Behavioral Ecology Vol. 13 No. 5: 657–663

Isolation from mammalian predators differentially affects two congeners

Daniel T. Blumstein and Janice C. Daniel
Department of Organismic Biology, Ecology, and Evolution, The University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA, and Department of Psychology and The Cooperative Research Centre for Conservation and Management of Marsupials, Macquarie University, Sydney NSW 2109, Australia

Evolutionary isolation from predators can profoundly influence the morphology, physiology, and behavior of prey, but little is known about how species respond to the loss of only some of their predators. We studied antipredator behavior of tammar wallabies (*Macropus eugenii*) and western gray kangaroos (*Macropus fuliginosus*) on Kangaroo Island (KI), South Australia, and at Tutanning Nature Reserve on the mainland of western Australia. Both species on KI have been isolated from native mammalian predators for several thousand years. On KI, wallabies (because of their size) are vulnerable to diurnal aerial predators. In contrast, on the mainland both species have been exposed continuously to native and introduced mammalian and avian predators. At both locations, wallabies modified the amount of time they allocated to vigilance and foraging in response to group size, whereas kangaroos did so only at the higher risk Tutanning site. Both species modified overall time budgets (they were warier at the higher risk site), and both species modified space-use patterns as a function of risk. At the higher risk site, tammars were closer to cover, whereas kangaroos were, on average, farther from cover. We hypothesize that the presence of a single predator, even if it is active at a different time of day, may profoundly affect the way a species responds to the loss of other predators by maintaining certain antipredator behaviors. Such an effect of ancestral predators may be expected as long as species encounter some predators. *Key words:* group size effects, habitat selection, macropod antipredator behavior, *Macropus eugenii, Macropus fuliginosus,* relaxed selection, tammar wallabies, time allocation, vigilance, western gray kangaroos. *[Behav Ecol 13:657–663 (2002)]*

Studies of populations on predator-free patches of habitat (Magurran et al., 1995; Riechert and Hedrick, 1990) or on predator-free islands (Kavaliers, 1990; Pressley, 1981; Van Damme and Castilla, 1996) and comparisons of species that evolved with and without certain predators (Coss and Goldthwaite, 1995; Goldthwaite et al., 1990) illustrate the remarkable variety of morphological, physiological, and behavioral changes that occur when animals are isolated from their predators (Magurran, 1999). Although we know that relaxed selection from predators has myriad effects (Coss, 1999), previous studies often have focused on the response of a single species to the loss of a key predator or to the loss of all its predators (Magurran et al., 1995). Isolation from all predators is probably a rare event. In this study we examined two closely related macropod marsupials found sympatrically at two locations with different evolutionary histories of exposure to predators to determine how species are differentially affected by the loss of some versus all of their predators.

The question of how populations respond to the loss of some rather than all predators has both theoretical and applied importance. Animals live in environments with multiple predators, yet many studies and models of antipredator behavior have focused on the effect of a single predator (but see Bouskila, 1995; Kotler et al., 1992; Lima, 1992; Sih et al., 1998). To better understand how relaxed selection acts on antipredator behavior, we must understand how it differentially affects species isolated from some versus all of their predators. An understanding of these effects has tremendous applied importance for species now found only on predator-free islands whose historic range extended onto predator-rich mainlands. In some places, conservationists translocate or reintroduce insular populations to the mainland (Johnson et al., 1989). Most translocations and reintroductions fail (Griffith et al., 1989; Wolf et al., 1996), and predation is often the factor responsible (McCallum et al., 1995). It follows that a fundamental understanding of how relaxed selection acts on antipredator behavior may enlighten conservation efforts.

We focused on two species both found on Kangaroo Island (KI), South Australia (35°52′ S, 136°53′ E) and Tutanning Nature Reserve, a mainland reserve in western Australia (32°32′ S, 117°19′ E). Tammar wallabies (*Macropus eugenii*) are mid-sized (maximum female mass = 6 kg, maximum male mass = 10 kg), moderately social, macropodid marsupials. On the mainland they fall prey to both mammalian and avian predators (Croft, 1989; Smith and Hinds, 1995). In protected areas on Kangaroo Island, wedge-tailed eagles are the tammar's only predator (Inns, 1980). Western gray kangaroos (*Macropus fuliginosus*) are relatively large (maximum female mass = 28 kg, maximum male mass = 54 kg), social macropodids (Croft, 1989; Poole, 1995). On the mainland, all age classes of kangaroos in their weight range may be preyed upon by terrestrial mammalian predators (e.g., Jarman and Wright, 1993), but adults face limited risk of predation by aerial predators. In protected areas on Kangaroo Island, adult kangaroos have little if any exposure to predators.

Kangaroo Island has been isolated from the Fleurieu Penninsula of South Australia for about 9500 years (Lampert, 1979). Early European explorers were amazed at the tameness of the wildlife and attributed it to a lack of predators—including humans (Peron, 1816). Aboriginal Australians last occupied Kangaroo Island about 4300 years ago (Lampert,

---

Address correspondence to D.T. Blumstein, Department of Organismic Biology, Ecology, and Evolution, The University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA. E-mail: marmots@ucla.edu.

Received 16 April 2001; revised 10 December 2001; accepted 19 December 2001.

1979), and Europeans primarily colonized the eastern part of the island in the mid-nineteenth century (Inns, 1980). With the Europeans came cats (*Felis cattus*) and farm dogs (*Canis familiaris*), which are now found around human settlements. The only historically important mammalian predator—the Tasmanian devil (*Sarcophilius harrisii*)—is known only from the fossil record (Pledge, 1979). There are no records of either thylacines (*Thylacinus cynocephalus*) or dingoes (*Canis lupus dingo*) having ever lived on the island. Wedge-tailed eagles (*Aquila audax*), a large diurnal raptor, are current residents (and presumably historical residents) of Kangaroo Island that may prey on small mammals. Only two smallish owl species live on Kangaroo Island (Ford, 1979); thus, there is no risk of nocturnal aerial predation for all but the smallest mammals.

Tutanning Nature Reserve, located in the western Australian wheat-belt, is a 4000-ha relict forest habitat surrounded by mixed farmland. Tutanning is one of a few locations where tammar wallabies did not go extinct on the mainland (Maxwell et al., 1996). The reserve is also home to western gray kangaroos. A fox baiting program begun in 1996 (Wyre, 1998) substantially increased the tammar population, and Tutanning has recently become a source of tammars for translocations to other mainland sites (Morris et al., 1998). Both wallabies and kangaroos at Tutanning have consistently been exposed to both mammalian and avian predators throughout their evolutionary history. Tammars survived the introduction of dingoes (about 3500 years ago; Corbett, 1995) and, more recently, red foxes.

To study antipredator behavior, we examined the time these species allocated to their most common behaviors, vigilance and foraging. Animals routinely trade-off antipredatory vigilance against foraging behavior (Bednekoff and Lima, 1998) and may become less vigilant if predators are removed or absent (Berger et al., 1983; Catterall et al., 1992; Hunter and Skinner, 1998). Patterns of time allocation can provide an indication of how animals perceive predation risk (Bekoff, 1995). A number of factors are suggested to influence the time animals allocate to antipredatory vigilance (Elgar, 1989). Two particularly important factors are the distance from protective cover (Lima, 1987) and the number of nearby conspecifics (Coulson, 1999). By comparing how these factors influence time allocation for wallabies and kangaroos, we aimed to better understand how antipredator behavior is differentially influenced by the loss of some versus all of a species' predators.

METHODS

Subjects and study site

We studied tammar wallabies and western gray kangaroos in Flinders Chase National Park (focusing on animals around the Rocky River ranger station and the Grassdale Conservation Park) on the western end of Kangaroo Island, and in Tutanning Nature Reserve. Both species spend their days in woodland or in dense, impenetrable scrub and emerge around dusk to forage in open meadows. We focused on adult and subadults and collected no data on young-at-foot.

General procedures

We video-recorded 5-min focal animal samples of animals from 1.5 h before sunset to 4.3 h after sunset on days without heavy rain. We stood or sat in locations where we had no obvious influence our focal subject's behavior. Tammars were typically observed between 11 and 50 m, and kangaroos were typically observed at distances >50 m.

We observed individuals as they moved out of cover to forage. Kangaroos emerged before tammars; thus some of our kangaroo focals were conducted before sunset (16/53 on KI; 59/103 at Tutanning), whereas most of our tammar focals were conducted after sunset (129/141 on KI; 104/104 at Tutanning). After sunset we affixed image intensifiers (ITT Nightcam 300) with 80–200 mm zoom camera lenses (Nikkor and Minolta) to the video cameras (Panasonic VX77A). We illuminated the image-intensified video field with either unfiltered, red-filtered, or yellow-filtered 1-W headlamps (Petzel). We observed no difference in the behavior of animals illuminated with the different color lights, nor did we detect any obvious effect of this temporary low-level illumination (see also Blumstein et al., 1999).

Individuals were not captured or marked. Kangaroos were relatively more active at dusk than were tammars, which were primarily active after dark. It was possible to discriminate most individual kangaroos, and some tammars, by day. After dark, individual discrimination was difficult. To avoid observing individuals more than once (i.e., to preserve statistical independence), we systematically walked through the meadows in which animals foraged and did not double-back on our paths. We are confident that most of the observations came from different individuals.

At the beginning of each focal sample, we noted the distance the focal animal was to protective cover and the group size, defined first as the number of conspecifics within 10 m and then as the number within 50 m (solitary animals were scored as being in a group size of one). Group size is one of the most important variables in explaining variation in wallaby time allocation (Blumstein et al., in press b). For macropods, the distance with which conspecifics are scored as being in a group varies between studies (50 m: Coulson, 1999; Heathcote, 1987; Jarman and Coulson, 1989; 30 m: Hoolihan and Goldizen, 1998; Johnson, 1989; 15 m: Jarman, 1987). We scored group size at two extremes, 10 m and 50 m, and judged from the animals' behavior how they perceived social companions (Blumstein et al., 2001).

All distances were measured or estimated from landmarks at known distance and classified into four categories: 0–1 m, 1–10 m, 10–50 m, and >50 m. We scored videotaped focals using event-recording software (Deni, 1996; Noldus Information Technologies, 1995) and noted the onset of each bout of foraging (included foraging on the ground and foraging on shrubby vegetation above the ground); looking while crouching, standing, or while rearing up (a look was scored each time an individual moved its head and fixated); locomotion, defined as pentapedal walking (kangaroos and wallabies move their back legs forward while balancing on their forepaws and tail) and hopping; grooming; affiliative behavior (sniffing); and aggressive behavior (displacements). We also noted when animals went out of sight and when they came back into sight. From the video record, we calculated the proportion of time allocated to each behavior as a function of the total time an animal was in sight. These analyses focus on the two most common behaviors, foraging and looking.

In the most commonly used habitat, grassland, we walked 50-m line transects and recorded the percent groundcover in 1.5-m diam circular plots and vegetation height (categorized as < 10 m or ≥ 10 m). At KI, we walked 4 lines through grassland leading to 44 plots. At Tutanning, we walked 16 lines through grassland, leading to 176 plots.

Statistical analyses

We used the individual and values based on aggregation of individuals as the unit of analysis. Statistical analyses were con-

Table 1

The final general linear models that explained the most variation in time allocated to vigilance and foraging

Effect	Vigilance *p* value	Foraging *p* value
Species	.002	.004
Site	.0001	.0001
Group size	.002	.003
Distance to cover	.002	.001
Species × site	.011	.010
Group size × species	.008	.009
Group size × site	.005	.030
Group size × distance to cover	.011	.024
Distance to cover × site	.279	.196
Group size × species × site	.005	.027
Group size × distance to cover × species	.010	(not in model)
Group size × distance to cover × site	.051	.083
Group size × distance to cover × species × site	.005	.043

[a] The vigilance model significantly explained 31.5% of the variation, and the foraging model significantly explained 28.3% of the variation.

ducted using StatView 5.0 (SAS Institute, 1998) and Super-Anova (Abacus Concepts, 1991).

In the subset of data for which age and sex were known, we used Mann-Whitney *U* tests to test for age and sex effects on time allocation. We also used Mann-Whitney *U* tests to compare estimates of percent cover and vegetation height in grassland, the most common microhabitat, between sites.

We fitted general linear models to explain variation in the time allocated to vigilance and foraging. We included four main effects: species, site, group size (defined as the number of conspecifics within 10 m), and distance to cover. We included all two-way, three-way, and four-way interactions; the results of some are more important to understand than others. For instance, the three-way interaction of group size × species × site provides a multivariate test of the hypothesis that group size effects are similar for the two species at the two sites. These initial models significantly explained variation in both variables, but we performed a backward-stepping algorithm to maximize the adjusted R^2 value (which initially increased after the removal of nonsignificant variables). The least significant variable was removed until the adjusted R^2 value began to decline, and we interpret these final models.

To study group size effects in more detail, we aggregated our set of focal observations to obtain the best possible estimate of the group-size effect at each group size (defined as the number of conspecifics within 10 m or 50 m). Antipredator models of vigilance and foraging group size effects predict a nonlinear relationship between group size and time allocation. Linear relationships between group size and time allocation may reflect intraspecific interference competition for limited resources modifying the nonlinear relationship and would illustrate a fundamental cost of sociality (Blumstein et al., 2001). We therefore regressed our aggregated group size against time allocation and fitted two models to these data: a logarithmic nonlinear model and a linear model.

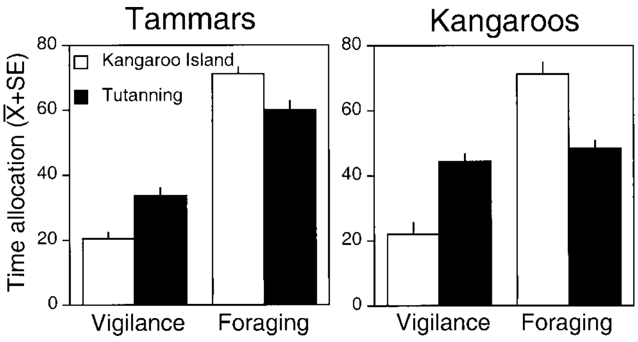

Figure 1
Percent time (mean + SE) allocated to vigilance and foraging in tammar wallabies and western gray kangaroos studied on Kangaroo Island, South Australia, and at Tutanning Nature Reserve on the western Australian mainland.

RESULTS

The final data set included focal observations where the subject was in sight for $\geq$ 2 min. Analyses are based on a total of 243 observations on tammars (140 at KI: 21 adult females, 15 adult males, 2 subadult females, 1 subadult male, 92 adults, 9 subadults; 103 at Tutanning: 15 adult females, 12 adult males, 49 adults, 7 subadults, 20 unidentified), and 155 observations on kangaroos (53 at KI: 21 adult females, 11 adult males, 1 subadult female, 2 subadult males, 18 unidentified; 102 at Tutanning: 36 adult females, 20 adult males, 10 subadult males, 15 unsexed adults, 6 unsexed subadults, 15 unidentified).

For the subset of available data, neither age nor sex significantly explained variation in time allocated to foraging or vigilance (foraging: age, all $p > .208$; sex, all $p > .07$; vigilance: age, all $p > .148$; sex, all $p > .063$).

There were differences in both potential food and in visibility in the grassland microhabitat where almost all focal observations were conducted. Tutanning grasslands had an average of 9% more groundcover than KI ($p = .010$). KI grasslands had significantly less tall vegetation ($\geq$ 10 cm) than Tutanning (Fisher's Exact test, $p = .029$).

For clarity, we report the results for vigilance; unless otherwise noted, foraging shows a reciprocal pattern. All main effects were significant (Table 1). Tammars were less vigilant than kangaroos. Animals at Tutanning were more vigilant than at KI (Figure 1). Animals were more vigilant when they were within 1 m of cover compared to farther away. Overall, vigilance decreased with group size.

Some two-way interactions were significant (Table 1). For species × site interactions, kangaroos increased vigilance more than did tammars between Tutanning and KI. For group size × species interactions, both species showed vigilance group-size effects, but the slope is steeper for tammars. In

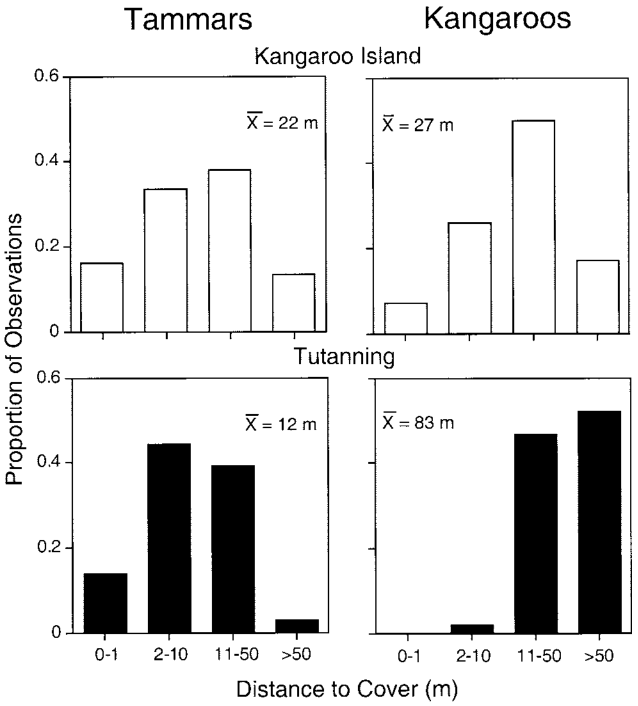

Figure 2
The distribution of foraging behavior in space with respect to nearest cover. Both tammars and kangaroos had significantly different distributions at the higher risk Tutanning site than the lower risk Kangaroo Island site.

contrast, for foraging, tammars, but not kangaroos, showed a significant group-size effect. For group size × site interactions, animals on Tutanning had steeper group-size effects than those on KI. Regarding group size × distance-to-cover interactions, there were significant group-size effects at 2–10 m and 11–50 m but not at < 1 m and > 50 m.

Some three-way interactions were significant (Table 1). The key three-way interaction of group size × species × site was significant: Tammars at Tutanning had steeper group-size effects than tammars at KI. Kangaroos at Tutanning had a significant group size effect but not at KI. For group size × distance to cover × species interactions, linear regressions of group size × time allocated to vigilance are only significant for tammars at 2–10 m and for kangaroos at 11–50 m. Small sample sizes prevented any other meaningful analysis. For group size × distance to cover × site interactions, there were no group-size effects on KI at any distance to cover while at Tutanning, there are significant group-size effects at all distances except 0–1 m from cover.

The four-way interaction of group size × distance to cover × species × site was significant (Table 1). There was a significant regression of group size for tammars at Tutanning when they were 2–10 m from cover. For kangaroos (again at Tutanning only), the distance was 11–50 m. Insufficient data prevented us from drawing any conclusions about the pattern < 10 m from cover.

At the higher risk Tutanning site (Figure 2), tammars foraged significantly closer to cover (means; Tutanning = 12 m, KI = 22 m, Mann-Whitney $p = .02$), while kangaroos foraged farther from cover (means; Tutanning = 83 m, KI = 27 m, Mann-Whitney $p < .001$).

The species perceived group-mates differently. For tammars, at both sites, more variation in the time allocated to vigilance and foraging was explained by the number of conspecifics within 10 m than within 50 m (Figure 3; KI: vigilance [log], adjusted $R^2 = .93$, $p = .001$ at 10 m vs. $R^2 = 0$, $p = .54$ at 50 m; foraging [linear], adjusted $R^2 = .93$, $p = .001$ at 10 m vs. a $R^2 = .18$, $p = .07$ at 50 m; Tutanning: vigilance [log], adjusted $R^2 = .58$, $p = .02$ at 10 m vs. $R^2 = .14$, $p = .16$ at 50 m; foraging [log], adjusted $R^2 = .42$, $p = .05$ at 10 m vs. $R^2 = .18$, $p = .13$ at 50 m). In contrast, the number of

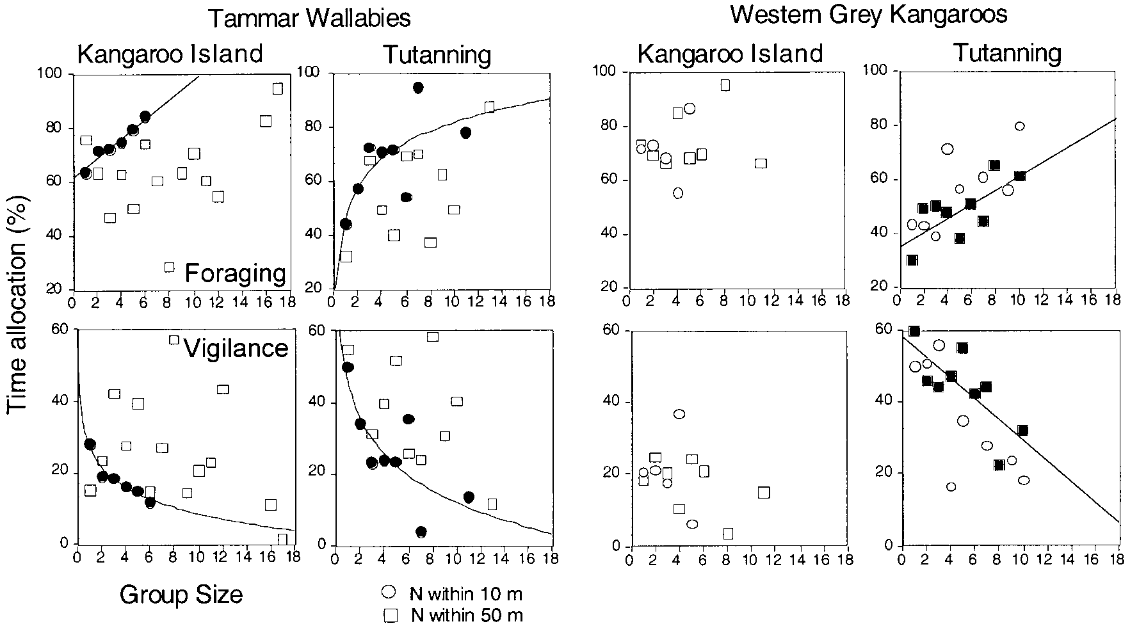

Figure 3
The relationships between time allocated to foraging (top graphs) and vigilance (bottom graphs) for tammar wallabies and western gray kangaroos at Kangaroo Island and Tutanning Nature Reserve. Group size was defined as the number of conspecifics within 10 m (circles) and the number within 50 m (squares). Linear and logarithmic regressions were fitted to the data; curves illustrate the better fit, and filled symbols illustrate the group size definition that explained more variation.

conspecifics within 50 m explained more variation in kangaroo group-size effects, although a significant group-size effect was only found at Tutanning (Figure 3; Tutanning: vigilance [linear], adjusted $R^2 = .52$, $p = .03$ at 10 m vs. $R^2 = .53$, $p = .02$ at 50 m; foraging [linear], adjusted $R^2 = .44$, $p = .04$ at 10 m vs. $R^2 = .47$, $p = .03$ at 50 m).

Tammars modified the time allocated to vigilance and foraging as a function of group size at both the lower-risk KI site and the higher risk Tutanning site (Figure 3). In contrast, western gray kangaroos only exhibited statistically significant group-size effects at the higher risk Tutanning site (Figure 3). When present, kangaroo group-size effects were linear; in contrast, nonlinear regression models explained more variation than linear regression models for most tammar group size effects.

DISCUSSION

Both tammar wallabies and western gray kangaroos modified how they allocated time to behavior in ways that suggest they were sensitive to the risk of predation. They modified their time budgets so that they were warier at the higher risk Tutanning site, and they foraged at different distances from cover. Tammars appeared to perceive cover as protective; they foraged closer to cover at the higher risk site. In fact, tammars routinely return to cover when alarmed. In contrast, gray kangaroos seemed to view cover as obstructive; they foraged farther from cover at the higher risk site. At Tutanning, kangaroos emerging from cover looked around briefly and then hopped to the center of the meadows, where they began foraging.

Two caveats must be made. First, like many other studies of geographic variation in behavior, our ''treatments'' are not replicated. These were the only two locations where we could study both tammar wallabies and Western gray kangaroos. We have gained statistical power by restricting our studies to these two locations where both species lived. Strictly, our conclusions are limited to these two model species in these two locations. We also must point out that these results may be influenced by the significantly different amounts of groundcover and/or the relative amount of deep vegetation at the two sites. We were unable to test specifically how these variables influenced time allocation because we did not record these at the points where subjects were observed foraging.

In the multivariate models, many terms explained significant variation in time allocation, but the key three-way interaction of group size × species × site reveals that group-size effects varied for the different species and at the different sites. Although we do not have specific data on the relative rates of predation at the sites, we do know about the presence of predators at the sites, and we can make inferences about the presence of predators in the past. We suggest that it is the different histories of predation that are responsible for the different patterns of group-size effects seen in kangaroos and wallabies. Tammars had significant group size effects at both sites, whereas kangaroos had group-size effects only at the higher risk site.

Group-size effects were found in some (Blumstein, unpublished observations; Coulson, 1999; Jarman, 1987), but not all (Colagross and Cockburn, 1993; Johnson, 1989), previous studies of macropodid time allocation, but it is possible that some studies which failed to detect group-size effects used an inappropriate (from the animal's perspective) distance to define a social group. For instance, Coulson (1999) used 50 m and found group-size effects in red-necked wallabies (*M. rufogriseus*), whereas Johnson (1989) used 30 m and did not find group-size effects.

The degree to which antipredator behavior requires experience, and hence its phenotypic plasticity, varies. Behaviors such as time allocation and space use seem to be relatively plastic: They varied for both species at both sites and hence are likely to rely on experience (see also Hunter and Skinner, 1998). In contrast, the degree to which cover was obstructive or protective, and whether or not group-size effects were detected, are seemingly more constrained and thus are less likely to rely on experience. Why might tammar group-size effects persist under relaxed selection?

The ''ghost of predators past'' hypothesis (e.g., Byers, 1997; Peckarsky and Penton, 1988) predicts that tammars have not lost their antipredator behavior because they were historically subjected to intense predation. Before the Pleistocene extinctions, mainland Australia had a rich predator community of thylacinids (marsupial lions/tigers) and dasyurids (quolls, tiger cats, and devils) (Archer, 1981; Robertshaw and Harden, 1989). Although this may explain the persistence of complex antipredator behavior in some species subjected to relatively relaxed predation pressure since the Pleistocene extinctions (e.g., Byers, 1997), other species subjected to a history of predation may lose the ability to recognize predators eliminated by humans in the past century (e.g., Berger, 1998). Whether a species quickly loses antipredator behavior following relaxed selection depends in part on the degree to which behavior is experience dependent (i.e., learned or ''innate'') and, ultimately, on its cost.

The ghost hypothesis assumes that there are no substantial costs to maintaining antipredator behavior. Tammars may gain other benefits from aggregating. For instance, rates of affiliative behavior increase with group size (Blumstein et al., 1999), and if kin aggregate and engage in beneficial behavior (Blumstein et al., in press a), then group-size effects may be maintained by their net benefit.

Lima (1992) modeled the effects of multiple predators on vigilance behavior in prey and discovered that one or more relatively innocuous and/or rare predators can have a substantial impact on prey vigilance. He concluded that more attention should be paid to the combined effects of predators on prey, a point echoed by others (Magurran, 1999). Previous studies assumed that the antipredator behavior we see occurs when predators are potentially active. Our results suggest that relatively sophisticated antipredator behavior can be maintained during times when there is no risk of predation (e.g., eagles do not hunt after sunset).

Coss (1999) noted that evolutionary persistence of antipredator behavior is expected for functionally integrated activities. Underlying physiological mechanisms for responding to predators and managing predation risk may be shared regardless of predator type (e.g., Blanchard et al., 1989, 1990). At a genetic level, pleiotropy will prevent or slow the rate of the loss of formerly adaptive traits (Byers, 1997) such as nocturnal antipredator behavior. We hypothesize that the presence of predators by day will help maintain antipredator behavior at night because it may be a factor that selects for maintaining integrated antipredator systems. Although this hypothesis needs a more detailed evaluation, we should note that without substantial costs for their maintenance, these mechanisms may be sufficient to explain evolutionary persistence of antipredator behavior in tammar wallabies.

Wildlife managers planning translocations should pay particular attention to the history of predation in their source population. Fortunately, our results suggest that some antipredator behavior (group-size effects) may persist despite isolation from some predators, while others (space use and wariness) appear flexible enough for animals to learn themselves (Hunter and Skinner, 1998) upon release.

We thank Des Cooper and Bob Inns for advice on Kangaroo Island tammars; Robert Ellis and the staff at Flinders Chase National Park for hospitality and advice on where to find tammars in the park; the University of Adelaide for access to their biology field station; The Western Australia Department of Conservation and Land Management for permission to work in Tutanning; Les and Cindy Marshall for housing and hospitality while working at Tutanning; Ian McLean for general logistical support in Western Australia; Chris Evans for access to facilities at Macquarie University; Helena Bender, Amos Bouskila, Graeme Coulson, Chris, Andrea Griffin, and Ian for recent discussions about antipredator behavior; and Chris, Andrea, John Byers, Ron Ydenberg, and two helpful anonymous reviewers for comments on previous versions of the paper. Fieldwork was supported by grants to D.T.B. by the Australian Research Council (APD and Small Grant), the Australian Government Cooperative Research Programme, and by Macquarie University (MURG funds). Research protocols were approved by the South Australian Animal Care and Ethics Committee (approval #23/98) and the Macquarie University Animal Ethics Committee (approval #99018), and permits to work with wildlife were issued by the Government of South Australia (license #57) and the Western Australian Department of Conservation and Land Management (license #SF3005).

REFERENCES

Abacus Concepts, 1991. SuperAnova. Berkeley, California: Abacus Concepts.

Archer M, 1981. A review of the origins and radiations of Australian mammals. In: Ecological biogeography of Australia (Keast A, ed). The Hague: W. Junk; 1436–1488.

Bednekoff PA, Lima SL, 1998. Randomness, chaos and confusion in the study of antipredator vigilance. Trends Ecol Evol 13:284–287.

Bekoff M, 1995. Vigilance, flock size, and flock geometry: information gathering by western evening grosbeaks (Aves, Fringillidae). Ethology 99:150–161.

Berger J, 1998. Future prey: some consequences of the loss and restoration of large carnivores. In: Behavioral ecology and conservation biology (Caro TM, ed). New York: Oxford University Press; 80–100.

Berger J, Daneke D, Johnson J, Berwick SH, 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biol Conserv 25:193–208.

Blanchard RJ, Blanchard DC, Hori K, 1989. An ethoexperimental approach to the study of defense. In: Ethoexperimental approaches to the study of behaviour (Blanchard RJ, Bain PF, Blanchard DC, Parmigiani S, eds). Dordrecht: Kluwer Academic; 114–136.

Blanchard DC, Blanchard RJ, Rodgers RJ, 1990. Pharmacological and neural control of anti-predator defense in the rat. Aggress Behav 16:165–175.

Blumstein DT, Ardron JG, Evans CS, in press a. Kin discrimination in a macropod marsupial. Anim Behav.

Blumstein DT, Daniel JC, Ardron JG, Evans CS, in press b. Competition for food increases aggression but not the trade-off between foraging and vigilance in tammar wallabies. Ethology.

Blumstein DT, Daniel JC, Evans CS, 2001. Yellow-footed rock-wallaby group size effects reflect a trade-off. Ethology 107:655–664.

Blumstein DT, Evans CS, Daniel JC, 1999. An experimental study of behavioural group size effects in tammar wallabies (*Macropus eugenii*). Anim Behav 58:351–360.

Bouskila A, 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. Ecology 76:165–178.

Byers JA, 1997. American pronghorn: social adaptations and the ghosts of predators past. Chicago: University of Chicago Press.

Catterall CP, Elgar MA, Kikkawa J, 1992. Vigilance does not covary with group size in an island population of silvereyes (*Zosterops laterlis*). Behav Ecol 3:207–210.

Colagross AML, Cockburn A, 1993. Vigilance and grouping in the eastern grey kangaroo, *Macropus giganteus.* Aust J Zool 41:325–334.

Corbett L, 1995. The dingo in Australia and Asia. Sydney: University of New South Wales Press.

Coss RG, 1999. Effects of relaxed natural selection on the evolution of behavior. In: Geographic variation in behavior: perspectives on evolutionary mechanisms (Foster SA, Endler JA, eds). New York: Oxford University Press; 180–208.

Coss RG, Goldthwaite RO, 1995. The persistence of old designs for perception. Perspect Ethol 11:83–148.

Coulson G, 1999. Monospecific and heterospecific grouping and feeding behavior in grey kangaroos and red-necked wallabies. J Mammal 80:270–282.

Croft DB, 1989. Social organization of the Macropodoidea. In: Kangaroos, wallabies and rat-kangaroos, vol. 2 (Grigg G, Jarman P, Hume I, eds). Chipping Norton, New South Wales: Surrey Beatty & Sons; 505–525.

Deni R, 1996. Observe software v2.1 for the Macintosh. Lawrenceville, New Jersey: Richard Deni.

Elgar MA, 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol Rev 64:13–33.

Ford H, 1979. Birds. In: Natural history of Kangaroo Island (Tyler MJ, Twidale CR, Ling JK, eds). Adelaide: Royal Society of South Australia; 103–114.

Goldthwaite RO, Coss RG, Owings DH, 1990. Evolutionary dissipation of an antisnake system: differential behavior by California and arctic ground squirrels in above- and below-ground contexts. Behaviour 112:246–269.

Griffith B, Scott JM, Carpenter JW, Reed C, 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Heathcote CF, 1987. Grouping of eastern grey kangaroos in open habitat. Aust Wildl Res 14:343–348.

Hoolihan DW, Goldizen AW, 1998. The grouping dynamics of the black-striped wallaby. Wildlife Res 25:467–473.

Hunter LTB, Skinner JD, 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135:195–211.

Inns RW, 1980. Ecology of the Kangaroo Island wallaby, *Macropus eugenii* (Desmarest), in Flinders Chase National Park, Kangaroo Island (PhD dissertation). Adelaide: University of Adelaide.

Jarman PJ, 1987. Group size and activity in eastern grey kangaroos. Anim Behav 35:1044–1050.

Jarman PJ, Coulson G, 1989. Dynamics and adaptiveness of grouping in macropods. In: Kangaroos, wallabies and rat-kangaroos, vol. 2 (Grigg G, Jarman P, Hume I, eds). Chipping Norton, New South Wales: Surrey Beatty & Sons; 527–547.

Jarman PJ, Wright SM, 1993. Macropod studies at Wallaby Creek. IX. Exposure and responses of eastern grey kangaroos to dingoes. Wildl Res 20:833–843.

Johnson CN, 1989. Grouping and the structure of association in the red-necked wallaby. J Mammal 70:18–26.

Johnson KA, Burbidge AA, McKenzie NL, 1989. Australian Macropodoidea: status, causes of decline and future research and management. In: Kangaroos, wallabies and rat-kangaroos, vol. 2 (Grigg G, Jarman P, Hume I, eds). Chipping Norton, New South Wales: Surrey Beatty & Sons; 641–657.

Kavaliers M, 1990. Responsiveness of deer mice to a predator, the short-tailed weasel: population differences and neuromodulatory mechanisms. Physiol Zool 63:388–407.

Kotler BP, Blaustein L, Brown JS, 1992. Predator facilitation: the combined effects of snakes and owls on the foraging behavior of gerbils. Ann Zool Fenn 29:199–206.

Lampert RJ, 1979. Aborigines. In: Natural history of Kangaroo Island (Tyler MJ, Twidale CR, Ling JK, eds). Adelaide: Royal Society of South Australia; 81–89.

Lima SL, 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. Behaviour 102:231–238.

Lima SL, 1992. Life in a multi-predator environment: some considerations for anti-predatory vigilance. Ann Zool Fenn 29:217–226.

Magurran AE, 1999. The causes and consequences of geographic variation in antipredator behavior: perspectives from fish populations. In: Geographic variation in behavior: perspectives on evolutionary mechanisms (Foster SA, Endler JA, eds). New York: Oxford University Press; 139–163.

Magurran AE, Seghers BH, Shaw PW, Carvalho GR, 1995. The behavioral diversity and evolution of guppy, *Poecilia reticulata,* populations in Trinidad. Adv Study Behav 24:155–202.

Maxwell S, Burbridge AA, Morris K (eds), 1996. The 1996 action plan for Australian marsupials and monotremes. Canberra: Wildlife Australia.

McCallum H, Timmers P, Hoyle S, 1995. Modelling the impact of predation on reintroductions of bridled nailtail wallabies. Wildl Res 22:163–171.

Morris K, Armstrong R, Orell P, Vance M, 1998. Bouncing back: Western Shield update. Landscope 14:28–35.

Noldus Information Technologies, 1995. The Observer 3.0. Wageningen, The Netherlands: Noldus Information Technologies.

Peckarsky BL, Penton MA, 1998. Why do *Ephemerella* nymphs scorpion posture: a "ghost of predation past"? Oikos 53:185–193.

Peron F, 1816 [1979]. Historical perspective: Kangaroo Island—1803. In: Natural history of Kangaroo Island (Tyler MJ, Twidale CR, Ling JK, eds). Adelaide: Royal Society of South Australia; 177–184.

Pledge NS, 1979. Fossil vertebrates. In: Natural history of Kangaroo Island (Tyler MJ, Twidale CR, Ling JK, eds). Adelaide: Royal Society of South Australia; 123–127.

Poole WE, 1995. Western grey kangaroo. In: The mammals of Australia (Strahan R, ed). Chatswood, New South Wales: Reed Books; 332–334.

Pressley PH, 1981. Parental effort and the evolution of nest-guarding tactics in the threespine stickleback, *Gasterosteus aculeatus* L. Evolution 35:282–295.

Riechert SE, Hedrick AV, 1990. Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta*. Anim Behav 40:679–687.

Robertshaw JD, Harden RH, 1989. Predation on Macropodoidea: A review. In: Kangaroos, wallabies and rat-kangaroos, vol. 2 (Grigg G, Jarman P, Hume I, eds). Chipping Norton, New South Wales: Surrey Beatty & Sons; 735–753.

SAS Institute, 1998. StatView 5.0. Cary, North Carolina: SAS Institute.

Sih A, Englund G, Wooster D, 1998. Emergent impacts of multiple predators on prey. Trends Ecol Evol 13:350–355.

Smith MJ, Hinds L, 1995. Tammar wallaby. In: The mammals of Australia (Strahan R, ed). Chatswood, New South Wales: Reed Books; 329–331.

Van Damme R, Castilla AM, 1996. Chemosensory predator recognition in the lizard *Podarcis hispanica*: effects of predation pressure relaxation. J Chem Ecol 22:13–22.

Wolf CM, Griffith B, Reed C, Temple SA, 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conserv Biol 10:1142–1154.

Wyre G, 1998. Operation Western Shield. In: Mammal conservation in Western Australia (Perth Zoo, ed). Perth: Perth Zoo; 25–32.