Ethology Ecology & Evolution 15: 159-172, 2003

Tammar wallabies (*Macropus eugenii*) associate safety with higher levels of nocturnal illumination

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Received 29 October 2002, accepted 25 March 2003

Moonlight is commonly reported to increase the time nocturnal animals allocate to antipredator vigilance and to affect space use patterns because predation risk increases as a function of light intensity. The majority of studies reporting moon-light effects have been conducted on small-body sized mammals which are relatively vulnerable to a variety of predators. Moonlight effects were studied experimentally on a mid-sized mammal, the tammar wallaby (*Macropus eugenii*), a macropodid marsupial. Four groups of six adult female wallabies were observed for 6 days during each of three moon phases (no moon, quarter moon and full moon). In addition to natural illumination, wallabies were exposed to 2 days each of three artificial light treatments (no light, red light, white light) during each moon phase treatment. Subjects were videotaped at night with an image intensifier affixed to a video camera. Time budgets were calculated from the video record, and later analyzed in a repeated-measures factorial ANOVA. There was no effect of natural moonlight on time allocation, suggesting that wallabies had no endogenous cycle associated with moonlight. There were effects of artificial illumination and of the experimental group on time allocation. Wallabies tended to forage more and allocate less time to antipredator vigilance under the two light treatments, suggesting that, unlike previous studies on a variety of other taxa, they associated safety with increased illumination. We speculate that differences among groups might reflect the different seasons over which wallabies were studied. Results suggest that the nocturnally active tammar wallaby exercises caution in the dark.

KEY WORDS: antipredator behavior, moonlight effects, tammar wallaby.

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INTRODUCTION

Predation risk can be defined as the probability of an animal being killed during a certain time period. Some periods are more dangerous than others because of spatial and temporal variation in predator activity (LIMA & DILL 1990). Light intensity, through its effect on the visual abilities of both predator and prey, is an environmental determinant of risk which, theoretically, can be easily assessed by the prey and used as an indicator of predation risk. Illumination could influence risk in several ways. Illumination can increase predator "lethality" (BROWN 1999) by increasing predator hunting success. Alternatively, it could decrease risk if the effectiveness of prey at detecting predators increases (BROWN 1999). The integration of these forces should be reflected in how prey allocate time to various activities and utilize their habitat under different levels of illumination (LIMA & DILL 1990, CLARKE et al. 1995, BROWN 1999, KOTLER et al. 2002).

Previous studies investigating the effects of artificial or lunar light on activity patterns generally focused on small mammals (mainly desert rodents) as well as a few small marsupials (e.g., LOCKARD & OWINGS 1974a, 1974b; KAUFMAN & KAUFMAN 1982; KOTLER 1984; PRICE et al. 1984; GOLDINGAY & KAVANAGH 1986; BOWERS 1988; BROWN et al. 1988; KOTLER et al. 1988, 1991, 1994, 2002; WOLFE & SUMMERLIN 1989; LONGLAND & PRICE 1991; DICKMAN 1992; HUGHES et al. 1994; BOUSKILA 1995; SUTHERLAND & PREDAVEC 1999; TOPPING et al. 1999; HAYTHORNTHWAITE & DICKMAN 2000). Fewer studies investigated the behavior of larger body-sized mammals (seals: TRILLMICH & MOHREN 1981; porcupines: ALKON & SALTZ 1988; lagomorphs: GILBERT & BOUTIN 1991; KOLB 1992; opossums: JULIEN-LAFERRIÈRE 1997; primates: DONATI et al. 2001). Moonlight avoidance is widespread, and a general pattern emerging from these studies is that, with high levels of illumination, animals decrease the time allocated to foraging and shift their microhabitat use from open habitats towards cover (typically "bush" microhabitat). Because investigations of predation rates have shown that the risk of predation is higher in the open than in the bush microhabitat, and that this risk increases with increased illumination, it is believed that this moonlight avoidance response is an effective adaptation to reduce the risk of being killed by visually oriented nocturnal predators (BROWN et al. 1988; KOTLER et al. 1988, 1991).

We conducted an experimental study of moonlight effects on tammar wallabies, a mid-sized (6-10 kg), nocturnal macropodid marsupial (SMITH & HINDS 1995) because much was known about other components of their antipredator behavior and time allocation. Nothing specifically was known about how moonlight influenced their behavior. Captivity provided the necessary control to focus specifically on moonlight effects. We studied time allocated to different behaviors at night, when the wallabies were most active, to determine whether and how illumination affected their behavior.

Our subjects were captive-bred offspring from Kangaroo Island, South Australia. Despite about 9500 years of isolation from mammalian predators (BLUMSTEIN et al. 2000a), Kangaroo Island tammar wallabies maintained a variety of antipredator behaviors designed to minimize risk (BLUMSTEIN & DANIEL 2002), as well as the ability to respond to visual, but not acoustic or olfactory cues associated with predators (BLUMSTEIN et al. 2000a, 2002b). For example, tammars decreased time allocated to foraging and increased time allocated to vigilance and locomotion in response to variation in group size (BLUMSTEIN et al. 1999). Kangaroo Island tammars also responded to the sight of novel mammalian predators (BLUMSTEIN et al. 2000a), and were able to be trained to be more responsive specifically to the sight of predators, but not non-predators (GRIFFIN et al. 2001, 2002). Previous studies have shown that wallabies engage in more "relaxed postures" and social interactions as perceived predation risk declines (BLUMSTEIN et al. 1999). Time allocated to grooming and aggression seems to be affected by social factors more than by perceived predation risk (BLUMSTEIN et al. 1999).

Specifically, we studied the effects of the natural moon-cycle and different artificial ambient light levels or colors on the nocturnal behavior of tammar wallabies by addressing two questions:

(1) Does wallaby behavior follow an endogenous cycle related to moon phase?

(2) Does time allocation to vigilance and other behavior vary with levels of illumination, and do wallabies use light intensity as a cue for predation risk?

If there was an endogenous cycle involved, we expected tammars to respond differentially according to moonphase. If the wallabies used light intensity as a cue for increased predation risk, we expected a significant difference between no light and white light treatments. Specifically, we expected tammar wallabies to increase their vigilance and locomotion, and to decrease time allocated to foraging, relaxed behaviors and social interactions with increased levels of illumination. Time allocated to grooming and aggression might not change because those behaviors are likely more affected by a social factor than by perceived predation risk. We might also expect some seasonal variation in the response to light levels, because the study was conducted from late Austral summer until winter. Seasonal variation might reflect changes in reproductive status, night length (and therefore available foraging time), as well as differences in ambient temperature (which could influence the marginal benefits of foraging).

METHODS

Subjects and husbandry

We studied adult female tammar wallabies at the Macquarie University Fauna Park, Sydney, New South Wales, Australia, from February to July 2001. When not participating in the experiment, the wallabies lived in mixed-sex, female-biased or all female groups. For this study, we temporarily placed six mature females, with or without pouch young, in an observation yard measuring 11 × 28 m. The yard was beneath a dense forest canopy; some, but not much, natural moonlight illuminated the yard. The fences of the enclosure were covered with a 2 m high shade-cloth, preventing animals from seeing conspecifics in the three adjacent yards and by being disturbed by people walking through the park. Wallabies were fed ad libitum kangaroo pellets (Gordon's stock feed) in a food bin placed in the center of the yard, and were provided with ad libitum water. They also fed on natural vegetation (tree roots and bark, fallen leaves, twigs and branches). The observation yard contained natural shade from trees and an artificial cover, consisting of wood piles, but low-lying bushes were removed to allow maximum visibility from the observer's hide. Compared to their natural habitat, this would be viewed as 'open' from the wallabies' perspective.

For ethical reasons, we used the smallest possible sample of animals. By selecting animals from the Fauna Park breeding colony, and by observing them in semi-natural conditions under a variety of weather conditions, we believe our results should be generalizable to other tammars. We tried to limit the influence of factors that could influence time allocation in tammar wallabies by testing only mature females and by observing them at the same relative time of day (from 1 hr after sunset to 3-3.5 hr after sunset). Moreover, food, water and availability of cover were identical during all treatments. We used female wallabies because their agonistic interactions were mainly simple displacements; chases were infrequent. The presence of a male in our group would have enhanced the females' aggressiveness.

For this experiment, we randomly selected six mature female tammar wallabies for each of the four experimental groups, providing a total study population of 24 animals. The subjects ranged between 1 and 5 years from four different breeding yards and weighed between 3.4 and 6.6 kg. No animal was used in more than one experimental group. Subjects were given at least 4 days to habituate before the experiments started and they generally "relaxed" within a day or two of being introduced to the observation yard: they decreased exploring the perimeter of the enclosure, they looked less tense than when initially introduced, and they behaved similarly to individuals in other yards. While being observed, each subject wore a 1 cm wide cat collar with a coloured plastic key chain (measuring 2.2 × 5.0 cm) with reflective tape on both the collar and the key chain creating a unique pattern. These patterns permitted subjects to be unambiguously identified both day and night. Wallabies quickly habituated to the collars which had no obvious adverse effects. Identical collars have been used to identify individuals in several previous studies (e.g., BLUMSTEIN et al. 1999, ORD et al. 1999, GRIFFIN et al. 2001). Following the experiment, each female was moved back to her original yard, and her collar was removed.

Experimental design

For the purpose of this experiment, we divided the moon cycle into three phases. Full moon, spanned 6 consecutive nights around the full moon. Quarter moon, spanned 6 consecutive nights around the first or last quarter. New moon, spanned 6 consecutive nights around the new moon. During each phase, three light treatments were tested: "no light", "red light" and "white light"; each light treatment lasted 2 consecutive nights. The combination of moonphase and light treatment thus gave us nine different treatments. Each group experienced the light treatments in a random order. Additionally, the starting moon phase was systematically varied among the different groups so that all groups did not start at the same phase. Observations were conducted during the late summer, between 21 February and 14 March, for group 1; during autumn, between 1 and 30 April and between 7 and 25 May for group 2 and 3; and in winter, between 10 June and 12 July for group 4.

Observation procedure

To illuminate the observational yard, we used six 4-w garden lights affixed to the fence on one side of the yard. White light was used to mimic the illumination under a natural full moon. Red filters are often used by fieldworkers when spot-lighting nocturnal animals to reduce disturbance while still permitting identification. Red light was obtained by placing a red plastic pool filter in front of the garden lights. Finally, under no light treatment, the yard was bathed only in natural moonlight. We obtained a relative measure of light intensity by using a camera on a moonless night. We set the camera's aperature to 4.5 (ASA 400) and recorded the shutter speed for each of the treatments (1/20 for white light, 1/10 for red light and 30 sec for no light). Red light thus was 50% less intense than white light and no light was 0.17% less intense than white light. While not quantified, these light treatments reflected the range of variation in natural moonlight seen when observing foraging wallabies on Kangaroo Island (D.T. Blumstein unpublished observations).

Proportion of time allocated to foraging varies throughout the day and night (D.T. Blumstein unpublished observations). Rather than beginning our observations after moonrise (which varies), we elected to control for diel variation in behavior by setting the time of our observations to sunset. This permitted us to test for variation attributable specifically to moonphase, and thus to determine if there was an endogenous cycle, rather than ambient light (which varied considerably due to cloud cover). Each observation night began 1 hr after sunset, when the lights were switched on (or not in case of the no light treatment), and the first focal animal sample began ≥ 20 min later (this delay provided time for the subjects to habituate to the light and the observer's presence). Each subject was filmed twice for 5 min each observation night, producing two 5-min focal animal samples (Martin & Bateson 1993).

Animals were videotaped using a tripod-mounted Panasonic NV-VX77 video camera with an ITT Nightcam 300 image intensifier, and a Tamron 80-210 mm zoom lens attached. For all treatments, we used a 1w hand-held flashlight to provide sufficient illumination so that we could unambiguously score wallaby behavior.

In total we obtained 20 min observation per individual, per treatment, per moon phase (for 2 observation nights), resulting in 2 hr of observation for each group, per treatment, per moonphase. The sequence of the focal animals was determined randomly at the beginning of each 6-night observation block, and the last focal animal sample was generally completed 3 to 3.5 hr after sunset.

Data analysis

The resulting focal sampling observations were scored in real time from video tapes, using JWatcher, an event recorder program designed for the analysis of focal animal samples (Blumstein et al. 2000b). We scored the behaviors based on a previously published tammar ethogram (Blumstein et al. 1999). Using JWatcher, we calculated the proportion of time in sight for each behavior and for each focal sample. We then combined behaviors to generate composite behaviors for final analysis. The behaviors analyzed included: foraging (included foraging and drinking), vigilance (included looking while in all postures except lying down or sitting), relaxed behavior (included lying down and sitting), grooming (included all forms of self-grooming), aggression, social behavior, locomotion (included pentapedal walking and bipedal hopping), and out-of-sight. For each behavior we averaged the results of the four 5-min focal samples for each individual during each treatment to obtain a mean proportion of time in sight for each individual and each treatment.

Statistical analyzes were conducted using SPSS 10 (SPSS Inc. 2000). We fitted a repeated-measures factorial ANOVA to study the effects of moon phase and the light treatment (within subjects factors), and the experimental group (a between subjects factor). The α level was set at 0.05. We used arcsine-square root transformations of the proportion of time in sight for all analyzes (Martin & Bateson 1993), and report the Greenhouse-Geisser corrected P-values and η^2 as a measure of effect size (Cohen 1988). We also conducted paired sample t-tests when the results for the repeated-measures ANOVA were significant.

RESULTS

Moon phase explained no significant variation in the time allocated to behavior (Table 1; Fig. 1). However, variation in the time allocated to aggression was significantly explained by a two-way interaction between moon phase and group, and there was a significant three-way interaction between moon phase, treatment and

Table 1.

Results from factorial ANOVA designed to explain variation in the proportion of time in sight allocated to each of the six behaviors. Significant P-values (Greenhouse-Geisser for tests of the within-subjects effects) are in italic.

	Foraging		Vigilance	
	P-value	η^2	P-value	η^2
Moon	0.624	0.022	0.569	0.026
Treatment	*0.022*	0.174	*0.005*	0.245
Group	*0.046*	0.324	*0.039*	0.335
Moon × Group (interaction)	0.236	0.176	0.145	0.208
Treatment × Group	0.143	0.204	*<0.001*	0.510
Moon× Treatment	0.278	0.050	0.434	0.044
Moon × Treatment × Group	*<0.001*	0.385	*0.014*	0.281

	Locomotion		Grooming	
	P-value	η^2	P-value	η^2
Moon	0.068	0.131	0.071	0.131
Treatment	0.107	0.109	0.897	0.005
Group	*0.007*	0.448	*0.007*	0.448
Moon × Group (interaction)	0.791	0.069	0.513	0.115
Treatment × Group	0.036	0.284	0.831	0.065
Moon × Treatment	0.314	0.057	0.246	0.066
Moon × Treatment × Group	*<0.001*	0.418	0.351	0.146

	Social		Aggression	
	P-value	η^2	P-value	η^2
Moon	0.884	0.004	0.502	0.032
Treatment	0.555	0.027	0.506	0.031
Group	0.617	0.084	*0.004*	0.475
Moon × Group (interaction)	0.149	0.209	*<0.001*	0.478
Treatment × Group	0.374	0.143	0.213	0.185
Moon× Treatment	0.820	0.014	0.386	0.049
Moon × Treatment × Group	0.522	0.120	0.123	0.200

	Relaxed	
	P-value	η^2
Moon	0.529	0.027
Treatment	0.262	0.065
Group	0.106	0.258
Moon × Group (interaction)	0.271	0.169
Treatment × Group	0.254	0.170
Moon× Treatment	0.723	0.024
Moon × Treatment × Group	*<0.001*	0.359

group for locomotion. Significant differences were also found between experimental groups for time allocated to vigilance, locomotion, foraging, grooming and aggression (Table 1; Fig. 2).

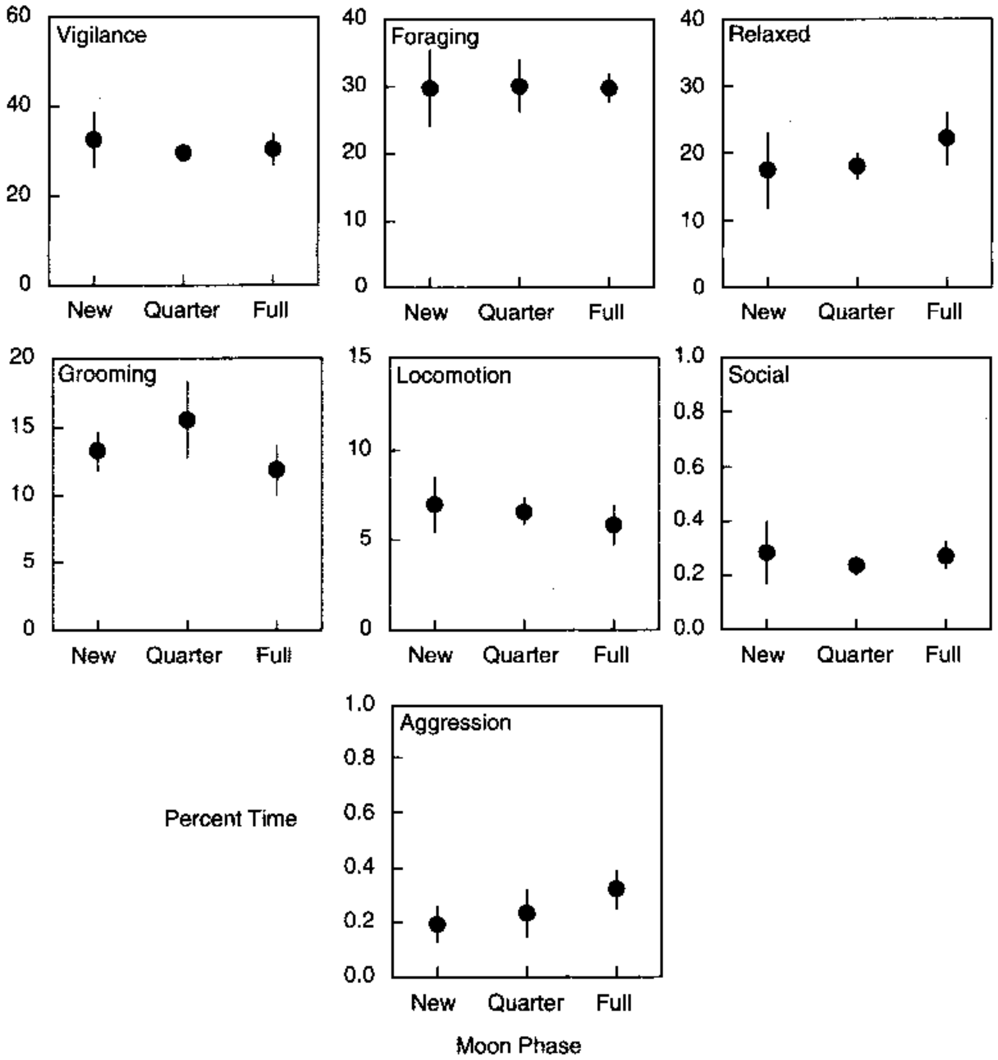

Fig. 1. — Average (± SEM) percent time tammar wallabies allocated to behavior as a function of moon-phase (note: scales differ among graphs). Statistical analyzes were conducted on angularly-transformed data (see text for details and Table 1 for results).

The artificial illumination treatments explained significant variation in time allocated to foraging and vigilance (Table 1; Fig. 3). Paired t-tests revealed tendencies for wallabies to forage significantly more under the red or white light treatments compared to the no light treatment (no light vs white light: *P* = 0.028; no light vs red light: *P* = 0.082; red light vs white light: *P* = 0.364; Bonferonni-adjusted *P*-critical = 0.015). Wallabies were significantly less vigilant when illuminated by red light compared to no light (no light vs red light: *P* = 0.013; no light vs white light: *P* = 0.255; red light vs white light: *P* = 0.092; Bonferonni-adjusted *P*-critical =

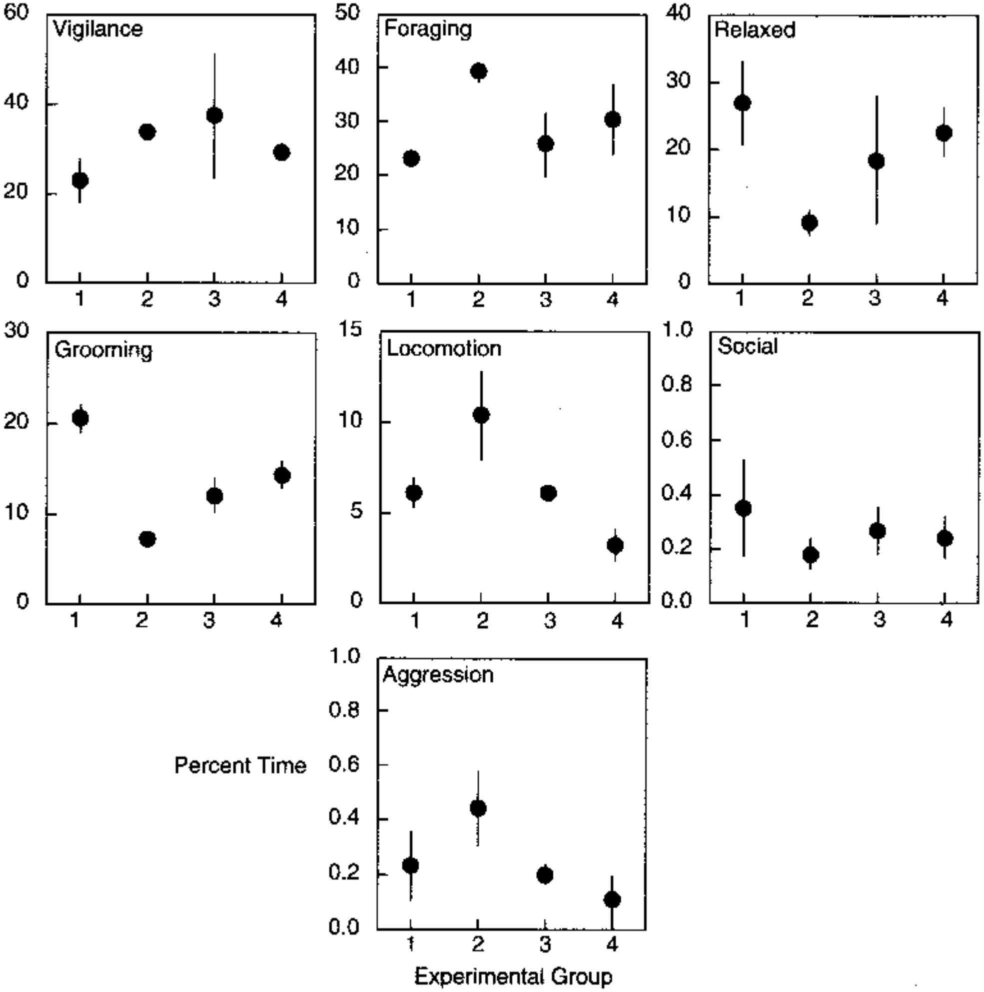

Fig. 2. — Average (± SEM) percent time tammar wallabies allocated to behavior as a function of experimental group (note: scales differ among graphs). Statistical analyzes were conducted on angularly-transformed data (see text for details and Table 1 for results).

0.015). Treatment had a relatively large effect on foraging and vigilance, although the size of the experimental group and the interactions were relatively larger than other factors (Table 1).

DISCUSSION

We studied the effects of the natural moon cycle and artificial illumination on the nocturnal behavior of tammar wallabies. We expected that tammars would

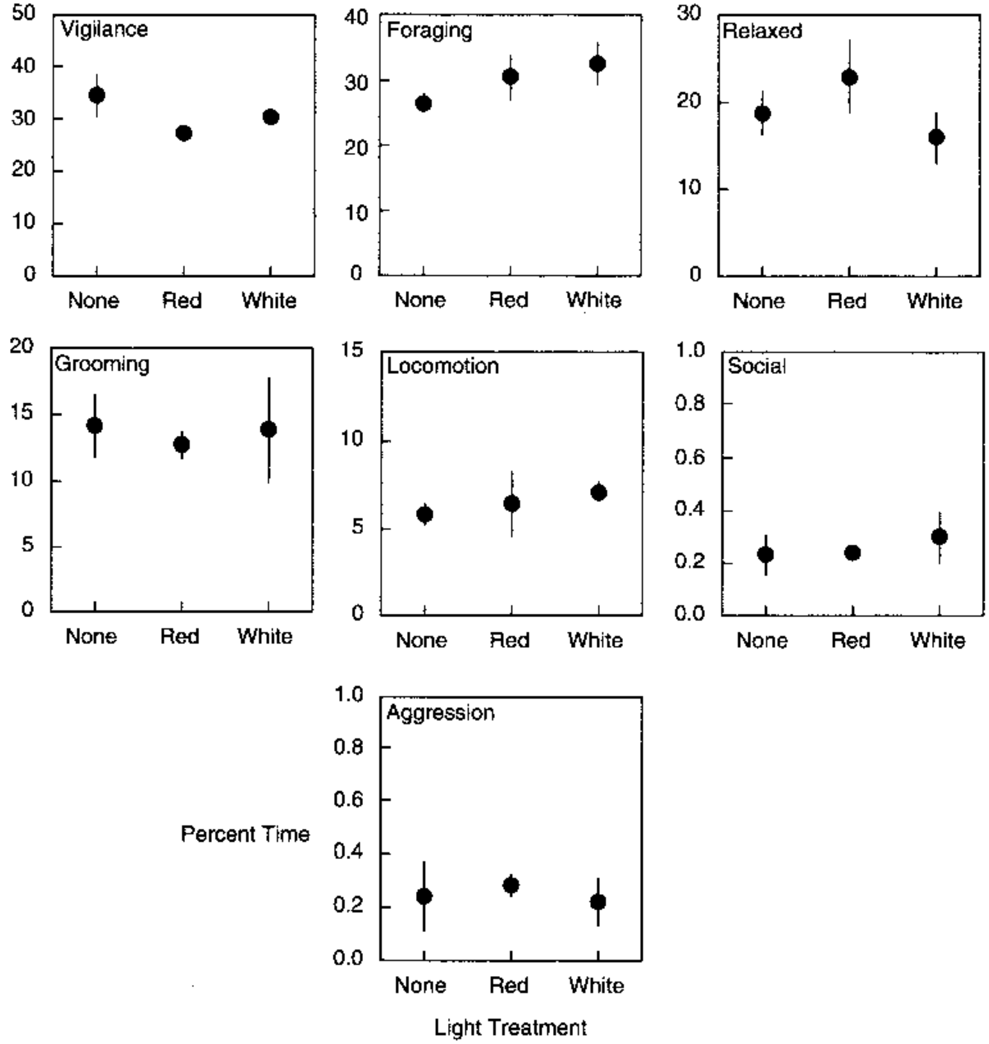

Fig. 3. — Average (± SEM) percent time tammar wallabies allocated to behavior as a function of artificial light treatment (note: scales differ among graphs). Statistical analyzes were conducted on angularly-transformed data (see text for details and Table 1 for results).

increase the time they allocated to vigilance and locomotion and to decrease the time they allocated to foraging, relaxed behaviors and social interactions with increased levels of illumination. We did not expect differences in the time allocated to grooming and aggression.

We found no main effect of moon cycle on wallaby behavior, although there were some uninterpretable interactions of moon phase and other factors. This suggests that there is no obvious endogenous cycle of wallaby behavior in response to natural moon cycles.

Both illumination treatment and the experimental group affected wallaby behavior. However, the increase in the proportion of time spent foraging under white light compared to no light was contrary to our expectations. Theory predicts that if predator lethality (BROWN 1999) is greater on moonlit nights, and that if the increase in the effectiveness of prey vigilance does not reduce this risk, then animals should behave more cautiously (BROWN 1999). Consistent with this theory, most previous light effect studies in mammals found a decrease in foraging behavior with increased levels of illumination (e.g., KOTLER 1984; BOWERS 1988; KOTLER et al. 1991, 1993, 1994), although some studies found no significant effect (e.g., SUTHERLAND & PREDAVEC 1999, HAYTHORTHWAITE & DICKMAN 2000). Previous studies suggested that the animals perceived a greater risk of predation with increased illumination, and concluded that for the species they studied, increased light levels were tantamount to increased predation risk. Because previous studies of tammar antipredator behavior (e.g., BLUMSTEIN et al. 1999, 2000a; GRIFFIN et al. 2001) have showed that tammars respond to increased predation risk by decreasing time allocated to foraging, we suggest that tammars perceived a greater risk of predation under dark conditions than under brighter light. While not significant, the wallabies tended to decrease vigilance and there was a non-significant tendency to increase time spent in relaxed behaviors when artificial illumination was high. These findings are consistent with the hypothesis that they perceived a greater risk in the dark. CLARKE et al. (1995) reported that eastern grey kangaroos (*Macropus giganteus*) needed more time to select their food in darkness, but this did not seem to be the case in our study; possibly because supplemental food was freely available. Our finding is also consistent with LENTLE et al.'s (1998) report that darkness does not influence the rate of food selection in tammar wallabies. One interpretation for this is that their night vision is more refined than in more diurnally active macropods such as the eastern grey kangaroo. It is also possible that changes in time allocation as a function of artificial illumination were influenced by social factors, not predation risk. We find this to be a less compelling explanation because resources were not limited and we have no a priori reason to expect that illumination directly influences the marginal value of foraging (e.g., BROWN 1999).

At night on the mainland, tammars were historically preyed on by mammalian predators (thylacines — *Thylacinus cynocephalus*; devils — *Sarcophilus harrisii*; and later dingoes — *Canis lupus dingo*; red foxes — *Vulpes vulpes*, and possibly cats — *Felis catus*), and avian predators such as large owls (*Ninox syrenua*). In contrast, Kangaroo Island tammars have probably not been exposed to nocturnal predation risk for 9500 years since the island was isolated from the mainland (BLUMSTEIN et al. 2000a), but seemingly remain cautious in low light levels. BLUMSTEIN et al. (2000a, 2002b) also showed that tammar wallabies recognize predators by visual, but not by acoustic or olfactory cues. This may explain why tammars felt more secure with higher levels of ambient light, as they would be more able to detect predators in higher ambient light levels.

The color or intensity of the ambient light also affected tammar wallaby time allocation. Wallabies significantly decreased the time allocated to vigilance under red light and tended to increase time allocated to foraging and relaxed behaviors suggesting that they also perceived a lower risk of predation under red light. Under red light, wallabies were the least vigilant and engaged in the most relaxed behavior. The intensity of the red light was 50% of that of white light, whereas no light was only 0.17% of the white light intensity. Thus, the no light treatment could be considered as the most dangerous by the wallabies because it limited their visual capacities while red light provided sufficient illumination for predator detection yet still allowed some degree of crypsis. Further investigation, for example by observing wallaby behavior under different intensities of white and red light, will be required to determine whether wallabies used variation in colour or intensity to assess risk.

Previous studies of other species suggested that seasonal variations in response to light were mainly due to night length and food availability, although temperature or other social or reproductive factors may also be important (e.g., LOCKARD & OWINGS 1974a, 1974b; ALKON & SALTZ 1988). Aggressive and social interactions are probably influenced by individual differences within groups, as well as by social factors. Kinship may influence these interactions because there is a continued tolerance between related females (VUJCICH 1979, JOHNSON 1989, RUSSELL 1989), and previous studies have demonstrated a kinship effect on the rate of aggressive behavior in tammars (BLUMSTEIN et al. 2002a). We had no information about the relatedness of subjects in this experiment, but had information about recent familiarity. Groups 1 and 4 both contained individuals from two different yards while groups 2 and 3 were composed by animals originating from the same yard. This did not seem to affect aggressive and social interactions because aggressive interactions were the highest for group 2 and the lowest for group 4; we would have expected the opposite based on familiarity alone. A similar pattern was seen with social interactions; which were the highest for group 1 and the lowest for group 2, even though individuals in group 1 were not familiar but the ones in group 2 were. Thus, there seem to be more complex factors regulating aggressive and social interactions.

Fundamental knowledge of antipredator behavior has important implications for conservation biologists (BLUMSTEIN 2000), particularly when animals are to be translocated or reintroduced (KLEIMAN 1989, WOLF et al. 1996). Our results suggest that (unless there was a substantial increase in predator activity), translocations into open habitat (where natural moonlight is the main source of light) might best be conducted around the full moon to maximize the likelihood that tammars can detect predators.

In conclusion, we found no evidence for an endogenous cycle involved in the response to light levels, and, contrary to what has been reported in many other small mammals, tammar wallabies considered increased illumination as safer than low illumination. This effect seemingly persisted despite 9500 years of isolation from nocturnal predation. Future studies could focus specifically on teasing apart the mechanisms responsible for this effect — variation in light intensity versus colour. Regardless, the nocturnal tammar wallaby appears to be afraid of the dark.

ACKNOWLEDGEMENTS

We are extremely grateful to Chris Evans and the Animal Behaviour Laboratory at Macquarie University for providing equipment and logistical support; Chris and Janice Daniel for discussions about experimental design; Janice, and especially Alan Taylor, for statistical advice; Chris, Janice and Andrea Griffin for on-going discussions about wallaby antipredator behavior; Ron Claassens, Anne Mouland, and Scott Peel for wallaby wrangling; Des Cooper, John Rodger, and The Marsupial CRC for access to animals and facilities. We are grateful for the support from the Australian Research Foundation (via an ARC-APD to DTB), and the Australian Cooperative Research Centre Programme. The research was conducted under Macquarie University Animal Research Protocols No. 99019. Animals were held under permit No. 62131 by the New South Wales National Parks and Wildlife Service. By design, animals were not harmed during the course of this study. Finally, we thank Janice Daniel, Burt Kotler, and two anonymous referees for constructive comments on the manuscript.

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