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Provisioning by tourists affects the behaviour but not the body condition of Mareeba rock-wallabies (*Petrogale mareeba*)

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Abstract. Feeding free-ranging native animals is a form of wildlife-based tourism that is particularly popular in Australia as a result of the cryptic nature of many native species. The colony of Mareeba rock-wallabies (*Petrogale mareeba*) at 'Granite Gorge', North Queensland, where tourists feed a spatially defined subset of animals daily, was studied to determine the effects of provisioning on their behaviour and body condition. Provisioned *P. mareeba* had higher activity levels, including higher aggression levels, and spent more time performing contact behaviours (including mutual and non-mutual allogrooming) than did non-provisioned animals. Possible explanations for increased aggression include competition over provisioned food and territorial defence. Increased contact behaviours may serve to reduce tension caused by provisioning. The diurnal activities of the provisioned rock-wallabies were dictated by the activities of tourists. Provisioned rock-wallabies emerged from their shelters to receive food much earlier each afternoon than did the unprovisioned animals. The level of autogrooming exhibited by the provisioned wallabies was much higher than that of the unprovisioned animals, presumably as a thermoregulatory response to the high afternoon temperatures. Although provisioned *P. mareeba* feed more, their higher activity levels explain the lack of difference in the body condition between the two groups.

Introduction

As wildlife-based tourism becomes increasingly popular, the impact of the activities of tourists on wildlife requires evaluation (Jacobson and Lopez 1994). When tourists are focusing directly on one species, behavioural studies can be useful as a way to assess impacts. These impacts represent a cost that must be weighed against the possible conservation benefit achieved through wildlife tourism, and are important when dealing with species that are considered at risk of extinction.

The cryptic nature of many species of native Australian wildlife encourages provisioning to make these animals more visible to tourists. Nocturnal and crepuscular species can be lured from their resting sites through regular feeding, providing tourists with the opportunity to view and interact with these animals. At 'Granite Gorge' on the Atherton Tablelands, Mareeba rock-wallabies (*Petrogale mareeba*) are fed regularly by organised tour groups. Mareeba rock-wallabies have only recently been recognised as a separate species, having formerly been classified as a sub-species of the allied rock-wallaby (*P. assimilis*) and referred to as the Mareeba race (Eldridge and Close 1992). Mareeba rock-wallabies are classified as a 'rare' species under Queensland's *Nature Conservation (Wildlife) Regulation (1994)*.

In order to quantify the effects of provisioning on rock-wallabies, we compared the social behaviour, diurnal activity patterns, activity levels and body condition of provisioned and unprovisioned subcolonies of rock-wallabies at Granite Gorge. There have been no previous behavioural studies of Mareeba rock-wallabies, so we compare our results with the behaviour of the (better-studied and closely related) allied rock-wallabies.

Methods

Study site and setting

The study was conducted at 'Granite Gorge' (145°20′30″S, 17°02′00″E; elevation 400 m), on the Atherton Tablelands, Queensland, Australia. Annual minimum and maximum mean temperatures are 16.1°C and 28.8°C respectively, and the area receives an average of 912 mm rain per year. The gorge comprises large outcropping granite domes, boulder piles and steep rocky slopes extending ~2 km on either side of Granite Creek (Fig. 1). The surrounding vegetation is

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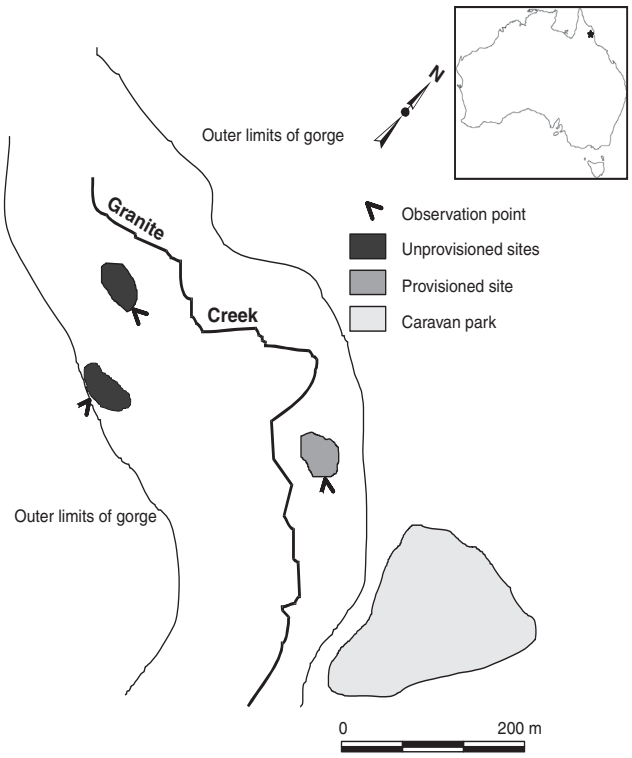

Fig. 1. Map of 'Granite Gorge' showing the three behavioural observation sites (one provisioned and two unprovisioned), 'Granite Creek' separating the provisioned and unprovisioned subcolonies, and the location of the caravan park. Insert shows the location of Granite Gorge (indicated by black star) in Queensland, Australia.

eucalypt-dominated tropical woodland with a grass understorey. Land extending beyond the area of the gorge has mostly been cleared for agriculture. Adjacent to the gorge is a caravan park on private property. At least 46 Mareeba rock-wallabies inhabited 'Granite Gorge' in 1997 (Hodgson 1998), occupying the rock outcrops on either side of the creek and feeding in the caravan park and in the surrounding vegetation at night. Within the gorge there are two distinguishable subcolonies, only one of which is provisioned by visitors to the caravan park. These subcolonies are separated by 'Granite Creek' and were never observed intermixing (Fig. 1).

During 1998, two companies took tourists to the gorge to feed the wallabies daily. Tourists were provided with either rolled oats or kangaroo pellets ('Gold Medal' brand), which were fed by hand to the provisioned wallabies.

The provisioned subcolony was observed from a rock above the area where the rock-wallabies were fed by tourists. It was possible to observe almost all occurrences of feeding of wallabies by humans, as well as the activities of the provisioned wallabies at dawn and dusk. Two sites were used to observe unprovisioned rock-wallabies, which was necessary to observe the same number of individuals as at the single provisioned site (Fig. 1). This study lacks replication, being limited to two subcolonies (provisioned and unprovisioned) at a single site ('Granite Gorge'). This was unavoidable as there was no second site available to replicate the study.

Observations

Rock-wallabies were observed for 36 days in September–November 1997. Observations were carried out during dawn and dusk as rock-wallabies are crepuscular (Sharman and Maynes 1995). Tourists fed the rock-wallabies daily between 1500 and 1630 hours so dusk observations of the provisioned subcolony were extended to include this period. Dawn and dusk observation sessions were alternated between the provisioned and unprovisioned subcolonies.

Focal sampling

Individual rock-wallabies were identified by means of distinguishable physical characteristics such as facial markings, ear marks, body and tail colouring, scars and reproductive status. Continuous recordings were made of focal individuals (Altmann 1974) during sampling sessions of 30 min each. Focal individuals were chosen on the basis of their age–sex class and we attempted to sample each class equally and in random order. Data were recorded at regular intervals of 30 s on the focal individual's posture, and the identification of, and distance to, its nearest neighbour. Units of behaviour and postures were classified according to those described in Horsup (1986, 1996) and Barker (1990). Additional postures and behaviours observed during this study were added to this repertoire.

Scan sampling

Scan sampling (Altmann 1974) was conducted as an alternative to focal sampling to provide information on group size and activity levels of rock-wallabies within each focal site. The posture or behaviour of all visible individuals was instantaneously sampled at 2-min intervals.

Classification of units of behaviour

Units of behaviour were divided into six main classes:

1. Aggressive – including aggressive approach, aggressive stare, aggressive vocalisation, aggressive chase, back jump, bite, forepaw strike, head thrust, and sparring/fighting (Horsup 1986, 1996).
2. Submissive – including retreat, flight, submissive vocalisation, stare avoidance, and hop (Horsup 1986, 1996).
3. Sexual – including sexual approach, sexual checking, sexual marking, sexual follow, clawing, clasping, erection, and copulation (Horsup 1986, 1996).
4. Contact – all behaviours not deemed aggressive, submissive or sexual, but involving an interaction between two or more individuals, including allogrooming, mutual allogrooming and mutual nose sniffs.
5. Autogrooming – all forms of autogrooming.
6. Feeding – natural and 'unnatural' foraging (feeding of wallabies by tourists and foraging by wallabies on food provided by humans), drinking and merycism (regurgitation and redigestion of food).

Age–sex classes

Three age–sex classes were identified: adult males, adult females, and juveniles (smaller individuals whose external genitalia were not readily distinguishable during behavioural observations).

Behavioural analysis

The difference in levels of each behaviour class performed by individuals in each subcolony was examined using a two-way ANOVA with subcolony and sex as fixed factors, and individuals as replicates. Levels of behaviour were measured in two ways: (1) the number of behaviours per individual per hour, and (2) the proportion of time spent performing each class of behaviour. The variances of the responses for each individual were weighted relative to the total focal time per individual by using the square root of the total focal time in hours.

Data from scan sampling were used to analyse activity levels in the two subcolonies, where the proportion of 2-min samples spent stationary (where a posture was recorded rather than an active behaviour) was calculated for each individual. The result for each

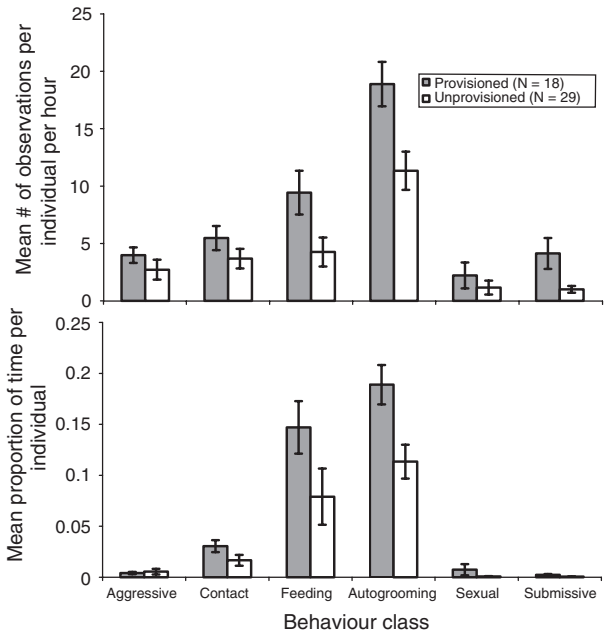

Fig. 2. Mean number of observations recorded per individual per hour and mean proportion of time that individuals were observed carrying out each behaviour class in provisioned and unprovisioned subcolonies (±s.e.) (where N = number of individual rock-wallabies).

individual was the dependent variable in a repeated-measures ANOVA, comparing time of day (morning or afternoon) within subcolonies. The data were transformed using arcsin-square-root and only individuals recorded in both the morning and afternoon were used in this analysis.

Body condition

Unprovisioned rock-wallabies were trapped (9–16 December 1997) in wire cage, treadle-release traps. The back end of each trap was padded with foam to provide protection for the wallabies against trap damage. Traps were baited with a mixture of rolled oats, peanut butter and honey, and were set overnight and emptied twice each night. Provisioned wallabies were hand-caught by inducing them with bait, grasping them by the base of the tail and placing them in opaque cloth (hessian) sacks.

The pouches of all females with large pouch young were taped closed prior to release, and these females were released directly into a cave, in an attempt to minimise the chance of losing pouch young. Body weight (to 1 g, including pouch young) and head length (to 0.1 mm) were recorded for each individual captured. The head lengths of pouch young with females from the provisioned and unprovisioned subcolonies were compared using a *t*-test, to check for any bias that may be introduced by including pouch young in weight measurements.

An index of condition was calculated for each adult (Krebs and Singleton 1993), where the index is the ratio of the observed body mass to the mass predicted using the regression of head length and body weight. The regression was calculated using data from individuals heavier than 2000 g as this is the minimum weight at which the sibling species, *P. assimilis*, reaches sexual maturity (Delaney 1997).

Results

Feeding by tourists

On average, a single tour group spent 13 min (range 7–25 min) feeding the provisioned rock-wallabies. Up to 5 tour groups visited the gorge each day, with each group usually feeding the wallabies at separate times. Groups consisted of up to 20 people and there was no defined limit to the amount of oats or pellets they could feed to the wallabies.

Although some rock-wallabies aggregated while provisioning was taking place, provisioning was limited to 16 of the 23 individuals visible from the observation site. These 16 individuals were consistently observed both during feeding and non-feeding times, within the area where provisioning occurred. The remaining animals were most commonly observed on the perimeter of this area.

Levels of behaviour within each subcolony

Provisioned individuals performed more aggressive behaviours per hour than did unprovisioned individuals ($P = 0.04$, for all ANOVAs d.f. = 1,43), but the proportion of time spent exhibiting these behaviours did not significantly differ between the two groups (Fig. 2). The provisioned rock-wallabies also fed more times per hour ($P < 0.01$) and spent a higher proportion of time feeding ($P < 0.01$) than did the unprovisioned rock-wallabies. Autogrooming behaviours were exhibited more often per hour by provisioned individuals than by unprovisioned ($P < 0.01$) and a higher proportion of time was spent autogrooming by the provisioned individuals than by the unprovisioned ($P < 0.01$). The provisioned rock-wallabies spent a higher proportion of time performing contact behaviours than did the unprovisioned ($P = 0.01$) but did not perform these behaviours more times per hour. Levels of sexual and submissive behaviours are shown in Fig. 2 but sample sizes were too small to be analysed statistically.

Activity levels

Members of the unprovisioned subcolony spent a higher proportion of time stationary than did those of the provisioned subcolony ($P < 0.01$, d.f. = 1,25), indicating that individuals in the provisioned subcolony were more active. Morning and evening activity levels did not differ within each subcolony, with the proportions of time spent stationary being 75% (±0.04%, s.e.) and 68% (±0.03%, s.e.) in the provisioned subcolony and 82% (±0.05%, s.e.) and 92% (±0.02%, s.e.) in the unprovisioned subcolony respectively.

Diurnal patterns of behaviour

During all of the 14 half-hour periods during which behavioural observations were conducted, more of the known provisioned population was visible than of the known unprovisioned population (Fig. 3). A substantial proportion of the provisioned subcolony (40.6% ± 1.85%, s.e.) was still visible when morning scan sampling sessions ended 2.5 h after sunrise, while there were never any unprovisioned rock-wallabies visible at the end of morning sessions. Many provisioned individuals were already visible 3.5 h before sunset, while in the unprovisioned subcolony, no individual was seen more than 1.5 h before sunset.

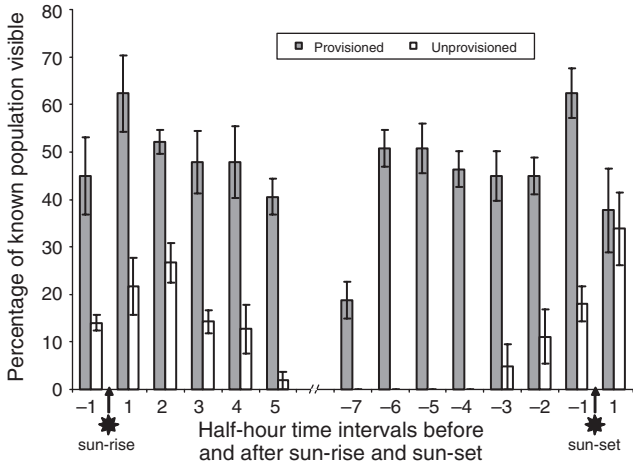

Fig. 3. Percentage of the known population visible within the provisioned and unprovisioned subcolonies (represented by bars, ±s.e.), according to number of minutes after sunrise and before sunset.

The proportion of the known population visible in the evening peaked earlier for the provisioned subcolony (0–29 min before sunset), than for the unprovisioned subcolony (30–59 min before sunset). While the provisioned rock-wallabies began to leave the observation site up to half an hour before sunset, the number of unprovisioned rock-wallabies tended to increase at this time and they remained at the observation sites until it was too dark to observe them. Thus behavioural sampling sessions were usually ended before the unprovisioned individuals left the observation sites. These results were not subject to statistical testing as data on the unprovisioned animals were clearly right-censored, but data on the provisioned animals were not.

Body condition

There was no significant difference in the mean head lengths of pouch young with females from the provisioned (54.0 mm ± 15.9 mm s.e., $N = 6$) and unprovisioned (35.1 mm ± 7.3 mm s.e., $N = 10$) subcolonies. Therefore it was assumed that no bias was caused by including pouch young in the weight of females from both subcolonies.

The mean condition index (Krebs and Singleton 1993) for rock-wallabies in the provisioned subcolony was 0.99 (±0.021 s.e., $N = 14$), and for the unprovisioned colony 1.01 (±0.012 s.e., $N = 25$). These values are very close to 1.0, which by definition is the average index of all animals measured (Krebs and Singleton 1993), and did not differ significantly ($F = 0.841$, d.f. = 1,35, $P = 0.36$).

Discussion

Resource distribution affects the social behaviour of a species by influencing the distribution of individuals and increasing group size (Slobodchikoff and Shields 1988). Clumped food sources often result in animals feeding in aggregations (Morse 1980). The provision of extra food to a group of individuals has the potential to influence the behaviour of individuals in that group, as it creates a plentiful food source that is concentrated in both space and time (Hill 1994). Provisioning results in larger groups of mammals as individuals aggregate around supplemental food sources (Ims 1987; Lyndaker 1987).

Provisioned rock-wallabies were more active than the unprovisioned rock-wallabies. The higher levels of activity in the provisioned subcolony can be attributed to their higher rates of aggressive, feeding and grooming behaviours and the fact that they spent a higher proportion of their time feeding, grooming and performing contact behaviours (Fig. 2).

Increased aggression amongst provisioned animals has been observed in primates, including chimpanzees (*Pan troglodytes*) (Wrangham 1974), rhesus monkeys (*Macaca mulatta*) (Hill 1994), Japanese macaques (*Macaca fuscata*) (Hill 1999) and Hamadryas baboons (*Papio hamadryas*) (Kamal *et al*. 1997). The highest level of aggression has been observed when there is increased competition because of restricted access to the available food source (Wrangham 1974; Southwick *et al*. 1976). Increased aggression is also a result of aggregations of individuals that do not necessarily occur naturally. Plantations of exotic plants may produce a similar result; for example, Barker (1990) found that rock-wallabies aggregating and feeding on watered lawns have high aggression levels. During provisioning of rock-wallabies by tourists at Granite Gorge, the volume of the provisioned food was not limited. However, the time and sources were. Typically, there were more rock-wallabies than tourists feeding them, and this promoted competition among the rock-wallabies to gain access to the food sources.

Rock-wallabies generally defend territories (Horsup 1994). Adult allied rock-wallabies at ‘Black Rock’ exhibited extremely strong fidelity to their home ranges, and had well defined rock pile ranges (the area used by the rock-wallaby on the rock pile) with little overlap between the ranges of individuals of the same sex (Horsup 1994; Spencer 1996). Individuals of the same sex were never seen on the same rock unless they were interacting agonistically (Horsup 1994). Although home ranges of *P. mareeba* at ‘Granite Gorge’ were not investigated, it is likely that the area in which provisioning takes place is part of, or adjacent to, the territories of the 16 individuals that were observed being provisioned. These territories may be defined only loosely during provisioning times, as the benefits of accepting provisioned food outweigh the benefits of asserting territorial defence. Nonetheless, the defence of territories may promote aggression when individuals are aggregating prior to, and remain aggregated following, provisioning. This may also be preventing larger aggregations of rock-wallabies in the provisioning area, as other individuals that were often seen on the perimeter of this area were never seen accepting food from tourists.

Contact behaviours included allogrooming and mutual allogrooming, both of which are rare amongst macropods except between mothers and juveniles (Hume *et al*. 1989). Horsup (1996) observed allogrooming between adult male and female *P. assimilis*, where it served to reinforce pair-bonds. While allogrooming was observed between adult males and females in this study, dyads were not exclusive and neither the provisioned or non-provisioned individuals were considered to form long-term pair-bonds (Hodgson 1998). In other species, allogrooming promotes group bonding (Russell 1984) and Kaufmann (1974) suggests that this is particularly the case in species that exhibit high levels of aggression when in groups, where allogrooming probably reduces intra-group tension. While this explanation of the function of allogrooming in *P. mareeba* is purely speculative, it is possible that the higher rate of aggressive behaviours is related to individuals in the provisioned subcolony spending more time performing contact behaviours. Allogrooming may serve to appease neighbours within the provisioning area. Alternatively, the higher levels of contact behaviours may result from the larger amount of time provisioned individuals spend in close proximity, as a result of the relatively small area in which provisioning occurs, and the increased opportunity for contact behaviours to occur.

Increased autogrooming appears to be a thermoregulatory response as, unlike unprovisioned individuals, provisioned rock-wallabies spend time out of their shelter during the relatively high mid-afternoon temperatures. The use of shelters by rock-wallabies is also a thermoregulatory behaviour (Croft 1989). Diurnal activities of allied rock-wallabies are usually dictated by variations in temperature, light intensity, and daylength and they groom more during the hotter months (Horsup 1986). In contrast, the diurnal activities of provisioned rock-wallabies at 'Granite Gorge' are dictated by the activities of tourists, resulting in the rock-wallabies spending less time in their shelters.

The higher activity levels in the provisioned subcolony explain the lack of a significant difference in body condition between the two subcolonies. This result was unexpected, particularly during the dry season when the study was conducted, and when natural food is of low nutritional quality (Horsup and Marsh 1992). It is likely that there was a trade-off between the higher intake of energy by the provisioned rock-wallabies, and the higher expenditure of energy due to high activity levels.

Conclusions

Provisioning Mareeba rock-wallabies at 'Granite Gorge' changes their diurnal activity patterns and causes some individuals to aggregate. As a result, these individuals display a higher rate of aggression and spend more time performing contact behaviours. The higher level of autogrooming within the provisioned subcolony may have been a thermoregulatory response to the greater proportion of the day that the provisioned subcolony spent out on the rocks rather than in their rock shelters. Although the provisioned individuals spend more time feeding, this does not appear to affect their condition, presumably because these individuals also have higher activity levels. Our study could not quantify other potential effects of provisioning such as whether provisioned rock-wallabies were more at risk of predation, or whether the increased interaction between individuals was likely to exacerbate the possible spread of disease in the provisioned subcolony. This study is limited to a single sampling period and further research is required to account for the effects of varying weather conditions across seasons and years on the behavioural responses of *P. mareeba* to provisioning.

Wildlife tours such as those that visit 'Granite Gorge' offer an opportunity to educate tourists about native fauna. Further research should determine the conservation value and demand from tourists for direct contact with the rock-wallabies through hand feeding, as opposed to viewing the natural, undisturbed behaviour of these animals. A tourism strategy could then be devised that accounts for the conservation status of targeted species, such as the rare Mareeba rock-wallaby.

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