

Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands

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ABSTRACT

Approaching wildlife to attain a closer viewing experience is common amongst visitors to natural areas. We examined how tourists approach free-living kangaroos during encounters in a popular tourism destination in South Australia. We then simulated the typical properties of approaches to quantify the behavioural reactions of two kangaroo species—the Red Kangaroo (*Macropus rufus*) and the Euro (*M. robustus erubescens*). We also accounted for the disturbance context such as varying environmental conditions (time of day, cover, wind speed) and other factors (species, sex class, grouping) that potentially modify the kangaroos' flight response.

Approach varied by access (on-trail, off-trail), transport (on-trail: hiking, driving; off-trail: hiking) and approach style (on-trail: tangential/continuous, tangential/stop-and-go; off-trail: direct/continuous, direct/stop-and-go, direct/stop-and-go/talking, tangential/zigzag/stop-and-go). On-trail, 53% of kangaroos took flight when the closest distance to them was approached whilst (by design) all subjects off-trail took flight. The mean (± 1 SE) flight initiation distance (FID) was significantly shorter following an on-trail (78 ± 2.7 m) than an off-trail approach (90 ± 2.7 m). Kangaroos fled less often (41% vs. 75%) and spent more time in maintenance activities (40% vs. 10%) if approached in a vehicle than on foot. The mean FID and flight length (FL) after approach on foot was reduced when made in a stop-and-go fashion without talking. Euros fled at a significantly shorter FID with a shorter FL than Red Kangaroos, and so did females with obvious pouch-young compared to females with young-at-foot. FID was shortest if the approach was made in the evenings, the habitat provided cover and the day was calm.

The results suggest that wildlife tourists should be educated to the best choice of approach behaviour and viewing conditions to reduce aversive reactions in kangaroos and mediate closer observations to the visitors' greater satisfaction and the kangaroos' better welfare. Our study also shows the benefit of a two-stage approach where the detailed observation of human behaviour serves as a prerequisite to an experimental study on wildlife response.

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1. Introduction

Close encounter with animals in their natural environment is a key factor for determining visitor satisfaction with non-consumptive wildlife tourism experiences (Moscardo and Saltzer, 2005). Distance is often overcome by approaching wildlife but they in turn perceive humans as potential threats (predation/displacement), especially in

non-captive settings, where irregular visitation and the unpredictable behaviour of people due to a lack of constraining barriers reduce the likelihood for habituation (reviewed by Knight and Gutzwiller, 1995).

Disturbed animals will assume vigilance behaviour to evaluate potential danger (Dyck and Baydack, 2003) or undertake evasive actions (Cassirer et al., 1992). The consequence is that less time can be spent on body maintenance through feeding and resting (Lott and McCoy, 1995; Roe et al., 1997) or on social interaction (Edington and Edington, 1990). Furthermore, tourists can drive animals from habitats with better quality resources (Griffiths and van Schaik, 1993). Hence, the individual's current energy levels are depleted by physiological defence reactions as well as additional vigilance and flight (Giese, 1998), less new energy can be consumed due to reduced body maintenance activities, and the actual intake will be less efficient if displacement from optimum foraging places and times occurs. Therefore, if tourism disturbance persists or occurs frequently, changes in key behaviour may result in adverse, long-term effects for survival and reproduction (reviewed by Green and Giese, 2004).

Given that vigilance and flight behaviour are costly activities, prey need to decide whether to disregard the threat, attend to it or to flee; and if taking flight, when to flee, how far and on what trajectory (Lima and Dill, 1990). A major factor influencing these decisions in encounters with people is the person's starting (Blumstein, 2003) and ending distance (Cassini, 2001) and the mode of their approach to the animal. Leaving a frequently used track to approach off-trail seems to augment the response more than an on-trail approach (Mainini et al., 1993; Miller et al., 2001). Foot approach tends to elicit a greater response than a vehicle approach because of the longer history of ambulatory hunting (McLellan and Shackleton, 1989). Furthermore, behavioural responses depend on the direction (Richens and Lavigne, 1978) and speed (Burger, 1981) of the approaching person. The intensity of the response may also depend on a variety of modifying factors like species (Blumstein and Daniel, 2002), group size (Blumstein and Daniel, 2003b), time of day (Taylor and Knight, 2003b) and habitat cover (Burger and Gochfeld, 1990). Finally, experience with similar stimuli plays a role and habituated animals may react less strongly to tourism activities (MacArthur et al., 1982).

In Australia, encounters with kangaroos (a collective term for six species of kangaroos and wallaroos) are a highly sought after attraction (Croft, 2001) that brands the continent as a tourism destination abundant with unique wildlife. Even though the tourist–kangaroo interface has rarely been investigated, experiments to elucidate the relationship between kangaroos and their predators (Blumstein and Daniel, 2003a) suggest that kangaroos react sensitively to human approach, which may lead to short-term behavioural changes such as flight. Fleeing from a potential threat is an energy-demanding process for kangaroos (Dawson and Taylor, 1973). Thus, there is a likely trade-off between this expenditure of energy as well as time spent on behaviour that protects against disturbance, and that invested in fitness-maximizing maintenance activities (Frid and Dill, 2002).

We simulated the most common approach behaviour that we had previously observed (Wolf, 2009) amongst driving and hiking tourists during kangaroo encounters to identify the least intrusive behaviour as a guide for tourism management. We assumed that greater perceived risk of harm from an approaching person would be indicated by: a greater percentage of kangaroos taking flight, longer flight initiation distances (distance at which an animal takes flight from an approaching threat, Dill and Ydenberg, 1987) and flight lengths, and more time spent in alertness and flight vs. maintenance behaviour. There were two aims in this study. The first was to determine flight reactions and behavioural time budgets of Red Kangaroos (*Macropus rufus*) and Euros (*M. robustus erubescens*—an arid-dwelling subspecies of the Common Wallaroo) in relation to different modes of approach. The second was to ascertain if these depended on the “disturbance context” (Steidl and Anthony, 1996: 484); namely environmental conditions (time of day, availability of cover, wind speed) and other potentially modifying factors (species, sex class, grouping).

2. Methods

2.1. Study areas

This study was conducted in the Flinders Ranges National Park (FRNP) and at the University of New South Wales Arid Zone Research Station at Fowlers Gap (FG). The FRNP (lat. 31° 27' S, long. 138° 41' E) covers 95 000 ha in central South Australia. The Park is a popular nature-based tourism destination that offers a wide range of activities including bushwalking and scenic touring. The vegetation is a mixture of arid-adapted species on shales or slopes and moist-adapted species in gorges. It includes woodlands of mallee (*Eucalyptus* spp.), Black Oak (*Casuarina cristata*) and porcupine (*Triodia scariosa*) grasslands. In 2009, Red Kangaroo and Euro densities were estimated to be around 15–25 and 5–10 individuals km⁻² (Peter Watkins, Manager Operation Bounceback, pers. comm.), respectively. There is some culling of the Euro to allow regeneration of native vegetation. Culling typically occurs by spotlight shooting from a vehicle at night, totalling approximately 30 nights per year. Our study was undertaken within the culled areas of Mt Sunderland and Pantapinna. Albeit kangaroos and wallaroos are differentiated by their morphology we refer to Euros and Red Kangaroos collectively as ‘kangaroos’ consistent with the conventional usage (Dawson, 1995) of this term.

FG (lat. 31° 05' S, long. 141° 43' E) covers an area of 39 888 ha in western New South Wales and is held by the University of New South Wales, Sydney, for the purpose of research, teaching and tourism. The climate is dry and mildly arid (Bell, 1973) and similar to FRNP. The station is typical of Australia's southern sheep rangelands with a chenopod shrub steppe and scattered trees such as Mulga (*Acacia aneura*) and Black Oak. The densities of Red Kangaroos (estimated between 1985 and 1987; Edwards et al., 1996) and Euros (estimated between 1984 and 1986; Clancy, 1989) are typically at around 10–20 and 3–20 individuals km⁻², respectively. There is no culling of kangaroos.

Dingoes (*Canis lupus dingo*), the replacement of now-extinct natural predators of kangaroos, have been excluded from both study areas by ongoing control and the trans-continental 'Dingo Barrier Fence'.

2.2. Tourist behaviour during kangaroo encounters

The behaviour of tourists ($n_{\text{drivers}} = 278$; $n_{\text{hikers}} = 200$) during encounters with kangaroos was recorded using ad libitum sampling (Altmann, 1974) from several areas in FRNP from 09:00 to 17:00 h on randomly chosen days. Sites were established in characteristic kangaroo habitat where tourists could expect to encounter kangaroos after reading the Park's interpretative materials. For each passing tourist group, we recorded the occurrence of different approach styles.

Tourists commenced all kangaroo observations with an on-trail approach along recreational paths that lead by/towards the kangaroos, and in some cases (disembarked drivers: 15%, hikers: 20%) continued off-trail. The direction of an on-trail approach was always tangential to the kangaroo (since the trail never lead directly to the kangaroo) whereas the direction of an off-trail approach was either direct or tangential. The most commonly adopted on-trail approach styles (from a repertoire of five observed) amongst both drivers and hikers were a tangential/stop-and-go approach (stop-and-go approach with intermittent periods of observation) and a tangential/continuous approach (after initial discovery from a distance the kangaroo was approached without intermissions to the closest distance that could be reached on-trail). Three types of off-trail approach were observed: direct/continuous, direct/stop-and-go and tangential/zigzag/stop-and-go (includes a zigzag motion towards the animal).

2.3. Study transects

We established six line-transects in FRNP (four trails, two roads) and four line-transects at FG (two trails, two roads) along which we approached kangaroos to determine flight reactions and behavioural time budgets to varying approach behaviour on foot or by vehicle. The transects averaged (± 1 SE) 9 ± 0.5 km for foot and 19 ± 3.6 km for in-vehicle approaches. The potential for pseudoreplication through re-sampling the same kangaroo individuals was minimized by using two geographic regions and spatially distinct areas so that within each region the centre points of the (loop) transects were between 3 and 8 km apart. Starting points of hikes were at least 1 km apart. Further, hiking transects led into different directions demarcated by ridges or roads that traverse FRNP and FG. Finally, the same transect was never sampled during two consecutive observation periods.

Kangaroo-human encounters (mainly station/park workers, some researchers and drive-through traffic, a few tourists) in these areas were somewhat infrequent. The transects sampled representative habitat for the Euro (hills and slopes) and the Red Kangaroo (open plains) (Dawson, 1995).

2.4. Approach of kangaroos and sampling of the behavioural response

Each of two observers in drab clothing walked singly on two randomly chosen transects per day in the 3 h past sunrise or before sunset from September 2007 to February 2008 so that all transects were equally sampled. The direction of the walks was rotated daily to reduce temporal biases. The two observers collaborated in a pilot study to standardize their behaviour and ensure inter-observer reliability. No observer effect was found in the analysis of the results. Days with unusual weather (e.g., rain) were excluded for possible effects on kangaroo reactivity (Croft, 1981).

The individual closest to the observer was chosen as the focal animal. Groups were defined as two or more animals of the same species within a distance of 50 m (Heathcote, 1987) that are able to communicate visually with each other (Colagross and Cockburn, 1993). To determine the importance of the disturbance context for flight reactions of kangaroos, we recorded the focal animal's species, sex class, grouping and the availability of cover (natural features suitable for hiding and covering more than 30% of the kangaroo) within 2 m from a Bushnell rangefinder Yardage Pro 1000 (Bushnell, Overland Park, Kansas, USA). The rangefinder was shaped like compact binoculars which might typically be used by a tourist. We also recorded the time of day and wind speed (from a Kestrel anemometer Pocket Weather Meter 2000; Kestrel, Sylvan Lake, Michigan, USA) and the distance at which the animal became alert to the observer to account for the potential effect of the observer's starting distance (after Blumstein, 2003). The observer approached the focal animal at a constant pace (Burger and Gochfeld, 1990) by using one of eight different approach treatments (see below in this section; Table 1) that was chosen randomly for each occasion from the treatments that had not yet been administered in a particular run. The quota for on-trail approaches was set higher than those for off-trail approaches to compensate for the lower percentage of kangaroos taking flight. Once the focal animal took flight (aversive movements away from the observer following an alert/orientation response towards the observer) the approach was stopped and the kangaroo observed until it stopped.

The following measurements were taken: The distance between the observer's current position and the focal animal's position at the commencement of flight (memorized from visual landscape cues; Taylor and Knight, 2003b) was measured from the rangefinder as the flight initiation distance (FID). We use the term 'flight initiation distance' as its meaning is unequivocal compared to other possible terms (as listed in Taylor and Knight, 2003a). The distance between the observer's current position and the focal animal's final position after the flight was recorded as the final flight distance. The angle between the FID and final flight distance vectors was measured with a Suunto compass DS 56 (Suunto, Vantaa, Finland). FID, final flight distance and the angle were used to calculate the flight length (FL) – the distance between the initial and final position of the focal animal – by means of simple trigonometric relationships. The safety distance kangaroos gained to the observer

Table 1

Modes of simulated tourist approach and its intrinsic properties to which Euros and Red Kangaroos were subjected.

Access	Transport	Approach style	Predictable	Direct	Continuous	Change of direction	Extra behaviour ^a
On-trail	Driving	Tangential/continuous	X		X		
		Tangential/stop-and-go	X				
	Hiking	Tangential/continuous	X		X		
		Tangential/stop-and-go	X				
Off-trail	Hiking	Direct/continuous		X	X		
		Direct/stop-and-go		X			
		Direct/stop-and-go/talking		X			X
		Tangential/zigzag/stop-and-go				X	

^a Behaviour (talking) added onto the baseline approach behaviour.

by fleeing was calculated by subtracting FID from the final flight distance. The safety distance gained is only equal to the FL if the kangaroo hops directly away from the observer whereas most kangaroos fled tangentially to the observer, and so for every metre of safety distance gained most kangaroos hopped additional metres. We defined the ratio of FL to safety distance as the 'flight effort' because as the ratio increases the kangaroo needs to hop additional metres for every metre of safety distance gained.

The choice of approach treatments (Table 1) was guided by the range and frequencies of behaviour encountered during the tourist observations. Thus on-trail the observer approached the kangaroo in a tangential/continuous or tangential/stop-and-go fashion, either on foot or by vehicle. Approach on foot took place at a constant walking pace of about 0.5 m s⁻¹ and (sport utility) vehicle approach at about 20 km h⁻¹, equal to the average pass-by speed for visitors observing wildlife from their vehicle. As we saw no visitor drive off a formed track but some hikers (or disembarked drivers) did leave the trail, we confined off-trail approaches to those on foot. The principal types of off-trail approach that we tested were direct/continuous, direct/stop-and-go, tangential/zigzag/stop-and-go. A stop-and-go approach was standardized to a stop of 15 s after every five paces. A tangential off-trail approach was conducted at a 45° angle to the direct line between observer and kangaroo. After every five paces the observer stopped for 15 s and a turn of 90° was made towards the opposite direction, after which the observer continued to move towards the kangaroo at a 45° angle. A tangential on-trail approach could not be standardized to a specific approach angle since that was determined by the course of the track. Given that talking was a very common form of supplementary behaviour for hiker groups, we tested for its additional effects by performing the direct/stop-and-go approach off-trail with or without talking. The observer talked during the stops at a medium voice level.

By design the observer approached kangaroos off-trail until they took flight, whereas on-trail approaches did not always trigger flight. In the latter case we measured the closest distance (instead of the FID) to the kangaroo that one could attain by remaining on the trail. Further, an additional response measure was taken: the behaviour of the focal animal for 5 min immediately after an on-trail approach to the closest distance or FID. We calculated the percentage of time spent in vigilance behaviour, hiding and aversive movements vs. maintenance activities such as feeding, grooming and social interactions (after King et al.,

2005). Subjects were deemed to be 'hiding' if flight placed them in cover that obscured them from the observer. The recording of the behaviour of kangaroos that took flight commenced when they came to rest.

2.5. Data analyses

Chi-square tests were used to compare the number of kangaroos that took flight in response to access (on-trail vs. off-trail), transport (on-trail: hiking, driving; off-trail: hiking) and approach style (on-trail: tangential/continuous, tangential/stop-and-go; off-trail: direct/continuous, direct/stop-and-go, direct/stop-and-go/talking, tangential/zigzag/stop-and-go). The individual animal was taken as the unit of replication.

To test for the influence of access style on mean FID, FL and flight effort we conducted ANOVAs using data from on- and off-trail approach; however, we only used data from the hiker approach and the off-trail direct/stop-and-go and direct/continuous approach, as only these treatments were common to both on- and off-trail observations.

To examine the effects of transport (only for on-trail approach) and approach style on mean FID and FL, multi-factorial ANOVA models were fitted on data sets partitioned into on- and off-trail approach treatments. The disturbance context was accounted for by including the factors species (Euros vs. Red Kangaroos), sex class (female with no obvious young vs. male vs. female with young-at-foot vs. female with visible pouch-young), grouping (solitary vs. grouped), availability of cover (none vs. some), time of day (mornings vs. evenings) and wind speed (<10 km h⁻¹ vs. ≥10 km h⁻¹). Wind speed was originally measured as a continuous variable and then categorized as scatterplots suggested a cut-off point in FID and FL values at the 10 km h⁻¹ level. We optimized the original ANOVA models, containing all main effects and biologically relevant first order interactions, by excluding factors with *P*-values > 0.25 (Winer et al., 1991; Underwood, 1997) from initial models in a manual, stepwise backward selection procedure (Crawley, 2007). Therefore, starting distance, which had initially been included as a covariate (Blumstein, 2003), was not retained.

The nature of significant differences for factors with more than two levels was assessed with Hochberg's GT2 post hoc comparison because it offers good power for unbalanced data sets (Field, 2005). If significant interaction effects were detected, simple main effect analyses (Field, 2005) were conducted to identify the level of one factor at

Table 2

Final ANOVA models including all main effects and first order interactions which significantly (bold) explained variation in the mean flight initiation distance (FID) and mean flight length (FL) of Euros and Red Kangaroos in relation to simulated tourist (a) on-trail and (b) off-trail approach.

Factor	(a) On-trail						(b) Off-trail						
	df		F		P		df		F		P		
	FID	FL	FID	FL	FID		FL	FID	FL	FID	FL	FID	FL
Transport style	1, 379	1, 346	0.24	8.45	0.622	0.004							
Approach style	1, 379	1, 346	9.53	0.26	0.002	0.612	3, 409	3, 396	9.71	6.01	<0.001	0.001	
Approach style × transport style	1, 379	1, 346	4.37	8.83	0.037	0.003							
Species	1, 379	NA NA	22.59	NA	<0.001	NA	1, 409	1, 396	50.69	18.00	<0.001	<0.001	
Sex class	3, 379	NA NA	5.06	NA	0.002	NA	3, 409	NA 396	9.49	NA	<0.001	NA	
Time of day	1, 379	1, 346	8.34	19.39	0.004	<0.001	NA NA	1, 396	NA	5.67	NA	0.018	
Cover	1, 379	1, 346	24.44	9.29	<0.001	0.002	1, 409	NA 396	11.37	NA	0.001	NA	
Time of day × cover	NA NA	1, 346	NA	8.96	NA	0.003	NA	NA	NA	NA	NA	NA	NA
Wind speed	1, 379	NA NA	9.15	NA	0.003	NA	1, 409	1, 396	9.03	6.90	0.003	0.009	

Note: Terms for which $P > 0.25$ (Winer et al., 1991; Underwood, 1997) were excluded from final models (denoted as 'NA') unless they figured in higher order terms. The factors observer, transect, grouping and starting distance were excluded because of $P > 0.25$ for all effects. Empty cells indicate that the factor was not part of the experimental design. On-trail: $n_{(FID)} = 390$; $n_{(FL)} = 353$; $R^2_{FID\text{ model}} = 0.23$; $R^2_{FL\text{ model}} = 0.15$. Off-trail: $n_{(RD)} = 419$; $n_{(FL)} = 403$; $R^2_{FID\text{ model}} = 0.29$; $R^2_{FL\text{ model}} = 0.13$.

which significant differences of the other factor occurred. The validity of the ANOVA models was justified by checking the assumptions of normality and homogeneity of variance by means of inspecting frequency histograms of standardized residuals with normal curves fitted, $Q-Q$ plots and boxplots. For all analyses the α -level of the P -value was set to 0.05.

The percentage of time spent with different activities was examined with a Kruskal–Wallis test, a non-parametric test to compare differences between two or more groups, since percent data with their binomial distribution do not comply with assumptions for parametric tests such as normal distribution. A Mann–Whitney U -test was used for post hoc analyses (Field, 2005).

All statistical analyses were carried out with SPSS for Windows 17.0 (SPSS Inc., Chicago, USA).

3. Results

Over 4 months we recorded data from 620 encounters with Red Kangaroos and 159 encounters with Euros during on-trail approaches and 279 encounters with Red Kangaroos and 175 encounters with Euros during off-trail approaches with no bias towards morning or evening walks. In 365 on-trail cases subjects did not flee (thus data on behavioural time budgets but no data on FID and FL). In total (on- and off-trail), 32 subjects took flight at first sight before any approach treatment could be applied (excluded from the data set) and in 61 cases subjects went out of sight after the approach (no FL data). Several subjects were excluded from further analysis because of missing data. Altogether, 809 FID and 756 FL were estimated and 744 behavioural time budgets calculated, with similar numbers for all treatments. The pattern of the flight response to the approach treatments for most variables was not significantly different between species and so data were pooled unless stated otherwise.

By design all subjects off-trail took flight as this was the end-point of the approach. In contrast, flight was provoked in only 53% of all cases when closest distance was

approached or attained on-trail. Flight was significantly more likely if the approach was on foot (75%) than in a vehicle (41%) ($\chi^2_{(1)} = 72.55$, $P < 0.001$). By either method a tangential/stop-and-go (59%) was slightly more likely to provoke flight than a tangential/continuous (50%) approach ($\chi^2_{(1)} = 5.62$, $P = 0.018$).

Mean FID (± 1 SE) was significantly shorter following an on-trail (78 ± 2.7 m) than an off-trail approach (90 ± 2.7 m) ($F_{(1,412)} = 13.83$, $P < 0.001$). On-trail, we found a significant interaction between type of approach and transport (Table 2a) for FID (Fig. 1a) and FL (Fig. 1b). On foot a tangential/stop-and-go approach significantly reduced FID and FL but there was no such effect if driving.

Off-trail approach style likewise significantly influenced mean FID and FL (Table 2b, Fig. 2). The shortest FID was with a direct/stop-and-go approach and the longest with a tangential/zigzag/stop-and-go. The other two off-trail approach styles caused an intermediate FID and were not significantly different from each other. FL was significantly shorter after a direct/stop-and-go approach compared to the other styles (trend for direct/continuous). Thus, talking significantly augmented the flight response compared to a direct/stop-and-go approach without talking.

Species, sex class, time of day, cover and wind speed significantly influenced mean FID and FL (Table 2). The pattern of influence and its magnitude were similar between an on- and an off-trail approach and so only the latter are given. Euros fled at a significantly shorter FID than Red Kangaroos and showed a significantly shorter FL as well (Fig. 3a). FID was longest in females with young-at-foot and shortest in females with obvious pouch-young. Males and females unencumbered with obvious young had an intermediate FID (Fig. 3b). There was a trend for singletons (85 ± 3.0 m) to have a shorter FID than groups (102 ± 2.0 m). FL was significantly shorter in the evenings (74 ± 3.0 m) than in the mornings (89 ± 3.0 m), and FID was significantly shorter in habitat with cover (89 ± 2.0 m; no cover: 108 ± 3.0 m). On-trail, FL was significantly reduced in the evenings if the habitat contained cover (evening/cover: 50 ± 3.6 m; evening/no cover: 86 ± 3.6 m; morning/cover: 78 ± 5.5 m; morning/no cover: 86 ± 3.4 m). FID and FL were signifi-

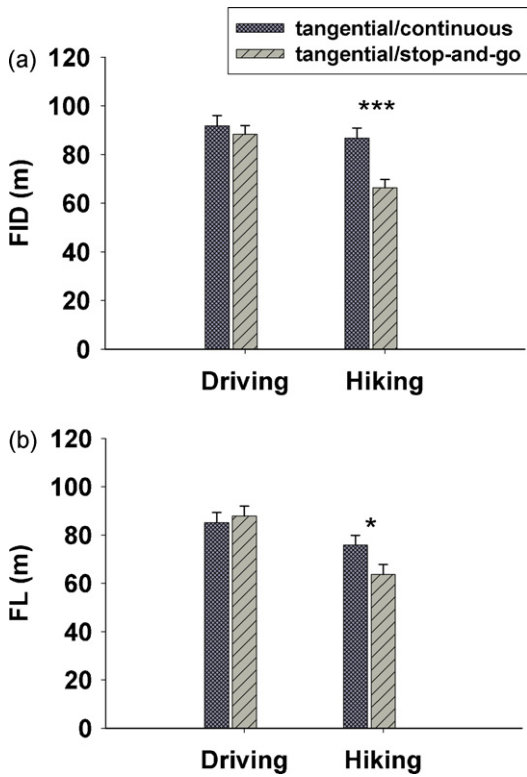


Fig. 1. Mean (+1 SE) (a) flight initiation distance (FID) and (b) flight length (FL) of Euros and Red Kangaroos in relation to transport and on-trail approach styles of simulated tourist approach. Asterisks indicate significant effects (* $P < 0.05$, *** $P < 0.001$) of an approach style at a particular transport level.

cantly shorter on calm (FID: 94 ± 2.0 m; FL: 79 ± 2.0 m) than windy days (FID: 112 ± 5.2 m; FL: 94 ± 5.0 m).

Through flight, both species gained on average about 25 m in safety distance to the observer independent of access type. However, there was a significant interaction effect between species and type of access on mean

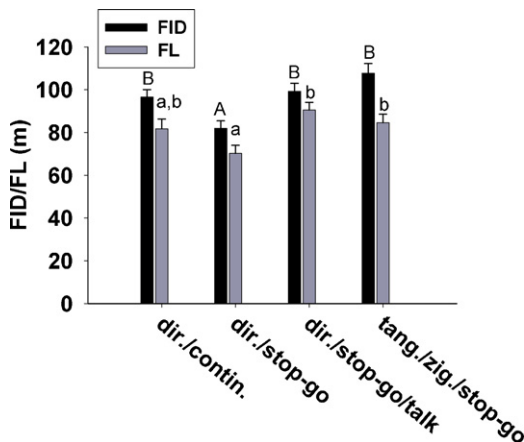


Fig. 2. Mean (+1 SE) flight initiation distance (FID) and flight length (FL) in relation to off-trail approach styles. Within FID or FL error bars that do not share a common letter are significantly different (Hochberg's GT2 post hoc test, $P < 0.05$).

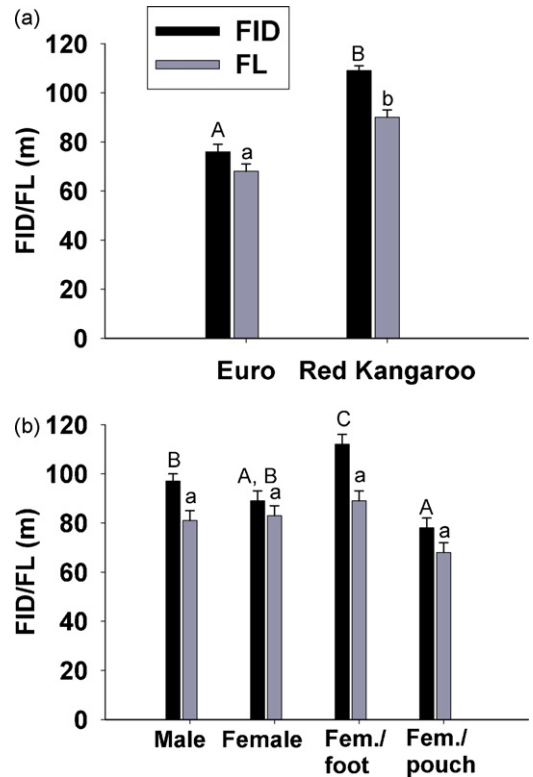


Fig. 3. Mean (+1 SE) flight initiation distance (FID) and flight length (FL) of Euros and Red Kangaroos after simulated tourist off-trail approach in relation to (a) species and (b) sex class (female = kangaroos without offspring that was obvious to the observer; fem./foot = female with young-at-foot; fem./pouch = female with pouch-young). Similar patterns and magnitude of effects were found in response to on-trail approach. Within FID or FL error bars that do not share a common letter are significantly different (Hochberg's GT2 post hoc test, $P < 0.05$).

flight effort ($F_{(1,304)} = 5.34$, $P = 0.02$). For every safety metre gained, Euros had to hop about 4 m independent of type of access, whilst for Red Kangaroos flight effort almost doubled from 3.8 to 7.8 when approached off-trail ($F_{(1,304)} = 11.48$, $P = 0.001$).

On-trail, both species invested 40% of their time in maintenance activities following a vehicle approach compared to 10% if the approach was on foot ($\chi^2_{(1)} = 85.16$, $df = 1$, $P < 0.001$). On-trail approach style caused no significant difference.

4. Discussion

When humans disturb wildlife the same economic principle used by prey encountering predators should govern the animal's response (Gill and Sutherland, 2000): the greater the perceived risk from the disturbance, then the stronger is the response elicited. To determine the level of risk, animals track short-term changes in a combination of factors that characterize the disturbance (Frid and Dill, 2002). In our study, these included the mode of human approach and its intrinsic properties (Table 1) staged in a varying disturbance context.

4.1. Kangaroo response to different modes of human approach

The intrusiveness of on- vs. off-trail approach was determined by two intrinsic properties of the disturbance: the predictability of the route resulting from travel along designated tracks and the directness of the approach (itself a function of the approach angle; [Burger and Gochfeld, 1990](#)). Both need to be considered – an oversight in some studies ([Freddy et al., 1986](#); [Mainini et al., 1993](#)) – as the directness is only negligible if the off-trail approach is applied directly parallel to the trail (as in [King et al., 2005](#)).

If animals know from previous experience that they have nothing to fear from visitors that travel along recreational tracks, and they come to expect them to stay on a particular route, then they might habituate ([Whittaker and Knight, 1998](#)). Indeed when the two species of kangaroos took flight following an on-trail approach the FID was shorter by 13% than off-trail. A similar response was found by [Taylor and Knight \(2003b\)](#) for American Bison (*Bison bison*), Mule Deer (*Odocoileus hemionus*) and Pronghorn Antelope (*Antilocapra americana*). Confinement of visitor use to designated tracks is less extreme than fencing off whole areas from visitor use, which has also been reported to relax animals ([Cassini, 2001](#); [Ikuta and Blumstein, 2003](#)). Even so both management actions enable animals to decide how close they get to the prospective observer's location and not vice versa provided that tourists comply with track use. In addition, if tourists stay on-trail then their approach will typically be less direct to a wildlife subject than any unconstrained off-trail approach. Subjects may perceive intruders approaching more directly as a greater threat than those passing by at an oblique angle ([Walther, 1969](#)), because directness may convey detection and intent to harm or displace.

A novel result that we discovered was that flight effort depended on the interaction between type of access and species. Whilst flight effort was independent of type of access for Euros, Red Kangaroos hopped almost twice as many metres for every metre of safety distance gained, despite similar average values for safety distance, when they were approached off-trail. This was not a function of a constraint on Red Kangaroos (a greater tendency to hop along flat ground than the hill-dwelling Euro) as might occur if trails meandered through tight gorges. Rather Red Kangaroos had a lower flight efficiency than Euros after off-trail approach and this may be some sort of strategy to circle the threat with a resultant increase in energy expenditure counter-balanced by the high energy costs of ascending the slopes of hills (typical of Euros).

Another significant predictor for the risk level perceived by animals is the means of transport used to approach wildlife. In our study area as well as many other nature-based tourist destinations worldwide, visitors typically approach on foot or by car. We observed that a significantly lower proportion of the two kangaroo species took flight when approached by car in support of previous conclusions that pedestrians induce a more intense wildlife response than motorized vehicles; for example, a higher percentage of flush response ([Klein, 1993](#); [Gonzalez et al., 2006](#)) or a longer FID ([Andersen et al., 1996](#); [King et al., 2005](#)). More-

over, our behavioural observations showed that the two kangaroo species treated an approach on foot with more alarm than a vehicle approach as the time spent in vigilance behaviour, hiding or aversive movements increased by 30%. Like other species that have suffered harm from pedestrian hunters ([McLellan and Shackleton, 1989](#)), kangaroos have had little time to adapt from a long history of close-range daytime hunting on foot by people (~50 000 years) to predominantly long-range night-time hunting from a vehicle (~60 years). Furthermore, vehicles were likely to be noticed from a greater distance so that the kangaroos were less startled as they drew closer ([Papouchis et al., 2001](#)).

In our study area, tourists approached kangaroos either in a continuous movement pattern or with momentary stops. The importance of such movement patterns in the animal's response to an approach is frequently overlooked. [Taylor and Knight \(2003a\)](#), who reviewed 54 papers that examined wildlife response distances to human activity, found that 30 papers did not specify the pattern of movement towards their study animals at all. Further, there were no papers which explicitly compared the flight response between continuously approached animals and those approached with interruptions. An interrupted versus a continuous movement pattern could have one of two effects. Either the stop-and-go approach elicits a shorter FID and/or FL, because of its more tentative nature, or a pattern of stopping could indicate a furtive attempt to pursue the animal. Our results clearly support the former given the significant reduction in the FID for a stop-and-go approach afoot (on-trail or off-trail) in comparison to its continuous counterpart. The two kangaroo species visibly relaxed during the stops with some of them changing from a more upright alert stance to a lower one, making fewer movements with their ears and/or showing less body tension. However, an interrupted approach only reduced the FID if the observer was on foot. The repeated stopping and starting of our vehicle was perhaps atypical and alarmed kangaroos as drivers normally pass through the study sites or stop once to examine some phenomenon.

Tangential approach, in spite of being less direct, was not associated with the shortest FID and FL relative to any of the direct approaches. We attribute this to the presence of another risk factor, the change in approach direction. Following our observations of actual tourist behaviour, we applied our tangential off-trail approach in combination with a zigzag motion. The two kangaroo species may have perceived such a change in the person's approach path as a higher threat due to its unpredictable nature where the risk of being harmed suddenly increases when bypassing observers turn towards the animals ([Cooper, 1998](#)).

We witnessed a large variety of tourist behaviour that may add to the impact of approach behaviour towards wildlife. Key amongst these is talking within the group or directed towards the animal. Consistent with our expectation that ambient noise would increase the magnitude of the stimulus presented to the kangaroo species, talking significantly lengthened FID relative to a mute direct/stop-and-go approach. [Cassini et al. \(2004\)](#), who used voice level as one factor in rating intrusiveness of tourists that were approaching South American Fur Seals (*Arctocephalus australis*), observed a much higher percentage of flush

response and aggressive seal behaviour, when the intruders' behaviour was classified as intermediately to intensely disturbing rather than calm.

4.2. Disturbance context

The response of wildlife to a human approach has consistently been reported to be a function of its disturbance context (Steidl and Anthony, 1996). In our study, intrinsic characteristics of the kangaroos such as species and sex class were influential. Grouping played only a minor role. Habitat cover, time of day and wind speed were important environmental factors.

Flight response as a species-specific trait has been reported in numerous mammal studies (e.g., Borkowski et al., 2006). In our study, Red Kangaroos were more flighty than Euros. This difference may be related to habitat preferences: Red Kangaroos inhabit open plains and so may be more wary since they are more easily discovered by predators. Flight over plains might also be less costly than in the hilly terrain, where the Euros tend to dwell, and therefore not delayed as long. Red Kangaroos were also more affected by an off-trail approach than Euros, expressed in the greater flight effort. Perhaps their flight becomes less efficient when faced with a new or less common form of approach.

We observed a high level of variability in the flight response between the four sex classes that we differentiated. Since reproductive females with young are most sensitive to predation (Dawson, 1995; Banks, 2001), and numerous mammal studies have found higher reactivity of females to disturbance (e.g., Bullock et al., 1993; Vandenheede and Bouissou, 1993), we expected females in general to exhibit the largest FID and/or FL. However, our more complex result suggests a different flight strategy when protection of the young is a high priority (Recarte et al., 1998): Females with obvious pouch-young might delay flight as long as possible and flee only as far as necessary because they carry the considerable extra weight of the young (Colagross and Cockburn, 1993) and face the risk that it is being expelled from the pouch (Stuart-Dick, 1987). Females with young-at-foot, on the other hand, have to consider the lower flight efficiency of their young, and might therefore flee early and further.

Habitat cover may allow animals to outwait a predator until a particular approach distance threshold (Frid and Dill, 2002) has been exceeded but can also obstruct the animal's view of approaching predators (Elton, 1939). Our study sites were typical of the open habitat of the Australian arid lands (Williams, 1979) with its comparatively sparse cover. Even so, the results were congruent with the decreased level of vigilance or flight reported by other studies on various species in habitat with cover (Bleich, 1999; Papouchis et al., 2001). However, whilst the FL after an on-trail approach in the mornings remained long, independent of habitat cover, it was reduced by 30 m in areas with cover in the evenings. Kangaroos seek 'run-on' areas where nutrients, water and organic matter collect as they provide the first and last places for grazing in arid lands (Montague-Drake and Croft, 2004). Such areas are likely to have more cover and so kangaroos might be reluctant

to leave, especially in the evening when feeding is of high priority. Higher activity in the mornings when kangaroos are close to satiation from feeding throughout the night (Watson and Dawson, 1993) and move towards rest sites may lead to higher reactivity towards disturbance.

Finally, the weather can determine the prey's perceived risk level of a situation as it affects predator detection rates. Wind, for instance can carry away olfactory cues or mask auditory cues of predators. This likely explains that the two kangaroo species took flight more readily with stronger winds consistent with other studies (Blumstein and Daniel, 2003a; Carter and Goldizen, 2003).

5. Conclusion

From our results, an approach of free-living kangaroos on foot should be on-trail by using a stop-and-go movement pattern but a zigzag motion and talking should be avoided to minimize energy-demanding processes such as flight and an aversion from fitness-maximizing maintenance activities. Disturbance will be less for both hiking and driving tourists if the habitat has some cover and calm evenings are chosen for the excursion. Importantly, education programmes need to inform park visitors on the consequences of kangaroos' response to human approach and provide them with easy-to-follow instructions on the least intrusive viewing behaviour that allows for a more rewarding wildlife experience with closer and longer-lasting observations.

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References

- Altmann, J., 1974. Observational study of behavior. *Behaviour* 49, 227–267.
- Andersen, R., Linnell, J.D.C., Langvatn, R., 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biol. Conserv.* 77, 169–176.

- Banks, P.B., 2001. Predation-sensitive grouping and habitat use by Eastern Grey Kangaroos: a field experiment. *Anim. Behav.* 61, 1013–1021.
- Bell, F.C., 1973. Climate of Fowlers Gap Station. In: Mabbutt, J.A. (Ed.), *Lands of Fowlers Gap Station, New South Wales*. The University of New South Wales, Sydney, pp. 45–63.
- Bleich, C.V., 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *J. Mammal.* 80, 283–289.
- Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* 67, 852–857.
- Blumstein, D.T., Daniel, J.C., 2002. Isolation from mammalian predators differentially affects two congeners. *Behav. Ecol.* 13, 657–663.
- Blumstein, D.T., Daniel, J.C., 2003a. Foraging behavior of three Tasmanian macropodid marsupials in response to present and historical predation threat. *Ecography* 26, 585–594.
- Blumstein, D.T., Daniel, J.C., 2003b. Red Kangaroos (*Macropus rufus*) receive an antipredator benefit from aggregation. *Acta Ethol.* 5, 95–99.
- Borkowski, J.J., White, P.J., Garrott, R.A., Davis, T., Hardy, A.R., Reinhart, D.J., 2006. Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. *Ecol. Appl.* 16, 1911–1925.
- Bullock, D.J., Kerridge, F.J., Hanlon, A., Arnold, R.W., 1993. Short-term responses of deer to recreational disturbances in two deer parks. *J. Zool. (Lond.)* 230, 327–332.
- Burger, J., 1981. Effects of human disturbance on colonial species, particularly Gulls. *Colon. Waterbirds* 4, 28–36.
- Burger, J., Gochfeld, M., 1990. Risk discrimination of direct versus tangential approach by basking Black Iguanas (*Ctenosaura similis*): Variation as a function of human exposure. *J. Comp. Physiol. B: Biochem. Syst. Environ. Physiol.* 104, 388–394.
- Carter, K., Goldizen, A.W., 2003. Habitat choice and vigilance behaviour of Brush-tailed Rock-wallabies (*Petrogale penicillata*) within their nocturnal foraging ranges. *Wildl. Res.* 30, 355–364.
- Cassini, M.H., 2001. Behavioural responses of South American Fur Seals to approach by tourists—a brief report. *Appl. Anim. Behav. Sci.* 71, 341–346.
- Cassini, M.H., Szteren, D., Fernández-Juricic, E., 2004. Fence effects on the behavioural responses of South American Fur Seals to tourist approaches. *J. Ethol.* 22, 127–133.
- Cassirer, E.F., Freddy, D.J., Ables, E.D., 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildl. Soc. Bull.* 20, 375–381.
- Clancy, T.F., 1989. Factors Influencing Movement Patterns of the Euro, *Macropus robustus erubescens*, in the Arid Zone. School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney.
- Colagross, A.M., Cockburn, A., 1993. Vigilance and grouping in the Eastern Grey Kangaroo, *Macropus giganteus*. *Aust. J. Zool.* 41, 324–325.
- Cooper Jr., W.E., 1998. Direction of predator turning, a neglected cue to predation risk. *Behaviour* 135, 55–64.
- Crawley, M.J., 2007. *The R Book*, second ed. Wiley & Sons, Chichester.
- Croft, D.B., 1981. Behaviour of Red Kangaroos, *Macropus rufus* (Desmarest, 1822) in northwestern New South Wales, Australia. *Aust. Mammal.* 4, 5–58.
- Croft, D.B., 2001. Rangeland Kangaroos: A World Class Wildlife Experience, Wildlife Tourism Report Series: No. 16. Cooperative Research Centre for Sustainable Tourism, Gold Coast.
- Dawson, T.J., 1995. Kangaroos: Biology of the Largest Marsupials. Cornell University Press, New York.
- Dawson, T.J., Taylor, C.R., 1973. Energy cost of locomotion by kangaroos. *Nature* 246, 313–314.
- Dill, L., Ydenberg, R., 1987. The group size-flight distance relationship in water striders (*Gerris remigis*). *Can. J. Zool.* 65, 223–226.
- Dyck, M.G., Baydack, R.K., 2003. Vigilance behaviour of Polar Bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biol. Conserv.* 116, 343–350.
- Edington, J.M., Edington, M.A., 1990. *Ecology, Recreation and Tourism*. Cambridge University Press, Cambridge.
- Edwards, G.P., Croft, D.B., Dawson, T.J., 1996. Competition between Red Kangaroos (*Macropus rufus*) and sheep (*Ovis aries*) in the arid rangelands of Australia. *Aust. Ecol.* 21, 165–172.
- Elton, C., 1939. On the nature of cover. *J. Wildl. Manage.* 3, 332–338.
- Field, A.P., 2005. *Discovering Statistics Using SPSS*. Sage Publications, London.
- Freddy, D.J., Bronaugh, W.M., Fowler, M.C., 1986. Responses of Mule Deer to disturbance by persons afoot and snowmobiles. *Wildl. Soc. Bull.* 14, 63–68.
- Frid, A., Dill, L.M., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11.
- Giese, M., 1998. Guidelines for people approaching breeding groups of Adélie Penguins (*Pygoscelis adeliae*). *Polar Rec.* 34, 287–292.
- Gill, J.A., Sutherland, W.J., 2000. Predicting the consequences of human disturbance from behavioural decisions. In: Gosling, L.M., Sutherland, W.J. (Eds.), *Behaviour and Conservation*. Cambridge University Press, Cambridge, pp. 51–64.
- Gonzalez, L.M., Arroyo, B.E., Margalida, A., Sanchez, R., Oria, J., 2006. Effect of human activities on the behaviour of breeding Spanish Imperial Eagles (*Aquila adalberti*): Management implications for the conservation of a threatened species. *Anim. Conserv.* 9, 85–93.
- Green, R., Giese, M., 2004. Negative effects of wildlife tourism on wildlife. In: Higginbottom, K. (Ed.), *Wildlife Tourism: Impacts, Management and Planning*. Sustainable Tourism Cooperative Research Centre, Gold Coast, pp. 81–98.
- Griffiths, M., van Schaik, C.P., 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conserv. Biol.* 7, 623–626.
- Heathcote, C.F., 1987. Grouping of Eastern Grey Kangaroos in open habitat. *Aust. Wildl. Res.* 14, 343–348.
- Ikuta, L.A., Blumstein, D.T., 2003. Do fences protect birds from human disturbance? *Biol. Conserv.* 112, 447–452.
- King, N.G., Higginbottom, K.B., Bauer, J.J., 2005. Terrifying tourists and wary wallabies: responses of macropodid species to the presence of humans. *Pac. Conserv. Biol.* 11, 64–72.
- Klein, M.L., 1993. Waterbird behavioral responses to human disturbances. *Wildl. Soc. Bull.* 21, 31–39.
- Knight, R.L., Gutzwiller, K.J., 1995. *Wildlife and Recreationists: Coexistence Through Management and Research*. Island Press, Washington, DC.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Lott, D.F., McCoy, M., 1995. Asian Rhinos *Rhinoceros unicornis* on the run? Impact of tourist visits on one population. *Biol. Conserv.* 73, 23–26.
- MacArthur, R.A., Geist, V., Johnston, R.H., 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. *J. Wildl. Manage.* 46, 351–358.
- Mainini, B., Neuhaus, P., Ingold, P., 1993. Behaviour of marmots *Marmota marmota* under the influence of different hiking activities. *Biol. Conserv.* 64, 161–164.
- McLellan, B.N., Shackleton, D.M., 1989. Immediate reactions of Grizzly Bears to human activities. *Wildl. Soc. Bull.* 17, 269–274.
- Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. *Wildl. Soc. Bull.* 29, 124–132.
- Montague-Drake, R., Croft, D.B., 2004. Do kangaroos exhibit water-focused grazing patterns in arid New South Wales? A case study in Sturt National Park. *Aust. Mammal.* 26, 87–100.
- Moscardo, G., Saltzer, R., 2005. *Understanding Tourism Wildlife Interactions: Visitor Market Analysis*. Sustainable Tourism Cooperative Research Centre, Gold Coast.
- Papouchis, C.M., Singer, F.J., Sloan, W.B., 2001. Responses of Desert Bighorn Sheep to increased human recreation. *J. Wildl. Manage.* 65, 573–582.
- Recarte, J.M., Vincent, J.P., Hewison, A.J.M., 1998. Flight responses of park Fallow Deer to the human observer. *Behav. Process.* 44, 65–72.
- Richens, V.B., Lavigne, G.R., 1978. Response of White-tailed Deer to snowmobiles and snowmobile trails in Mains. *Can. Field-Nat.* 92, 334–344.
- Roe, D., Leader-Williams, N., Dalal-Clayton, B., 1997. *Take only Photographs, Leave only Footprints: The Environmental Impacts of Wildlife Tourism*. International Institute for Environment and Development, London.
- Steidl, R.J., Anthony, R.G., 1996. Responses of Bald Eagles to human activity during the summer in interior Alaska. *Ecol. Appl.* 6, 482–491.
- Stuart-Dick, R.I., 1987. Parental investment in the Eastern Grey kangaroo. Ph.D. Thesis, University of New England, Armidale.
- Taylor, A.R., Knight, R.L., 2003a. Behavioral responses of wildlife to human activity: terminology and methods. *Wildl. Soc. Bull.* 31, 1263–1271.
- Taylor, A.R., Knight, R.L., 2003b. Wildlife responses to recreation and associated visitor perceptions. *Ecol. Appl.* 13, 951–963.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.
- Vandenheede, M., Bouissou, M.F., 1993. Sex differences in fear reactions in sheep. *Appl. Anim. Behav. Sci.* 37, 39–55.
- Walther, F.R., 1969. Flight behaviour and avoidance of predators in Thomson's Gazelle (*Gazella Thomsoni* Guenther 1884). *Behaviour* 34, 184–220.
- Watson, D.M., Dawson, T.J., 1993. The effects of age, sex, reproductive status and temporal factors on the time-use of free-ranging Red Kangaroos (*Macropus rufus*) in Western New South Wales. *Wildl. Res.* 20, 785–801.

- Whittaker, D., Knight, R.L., 1998. Understanding wildlife responses to humans. *Wildl. Soc. Bull.* 26, 312–317.
- Williams, O.B., 1979. Australia. In: Goodall, D.W., Perry, R.A. (Eds.), *Aridland Ecosystems: Their Structure, Functioning and Management*. Cambridge University Press, Cambridge, pp. 145–212.
- Winer, B.J., Brown, D.R., Michels, K.M., 1991. *Statistical Principles in Experimental Design*. McGraw-Hill, New York.
- Wolf, I.D., 2009. *Towards Sustainable Tourism in Outback Australia: The Behaviour and Impact of Nature-based Tourists on Vegetation and Selected Wildlife Species*. The University of New South Wales, Sydney.