Animal Conservation

Are tourism and conservation compatible for ‘island tame’ species?

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Abstract

Islands play an important conservation role due to high rates of speciation as well as providing a predator-free refuge environment for species that are vulnerable to terrestrial predation on the mainland. Many animals show marked ‘island tameness’ on predator-free islands, reducing costly escape responses in the absence of predation threat. Island tameness also translates to altered responses towards humans, making many island species attractive for wildlife tourism. We explored temporal and spatial differences in behavioral responses on the Rottnest Island quokka (*Setonix brachyurus*). This marsupial is an excellent species to test for effects of ecotourism, as well as of being conservation significance (IUCN-listed as Vulnerable). Comparing escape responses for n=339 individuals in high tourism and low tourism seasons, quokkas at tourism sites allowed a person to approach closer before moving away compared with non-tourisms sites, and two-thirds of individuals around tourism sites allowed a person to approach within 1m (compared with 14% of individuals at non-tourism sites). For n=67 *ad hoc* interactions with tourists, quokkas would only move away from an interaction with a tourist when the tourist group was noisy or there was an attempt to touch the animal. Time budgets (n=379 individuals) showed that quokkas spent more time in group behavior and locomotion but less in vigilance and feeding for tourism sites compared with non-tourism sites. Understanding the impact of ecotourism on animal behavior will help to frame conservation management actions to ensure persistence of threatened wildlife species. We propose two models describing animal responses towards ecotourism: spatial separation according to animal temperament, or temporal adjustment due to learned habituation. These models are not mutually exclusive and we suggest that both spatial separation and habitation are likely evident for Rottnest quokkas. We discuss implications of these results for protection of animals on the island as well as for species conservation.

**Keywords**: FID; alert distance; tameness; island; habituation; conservation

# Introduction

Island faunas are ‘unbalanced and impoverished compared with continental faunas’, and do not tend to support a high diversity of large predators (Alcover *et al.*, 1998). Because of the relaxed selection they experience on isolated predator-free islands, many species therefore show reduced reactivity towards predators (Blumstein, 2002, Cooper *et al.*, 2014, Coss, 1999). These changes to responsiveness can happen over short times (Blumstein, 2002); for example, tammar wallabies (*M. eugenii*) introduced to New Zealand lost any effect of group size on vigilance after just 130 years of isolation from predators (Blumstein, 2002, Blumstein *et al.*, 2004). This ‘island tameness’ has been recorded in multiple taxa, including reptiles (e.g. Cooper *et al.*, 2014), birds (e.g. Beauchamp, 2004, Humphrey *et al.*, 1987) and mammals (e.g. Blumstein and Daniel, 2005, Coulson, 1996).

A lack of aversion for island fauna is often transferred to a lack of fear of humans. Darwin (1839) noted that animals on islands with few predators did not react adversely towards humans. The arrival of humans and associated changes due to altered land use, as well as the introduction of domestic and commensal species to islands have probably been responsible for the extinction of 35% of terrestrial mammals on the world’s islands (Alcover *et al.*, 1998), while the loss of bird species in the tropical Pacific may represent 20 percent of the worldwide reduction in the number of bird species (Steadman, 1995). Even large islands have been vulnerable to mass scale extinctions after the arrival of humans (Burney and Flannery, 2005). The loss of appropriate antipredator responses is likely to have contributed to the vulnerability to extinction of island fauna.

Island tameness makes wildlife species particularly appealing targets for ecotourism ventures, where animals will accept hand-feeding, close-up photography, and occasionally even tolerate being touched (e.g. Hines, 2011). Unfortunately, their tolerance towards people can increase the expose of island-tame animals to potential threat from people and risks associated with tourism activity. For example animals exposed to nature-based tourism activities may have increased risk of disease or collisions with vehicles, altered diet due to a variety of available food sources and hand feeding (e.g. Newsome and Rodger, 2013, Orams, 2002, Price and Lill, 2011), while congregations can increase social conflict and competition for resources (Price and Lill, 2011, Semeniuk and Rothley, 2008). Animals can also be more susceptible to direct injury from human contact (Green and Giese, 2004) or have reduced vigilance towards natural predators (Geffroy *et al.*, 2015). Interactions with tourists can therefore have major impacts on wildlife, leading to overall declines in animal health (e.g. Gilliam and Sullivan, 1993, Orams, 2002, Semeniuk and Rothley, 2008), or causing animals to increase vigilance and alert behaviour, decrease feeding and maintenance behaviour, or even leave a location (e.g. Amo *et al.*, 2006, King *et al.*, 2005, Sherwen *et al.*, 2015, Thiel *et al.*, 2007). Species that are breeding or have dependent young when visited suffer greater stress than animals that are merely foraging (e.g. Burger and Gochfeld, 1993, Karp and Root, 2009), and over time, these changes can impact on breeding success and long-term individual and population health (e.g.Johnson *et al.*, 1996, Orams, 2002).

Rottnest Island, off the coast of Western Australia, is an A-Class Reserve island – representing the greatest level of Western Australian governmental protection due to high conservation and community value. The island receives 450,000-550,000 tourists annually (Rottnest Island Authority 2014). A focal tourist attraction for the island is the quokka (*Setonix brachyurus*), a small nocturnal macropod the size of a domestic cat which is listed by the IUCN as Vulnerable due to the marked decline of mainland populations (de Tores *et al.*, 2007). In its ~7,000 years isolation from the mainland, there has been no terrestrial predators and the quokkas are island tame – previous studies describe Rottnest quokkas as ‘habituated’, ‘tame’, and ‘unperturbed by human activity’ (Blumstein *et al.*, 2003, Mclean *et al.*, 2009). Rottnest quokkas are regularly approached by tourists (on foot or by bicycle), photographing, provisioning, or touching the animals. There are differences in the impact of ecotourism across Rottnest, with remote parts of the island having less tourist activity than more accessible sites. Seasonal fluctuations also contribute temporal variation in the impact of ecotourism. This makes the Rottnest quokka an excellent model to study the applicability of optimal escape theory in a highly island-tame species.

We examined whether tourist behavior influences wariness responses (i.e. avoidance) in quokkas (Study 1) and predicted that if optimal escape theory still applied to these island-tame animals, then quokkas would be more wary of approaches on bicycles (which are generally faster) than approaching pedestrians; would be more wary of large, noisy groups of tourists than small, quiet groups due to the perceived danger associated with greater numbers of people and noise associated with group size; would be more wary of interactions where they were touched or photographed but less wary of interactions where they were provisioned.

We also examined how quokkas respond to people across spatial and temporal scales, comparing time budgets (Study 2) and antipredator responses (Study 3), predicting that quokkas inhabiting the tourism sites and during the tourism season would be more habituated to human approach and therefore exhibit less vigilance, more maintenance behavior (i.e. social behavior, grooming), and have shorter alert distance (AD) and flight initiation distance (FID) compared with quokkas located in non-tourism sites and out of tourism season.

# Materials & Methods

This study was approved by the Murdoch University Animal Ethics Committee (O2413/11).

Rottnest Island is a 1,950 ha island 18 km off the coast adjacent to Perth, Western Australia (115° 30.65' E 32° 0.44' S). This study was carried out in 2011, when over 500,000 visitors to the island were recorded (Rottnest Island Authority, 2011). We worked at two main study areas: sites around Thomson Bay Settlement (‘high tourism site’ on the east side of the island around the main tourism precinct, where buildings, food shops, and most human activity on the island is focused); and sites around the West End (‘non-tourism sites’, where fewer people visit, largely only during the daytime as there is no accommodation or facilities; this part of the island is transected by infrequently used roads and tracks, and access for tourists is principally via bicycle or a limited bus service that does a circuit of the island). We carried out observations over summer (high tourism season) and winter (low tourism season).

Study 1: Tourist behavior that elicits wariness in quokkas

Interactions between quokkas and tourists were recorded opportunistically around the Settlement during summer and winter. Observations were carried out around food services (where tourists congregated during the middle of the day) between 11:00h and 15:00h. We could not reliably record interactions at our non-tourism site due to the unpredictable patterns of tourist visitation and low numbers of interactions.

An interaction was defined as a period of time in which a tourist paid specific attention to a quokka(s) and directed behavior towards an animal. Recording concluded after 10 min if the tourist had not already moved away (only one observation reached 10 min). Only interactions lasting more than 30 s, within a 50 m radius of the observer (TW), were recorded. How the tourist(s) approached and interacted with the quokka(s) were recorded, and wariness response of the focal quokka recorded (quokka did or did not move away). We used stepwise logistic regression to identify factors that were correlated with wariness behavior of the quokka (dependent variable). Categorical factors included in the analysis were mode of transport (bicycle/walking), level of noise (subjectively assessed as low/high), photographs taken (yes/no), and whether the animal was touched (yes/no) or provisioned (yes/no). Covariates included in the analysis the number of quokkas within a 20 m radius, tourist group size (estimated distance), and time (min) spent interacting.

Study 2: Time budget data

We worked 3 h in the morning (starting two hours before dawn) and 3 h in the evening (starting an hour before dusk) over a period of two weeks during each season. A head torch was used in periods of low light, as Blumstein *et al.* (2001) showed no negative response by quokkas towards researchers using low lighting. Sites were visited randomly with no site used at both time periods on one day. Observers followed transects in one direction during each sampling period to decrease the risk of observing a focal animal twice as quokkas are largely sedentary with small core home range areas (~0.64 ± 0.860ha, Phillips *et al.*, 2015). Focal quokkas were chosen randomly, and if animals were in a large group, a maximum of four observations were recorded.

After a 2 min settling period, a focal animal was identified and its time budget data recorded. We recorded number of conspecifics in a 20 m radius, number of people in a 50 m radius, and distance from protective cover (dense understorey vegetation). Quokka behavior was recorded continuously for 5 min using a voice recorder and later transcribed. Due to the continuous nature of time budget recordings, if a quokka was lost from sight for > 20s the observation was discontinued. If a quokka was lost from sight for < 20s and when sighted again had changed behavior, the behavior was recorded as starting from that point.

Time budgets were scored using JWatcher (Blumstein and Daniel, 2007, Blumstein *et al.*, 2006) for 10 mutually-exclusive behavior states (Table 1). These behavior states were *post hoc* grouped into four main categories (group behavior, locomotion, vigilance, foraging) due to low counts of some recorded behaviors. The proportion of time an animal spent in the four main behavioral categories was transformed using the arcsine square-root transformation, and then tested by three-way MANOVA with site (tourism or non-tourism), season (summer or winter), and time (am or pm) included as independent factors. Separate three-way ANOVA were then used on each of the four behavior categories (dependent variables) in response to site, season, and time (independent variables).

Study 3: Flight responses to human approach

After time budget data had been recorded, for a subset of the same focal animals, we recorded their flight response data – alert distance (AD; the point at which the quokka behavior suggested it was aware of the observer, i.e. lifting its head, increased vigilance) and flight initiation distance (FID; the point at which the quokka moved away). The focal quokka was approached by the observer walking at 1 m/sec on a tangential trajectory that would take the observer within 1 m of it. Animal that had not moved away were passed and their FID recorded as 0m. Markers were dropped to indicate starting point, the point where the quokka became aware of the approach (to estimate AD), and the point at which the quokka fled (to estimate FID). The distances were then measured (m) by pacing out with an approximated 1 m tread, practiced by observers. No transformation was required for alert distance data, while a square root transformation was applied to FID data.

Two separate ANCOVA were carried out to investigate how the dependent variables (AD and FID) were influenced by site, season, and time of day. Start distance was included as a continuous variable for both AD and FID, while AD was also included as a covariate for the analysis of FID. For the non-tourism site data, we also included the number of conspecifics in a 20 m radius, and distance to protective cover (m; tourism sites were characteristically devoid of suitable native vegetation cover) in additional separate analyses (excluding site).

**General**

All analyses were carried out using the R statistical programming language (R Development Core Team, 2010). Values are shown as means ±1 standard error (SE) throughout. We calculated effect sizes for responses in terms of Cohen’s *d*.

Results

Study 1: Tourist behavior that elicits wariness in quokkas

A total of 67 interactions were recorded across high tourism (summer n=47) and low tourism (winter n=20) seasons. Focal quokkas were generally close to at least one other quokka (mean 3, range 0–7 quokkas in 20 m radius) when interacting with a tourist, with only 12 interactions occurring when the focal quokka was alone. A greater number of interactions were for tourists that had approached on foot (84%) rather than on bicycle (16%). Tourist group size was usually small (mean 3, range 1–14 persons), tourists were generally quiet around animals (73%) and spent 3 min or less (67%) interacting with quokkas. Photographs were taken during 45% of interactions, tourists were observed provisioning quokkas during 27% of interactions, and quokkas were touched during 34% of interactions.

Wariness behavior (quokka moved away from interaction) was recorded in only 22% of total observations. Stepwise regression resulted in the retention of four of the nine factors considered (Table 2). Tourists that touched a quokka during their interaction (*P*=0.044) were more likely to prompt a wariness response, as were noisier tourist groups (*P*=0.036). Quokkas were less likely to move away when they were provisioned by tourists (*P*=0.082) or for shorter duration interactions (*P*=0.089).

Study 2: Time budget data

Time budget data were recorded for 379 focal quokkas; 187 in non-tourism sites (summer: 115, winter: 72) and 192 in the tourism sites (summer: 107, winter: 85). The MANOVA suggested that the main effects for season and site were statistically significant, as were season-site and season-time interaction effects (Table 3a).

Subsequent three-way ANOVAs for each behavioral category were carried out (Table 3b). These showed that group behavior was significantly different between sites (site: Cohen’s *d*=0.258), with quokkas in tourism sites engaging more often in social behavior (3.6±0.6%), such as allo-grooming, self-grooming, and aggressive behavior than those in the non-tourism sites (1.9±0.3%) (Fig. 1). Quokkas were also more likely to engage in group behavior in the morning than the evening.

In terms of locomotion, quokkas in tourism sites were more likely to move about (4.0±0.5%) than quokkas located in non-tourism sites (2.0±0.30%) (site: Cohen’s *d*=0.350). Quokkas also moved about more in winter (4.3±0.6%) than in summer (2.5±0.3%).

A significant season-site interaction for vigilance indicated that quokkas showed less vigilance in summer (24.4±2.2%) than winter (29.7±2.4%) around tourism sites, but quokkas were more vigilant in summer (32.8±2.2%) than in winter (23.5±2.5%) in non-tourism sites. The main effect of site was minimal (site data across both seasons: Cohen’s *d*=0.008), while the effect of season for the tourism sites only was stronger (Cohen’s *d*=0.236). There was also a significant season-time interaction, with quokkas more vigilant in the evening in summer (30.7±2.4%; compared to dawn: 26.7±2.0%), but more vigilant around dawn in winter (33.5±2.8%; compared to evening: 20.8±2.0%).

There was a significant season-site interaction for foraging, with quokkas in tourism sites spending less time feeding in winter (61.5±2.6%) than in summer (68.6±2.4%), while quokkas at the non-tourism sites spent more time feeding in winter (71.9±2.6%) compared to summer (62.9±2.2%). The main effect of site was minimal (site data across both seasons: Cohen’s *d*=0.003), while the effect of season for the tourism sites was stronger (Cohen’s *d*=0.290). A season-time interaction indicated more feeding in the evening than dawn in winter (73.6±2.1%; compared to dawn: 58.3±2.9%) but more feeding around dawn in summer (67.4±2.2%; compared to evening: 64.1±2.5%).

Study 3: Antipredator behavior in response to human approach

A total of 339 approaches towards focal quokkas were recorded; 163 in non-tourism sites (summer: 71, winter: 92) and 176 in the tourism sites (summer: 125, winter: 51). Researchers started to approach quokkas (starting distance) an average of 13.8±0.43m from the quokka in the tourism sites and 11.1±0.29m in the non-tourism sites (which were not significantly different).

Alert Distances were significantly shorter for quokkas at the tourism sites (5.4±0.34m) than for quokkas at non-tourism sites (6.5±0.27m) (*site*: Cohen’s *d*=0.273; Table 4a); similarly, FID were substantially shorter at the tourism sites (0.81±0.16m) than at non-tourism sites (3.18±0.23m) (*site*: Cohen’s *d*=0.931; Table 3b) (Fig. 2). There were some quokkas at both sites that did not flee (FID=0m) when approached: 65.3% of 176 quokkas in tourism sites and 14.1% of 163 quokkas in non-tourism sites allowed the observer to pass them at 1m.

We found no seasonal effect on antipredator responses. Time of day was significantly associated with AD (but not FID) with shorter AD recorded in the evening (6.0±0.36m) compared to the morning (7.1±0.40m). AD was correlated with starting distance, while FID was correlated with AD. For the non-tourism sites, where there was native vegetation in proximity to the focal quokkas, AD (but not FID) was correlated with initial distance to protective cover (average 3.8±0.55m), but we recorded no effect of group size on AD or FID (Table 4).

Discussion

Rottnest quokkas show a great degree of island tameness and many individuals appear almost oblivious to human presence, allowing tourists to approach them closely. Indeed, a high proportion of quokkas did not flee at all when approached (tourism sites: 65.3%; non-tourism sites: 14.1%). Quokkas also showed seasonal patterns in their time budgets (but not their antipredator responses) that may reflect habituation to increased numbers of tourists during summer. Together, these results indicate habituation to human presence and even a marked loss of antipredator responses on this island that is free of terrestrial predators, and where humans often provide food subsidies.

Ecotourism and nature-based tourism is a huge industry that is arguably the fastest growing tourism segment around the world (Ballantyne and Packer, 2013). This form of tourism is seen as positive, financially benefiting and educating human communities. We generally like to think of the interactions with wildlife as benign for the animals, although evidence indicates that ecotourism changes the behavior and physiology of target species (Bateman and Fleming, Submitted 28 Feb 2016 and references therein). Importantly, most species that are targets of ecotourism show behavioral habituation to tourism activities, appearing to become ‘tame’; however physiological measures suggest animals nevertheless respond to human presence (Bateman and Fleming, Submitted 28 Feb 2016). Over time, such changes can impact on breeding success and long-term individual and population health (Orams, 2002). Geffroy et al. (2015) warn that habituation towards tourists could increase the vulnerability of animals, making them more likely to fall victim to any predatory or other potentially fatal interactions. Being tolerant of people also exposes animals to potentially malicious attention.

We propose two models to describe animal responses towards ecotourism (Fig. 3). Both of these models may explain responses of animals towards benign ecotourism interactions and are not mutually exclusive. A spatial sorting model (Fig. 3a) suggests that some animals (shy/reactive individuals) will avoid tourism sites while others (bold/tame individuals) persist, despite high levels of human disturbance. A temporal adjustment model (Fig. 3b) suggests that animals exposed to increasing amounts of disturbance may initially show increased wariness, but will eventually habituate to this disturbance. This type of model could contribute to how we plan ecotourism ventures. Allowing animals to move away from exposure is important, and ensuring that animals do not become trapped within sites would support the more shy/reactive individuals that have less capacity to adapt to disturbance. Therefore designing facilities that allow animals a safe retreat would protect resident individuals; e.g. maintaining permeability of barriers like fencing, ensuring access to vegetation refuges.

Conservation of Rottnest quokkas requires increased understanding of factors influencing their behavior towards tourists. This information can also be used to improve visitor experiences and help ensure that tourists get the most out of their interactions with these charismatic animals. Tourists are discouraged from directly feeding quokkas on Rottnest, although quokkas will nevertheless forage on discarded anthropogenic food around tourism areas. Tourists should be advised that they will improve their experience by refraining from touching the animals and keeping their level of noise low. Additionally, reactions to human approach differ for quokkas located in tourism and non-tourism sites, with animals around the Settlement far more tolerant to being approached than those living on more remote parts of the island.

Although Rottnest quokkas are believed to be ‘comfortable’ or unperturbed by human contact (Blumstein *et al.*, 2001, Mclean *et al.*, 2000), we showed increased frequency of wariness by quokkas towards noisy tourist groups or where people attempt to touch them. Very close approach to touch or photograph animals has grown in popularity (Huang *et al.*, 2011, Reynolds and Braithwaite, 2001), and management of wildlife interactions at various sites differ in control, encouragement, and knowledge base of such tourist behavior (Orams, 2002). Although it makes a great impression on tourists (Ballantyne *et al.*, 2011, Rodger *et al.*, 2007), touching wildlife can disturb the focal animals to the point where it compromises key behavior (e.g. nesting, Johnson *et al.*, 1996). Several factors did not appear to influence quokka responses. Although other studies have found an effect of close-up photography on animals (Huang *et al.*, 2011), there was no influence of whether tourists were photographing quokkas on their wariness. We also found no evidence of an effect of tourist group size (but see Price and Lill, 2011). Quokkas did not respond differently to tourists that approached on bicycle or on foot (but see McLeod *et al.*, 2013, Wolf and Croft, 2010).

Quokkas are normally moderately social macropods, preferring to forage and rest alone or in small groups. Quokka movements are likely to be motivated by the availability of food and shelter resources, which are not evenly distributed across the island, especially around the Settlement, which lacks much natural cover and native food choices (Poole *et al.*, 2014). Here food sources, such as planted Morton Bay fig (*Ficus macrophylla*) trees and lawns, become focal foraging areas, resulting in large quokka congregations. Around the Settlement, quokkas spend more of their time in social behavior (aggressive behavior, allo-grooming and self-grooming; Table 5) than was evident for quokkas at West End.

The proportion of time quokkas spent in locomotion was greater around the Settlement. Although some animals shelter under buildings, radio-tracking individual quokkas indicates the least overlap between day (rest locations) and night (active locations) ranges for quokkas around the Settlement compared with other parts of the island, revealing that many individuals move into the settlement area to feed at night from diurnal rest sites in surrounding native vegetation (Phillips *et al.*, 2015).

Although we found little difference in overall vigilance behavior between sites, this was due to seasonal differences in patterns of vigilance. Quokkas showed less vigilance in summer for the tourist site, suggesting habituation to increased numbers of tourists during peak tourism season. Animals around the Settlement should therefore usually be in the right-hand part of Fig. 3b, where increasing amounts of disturbance result in habituation towards that disturbance. The data for time spent vigilant is supported by alert and flight initiation distances, which were significantly shorter for quokkas at the tourism sites than for quokkas at non-tourism sites. By contrast, at West End (where there is less frequent visitation by tourists), quokkas were more vigilant in summer when numbers of tourists increase. Animals at West End are therefore likely to be in the left-hand part of Fig. 3b, where increasing amounts of disturbance lead to increased wariness. This could suggest that animals away from the tourism sites retain the greatest wariness towards being approached.

Conclusion

Tourism is a double-edged sword – animals can benefit from human presence through access to food and water sources, reduced seasonality in food availability, or use of anthropogenic structures for shelter. However, they can also become more susceptible to disease or collisions with vehicles, congregating can increase social conflict and competition for resources, or the animals can be more susceptible to direct injury from human contact (Green and Giese, 2004). Habituated animals potentially also reduce vigilance towards natural predators (Geffroy *et al.*, 2015). The loss of reactivity towards predation threats and increased habituation towards humans therefore presents increased risk for island fauna that are the focus of ecotourism.

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**Table 1** Categories and singular behavior recorded during continuous 5-min time budgets of quokkas on Rottnest Island.

|  |  |  |
| --- | --- | --- |
| Categories | Category recorded | Description |
| Group behavior | Aggression | Focal quokka engaged in interaction with another quokka that caused one of those quokkas to move away (e.g. biting, jumping on, and hissing). |
|  | Grooming | Individual grooming itself or another animal. |
| Locomotion | Walking | Pentapedal movement |
|  | Hopping | Bipedal hopping |
| Vigilance | Rearing | Quokka lifted its head and actively looked around. |
|  | Standing | Quokka stretched up off its hind limbs in order to look about. |
|  | Crouching | Quokka’s forelimbs were close and/or on the ground while it looked around. |
| Foraging† | Foraging on ground | Quokka still or moved slowly with its head turned downwards towards the ground. |
|  | Foraging on shrubs | Quokka positioned in either a standing or crouching position. |

† Recording foraging only when an animal is eating can under-represent the time allocated to this behavior (Schmidt 1999). Consequently, quokkas were recorded as foraging when they were moving slowly, searching the ground and or shrubs for food.

**Table 2** Study 1 – quokka responses to tourists. Summary of stepwise regression on logistic model with wariness behavior (yes or no) as dependent variable.

|  |  |  |  |
| --- | --- | --- | --- |
| Factor† | β (std error) | z | P |
| Provisioning (no=0,yes=1) | -1.61 (0.93) | -1.73 | 0.082 |
| **Touched (no=0,yes=1)** | **1.39 (0.69)** | **2.01** | **0.044** |
| **Level of noise (low=0,medium=1)**  | **1.64 (0.78)** | **2.09** | **0.036** |
| Time spent interacting (minutes) | -0.30 (0.17) | -1.69 | 0.089 |

†Season, number of conspecifics, tourist group size, mode of transport and whether the quokkas were photographed were initially included in the analysis but were eliminated by the stepwise model selection algorithm. Bold indicates statistical significance (*P*<0.05).

**Table 3** Study 2 – time budget analyses for (a) all behavior categories considered together and (b) each of the four behavior categories.

|  |  |  |
| --- | --- | --- |
|  | a) all categories | b) Behavior categories |
| Independent Variables | Group Behavior | Locomotion | Vigilance | Foraging |
| F  | P | F  | P | F  | P | F  | P | F  | P |
| Season (summer vs. winter) | 3.49 | 0.030 | 0.24  | 0.624 | **10.27** | **<0.001** | 0.40 | 0.525 | >0.01 | 0.981 |
| Site (tourism vs. non-tourism) | **2.70** | **0.008** | **5.78** | **0.016** | **7.29** | **0.007** | 1.96 | 0.161 | >0.01 | 0.959 |
| Time (am vs. pm) | 1.35 | 0.211 | 2.92 | 0.054 | 0.69 | 0.498 | 1.09 | 0.336 | 1.99 | 0.137 |
| Season x Site | **3.09** | **0.015** | 0.74 | 0.387 | 0.85 | 0.355 | **10.48** | **0.001** | **10.13** | **0.001** |
| Season x Time | **3.58** | **0.006** | 0.11 | 0.732 | 0.79 | 0.372 | **12.72** | **<0.001** | **13.95** | **<0.001** |
| Site x Time | 0.39 | 0.811 | 0.01 | 0.896 | 0.69 | 0.405 | 0.04 | 0.831 | 0.039 | 0.842 |
| Season x Site x Time | 1.26 | 0.285 | 2.59 | 0.107 | 0.70 | 0.400 | 1.15 | 0.282 | 2.12 | 0.145 |

Bold indicates statistical significance for (a) Multivariate Analysis of Variance (MANOVA) for all behavior categories together and (b) two-way Analysis of Variance (ANOVA) for each of the four behavior categories (group behavior, locomotion, vigilance and feeding).

**Table 4** Study 3 – antipredator responses for (a) Alert Distance (AD) and (b) Flight Initiation Distance (FID) for all sites, and then for non-tourism sites only (where distance to cover could be estimated).

|  |  |  |
| --- | --- | --- |
|  | All sites | Non-tourism sites |
| a) Alert Distance (AD) | F | P | F | P |
| Site  | **9.73** | **0.001** |  |  |
| Season  | 1.81 | 0.179 | 1.96 | 0.163 |
| Time  | **6.76** | **0.009** | **6.72** | **0.010** |
| Start distance (m) | **154.81** | **<0.001** | **117.49** | **<0.001** |
| Distance to protective cover (m) |  |  | **5.17** | **0.024** |
| Number of conspecifics (count) |  |  | 3.00 | 0.084 |
| b) Flight Initiation Distance (FID) |  |  |  |  |
| Site  | **166.54** | **<0.001** |  |  |
| Season  | 0.44 | 0.505 | 2.04 | 0.154 |
| Time  | 1.24 | 0.264 | 0.54 | 0.462 |
| Start distance (m) | 2.29 | 0.130 | 0.27 | 0.599 |
| Alert distance (m) | **82.13** | **<0.001** | **77.06** | **<0.001** |
| Distance to protective cover (m) |  |  | 0.78 | 0.377 |
| Number of conspecifics (count) |  |  | 3.20 | 0.755 |

Bold indicates significance of ANCOVA with (a) Alert Distance and (b) Flight Initiation Distance as the dependent variables.

**Table 5** Summary of site and seasonal effects on time budget and antipredator behavior of quokkas at locations around the Thomson Bay Settlement (tourism sites) and West End of Rottnest Island (non-tourism sites), in summer (high tourism season) and winter (low tourism season).

|  |  |  |
| --- | --- | --- |
| Measure | Thomson Bay Settlement (tourism) | West End (non-tourism) |
| Time budgets: |  |  |
| 1. Group behavior
 | More group behavior | Less group behavior |
| 1. Locomotion
 | More locomotion | Less locomotion  |
| 1. Feeding
 | More time feeding in summer  | Less time feeding in summer  |
| 1. Vigilance
 | Less vigilance in summer (H) | More vigilant in summer (W) |
|  |  |  |
| Antipredator behavior: | Allow person to approach closer (H) |  |
| 1. Alert distance
 | - before showing alert behavior | Alert at a greater distance |
| 1. Flight initiation distance
 | - before fleeing | Flee at a greater distance  |

H indicates habituation, W indicates increased wariness in response to exposure to increased numbers of tourists.

Figures

**Fig. 1.** Summary of time budget data for 379 focal quokkas on Rottnest Island at Tourism and non-tourism sites, and recorded in the middle of peak tourism season (summer) or in mid-winter.

**Fig. 2.** Summary of differences in alert distance and flight initiation distance for tourism and non-tourism sites. There were no significant effects of season on these antipredator responses, and therefore the data for summer and winter are presented together.

**Fig. 3.** Two models showing alternative ideas that can explain animal habituation towards interactions with tourists (see also Martin and Réale, 2008). The graphs show changes in animal responses (*y*-axis; e.g. flight initiation distance or time spent in vigilance) against increasing levels of human interaction (*x*-axis). (a) Shy/reactive animals avoid sites with greater amounts of human interaction, while bold/tame animals do not. Demonstrating this self-selection effect would require recording space use by individual animals to determine how the animals respond to short-term changes in levels of exposure to tourists. (b) Habituation of resident animals towards tourists. For a continuum of increasing levels of tourism disturbance, animals may initially show increasing wariness towards greater amounts of disturbance, but where the costs of remaining prove to be less than the costs of moving away, animals can learn to become tolerant to disturbance, eventually showing increasing habituation. This learned response would be evident as altered responses for individual animals over time, requiring long term monitoring of individuals.

**Fig. 1.**

**Fig. 2.**



**Fig. 3**

spatial sorting model temporal adjustment model

