



Research Article

Body condition, breeding time and joey survival rates of the quokka (*Setonix brachyurus*) are improved in habitats developed for tourism on Rottnest Island, Western Australia

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Abstract

Tourism can modify habitats and can have both positive and negative effects on local wildlife species. Such effects include changes to body condition, reproduction and behaviour, and can significantly affect the long-term fitness of individuals and local populations.

With particular interest in the effects of tourism on the ecology of the quokka (*Setonix brachyurus*), we investigated the effects of season and habitat type on the body condition and reproduction of this endemic species on Rottnest Island, a popular tourist destination in Western Australia.

We trapped quokkas every season for two years within four habitat types with varying degrees of resource availability for the quokkas: coastal dune, grass/heath, woodland and the settlement areas that are highly developed for tourism.

We used tail circumference as a measure of body condition, and this was significantly greater in the high resource settlement areas than in the other habitat types ($p=0.02$). Condition was poorest in summer, a season with low rainfall and scarce food. The condition of males peaked in spring and was related to rainfall in the previous season. The condition of females peaked in winter and declined sharply in spring, likely because females are preparing for and meeting the demands of peak lactation.

A higher proportion of joeys were born in February and March in the settlement areas as opposed to March and April in other habitat types. There was no evidence that the period of seasonal anoestrus experienced by quokkas on the island was reduced or eliminated in the settlement areas. Weaning rates, not birth rates varied between habitat type, and were lowest in the poorly resourced coastal dunes and highest in the bountiful settlement areas.

Habitats modified by tourism are often considered to have negative impacts on the fitness of local wildlife. This study however, provides an example of how tourism can positively influence the fitness of a vulnerable species, the quokka, through increased body condition and improved joey survival rates. This has implications not just for the conservation management of the Rottnest Island quokka, but also for other species globally persisting in areas exposed to tourism.

Introduction

Factors such as the availability of food and shelter, population density, predation risk and interspecific competition all contribute to the quality of habitats and influence the fitness and demography of local species (Lindström, 1999; Pulliam, 2000; Lin and Batzli, 2001; Morris, 2003). Human development can disturb natural habitats and result in local changes to these ecological factors which can benefit the life history of more flexible species, adversely affect others, and in some cases can have both positive and negative effects (Higginbottom et al., 2001; Hoffman and O’Riain, 2011; Gentili et al., 2014).

Artificial increases to the availability of food in habitats modified for tourism for example can attract animals and can increase their fitness through improved body condition, reproductive success or survival (Orams, 2002; Prevedello et al., 2013). Golf courses for example can provide a ready availability of high quality forage for herbivorous species such as elk (*Cervus elaphus nelsoni*), or eastern grey kangaroos (*Macropus giganteus*), but can encourage local overabundance of these species (Lee and Miller, 2003; Herbert, 2004; Hodgkison et al., 2007; Tribe et al., 2014).

Crowded environments and greater exposure to tourists, however, can also reduce fitness through increased risk of injury, disease transmission and aggression, disruption of normal activities, increased levels of stress or ingestion of poor quality foods (Green and Higginbottom, 2000; Orams, 2002; Newsome and Rodger, 2008). Negative impacts associated with tourism have been reported in a wide range of wildlife species. Examples include reduced body condition in stingrays (*Dasyatis americana*), increased stress, lower breeding success and reduced fledging rates in endangered yellow eyed penguins (*Megadyptes antipodes*), increased aggression in Mareeba rock-wallabies (*Petrogale mareeba*) and modified activity patterns in Asiatic leopards (*Panthera pardus*; Hodgson et al., 2004; Ellenberg et al., 2007; Ngoprasert et al., 2007; Semeniuk and Rothley, 2008).

Understanding how local tourism may be affecting the fitness of local species is vital for their long-term management, and threatened species affected by tourism in particular should be monitored closely as small changes to threatened populations can greatly impact the survival probability of the species (Shaffer, 1981).

Rottnest Island off the coast of Western Australia is an A Class Conservation Reserve for the purpose of “Public recreation” and is a tourism Mecca in Western Australia. The island is also home to the only remaining high-density sub-population of the quokka (*Setonix brachyurus*), an endemic macropod listed as vulnerable by the IUCN (2011)

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having been decimated on the mainland through predation by the introduced European red fox (*Vulpes vulpes*) and through habitat alteration (Sinclair and Morris, 1996; de Tores et al., 2007, 2008).

At an estimated 4000 to 8000 quokkas, the Rottnest Island subpopulation accounts for a high proportion of the estimated 7850 to 17150 mature individuals remaining (IUCN, 2011). The island is therefore an important sanctuary for this threatened species, and although quokkas appear to be thriving here today, careful management, based on up-to-date ecological and demographic data, is vital in order to protect this important population into the future.

The success of quokkas on Rottnest Island may be attributed in part to human induced changes to the island's vegetation that have seen much of the island's extensive cover of low closed woodland replaced by low shrub and grassland, which is preferred habitat for the quokka (Kitchener, 1972; Pen and Green, 1983; Rippey et al., 2003; Poole et al., 2014). Further, fertilised and irrigated lawns and food from tourists greatly increases resource availability for quokkas in the highly developed settlement areas (Sinclair, 1998a).

The Quokka population is regulated, however, by seasonal declines, driven by the limited availability of food and water outside of the settlement areas during summer (Shield, 1958; Main, 1959; Storr, 1961; Holsworth, 1964). A period of anoestrus, not seen in mainland quokkas, coincides with the summer period and limits the breeding season to six to eight months per year, restricting females to producing one offspring per year (Shield, 1964). This period of anoestrus is lost when island quokkas are kept in captivity and may therefore be reduced or eliminated in quokkas that live near the high resource settlement areas (Sharman, 1955b; Shield, 1958, 1959b; Shield and Woolley, 1963).

In terms of management of the Rottnest Island quokka, two potential issues concerning the demographics and ecology of this subpopulation stand out. On the one hand, local environmental disturbance involving artificially increased food supply may drive potentially unsustainable increases in quokka numbers in affected areas. On the other hand, global climate change, which is forecast to result in warmer and drier conditions in South Western Australia (Gibson et al., 2010; Hughes, 2011), will likely result in extended periods of aridity, leading to increased morbidity and mortality, and this may pose a significant threat to the stability of the population in the future.

This study aimed to determine how resource availability, as it is affected by tourism and season, effects the body condition and reproduction of quokkas on Rottnest Island. We expected that high resource availability will be associated with improved body condition, reproductive performance, and joey survival rates. Conversely, we expected low resource availability to be associated with poorer body condition, reproductive performance and joey survival rates. This information will help to inform management decisions for the quokka, but may also be significant to other species affected by tourism globally.



Figure 1 – Aerial view of Rottnest Island (Western Australia) displaying the eight sites where quokkas (*Setonix brachyurus*) were sampled.

Methods

To test these hypotheses, we trapped quokkas each autumn, winter, spring and summer between April 2013 and January 2015. We used our collected data to model how factors such as, sex, habitat type and season affect body condition, birth times and reproduction in quokkas on Rottnest Island.

Study species

The quokka, a medium sized (1.6–4.5 kg) macropod that is endemic to the south west of Western Australia, is a ruminant like foregut fermenter and is primarily a herbivorous grazer (Shield, 1958; Storr, 1961). On Rottnest Island, the quokka can be omnivorous in its feeding habits however, consuming all manner of foodstuffs given or left by tourists, including processed meats such as sausage (V. Phillips personal observation). This behaviour is particularly common around the settlement areas where tourists gather. There have also been reports of quokkas feeding on other animals such as the legless lizard *Lialis burtanii* and the introduced snail *Helix pisana* (Erickson, 1951; Shield, 1958).

The Rottnest Island quokka has a small home range of approximately 0.13 to 4 ha (Kitchener, 1970; Holsworth, 1964). Quokkas are primarily nocturnal and rest under vegetative cover such as shrubs and bushes during the day, and move around to graze at night (Dunnet, 1962). Within the settlement areas however, some animals exhibit temporal shifts in activity patterns and move around during the day to scavenge from tourists (Wynne and Leguet, 2004). Most quokkas however, rest in densely vegetated areas outside of the settlement during the day and actively commute into them at night to feed on the highly palatable fertilised and irrigated couch grass (*Cynodon dactylon*), which is plentiful within the settlement areas and available year round. The large separation between daytime rest sites and night time feeding sites has not been observed in habitat types outside of the settlement areas (V. Phillips personal observation, 2016).

A seasonal anoestrus limits quokkas on Rottnest Island to producing one young per year, with the breeding season confined between late January and September and the majority of births occurring between March and April. Quokka young, also known as joeys, leave the pouch at approximately six months and are weaned at approximately nine months of age, and juveniles born earlier in the breeding season can breed at the commencement of their second year (Sharman, 1955a; Shield, 1958; Holsworth, 1964; Shield, 1964; Loh and Shield, 1977). Quokkas have been recorded living for up to 10 years on Rottnest Island (Holsworth, 1964).

Study sites

Rottnest (32°1' S, 115°50' E) is an island of approximately 19.5 km², which is located 2 km west of Perth and 18 km from the Australian coast. It has a Mediterranean climate and receives up to 80% of its average yearly rainfall of 561 mm between May and October, with June through August being the wettest and coolest months (Australian Bureau of Meteorology, 2015). The Island experiences hot conditions with little rainfall between November and April. As a result, there is little fresh water and nutritious herbage available outside of the developed settlement areas for the quokkas during the summer and early autumn months (Shield, 1958; Kitchener, 1972).

Eight sites, including two replicates from four key habitat types on the island were selected; these were: coastal dune, grass/heath, woodland and settlement (Fig. 1). Each habitat type had varying degrees of resource availability for the quokkas ranked as settlement > grass/heath > woodland > coastal dune, according to research conducted by Storr (1994) and Poole et al. (2014).

The settlement areas are highly developed for tourism and include buildings, roads, car parks and entertainment areas. Fertilised and irrigated couch grass (*Cynodon dactylon*) lawns are a common feature within the settlement, and the occasional native plant species such as *Melaleuca lanceolata*, lie mostly on the outskirts of these areas. There are also a number of introduced large *Ficus macrophylla* trees producing edible fruits and leaves. The settlement areas are often very busy with tourists, particularly during the summer and school holiday peri-

ods. The grass/heath habitat types include an abundance of two tussock grasses, *Stipa variabilis* and *Poa caespitosa*, but are dominated by the heath species *Acanthocarpus preissii*, *Austrostipa flavescens*, and the introduced rhizomatous herb *Trachyandra divaricata* (Storr, 1961; Rippey and Hobbs, 2003). The woodland habitats contain both native and introduced species including *Melaleuca lanceolata*, *Acacia rostellifera*, *Callitris preissii*, *Eucalyptus gomphocephala*, *Eucalyptus camaldulensis* and *Eucalyptus utilis*. *Acanthocarpus preissii* also commonly lines the understorey of these woodland habitats. The coastal dune habitats are comprised of sand dunes sparsely vegetated with *Scaevola crassifolia* and *Olearia axillaris*, but also contain occasional low thicket patches of *Acacia rostellifera*, and *Melaleuca lanceolata* (Storr, 1961).

Acanthocarpus preissii is also present in the coastal dunes but is more prolific at the edges of these habitat types.

Sites were selected through the use of vegetation maps provided by the Rottneest Island Authority, and on the ground inspection of vegetation. An average of 2196 ± 355.5 m separated each site.

Rainfall data

Rainfall data were obtained from the monthly climate statistics for Rottneest Island within the Australian Bureau of Meteorology Website (Australian Bureau of Meteorology, 2015). A missing value for July 2014 was replaced with rainfall data from the nearest available weather station, Fremantle (32.06° S, 115.75° E). Rainfall at Fremantle is higher on average than rainfall on Rottneest Island and for this reason winter rainfall for the year 2014 may be an overestimate. Total annual rainfall for 2013 was 590 mm, while total annual rainfall for 2014 was 550 mm (Fig. 2).

Trapping, animal handling and data collection

Between April 2013 and February 2015, we trapped quokkas at each of the eight sites in autumn, winter, spring and summer. Each trapping event lasted for a period of four nights and we sampled sites in the same order each season.

Outside of the settlement, quokkas were trapped using Thomas soft wall traps ($350 \times 350 \times 800$ mm, Sheffield Wire Works, Welshpool, Western Australia). Traps baited with pieces of apple were set at dusk and cleared at dawn. To eliminate the risk of tourists interfering with traps, quokkas were hand netted at night time within the settlement areas. To do this we traversed 25 permanently marked trap points within each site and made one attempt at netting a quokka if it was within 5 meters of the trap point.

Newly trapped quokkas were transported to the Nursery on Rottneest Island, anaesthetised through Isoflurane inhalation with a gas mask (in-

duced with 5% Isoflurane in oxygen and maintained at 3% Isoflurane in oxygen). We then weighed each animal and recorded its sex. We also measured the length of the right hind foot (pes), head, head/body, tail and the circumference of the base of the tail.

We marked each animal with two marks, so marks were not lost. Marks included a uniquely numbered aluminium ear tag (Monel #1), and a microchip (Allflex Australia), which was inserted subcutaneously between the shoulder blades of each animal.

Each quokka was also aged by molar eruption according to Holsworth (1964), and animals were classified as yearlings (7 months to 1 year), subadult (12–24 months) or adults (older than 24 months). Females were checked for the presence of pouch young or an elongated teat. Joeys deemed to be sufficiently developed (more than 40 mm, Waring et al., 1955) were sexed and their weight, crown to rump, and pes length were recorded. Animals were released at the point of capture after they had fully recovered from anaesthesia. Quokkas that were re-captured were weighed, measured and checked for the presence of pouch young on site, and released immediately.

Sex ratios of trapped individuals were calculated and compared to an assumed sex ratio of 1:1 using a goodness of fit Chi-square test with Yates correction for continuity.

All capture and animal handling procedures complied with the Australian code of practice for the care and use of animals for scientific purposes (NHMRC 2004), and were approved by the Animal Ethics Committee at The University of Western Australia (permit no. RA/3/100/1183). A licence to take fauna for scientific purposes (Reg. 17) was issued by the Department of Parks and Wildlife, Western Australia in 2013, 2014 and 2015 (Licence number: SF 009127).

Morphology and body condition

We used the statistics program SPSS Statistics 22 (SPSS) (IBM Corp. Armonk, N.Y.), to calculate mean values for body mass and morphological measurements within each sex, habitat type and season.

The circumference of the base of the tail was used as an indicator of body condition following Hayward et al. (2003). This is because quokkas store caudal fat in order to cope with extreme seasonal conditions (Bakker and Main, 1980; Hart et al., 1985; Sinclair, 1998b; Hayward et al., 2003). We included only adults in our analysis of body condition.

We used generalised linear mixed models in SPSS to test for the fixed effects of rainfall, habitat type, sex, season and the interactions “sex*season” and “sex*habitat” on tail circumference. Quokka ID was included as a random effect, and random intercepts were used (Gillies et al., 2006). Least 254 significant difference (LSD) was used to perform post hoc pairwise comparisons.

Birth and weaning rates

Birth rates were calculated as the highest proportion of individual adult and subadult females captured with a pouch young or elongated teat at any time during the breeding season, which runs from late January to September (Sharman, 1955b; Shield, 1959a; Chambers and Bencini, 2010). The sex ratios of pouch young were also calculated using all sex data recorded over the two-year period.

An elongated teat indicated that a joey had recently been weaned and we calculated weaning rates as the proportion of females with an elongated teat at the end of the breeding season in October or November each year (Shield, 1964).

We used Hierarchical log-linear analysis (SPSS) to test for the effects of habitat type and year on birth rates, weaning rates and pouch young sex ratios. Beginning with models that included all three way interactions (1. births \times habitat \times year; 2. weaning \times habitat \times year; 3. sex ratio \times habitat type \times year), non-significant variables were removed through backward elimination until only significant ($p < 0.05$) interaction terms remained.

Birth schedules

Birth schedules for each habitat type were calculated using the combined data from all joeys measured over the two-year study period. The

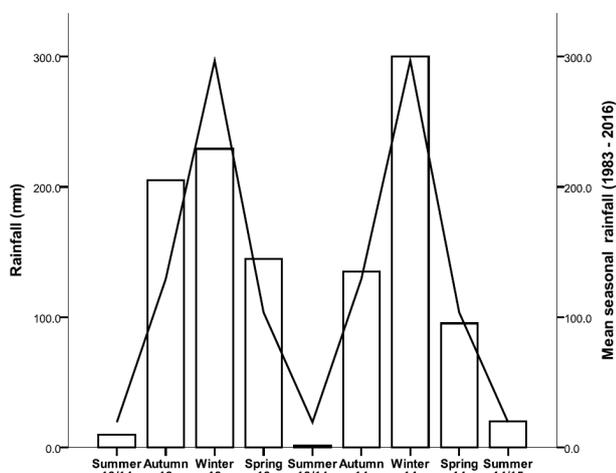


Figure 2 – Total seasonal rainfall for 2013 to 2015 (bars) and mean rainfall 1983–2016 (line) recorded at the Rottneest Island weather station (32.01° S, 115.50° E). A missing data point for July 2014 was replaced with data from the nearest available weather station, Fremantle (23.8 km east), and winter rainfall for that year may be an overestimate.

Table 1 – The total number of male and female adult, subadult and yearling quokkas caught in four habitat types on Rottne Island between April 2013 and February 2015. The numbers of individuals not previously captured are in parentheses.

Habitat type	Males			Females			Total	
	Adult	Subadult	Yearling	Adult	Subadult	Yearling	Individuals	Captures
Coastal dune	132 (29)	27 (12)	9 (6)	146 (39)	71 (30)	6 (5)	121	391
Grass/heath	187 (51)	28 (15)	3 (3)	112 (50)	64 (36)	5 (4)	159	399
Settlement	142 (110)	67 (53)	24 (22)	116 (98)	64 (55)	27 (25)	363	440
Woodland	232 (45)	40 (16)	7 (5)	181 (43)	64 (34)	7 (6)	145	531
Total	693 (235)	162 (96)	43 (36)	555 (230)	263 (151)	45 (40)	788	1761

ages of the joeys were estimated by comparing morphological measurements to growth curves (Shield and Woolley, 1961; Hayward et al., 2003) and their birth date was estimated by deducting their age from their date of capture. For each habitat type, birth schedules, calculated through the use of cumulative frequencies, were divided into monthly intervals beginning in January, and the schedules for each habitat type were compared using Kolmogorov–Smirnov two sample tests in SPSS, with p -values adjusted through the use of the Bonferroni correction (Chambers, 2009).

Results

Captures

Over 256 trap nights between April 2013 and February 2015, we captured 1761 quokkas, which included 788 different individuals of which 465 were mature adults (Tab. 1). The ratio of new males to females overall did not differ significantly from parity ($\chi^2=3.57$, $df=1$, $p=0.06$). The ratio of new adult males to females within each habitat type also did not vary significantly from the expected 1:1 ratio (coastal dunes: ($\chi^2=1.19$, $df=1$, $p=0.28$); grass/heath: ($\chi^2=0.01$, $df=1$, $p=1.0$); settlement: ($\chi^2=0.58$, $df=1$, $p=0.45$); woodland: ($\chi^2=0.01$, $df=1$, $p=0.92$).

Morphology and body condition

Quokkas on Rottne Island exhibited male-based sexual dimorphism, with the mean body mass (\pm S.E) of adult males over all habitat types and trapping sessions (3045.30 ± 21.04 g) being significantly greater than the females (2525.00 ± 14.39 g), $p<0.001$; Tab. 2). The heaviest male captured weighed 4420 g, while the heaviest female captured weighed 3550 g, and both of these animals were caught within the settlement. Males also had significantly larger head (96.00 ± 0.27 mm, $p<0.001$), head–body (510.80 ± 1.55 mm, $p<0.001$) and right pes lengths (103.90 ± 0.17 mm, $p<0.001$), compared to females (Tab. 2). There were no significant differences in body mass between the sexes for subadults ($F_{1,268}=3.22$, $p=0.07$) or yearlings ($F_{1,80}=2.56$, $p=0.11$).

The circumference at the base of the tail (mm), our indicator of body condition, was significantly larger in adult males (66.10 ± 0.34 mm) than in females (60.60 ± 0.33 mm) over all habitat types and seasons ($F_{2,772}=51.85$, $p<0.001$; Fig. 3).

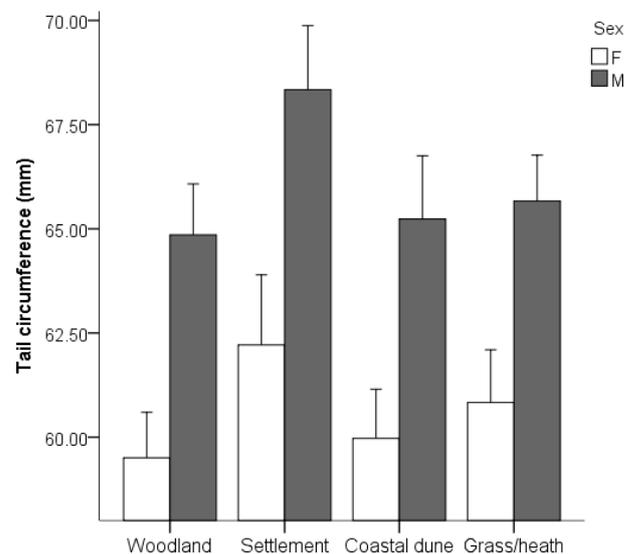
There was a significant effect of habitat type on overall tail circumference ($F_{3,772}=9.20$, $p<0.001$).

Quokkas in the settlement areas had significantly larger tail circumferences (65.90 ± 0.64 mm, $p=0.02$) than quokkas living in the coastal dunes (62.00 ± 0.51 mm), the woodland (62.40 ± 0.46 mm) and grass/heath (63.90 ± 0.45 mm) habitat types. There was a significant sex \times habitat type interaction ($F_{8,772}=16.55$, $p<0.001$), indicating that

some habitat types affect the body condition of males and females differently. Although tail circumference was significantly larger in the settlement than in other habitat types for both males (68.50 ± 4.94 mm, $p=0.011$) and females (62.40 ± 4.46 mm, $p<0.001$).

There was a significant effect of seasonal rainfall when the two years were combined on the tail circumference of female quokkas ($F_{1,351}=17.00$, $p<0.001$), but this effect was not seen in males ($F_{1,421}=0.56$, $p=0.45$). There was, however, a significant effect of rainfall in the previous season on the tail circumference of males ($F_{1,421}=9.09$, $p=0.003$; Fig. 5).

Season also had a significant effect on overall body condition ($F_{3,772}=4.83$, $p=0.002$), with tail circumference being significantly larger in winter at 64.3 ± 0.5 mm than in summer (62.50 ± 0.44 mm, $p=0.001$). A significant sex \times season interaction was detected ($F_{8,772}=15.76$, $p<0.001$). Female tail circumference was greatest in winter (62.80 ± 0.63 mm, $p<0.001$), and smallest in summer (58.90 ± 0.43 mm, $p<0.001$). Tail circumference was largest for males in spring (66.70 ± 0.62 mm) and smallest in summer (65.50 ± 0.49 mm; Fig. 4), although these differences failed to reach significance ($p>0.05$).

**Figure 3** – Mean (\pm S.E.) tail circumference (mm) as a measure of body condition for male and female quokkas (*Setonix brachyurus*) in four habitat types on Rottne Island, Western Australia.**Table 2** – Mean body mass and morphological measurements \pm standard errors for male and female adults, subadult and yearling quokkas on Rottne Island, all habitats combined.

	Adult Males	Adult Females	Subadults	Yearlings
Mass (g)	3045.30 \pm 21.04	2525.00 \pm 14.39	1907.70 \pm 22.29	1056.00 \pm 31.94
Head (mm)	96.00 \pm 0.27	91.30 \pm 0.24	85.20 \pm 0.35	72.90 \pm 0.72
Head Body (mm)	510.80 \pm 1.55	489.80 \pm 1.58	446.90 \pm 2.66	365.70 \pm 6.26
Right Pes (mm)	103.90 \pm 0.17	98.00 \pm 0.18	99.40 \pm 3.40	82.30 \pm 0.69
Tail circumference (mm)	66.10 \pm 0.34	60.60 \pm 0.33	55.20 \pm 0.39	44.80 \pm 0.74

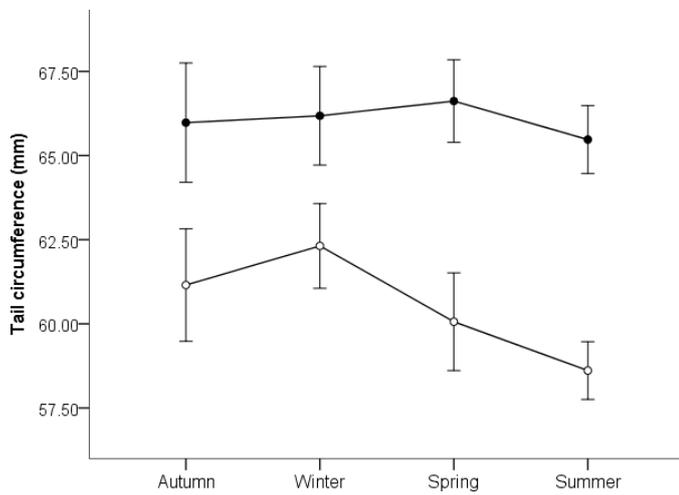


Figure 4 – Mean (\pm S.E.) tail circumference for male ($n=423$; black circles) and female ($n=349$; white circles) quokkas (*Setonix brachyurus*) in each season on Rottnest Island, Western Australia.

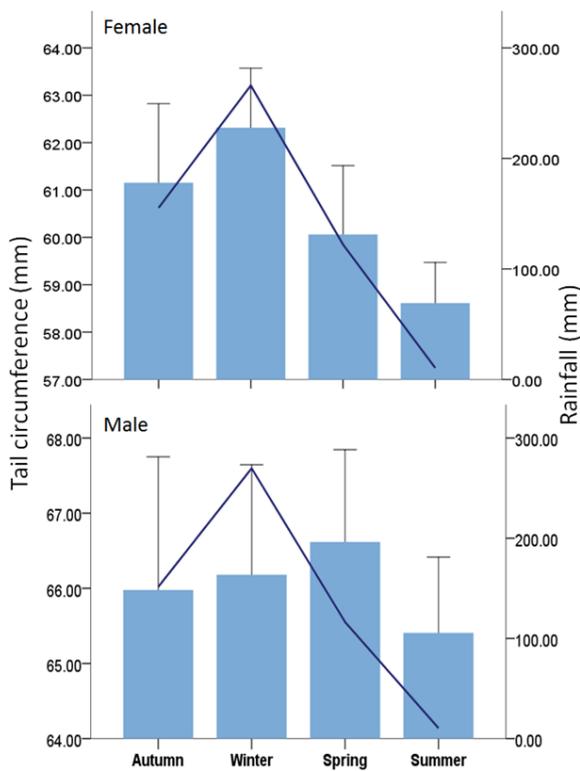


Figure 5 – Tail circumference \pm S.E. (bars) of female and male quokkas (*Setonix brachyurus*) and rainfall (line) in each of the four seasons on Rottnest Island, Western Australia. Data from 2013/14 and 2014/15 are pooled.

Reproduction

The average birth rate for subadult females overall was $41.00 \pm 5.84\%$, and it did not vary significantly between habitat types over the two-year period ($\chi^2=5.20$, $df=3$, $p=0.08$). The average subadult weaning rate overall was $13.50 \pm 5.70\%$.

We used hierarchical log linear modelling to test for differences in adult birth and weaning rates and the sex ratios of pouch young according to habitat type and year.

There was no significant three-way interaction for birth rates, although there was a strong trend towards significance ($\chi^2=7.77$, $df=3$, $p=0.06$). Further, there was no significant habitat \times birth interaction ($\chi^2=3.64$, $df=3$, $p=0.35$) or year \times birth interaction ($\chi^2=1.10$, $df=1$, $p=0.29$).

No significant three-way interaction was detected for weaning rates either ($\chi^2=1.76$, $df=3$, $p=0.62$). However year ($\chi^2=8.45$, $df=1$, $p=0.004$), and habitat type ($\chi^2=19.41$, $df=3$, $p<0.001$) both had significant two-way interactions with weaning rates. Overall, weaning rates were higher in 2014 than in 2013, while weaning rates were lowest in the coastal dunes and highest in the settlement areas (Tab. 3).

The sex ratio of pouch young varied from 0.84 males to every female in the coastal dunes in 2014/15 to 1.43 males to every female in the grass/heath in 2013/14 (Tab. 3). However, neither habitat type ($\chi^2=2.37$, $df=3$, $p=0.5$), or year ($\chi^2=0.05$, $df=1$, $p=0.83$) had a significant interaction with pouch young sex ratios.

Breeding season

The percentage of births peaked in February in the settlement areas, March in the grass/heath and woodland areas, and April in the coastal dune areas (Fig. 6).

The distribution of births between the settlement areas and all other three habitat types was significantly different (Kolmogorov–Smirnov two-sample test; coastal dune: $D=1.63$, $p=0.01$, grass/heath: $D=1.43$, $p=0.03$, woodland: $D=1.63$, $p=0.01$).

The distribution of births also differed between the woodland and the coastal dune habitat types ($D=1.43$, $p=0.01$). However, there was no significant difference in the distribution of births between the coastal dunes and the grass/heath habitats ($D=1.02$, $p=0.25$), or the woodland and the grass/heath habitats ($D=1.23$, $p=0.10$).

The birth month of the joeys was significantly affected by the body condition of their mothers ($F_{1,214}=4.99$, $p=0.03$), with body condition in January being highly significant in its effect ($p<0.001$) and body condition in February nearing significance ($p=0.056$).

Discussion

Body condition

Quokkas in areas highly developed for tourism on Rottnest Island were in significantly better condition compared to those from the less disturbed habitat types. This is what we expected as within the settlement areas on Rottnest abundant food resources from fertilised and irrigated lawns and tourists are available year round for local quokkas (Sinclair, 1998a; Hercocck, 2003).

Resource availability is a key factor affecting body condition, and the artificial increase of resources resulting from habitat modification and anthropogenic food sources have led to improved body condition in a great number of species globally. Such species include olive baboons, *Papio anubis*, racoons, *Procyon lotor* L., Columbian ground squirrels, *Spermophilus columbianus*, mongoose, *Mungos mungo* and tammar wallabies, *Macropus eugenii* (Dobson and Kjelgaard, 1985; Eley et al., 1989; Boutin, 1990; Rosatte et al., 1991; Moss and Croft, 1999; Otali and Gilchrist, 2004; Toïgo et al., 2006; Chambers and Bencini, 2010). Benefits of an increased food supply and improved body condition often include improved reproductive success and survival rates (Boutin, 1990; Orams, 2002; Ditchkoff et al., 2006; Senticchia et al., 2015). These factors, along with increased immigration to the settlement areas on Rottnest may result in density issues however, that could lead to increased levels of competition, aggression, disease transmission and risk of injury through collisions with vehicles or bicycles (Lin and Batzli, 2001).

Body condition, in herbivorous species in particular, can also be strongly affected by seasonal variation in the availability of resources. Californian voles (*Microtus californicus*) for example, have very low fat reserves in spring, when little green forage is available, and this leads to decreased survival rates (Batzli and Pitelka, 1971). We found that quokkas were in their poorest condition overall in summer, a season with greatly reduced access to nutritious food and water outside of the settlement areas. A rapid decline in the condition of quokkas on Rottnest Island during summer has also been recorded by Shield (1958), Holsworth (1964), Bakker and Main (1980) and Wake (1980), who all noted a significant seasonal mortality of quokkas on the island during this time.

Table 3 – Birth and weaning rates and the sex ratio of quokka pouch young born in four habitat types sampled on Rottnest Island in 2013 and 2014..

Year	Study Area	Birth Rate (%)	N	Weaning Rate (%)	N	Pouch young sex ratio (M:F)
2013/14	Coastal Dune*	96.43	28	62.50	8	17:12 (1.42:1)
	Grass/heath*	87.10	31	71.43	7	20:14 (1.43:1)
	Settlement	87.30	63	80.00	15	14:16 (0.88:1)
	Woodland*	93.33	30	75.00	12	18:17 (1.06:1)
	Total					69:59 (1.17:1)
2014/15	Coastal Dune*	88.23	34	72.73	11	16:19 (0.84:1)
	Grass/heath*	93.10	29	75.00	8	13:13 (1:1)
	Settlement	86.05	43	88.89	9	12:9 (1.33:1)
	Woodland	87.88	33	86.67	15	21:15 (1.4:1)
	Total					62:56 (1.11:1)

* Birth rates varied significantly from weaning rates ($p < 0.01$)

The season of peak condition differed between males and females however, with male condition peaking in spring, up to three months after peak rainfall. A similar correlation between body condition and rainfall in the previous 3 months has also been shown in male yellow footed rock wallabies, *Petrogale xanthopus* (sharp et al., 2006), and in black flanked rock wallabies, *Petrogale lateralis lateralis* (Willers et al., 2011).

Body condition of female quokkas, on the other hand, peaked in winter, along with a peak in rainfall. Female mammals store fat in preparation for lactation, one of the most energetically costly activities for female marsupials (Bronson, 1985; Gittleman and Thompson, 1988; Cripps et al., 2011). The increased body condition of female quokkas in winter is most likely because females are rapidly increasing their body fat reserves in preparation for peak lactation, which on Rottnest occurs between August and October (Sharman, 1955a; Shield, 1964; Loh and Shield, 1977). At peak lactation, the composition of quokka milk changes to meet the needs of the developing young and both the protein and lipid content of quokka milk increase dramatically as young are emerging from the pouch at around 180 days post-partum (Miller et al., 2009, 2010). The sharp decline in the condition of females in spring is therefore likely the result of mothers having mobilised their stored body lipids into milk lipids through lactation, a common trait in herbivorous mammals (Sadleir, 1969; Cork, 1991; Oftedal, 2000). A decrease in body condition throughout lactation has similarly been recorded in brushtail possums (*Trichosurus vulpecula*; Isaac, 2006).

Reproduction

We found that weaning rates, not birth rates, were affected by habitat type, with the highest weaning rates occurring the settlement and the lowest being found in the coastal dunes. Further, weaning rates were higher overall in 2014 than 2013.

Factors such as habitat type, timing of birth and rainfall all affect the availability of resources and have a strong influence on maternal condition and the survival rates of marsupial pouch young (Newsome, 1965; Dickman et al., 2001; Ficher et al., 2001; Wynd et al., 2006). In areas where food resources are readily available, pouch young survival rates may be significantly improved. For example, in a population of the dasyurid marsupial *Antechinus stuartii*, the survival of young significantly increased after the food supply was supplemented (Dickman, 1989). In the settlement areas of Rottnest Island, artificial increases to the food supply through habitat modification and anthropogenic sources likely lead to improved joey survival rates for quokkas in these areas, and we believe that improved weaning rates in 2014 also resulted from higher resource availability within that year.

Poorer or more variable resource availability, on the other hand, can often result in reduced pouch young survival in marsupials (Frith and Sharman, 1964; Newsome, 1965; Wynd et al., 2006).

For example, Frith and Sharman (1964) found that 83% of red kangaroo (*Macropus rufus*) pouch young failed to reach maturity in an area of drought because of failed lactation resulting from a heavily reduced food supply. We found that joey survival rates were lowest in the

coastal dunes, and this is likely related to the poor resource availability in this habitat type.

Marsupial females invest relatively little in pregnancy compared to eutherian females, and much of the cost of rearing pouch young occurs during the later stages of lactation. This means that less developed young can be easily abandoned if conditions are unfavourable, and explains why we found that weaning rates, not birth rates, differed between habitat types (Kirsck, 1977; Martin and Handasyde, 2007; Schwanz and Robert, 2012). Although quokkas are also able to store a quiescent blastocyst that can develop and replace young lost early in the breeding season, this reproductive function is less likely to occur under poor nutritional conditions and is not thought to be utilised by the Rottnest Island population (Shield and Woolley, 1963). Hayward et al. (2003) and Bain (2016) found that less than fifty percent of quokka joeys survived to independence on the mainland, and suggested that predation and habitat quality may be the primary limiting factors. It seems then, that for quokkas, joey survival rates are highly dependent on the availability of resources.

Birth schedules

We found that most quokka young are born between February and April as did past studies conducted on Rottnest Island. The young therefore leave the pouch between August and October, approximately 6 months post-partum, and continue to be suckled from outside the pouch for another 3 to 4 months prior to weaning (Sharman, 1955a; Shield, 1959a, 1964; Loh and Shield, 1977).

However, we were the first to compare differences between habitat types and we found that the distribution of birth dates varied significantly between the settlement and the other habitat types, with most joeys in the settlement being born earlier, in February and March instead of March and April.

A number of mammal species have been shown to time their breeding so that young benefit greatly from rainfall and resource availability peaks, including African buffalo (*Syncerus caffer*), wild boar (*Sus scrofa*), collared pikas (*Ochotona collaris*), Bennet's wallabies (*Macropus rufogriseus*) and western grey kangaroos (*Macropus fuliginosus*). This trait has also been suggested to exist in quokkas (Sharman, 1954; Bolton et al., 1982; Franken and Hik, 2004; Wynd et al., 2006; Ryan et al.; Canu et al., 2015). However, our data indicate that quokka young outside the settlement areas, particularly those in the coastal dunes, which are born later in April, would not leave the pouch until late spring. This means that peak lactation demand would coincide with the rapidly decreasing resource availability of late spring and that young would continue to be suckled throughout the summer when resource availability on Rottnest is extremely low (Shield, 1958; Kitchenner, 1970; Wake, 1980). Holsworth (1964) found that quokka joeys born later in the breeding season had lower survival rates and this is probably due to decreased resource availability for both the mothers and joeys.

In the settlement areas, however, food is available year round for the quokkas yet breeding is advanced. Increased food supply and improved body condition have been linked to advanced breeding times

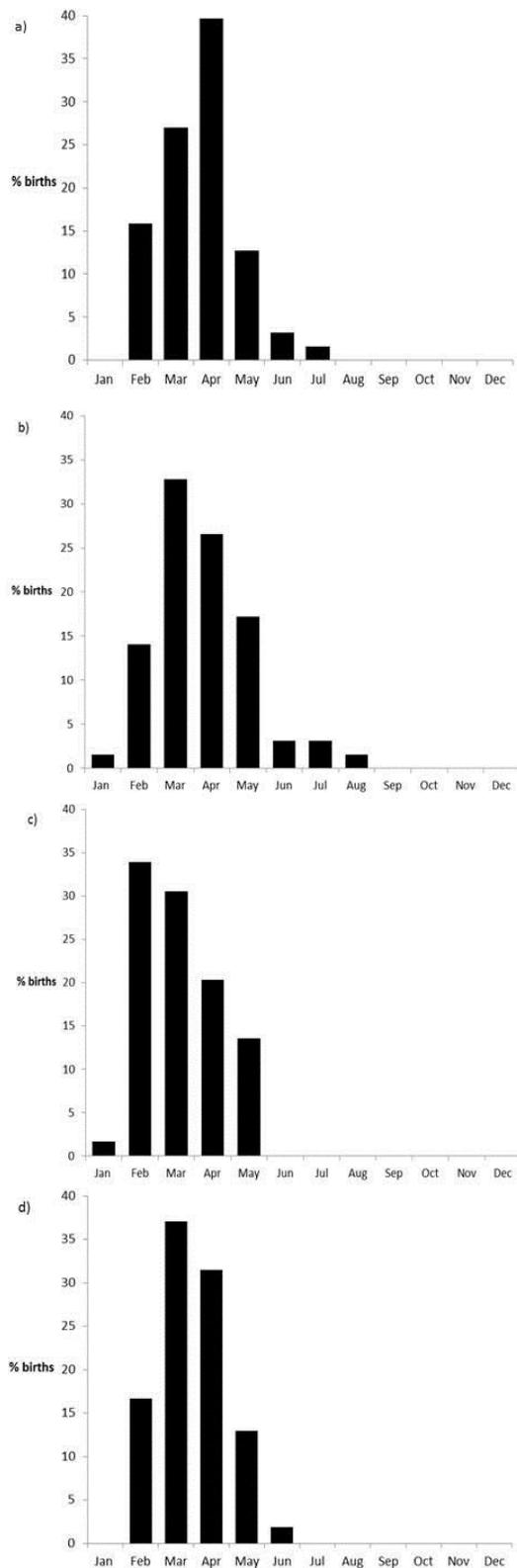


Figure 6 – Birth schedules for quokkas in four key habitat types on Rottneest Island, Western Australia a) coastal dune b) grass/heath, c) settlement, d) woodland. Data from 2013/14 and 2014/15 have been pooled.

in a number of mammals (Watts, 1970; Andrzejewski, 1975; Boutin, 1990; Schwanz and Robert, 2012; Senticchia et al., 2015). We found a significant relationship between the body condition of the mothers and joey birth month and therefore suggest that it is the body condition of the mothers, rather than the timing of breeding to suit optimal environmental conditions, that most significantly influences the birth dates of quokkas on Rottneest Island.

Shield (1964) reported having encountered quokkas breeding throughout the year in areas on Rottneest Island where artificial food

sources were available, such as the garbage dump, the settlement and the Research station. Despite detecting an advanced breeding season, we did not find any evidence of joeys being born outside of the breeding season within the settlement areas and must therefore reject our hypothesis that the period of anoestrus is reduced or lost in quokkas within the settlement areas.

We have shown that on Rottneest Island, Western Australia, the quokka benefits from habitats modified for tourism through improved body condition, advanced breeding times and improved joey survival rates. While these benefits improve the fitness of individuals in the short term, it is important that local populations are frequently monitored to ensure that negative impacts associated with high local densities, such as increased stress or disease transmission, do not threaten persistence of the species over the long term. This research has demonstrated that tourism can aid in the conservation of species, not just economically, but by improving fitness and maintaining local numbers through increased food supply. This is important not just for the conservation of the quokka, but for other opportunistic species that may persist in habitats highly modified by tourism. ☞

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