories (<300 m; ≥300 m) for examining the distance-to-observer effect. For *t*-tests where a Levene's test rejected the hypothesis of no differences in variances, we report the separate-variance *t*-test (SPSS Inc. 2000). In some cases, variables were not normally distributed. In those cases we explored a variety of transformations and non-parametric analyses. In all but one case (the presence of young-at-foot) there were no qualitative differences between the results. Thus, for consistency, we report the untransformed parametric statistics. For the presence of young-at-foot, and in contrast to the parametric results, the non-parametric Mann–Whitney *U*-test suggested that females with young-at-foot were more vigilant than those without young-at-foot (*P*=0.04). However, because this analysis was based on only 57 adult females, further exploration of the data in analysis of covariance (ANCOVA) models was not possible. Residuals from regression models were visually examined for normality.

Following bivariate analyses, we fitted fixed-factor ANCOVA models that included those factors that significantly explained variation in time allocation along with the covariate group size (defined as the number of conspecifics within 50 m). We also included all possible interactions. We employed a backward-stepping algorithm in which we removed the term with the largest P-value until the model's adjusted R^2 was maximized; we interpreted these final models. Residuals from ANCOVA models were visually examined for normality.

Results

Overall, red kangaroos foraged 60.2% (±26.6 SD, n=152) of the time, allocated 30.5% (±24.5) of their time to vigilance, locomoted an average of 5.8% (±5.4) of their time, and spent 2.4% (±4.5) of their time grooming. On average, kangaroos were 10.8 m (±10.5 SD, n=67) from their nearest conspecific.

When defined as the number of conspecifics within 50 m, group size explained significant variation in the time red kangaroos allocated to vigilance and foraging (Fig. 1) but not locomotion; logarithmic models explained more variation than did linear models (50 m log: vigilance: log adjusted R^2=0.60, P=0.015, linear adjusted R^2=0.462, P=0.038; foraging: log adjusted R^2=0.58, P=0.017, linear adjusted R^2=0.46, P=0.039; locomotion: log adjusted R^2=0, P=0.51, linear adjusted R^2=0, P=0.43). When defined as the number of conspecifics within 10 m, group size did not explain significant variation in time allocation (vigilance: log adjusted R^2=0.57, P=0.088, linear adjusted R^2=0.542, P=0.097; foraging: log adjusted R^2=0.05, P=0.35, linear adjusted R^2=0, P=0.44; locomotion: log adjusted R^2=0, P=0.41, linear adjusted R^2=0.195, P=0.25).

Kangaroos looked significantly more and foraged significantly less when in grassy habitat compared to scrubby habitat; locomotion was not influenced by microhabitat type (vigilance: P=0.009, n=117; foraging: P=0.006, locomotion: P=0.92). Distance to observer influenced time allocated to vigilance (P=0.036, n=139), but not to foraging (P=0.15) or locomotion (P=0.19). Kangaroos were less vigilant when far from the observer (mean_{far}=25.6±25.5 SD, $\text{mean}_{\text{close}}$=34.3±21.5 SD).

Other examined variables had no significant effects on time allocation. There was no effect of the distance to nearest conspecific on time allocation (vigilance: adjusted R^2=0, P=0.74, n=67; foraging: adjusted R^2=0, P=0.72; locomotion: adjusted R^2=0, P=0.98), of sex on time allocation (vigilance: P=0.91, n=82; foraging: P=0.68; locomotion: P=0.65), of having a young-at-foot on female time allocation (t-test vigilance P=0.16, n=57; foraging: P=0.17; locomotion: P=0.21; see Methods for non-parametric results), or of time of day scored as morning or evening observations on time allocation (vigilance: P=0.84, n=152; foraging: P=0.70; locomotion: P=0.83).

ANCOVA models revealed that group size defined as the number of conspecifics within 50 m explained significant variation in time allocated to vigilance and foraging after accounting for other factors (Table 1). The significant distance-to-observer*habitat type interaction was such that kangaroos reduced vigilance less when farther from the observer in grassy habitat compared to scrubby habitat.

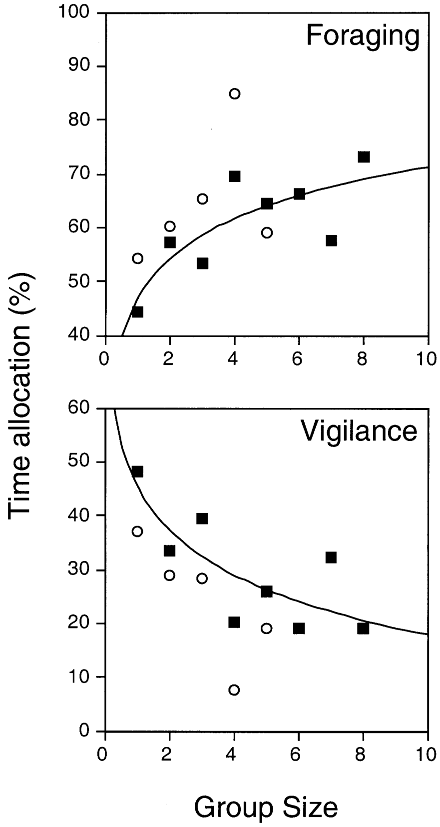

Fig. 1 The mean percentage of time that red kangaroos allocated to foraging and vigilance as a function of the number of conspecifics within 10 m (*open circles*) and 50 m (*solid squares*). Means were calculated from all observations of individuals foraging at a given group size for which we had at least 5 observations (n=54, 52, 35, 6, and 5 observations of animals foraging for group sizes of 1, 2, 3, 4, and 5 within 10 m; n=17, 33, 20, 36, 18, 11, 6, and 7 for group sizes of 1, 2, 3, 4, 5, 6, 7, and 8 within 50 m). For both behaviors, logarithmic regression models explained more variation than linear models. For logarithmic models, more variation was explained when group size was defined as the number of conspecifics within 50 m

Table 1 Final ANCOVA models after employing a backward-stepping algorithm designed to maximize adjusted R^2.*Group size* was defined as the number of conspecifics within 50 m for both analyses (foraging: n=117; vigilance: n=110)

Factor	Foraging	Vigilance
Model	P=0.002	P<0.0001
Group size	P=0.042	P=0.012
Habitat type	P=0.017	P=0.015
Group size*Habitat type	P=0.143	P=0.056
Distance-to-observer*Habitat type	Not in model	P=0.014
Adjusted R^2	0.096	0.160

Discussion

Red kangaroos treated those conspecifics within 50 m as 'group mates' and modified their time allocated to foraging and vigilance accordingly. That these relationships were non-linear suggests that red kangaroos received a net benefit from aggregation (Blumstein et al. 2001a).

Our logic underlying this interpretation notes that models of dilution (Hamilton 1971; Vine 1971) and models of detection (Pulliam 1973; Kenward 1978) both predict a non-linear decline in predation risk as a function of increasing group size if attack rate remains constant. Thus, if animals translate this non-linear reduction in predation risk into time allocation, they should forage more and look less and these relationships should be non-linear. Similar relationships have been reported in smaller macropods (Blumstein et al. 1999; Blumstein and Daniel 2002), but only one previous study of large-body macropods – eastern grey kangaroos (*M. fuliginosus*) – reported a non-linear relationship (Jarman 1987). The lack of other non-linear results might partially reflect the fact that previous studies by other authors typically fitted only linear models (e.g., Coulson 1996, 1999; but see Wahungu et al. 2001) or used ANOVA models and did not seek to understand the exact shape of the relationship (e.g., Colagross and Cockburn 1993). However, our previous studies (which fitted both linear and non-linear models) have, to date, not found non-linear relationships in kangaroos (Blumstein and Daniel 2002). Formal manipulative experiments (e.g., Lima et al. 1999; Blumstein et al. 2002) are required to support the hypothesis that intraspecific competition plays no role in these non-linear relationships. Nonetheless, our previous studies of macropodid time allocation suggest that species for which intraspecific competition is important (Blumstein et al. 2001a) have linear relationships, whereas species for which intraspecific competition is not important (Blumstein et al. 1999; Blumstein et al. 2002) have non-linear relationships. Finally, after accounting for non-significant variation explained by other potentially important factors (Elgar 1989), group size consistently explained significant variation in time allocation. Thus, we infer that red kangaroos perceived conspecifics as reducing the risk of predation.

Animals living in the open have a reduced set of options available to them to manage predation risk (Heard 1992). One such option is aggregation. Taken together, these results suggest that red kangaroos manage predation risk by relying on conspecifics. Competition, however, is an unavoidable cost associated with aggregation and there is both comparative evidence and evidence from single-species studies that macropods are sensitive to intraspecific competition (Jarman and Coulson 1989). Developing a detailed understanding of how red kangaroos reduce or manage intraspecific competition would be valuable. One such way might be by limiting maximum group size (Jarman and Coulson 1989). Both mean and ‘typical’ group sizes of red kangaroos are smaller than those of congeneric eastern (*M. giganteus*) and western grey kangaroos (Dawson 1995), suggesting that red kangaroos may be ‘trading off’ the benefits of aggregation with the costs of sharing food in their xeric environment.

The exact mechanisms by which red kangaroos benefit by aggregation remain unknown. It is possible that they benefit by having more eyes and ears to detect predators (e.g., Pulliam 1973; Powell 1974; Kenward 1978), or by simply ‘diluting’ predation risk (Vine 1971; Alexander 1974). Future experiments to elucidate the mechanism would make a valuable contribution to understanding antipredator behavior. Because their time allocation is not confounded by distance to cover or other factors, red kangaroos would represent an appropriate species in which to identify the ways in which animals benefit by aggregating.

Acknowledgements We thank David Croft and the staff at Fowlers Gap for making our stay both productive and enjoyable. Support for this project came from grants to DTB from the University of California Los Angeles, and from the Australian Cooperative Grants Programme (via The Marsupial CRC). Research protocols were approved by the Macquarie University Animal Care Committee (#99018) and research complied with current Australian law.

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