

# Home range overlap of the quokka *Setonix brachyurus* (Macropodidae: Marsupialia) suggests a polygynous mating system

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## ABSTRACT

The home range overlap of the quokka was investigated with the aim of elucidating the mating system of the species on mainland Australia. Fifty adult quokkas from five sites were radio collared for long enough to obtain stable home range estimates and the percentage that individual home ranges overlapped those of other conspecifics was calculated. Two sites were found to be anomalous due to a low population density and the threat of introduced predators, and were excluded from several comparisons and consequently there were no significant differences between sites. There was no significant difference in the degree of overlap of overall ranges, although male home ranges overlapped other males less than they overlapped females and less than females overlapped either sex. Female core home ranges overlapped other females significantly more than males. Because of the lack of significant results conclusions are tentative, however the fact that female home ranges overlap other ranges more than males do, combined with the male, weight-based dominance hierarchy, suggests the quokka operates a polygynous mating system, however variation in mating strategies may occur due to variations in prey density. Genetic analysis is recommended to confirm this hypothesis. The clumping behaviour of quokkas at the excluded Victor Road site is probably a predator-avoidance strategy.

Keywords: breeding strategy, mating system, predation, predator avoidance, polygyny, vulnerable, *Vulpes vulpes*

## INTRODUCTION

The mating systems of the larger macropodids are generally well understood, however those of the smaller members of the family are largely unknown due to their cryptic nature. The quokka (*Setonix brachyurus* Quoy & Gaimard 1830) is a medium-sized, macropodid marsupial that is listed as vulnerable according to IUCN criteria (Hilton-Taylor 2000). Despite extensive study on Rottneest Island in the 1950s, '60s and '70s (Kitchener 1972; Main et al. 1959; Packer 1965, 1969; Storr 1961) and on the mainland at the end of the last millennium (Hayward et al. 2005a; Hayward et al. 2005b; Hayward et al. 2007), the mating system of the quokka remains unknown (Hayward 2002).

Mating systems can be viewed as the outcomes of the behaviour of individuals competing to maximise their reproductive success (Davies 1991). Male mating behaviour varies among species according to four characteristics of females: 1) the extent to which female reproductive rate can be increased by male assistance in caring for the offspring; 2) the size of female home range;

3) the size and stability of female groups, and 4) the density and distribution of females in space (Clutton-Brock 1989).

Males can better monopolise several females when their assistance raising offspring is unnecessary, when females have small home ranges or when females live in small, stable groups (Davies 1991). Conversely, when females are solitary and use large home ranges, occur in unstable groups or where density is high, males are more likely to be monogamous or monopolise individual females successively (Davies 1991).

When male assistance is required for successful rearing of the young and females are territorial and solitary, obligate monogamy (e.g. gibbons *Hylobates sp.*, black-backed jackal *Canis mesomelas* and klipspringer *Oreotragus oreotragus*) or polyandry occurs (e.g. African wild dog *Lycan pictus*) (Davies 1991). Considering the parental investment typical of macropodids (Russell 1974) where forage is readily available and so assistance in food provisioning is unnecessary, it is unlikely that this form of mating system would apply to the quokka.

When male assistance is not required to rear the young, there are several options that have evolved. One male

defending solitary females with small ranges leads to monogamy (e.g. bushbabies *Galago sp.*) or several females with small home ranges leads to polygyny (e.g. tiger *Panthera tigris*) (Davies 1991). Variations in the number of males defending the ranges of several females lead to uni-male polygyny (e.g. black-tailed prairie dog *Cynomys ludovicianus*) or multi-male polygyny (e.g. lion *Panthera leo* and chimpanzee *Pan troglodytes*) (Davies 1991).

Alternatively, where males are not required to successfully raise the young and females occur in stable groups and undefendable ranges, harem polygyny may evolve. In red deer *Cervus elaphus* and gelada baboon *Theropithecus gelada*, one male defends a small, stable group of females (Clutton-Brock et al. 1985; Hill & Dunbar 1998), while in the multi-male polygynous African buffalo *Syncerus caffer* several males associate with large stable groups and individually defend receptive females (Sinclair 1977).

Finally, where males are not required to successfully raise their young and females occur in unstable groups in poorly defendable home ranges, three mating systems may result. Polygynous males may defend large, resource-based territories and mate with females from large unstable groups as they pass through (e.g. white rhinoceros *Ceratotherium simum*) (Davies 1991; Owen-Smith et al. 1997). Alternatively males may lek and defend small, clustered mating territories which females visit solely for mating (e.g. Uganda kob *Kobus kob*) (Clutton-Brock et al. 1993; Davies 1991). Scramble competition polygyny may arise when males search widely for solitary or small groups of receptive females which they may guard temporarily (e.g. polar bear *Ursus arctos* and African savannah elephant *Loxodonta africana*) (Davies 1991; Moss 2001). Finally, large unstable migratory herds where males may defend and mate with individual females or harems, or where they create temporary territories when the migration halts results in polygyny (e.g. blue wildebeest *Connochaetes taurinus*) (Davies 1991).

Evidence of similarity in home range size between male and female quokkas suggests monogamy may be the mating system (Hayward et al. 2004), although the male, weight-based dominance hierarchy (Kitchener 1972; Kitchener 1981; Packer 1969) indicates polygyny may be operating. I hypothesised that the degree of home range overlap of one sex on the same and other sex (as discussed) would indicate the type of mating system the species has. If male home ranges overlapped females extensively, but hardly overlapped those of other males, then polygyny is likely to be in operation (Fig. 1a). If female home ranges overlapped males extensively, but hardly overlapped those of other females then polyandry may be in operation (Fig. 1b). If home ranges of males and females overlapped equally, then the mating system may be monogamous (Fig. 1c).

## METHODS

Quokkas were trapped at five sites in the northern half of the jarrah forest bioregion (Hayward et al. 2003) (Fig. 2). Each of these sites was a swamp in the upper reaches of creek systems dominated by *Taxandria linearifolia* (Hayward et al. 2008). These sites are effectively isolated from other sites because the habitat changes in the lower reaches of creeks to become unsuitable for quokkas. Quokkas are almost entirely restricted to the swamps or their near surrounds (Hayward et al. 2004; Hayward et al. 2005b). Four of these sites were baited monthly with sodium monofluoroacetate poisoned dried meat baits targeting the European red fox (*Vulpes vulpes*), while the Victor Road site remained unbaited (Hayward et al. 2003).

Over 21,000 trap nights conducted seasonally at these five sites (range 2592 – 4976 trap nights), yielded 62 captures of new adult individuals and 186 recaptures (Hayward et al. 2003). Mark-recapture estimates suggested there were 10 individuals at Chandler (6

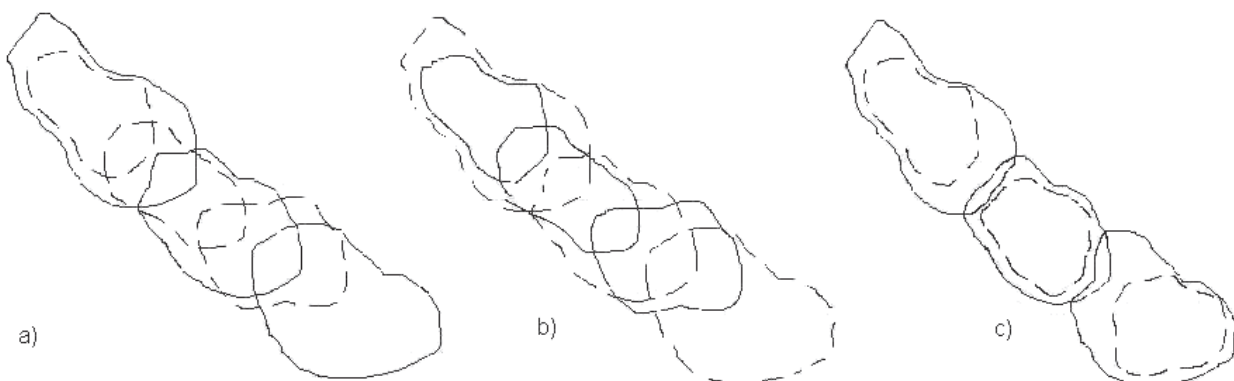


Figure 1. Schematic representation of how home range overlap can indicate the mating system of a species. In a), the home ranges of males (filled lines) overlap those of females (dashed lines) extensively but barely overlap other males – this implies polygyny. In b), the home ranges of males overlap those of other males extensively but females barely overlap other females, but overlap several males – this implies polyandry. In c), the home ranges of one male and one female overlap but are largely separate from adjoining home ranges indicating monogamy.

collared), 21 individuals at Hadfield (15 collared), 36 individuals at Kesners (18 collared) and nine individuals at Victor Road (all collared) (Hayward et al. 2004; Hayward et al. 2003). Only one quokka was trapped at the Rosella Road site despite 4607 trap nights (Hayward et al. 2003) so overlap analyses were not possible there. The study was conducted from spring 1998 until spring 2000, which was a period of average temperature and rainfall conditions (Hayward 2002).

Almost all captured quokkas were fitted with radio collars (50 of 62 captured adults) (Hayward et al. 2004). As such, we feel justified in using a simple percentage overlap measure as a predictor of mating system because it should be representative of the entire population, when compared with a null model of random distribution of individuals.

The dense vegetation of the quokkas' swampy habitat meant triangulation was used to locate individuals using the Locate II computer program (Nams 1990). Locations were taken both day and night, as nocturnal home ranges are significantly larger than diurnal ranges (Hayward et al. 2004). Entire home ranges were estimated using 95 percentile kernel estimates in the Ranges V computer program (Kenward & Hodder 1992) for individuals with more than the 40 locational fixes, as this number was found to provide accurate home range estimates (Hayward et al. 2004). Core home ranges were estimated using 50 percentile kernel estimates following identification by incremental area analysis (Hayward et al. 2004). Digitised boundaries of these home ranges were then exported into the MapInfo Professional Version 5.5 geographic information system (MapInfo Corporation 1985–1999) and the percentage overlap ( $O$ ) of home ranges was calculated by dividing the area that one home range covered another home range ( $a_1$ ) by the area of the original home range ( $a_o$ ) using the equation

$$O = \frac{a_1}{a_o} \times \frac{100}{1}.$$

Overlap was calculated for male home ranges overlapping other males, males overlapping females, females overlapping other females and females overlapping males, due to the differences in home range sizes of individual male and female quokkas (Hayward et al. 2004). The mean number of individuals of each sex overlapping other ranges is also reported.

### Data analysis

Non-parametric statistics were used after transformation attempts failed to normalise the data. The Kruskal-Wallis test was used to test differences between sites and the Mann-Whitney test was used to test differences between Kesners and Hadfield, after the eventual exclusion of the Chandler and Victor Road sites, and between the sexes. Chandler was excluded from subsequent analyses because the small population size meant that very few of the five animals collared overlapped one another. Individuals at the unbaited Victor Road site, where predation pressure

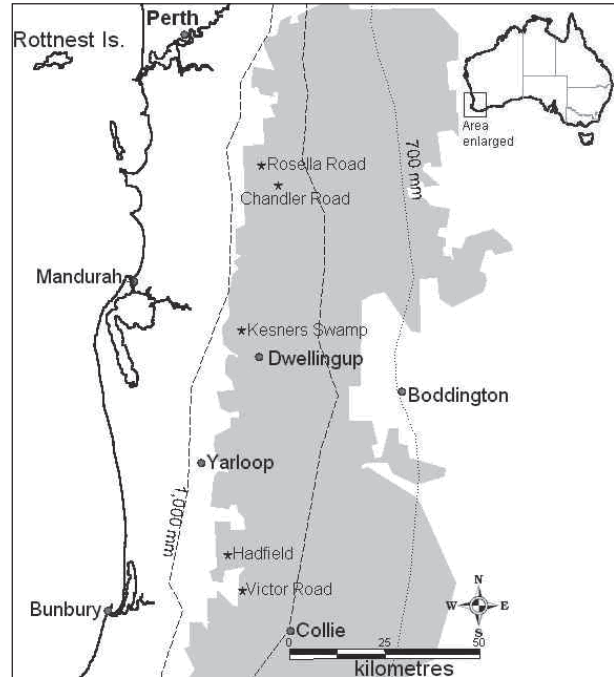


Figure 2. Map of the five study sites (stars) within the northern jarrah forest study region (shaded grey) of south-west Australia where quokkas were trapped and radio collared. Rainfall isohyets (700 and 1,000 mm) are also shown.

is considered higher than other sites, were excluded due to the high degree of home range overlap that has been hypothesised as being due to clumping associated with predator avoidance (Hayward 2002). Relationships between home range overlaps and population density and body mass were investigated using Spearman rank correlations. All tests were conducted in Statview for Windows V5.0 (SAS Institute 1992–1998) and sample means are presented with standard errors.

## RESULTS

Fifty-two percent of the average quokka home range is overlapped by home ranges of other quokkas. This home range overlap is substantially enlarged by individuals at the Victor Road site, where both males and females overlap significantly more than at other sites (Table 1; Fig. 3). Differences between sites arose through a significant negative relationship between home range overlap and population density, that is, as population density increases overlap decreases (Table 2). There is no such relationship between overlap and body mass (Table 2).

The average male quokka overlapped the ranges of four other males and eight females. The average female quokka overlapped the ranges of three other females and eight other males (Table 3). When we look at extensive home range overlaps (i.e. >50%), the average male overlapped the ranges of one other male and three females, while the average female overlapped the range of one other female and three males (Table 3).

The exclusion of the Chandler site, due to its low population density, and Victor Road site, due to clumping behaviour thought to be associated with the higher risk of predation there (Hayward 2002), removes these between sites differences (Table 4). In this case, the mean home range overlap is  $14.8 \pm 2.7\%$ . The mean male home range of 6.92 ha (Hayward et al. 2004) overlaps other

male ranges by  $9.0 \pm 1.5\%$  and females by  $14.5 \pm 2.7\%$  (Fig. 3). The mean female home range of 5.91 ha (Hayward et al. 2004) overlapped other females by  $20.4 \pm 3.8\%$  and males by  $15.0 \pm 2.7\%$  (Fig. 3). These differences were not significant (Table 5) and are illustrated by the real home range overlaps of three male and three female quokkas at the Hadfield site (Fig. 5). There are no changes

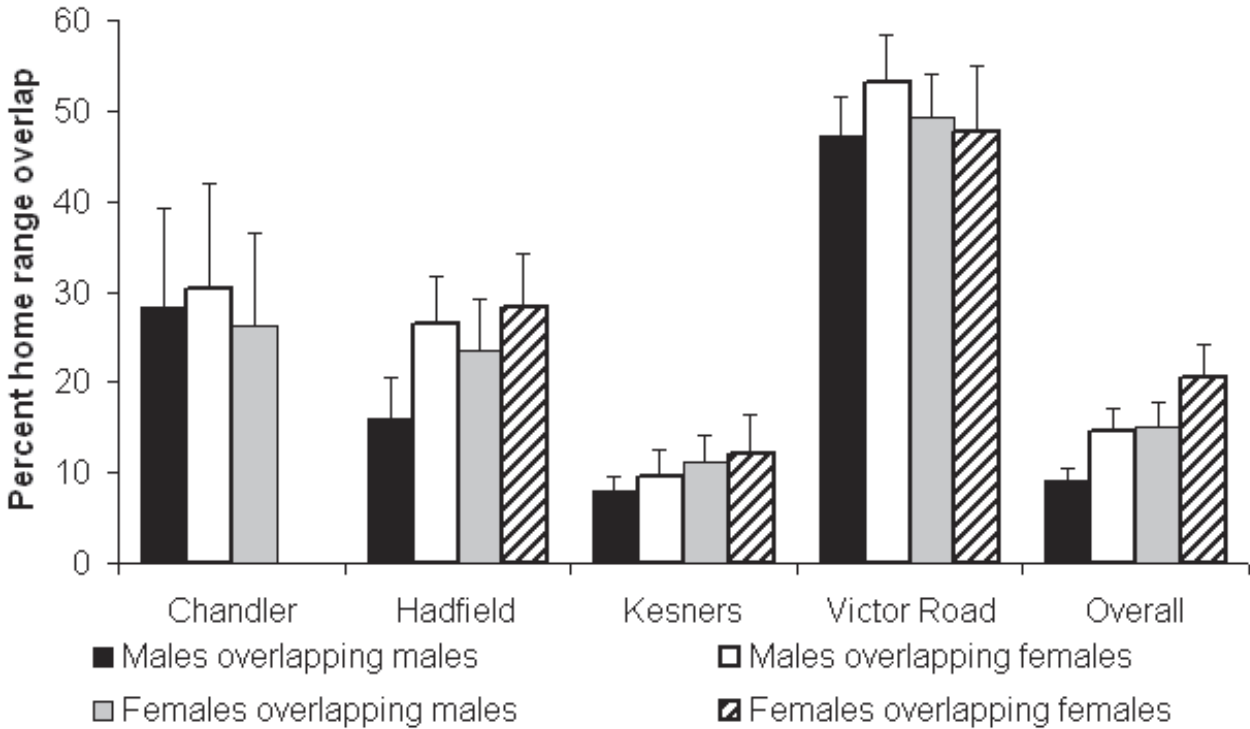


Figure 3. Mean ( $\pm$  s.e.) home range overlap for male and female quokkas at each site and overall (Hadfield and Kesners).

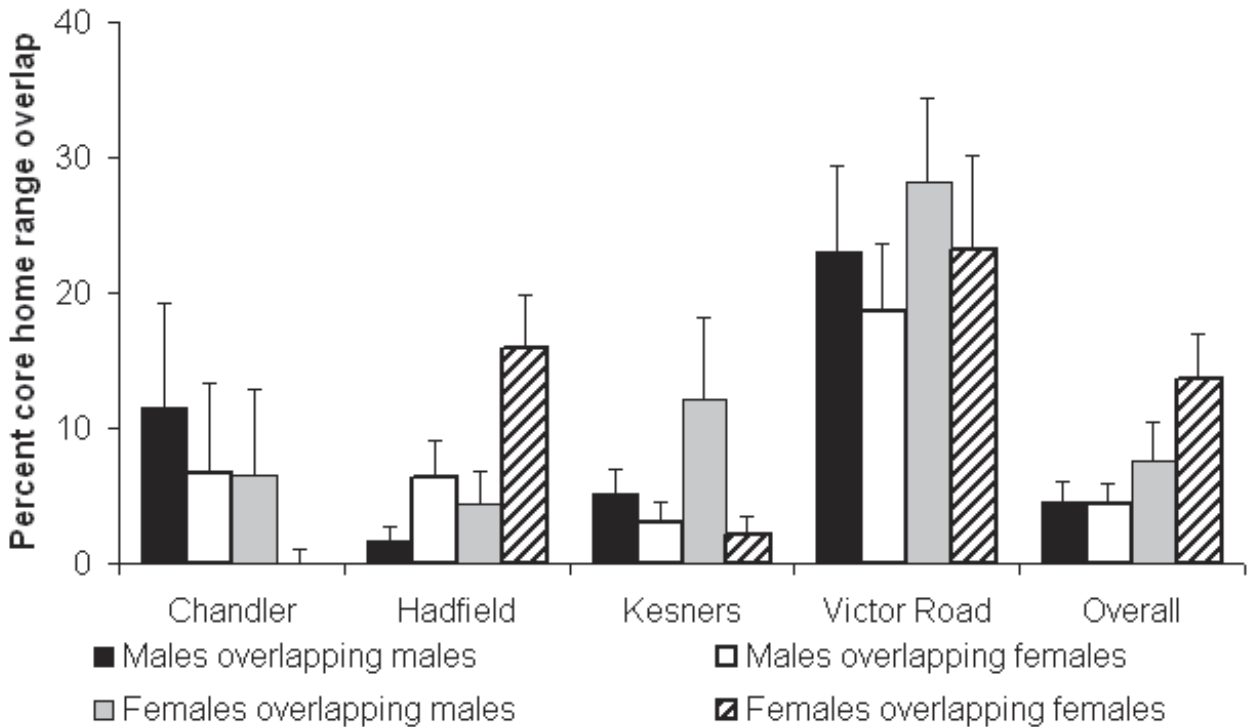


Figure 4. Mean ( $\pm$  s.e.) overlap of core home ranges of male and female quokkas at each site and overall (Hadfield and Kesners).

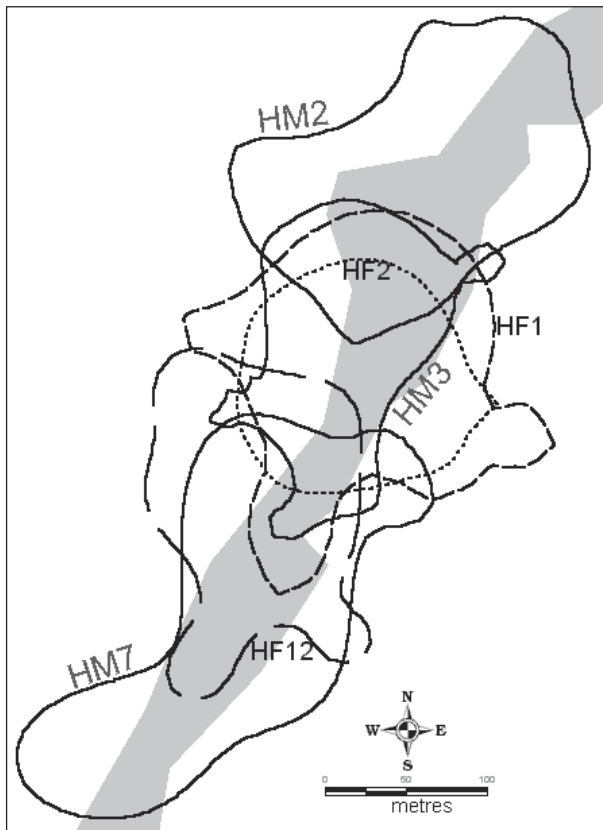


Figure 5. Home ranges of three male (solid lines) and three female (broken lines) quokkas at the Hadfield site showing a typical level of home range overlap for quokkas in the northern jarrah forest. The identification code beside each range refers to Hadfield (H), sex (M/F) and an individual number.

in the number of individual ranges overlapped by each sex with the exclusion of Chandler and Victor Road data.

The core home range overlap is similarly biased by the small population size and lack of abutting home ranges at Chandler and the clumping behaviour of quokkas under increased predation pressure at the Victor Road site, with significant differences existing amongst the sites (Table 1; Fig. 4). These differences cease to be significant with the exclusion of quokkas at these two sites in further analysis (Table 4) and the mean core home range is overlapped by conspecifics by  $7.5 \pm 2.3\%$ . The mean male core home range of 1.47 ha (Hayward et al. 2004) is overlapped by other males by  $4.5 \pm 1.6\%$  and by females by  $4.5 \pm 1.4\%$  (Fig. 4). The mean female core home range of 0.97 ha (Hayward et al. 2004) is overlapped by core ranges of other females by  $13.6 \pm 3.4\%$  and by males by  $7.5 \pm 2.9\%$  (Fig. 4). This increased overlap of female core ranges with other females is significantly larger than the degree of overlap of female core ranges with males (Table 5).

## DISCUSSION

Quokkas on the mainland are essentially solitary creatures unless threatened with high levels of predation (Hayward 2002). Such social behaviour is typical of

the small macropodids (Jarman 1989; Jarman & Coulson 1989).

The results from the overlap of entire home ranges revealed little about the mating system of the quokka, until the Chandler and Victor Road sites were excluded. The exclusion of these sites is justified by the small population size at Chandler (5 collared individuals over 11.3 ha) and the high degree of overlap occurring at Victor Road which probably stems from the higher predation risk there than at the other sites due to the lack of introduced predator control there. Although not significant, the smaller degree of overlap of males on males, once these sites were removed, compared to overlaps of females suggests males are avoiding each other.

With the Chandler and Victor Road sites excluded, the core home ranges of males overlapped other males and females almost equally, whereas core ranges of females overlapped those of other females significantly more than other males. The degree to which males are located by themselves suggests that they are not simply avoiding other males but females as well.

Based on the original hypotheses of this study and the male weight-based dominance hierarchy (Kitchener 1972; Kitchener 1981; Packer 1969), the more extensive home range overlap of males on females than on other males indicates polygyny may be the mating system of the quokka. Multi-male polygyny seems unlikely given the small degree of home range overlap amongst males. Similarly, the lack of observations of overlap between one male and several females suggests harem polygyny is not occurring. There was no evidence of lekking or migration so these forms of unstable group polygyny are also unlikely. The most likely mating system of the quokka is therefore uni-male polygyny where one male defends the ranges of a small number of females (e.g. Fig. 4). The lack of significant results however, means firm conclusions on the quokka mating system cannot be drawn.

An alternative hypothesis is that quokkas at the excluded sites (Chandler and Victor Road) were behaving naturally and reflect the natural flexibility in mating systems practiced by the quokka. At low population densities, the small population sizes might force quokkas to become monogamous due to the lack of mating opportunities, whereas at higher population densities polygyny may occur, and this may break-down at the highest population densities.

The only way to elucidate this feature of the ecology of the quokka with certainty is by conducting genetic analysis at sites of different densities to ascertain the relatedness of pouch young. If one male is siring the majority of offspring then polygyny is confirmed; if each male produces an equal number of offspring then monogamy may be occurring; and if one female has produced offspring from several different males over several breeding seasons then polyandry may be occurring.

The significant negative relationship between overlap and population density is interesting considering the similar significant negative relationship between home range size and population density (Hayward et al. 2004). Home ranges decreased in size and overlap together, rather

than the degree of overlap increasing with population density as more home ranges are fitted into the same bounded area of the swamp vegetation. In such circumstances, polygyny might break down.

The lack of a significant relationship between overlap and body mass is also interesting. For polygyny to occur, one might anticipate that heavier, dominant males would overlap a greater proportion of female home ranges and inhibit the overlap of other males. This is not the case.

The exceptionally high degree of home range overlap amongst individuals at the unbaited Victor Road site was anomalous compared to other sites and is considered a predator avoidance strategy. At Victor Road, the mean home range is overlapped by  $49.3 \pm 5.4\%$  compared to  $16.9 \pm 4.1\%$  at the other sites (Hadfield and Kesners). Proximity to conspecifics was found to minimise the risk of mortality in the quokka (Hayward 2002). Hence, this clumping behaviour is likely to be a feature used by quokkas to reduce predation risk from the introduced, European red fox.

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Table 1

Kruskal-Wallis test statistics for comparison between sites of the percentage of male, female and all home ranges that are overlapped by home ranges of other quokkas. *N* is the aggregate total of each individual's home range overlap with every other individual.

Comparison	Kruskal-Wallis H	d.f.	n	Probability
Sites (All)				
– % of all home ranges overlapped	41.371	3	602	<0.001
– % of male home ranges overlapped	31.476	3	366	<0.001
– % of female home ranges overlapped	36.153	3	236	<0.001
Core home ranges with sites (All)				
– % of all core home ranges overlapped	184.775	3	602	<0.001
– % of male core home ranges overlapped	76.402	3	366	<0.001
– % of female core home ranges overlapped	106.489	3	236	<0.001

Table 2

Spearman rank order correlations between the percentage of home range overlap and a) population density and b) body mass. Population density was calculated using the Jolly-Seber method (Hayward *et al.* 2003). *N* is the aggregate total of each individual's home range overlap with every other individual.

Comparison	Spearman rank correlation rho	Z-value	n	Probability
a) Overlap against population density (all sites)				
– % of all home ranges overlapped	-0.411	-3.701	602	<0.001
– % of male home ranges overlapped	-0.309	-2.783	366	<0.001
– % of female home ranges overlapped	-0.259	-2.333	236	0.003
b) Overlap against body mass				
– % of all home ranges overlapped	0.012	0.096	602	0.941
– % of male home ranges overlapped	0.021	0.176	366	0.915
– % of female home ranges overlapped	0.065	0.536	236	0.639

Table 3

Data on the number of individuals with overlapping home ranges. Overlaps of entire ranges are presented, along with extensive overlaps (i.e., overlaps of greater than 50% of the entire home range).

Site	Male – male	Female – female	Male – female	Male – male >50%	Female – female >50%	Male – female >50%
<i>Number of individuals with overlapping ranges</i>						
Chandler	4	0	3	2	0	1
Kesners	5	3	6	1	1	2
Victor Road	6	4	12	2	2	6
Hadfield	4	3	9	0	1	3
Mean	4	3	8	1	1	3
<i>Percentage of individuals at a site with overlapping ranges</i>						
Chandler	100%	0%	56%	50%	0%	22%
Kesners	39%	47%	35%	4%	8%	11%
Victor Road	70%	80%	95%	27%	36%	43%
Hadfield	72%	56%	83%	8%	22%	27%
Weighted average	62%	54%	65%	17%	19%	25%
S.E.	12%	17%	14%	10%	8%	7%

Table 4

Mann-Whitney test statistics for comparisons of the percentage of male, female and all home ranges that are overlapped by those of other quokkas between the sites when the anomalous Victor Road and Chandler sites are excluded.

Comparison between sites	Mann-Whitney U	d.f.	n	Probability
Entire home range				
– % of all home ranges overlapped	275.5	1	417	0.154
– % of male home ranges overlapped	284.5	1	255	0.205
– % of female home ranges overlapped	235.5	1	162	0.032
Core home ranges				
– % of all core home ranges overlapped	4952.0	1	367	0.195
– % of male home ranges overlapped	3994.0	1	176	0.623
– % of female home ranges overlapped	45724.0	1	191	0.179

Table 5

Mann-Whitney test statistics for comparisons of the percentage of male, female and all home ranges that are overlapped by those of other quokkas between the sexes with animals at Victor Road and Chandler excluded.

Comparison	Mann-Whitney U	d.f.	n	Probability
Sex – overall home range				
– % of all home ranges overlapped	848.000	1	82	0.851
Male mean rank 41.935; female 40.944				
– % of male home ranges overlapped	850.5	1	82	0.832
Male mean rank 41.989; female 40.875				
– % of female home ranges overlapped	892.000	1	82	0.547
Male mean rank 42.891; female 39.722				
Sex – core home ranges				
– % of male home ranges overlapped	2357.000	1	133	0.346
Male mean rank 64.838; female 69.262				
– % of female home ranges overlapped	2529.000	1	133	0.044
Male mean rank 62.309; female 71.908				