Home range and movements of the quokka *Setonix brachyurus* (Macropodidae: Marsupialia), and its impact on the viability of the metapopulation on the Australian mainland

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Abstract

The home range and movements of the quokka *Setonix brachyurus*, a medium-sized macropodid marsupial, were investigated using radio telemetry. Fifty-eight quokkas from five remnant mainland populations in the northern jarrah (*Eucalyptus marginata*) forest of Western Australia were radio-collared and monitored for up to 2 years between 1998 and 2000. Mean ($\pm$ SE) home-range sizes were 6.39 ± 0.77 ha and core ranges averaged 1.21 ± 0.12 ha. Male core home ranges were larger than those of females although not when corrected for body mass. Nocturnal ranges were larger than diurnal owing to nocturnal departures from the swamp. Ranges shifted to the edge of swamps in winter, as the swamps became inundated following rain, and toward the centre in autumn as the swamps dried. Quokka populations are thought to exist below carrying capacity at all sites and this probably caused the lack of dispersal observed in this study. We hypothesize that predation is suppressing population booms which would otherwise drive dispersal and thereby maintain metapopulation dynamics. Without dispersal to rescue unpopulated patches, we conclude that the original quokka metapopulation has collapsed and ameliatory measures are required.

Key words: colonization, dispersal, metapopulation, *Setonix brachyurus*, predation, vulnerable, *Vulpes vulpes*

INTRODUCTION

For collapsed or collapsing metapopulations, knowledge of the home-range size and dispersal distance of the species is important in determining the likelihood of restoring the metapopulation structure and identifying potential management methods. If movements are adequate to facilitate population mixing between patches, then little management may be required. If movements are too small to allow such mixing, then options for restoring connections need consideration, either through population augmentation or habitat management.

A metapopulation is defined here as a series of local populations that are partially reproductively isolated in distinct habitat patches and only occasionally mix through the dispersal of individuals (Chapin, Matson & Mooney, 2002: 306, 384). Local populations of the quokka *Setonix brachyurus* Quoy & Gaimard 1830 in the northern jarrah (*Eucalyptus marginata*) forest occur in distinct patches of *Agonis linearifolia* swamp shrubland that occur in the upper reaches of creek systems. These patches are not connected and are separated by at least a few hundred metres. Quokkas on the mainland have always been associated with such swamps and thickets (Gould, 1863; Shortridge, 1909; White, 1952). Genetic analysis shows that mainland populations once mixed more commonly than today but there is no evidence of panmixia (Sinclair, 1999, 2001; Alacs, 2001). There has been a reduction in gene transfer between populations since the arrival of Europeans to the south-west of Australia in 1829 (Sinclair, 2001). Consequently, we considered the quokkas of the northern jarrah forest to have originally existed as a metapopulation that has now collapsed (Hayward *et al.*, 2003).

The quokka is a vulnerable, macropodid marsupial endemic to the mesic south-west of Australia and two offshore islands (Rottnest and Bald) (Kitchener, 1995). The species suffered a substantial decline in the 1930s that coincided with the arrival of the European red fox *Vulpes vulpes* to the region (Hayward, 2002). At present on the mainland, local quokka populations are unconnected, widely scattered and rarely exceed 30 individuals (Hayward *et al.*, 2003). The quokka's preferred habitat type is common on the western side of the jarrah forest, yet many apparently suitable habitat patches remain unoccupied and it is unknown whether small movements

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of quokkas restrict their ability to colonize these adjacent patches.

There is no published study of the home-range size of quokkas on the mainland, however the movements of those on Rottnest Island have been investigated. Home ranges of six individuals estimated by spool and line using the minimum convex polygon method averaged 0.089 ha in May and 0.036 ha in November with an annual average of 0.13 ha (Kitchener, 1973). Trapping over 10 years on Rottnest Island identified overlapping individual home ranges of 6 ha and 50–100 individuals inhabiting non-overlapping, group territories of up to 15 ha (Holsworth, 1964).

Despite knowledge about the home ranges and movements of the quokka on Rottnest Island, extrapolation to the mainland populations is problematic owing to the vast environmental and ecological differences between the two areas (Main, Shield & Waring, 1959; Hayward, 2002). As well as the importance of determining home-range size on the mainland for management, knowledge of quokka movements is critical for identifying the functional status of the metapopulation following the species decline and ultimately to determine what is required to restore the metapopulation structure. If home ranges are small and traversing long distances does not occur then colonization of new habitat patches may be limited, whereas if home ranges and daily movements are large enough to reach a new patch then colonization is not restricted by movement capacity. As such, this study aimed to determine home range, dispersal and daily movement sizes of quokkas from five local populations at the northern limit of the species mainland distribution and compare these across space and time for each sex to determine if lack of movement is inhibiting metapopulation functioning.

MATERIALS AND METHODS

Study sites

The study was conducted at 5 sites (Chandler, Hadfield, Kesners, Rosella Road and Victor Road) in the northern half of the jarrah forest bioregion (Thackway & Cresswell, 1995) (hereafter termed 'northern jarrah forest') on mainland south-western Australia (Fig. 1). Each site consisted of swamp dominated by *Agonis linearifolia* that occurs in the upper reaches of creek systems on the western side of the jarrah forest and an area of surrounding jarrah (*Eucalyptus marginata*)–marri (*Corymbia calophylla*) forest communities. These 5 sites were the only known extant quokka populations in the northern jarrah forest when the study started.

Trapping and collar attachment

Quokkas were trapped seasonally between spring 1998 and summer 2000/2001 at sites, and using the techniques, described in Hayward et al. (2003). Quokkas were sedated using intramuscular injections with ketamine (9 mg kg^{-1})

and xylazil (2.5 mg kg^{-1}), which provided 30–60 min of sedation during which time most (50/62 adult and 8/15 juvenile) quokkas were fitted with radio-collars (Biotrack, Institute of Terrestrial Ecology, Wareham, U.K.). Three types of collar were used: a brass loop aerial (82%), a whip aerial (8%) and a breakaway variety (10%). Collars weighed 15–37 g (mean = 28 g) and most were < 1% of individual body mass, which is considered energetically costly (Berteaux et al., 1996). The heaviest collar by weight to body mass was 2.3% for a 670-g juvenile with a 15.25-g breakaway collar.

### Radio telemetry and triangulation

Triangulation was used to locate radio-collared quokkas because dense vegetation prevented direct observations. Compass bearings were taken from at least 3 telemetry stations in rapid succession (< 5 min). Telemetry stations were positioned with sub-metre accuracy using a differential global position system (GPS) (Magellan). To avoid the underestimation of home ranges caused by autocorrelation of fixes (Swihart & Slade, 1985; Rooney, Wolfe & Hayden, 1998; Otis & White, 1999), diurnal (daylight) and nocturnal locations were taken no more than once per day, with nocturnal locations occurring from 30 min after sunset until 30 min before dawn.

The Locate II computer program was used to determine the most likely position of a quokka within a 95% confidence or error ellipse (Nams, 1990). Only fixes with error ellipses of < 1 ha were used in the analyses after a pilot study showed that such error ellipses were within 15 m of the true location. The locations of trapped quokkas were also surveyed using differential GPS and were used as nocturnal fixes after incidental observations of traps found no quokkas were captured during the day. This did not lead to any autocorrelated fixes as telemetry was not conducted on trapped animals. Such locations did not extend the home-range size, as quokkas are extremely trap-shy (281 captures out of 21 287 trap nights from Hayward et al., 2003).

Home-range estimation and statistical analyses

Home range was considered to be the area within which an individual occurs 95% of the time. Three methods (minimum convex polygons (MCP); harmonic mean (Dixon & Chapman, 1980); kernel) were used to determine home-range size using the Ranges V computer program (Kenward & Hodder, 1992). All three methods were used after a review of home-range studies recommended a combination of techniques (Harris et al., 1990) and to allow comparison with other home-range studies that only use 1 estimation method.

Utilization plots (Kenward & Hodder, 1992) were used to identify the core home range of quokkas. Incremental area plots were used to determine the number of fixes required to accurately estimate the home range of the quokka (Kenward & Hodder, 1992). When
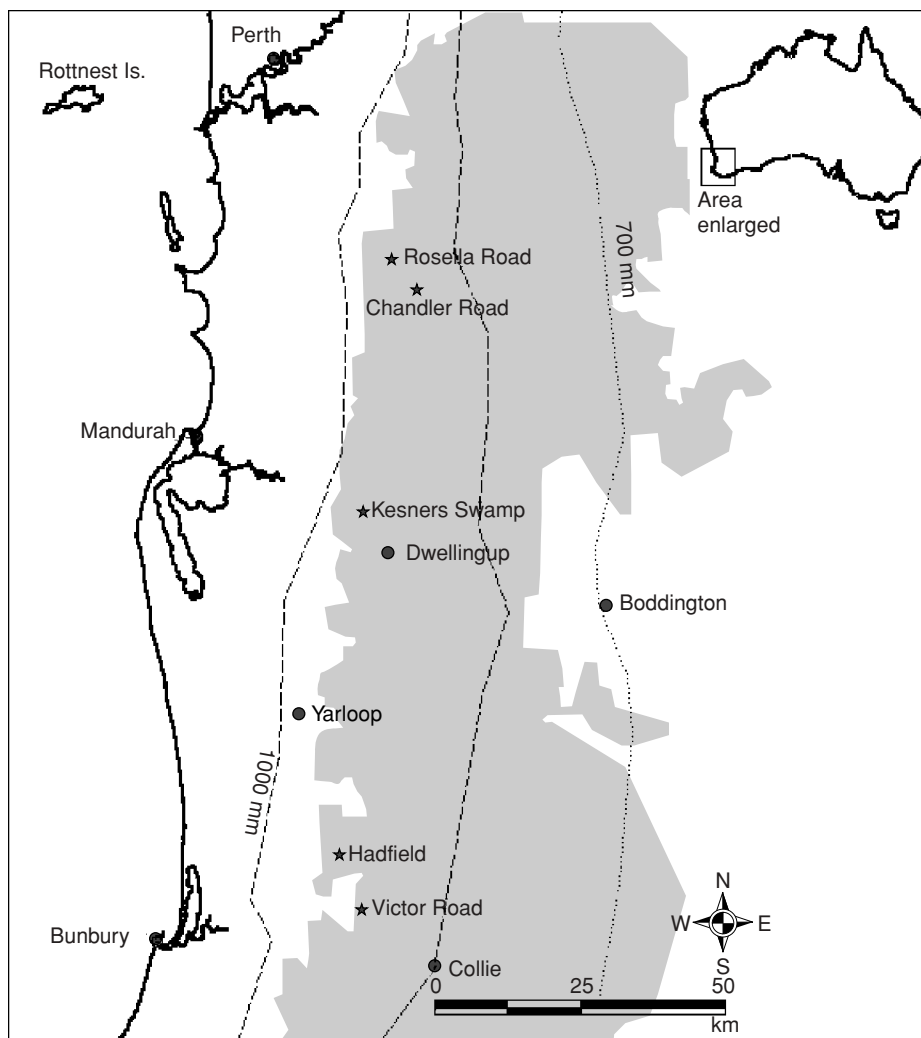
Fig. 1. Map of the study sites in the northern jarrah (*Eucalyptus marginata*) forest (shaded) of south-west Western Australia. Dotted line, 700 mm annual rainfall isohyet; dashed line, 1000 mm isohyet.

individual ranges were sub-divided (such as relative diurnal/nocturnal or seasonal range size), the number of fixes attained was greatly reduced and individual home ranges with 10 fixes or more were used to compare the relative sizes of these ranges. This is unlikely to be an accurate representation of the home-range size during these periods but has been included to compare relative differences between periods.

One individual that was thought to have dispersed was excluded from statistical analyses. Dispersal was considered to be a permanent change in the centre of a home range to a point outside the previous limits of that home range because we aimed to conservatively identify all dispersal events. We acknowledge this could simply define a range shift.

The Gaussian kernel estimate of the centre of each home range (Worton, 1989) was used to investigate seasonal shifts in range centres in a similar fashion to that used to investigate seasonal bird movements (Griffioen & Clarke, 2002). Once the seasonal range centre for each individual was determined, the shift along or across the

swamp between seasons was measured using the MapInfo Professional Version 5.5 geographic information system (MapInfo Corporation 1985–1999). Changes to the centre of the home range across and along the swamps were then tested non-parametrically using the sign test (Zar, 1996).

Population densities were taken from Hayward *et al.* (2003). Non-normal data were log transformed. Results are shown as mean ± standard error.

RESULTS

Between November 1998 and November 2000, 2060 discontinuous fix locations were taken of 58 individuals (33 males and 25 females) at the five sites. These individuals averaged 217 days with a functioning radio transmitter (range 3–612) for an average of 35 fixes (range 2–100). A two-factor ANOVA showed no significant difference between the sexes ($F_{1,3} = 0.817$, $P = 0.371$) or the sites ($F_{3,3} = 0.906$, $P = 0.445$) in the number of
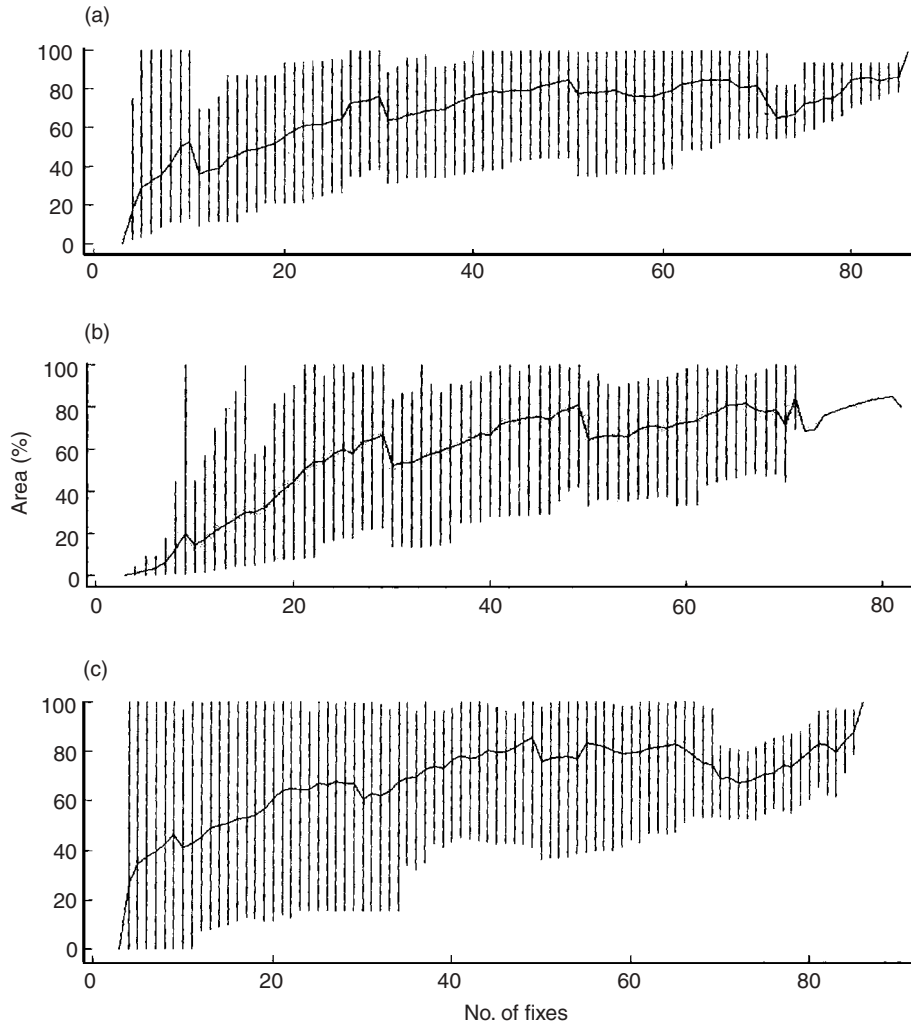
Fig. 2. Incremental area plots of all home ranges of quokkas *Setonix brachyurus* according to: (a) minimum convex polygon (MCP); (b) harmonic mean; (c) kernel methods. Area (%) of the *y*-axis, percentage of the total home range made up by a contour fitted using the number of fixes of the *x*-axis and the 95 percentiles are shown.

days individuals were monitored (interaction site × sex: $F_3 = 1.441$, $P = 0.242$). There was also no significant difference in the number of fixes taken between the sexes (two-factor ANOVA: $F_{1,3} = 0.840$, $P = 0.364$) or the sites ($F_{3,3} = 0.204$, $P = 0.893$) or site × sex ($F_3 = 2.136$, $P = 0.107$).

Incremental area plots showed that *c*. 30 fixes were needed to estimate within 10% of the final home-range size for the MCP method while 40 fixes were required for the harmonic mean and kernel estimators (Fig. 2). There were 27 individuals that had > 40 fixes and these averaged 68 fixes. Utilization plots indicated that the 50 percentile home range was a conservative estimate of the core area used by each animal (Fig. 3).

Despite being biased by outlying fixes (Harris *et al*., 1990), the MCP method generally gave the smallest estimate of home-range size (Table 1) with outliers affecting the shape (particularly length) of the range more than its size (Fig. 4). The harmonic mean method always provided the largest home-range estimate (Table 1, Fig. 4).
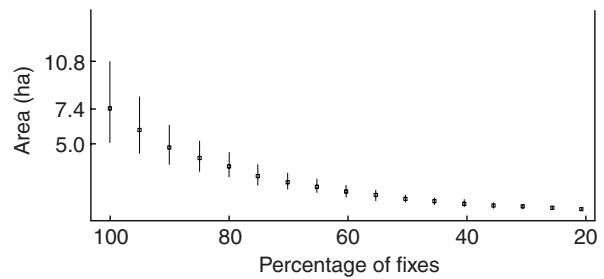

Fig. 3. Utilization plot of all home ranges of quokkas *Setonix brachyurus* determined by the kernel estimator. Smaller error bars and plateau in the decline in home-range size at 50% indicates that this is the percentage of location fixes that should be conservatively used to estimate the core range of quokkas.

The kernel estimator was generally sensitive enough to avoid areas not used (and by appearance not likely to be used) during the animals movements and was considered to be the most representative. It is used to define

Table 1. Mean (± SE) overall and core home-range sizes (ha) of quokkas *Setonix brachyurus* in south-west Western Australia derived by each of the three estimation methods. Individuals with 30 or more fixes (MCP) and 40 or more fixes (harmonic mean and kernel) were used for overall, male, female and site estimates. The sample size of collared individuals is shown in parentheses

Mean	Minimum convex polygons ± SE (*n*)		Harmonic mean ± SE (*n*)		Kernel ± SE (*n*)	
	Overall	Core	Overall	Core	Overall	Core
Overall	5.42 ± 0.51 (25)	0.95 ± 0.11 (25)	10.53 ± 1.39 (21)	1.18 ± 0.14 (21)	6.39 ± 0.77 (21)	1.21 ± 0.12 (21)
Male	6.39 ± 0.90 (11)	1.23 ± 0.19 (11)	11.22 ± 2.35 (10)	1.40 ± 0.22 (10)	6.92 ± 1.16 (10)	1.47 ± 0.18 (10)
Female	4.67 ± 0.52 (14)	0.71 ± 0.19 (14)	9.91 ± 1.66 (11)	0.99 ± 0.18 (11)	5.91 ± 1.07 (11)	0.97 ± 0.12 (11)
Diurnal	2.84 ± 0.31 (37)		5.01 ± 0.62 (37)		3.51 ± 0.40 (37)	
Male	3.04 ± 0.38 (20)		4.89 ± 0.72 (20)		3.60 ± 0.52 (20)	
Female	2.71 ± 0.48 (17)		5.17 ± 1.10 (17)		3.37 ± 0.66 (17)	
Nocturnal	4.56 ± 0.45 (26)		6.86 ± 1.11 (26)		5.48 ± 0.90 (26)	
Male	5.61 ± 0.92 (14)		7.68 ± 1.69 (14)		5.68 ± 1.35 (14)	
Female	4.08 ± 0.49 (12)		5.89 ± 1.45 (12)		5.25 ± 1.19 (12)	
Chandler	4.76 ± 0.96 (3)	1.29 ± 0.23 (3)	8.67 ± 3.68 (2)	1.49 ± 0.67 (2)	6.78 ± 2.83 (2)	1.41 ± 0.36 (2)
Hadfield	3.28 ± 0.40 (7)	0.90 ± 0.07 (7)	5.68 ± 1.70 (6)	0.60 ± 0.08 (6)	2.36 ± 0.23 (6)	0.66 ± 0.08 (6)
Kesners	5.67 ± 0.81 (9)	1.07 ± 0.15 (9)	10.08 ± 1.42 (6)	1.21 ± 0.14 (6)	6.27 ± 0.92 (6)	1.46 ± 0.22 (6)
Rosella	10.60 (1)	1.51 (1)	28.19 (1)	2.37 (1)	8.79 (1)	1.88 (1)
Victor Road	7.89 ± 0.97 (6)	1.04 ± 0.33 (6)	13.54 ± 1.99 (6)	1.46 ± 0.30 (6)	10.01 ± 0.93 (6)	1.34 ± 0.20 (6)
Autumn	3.48 ± 0.45 (32)		7.89 ± 0.97 (32)		7.89 ± 0.97 (32)	
Winter	2.87 ± 0.42 (18)		3.13 ± 0.39 (18)		3.56 ± 0.61 (18)	
Spring	1.62 ± 0.29 (17)		2.494 ± 0.915 (17)		2.098 ± 0.532 (17)	
Summer	1.79 ± 0.38 (19)		3.260 ± 1.472 (19)		2.854 ± 0.724 (19)	
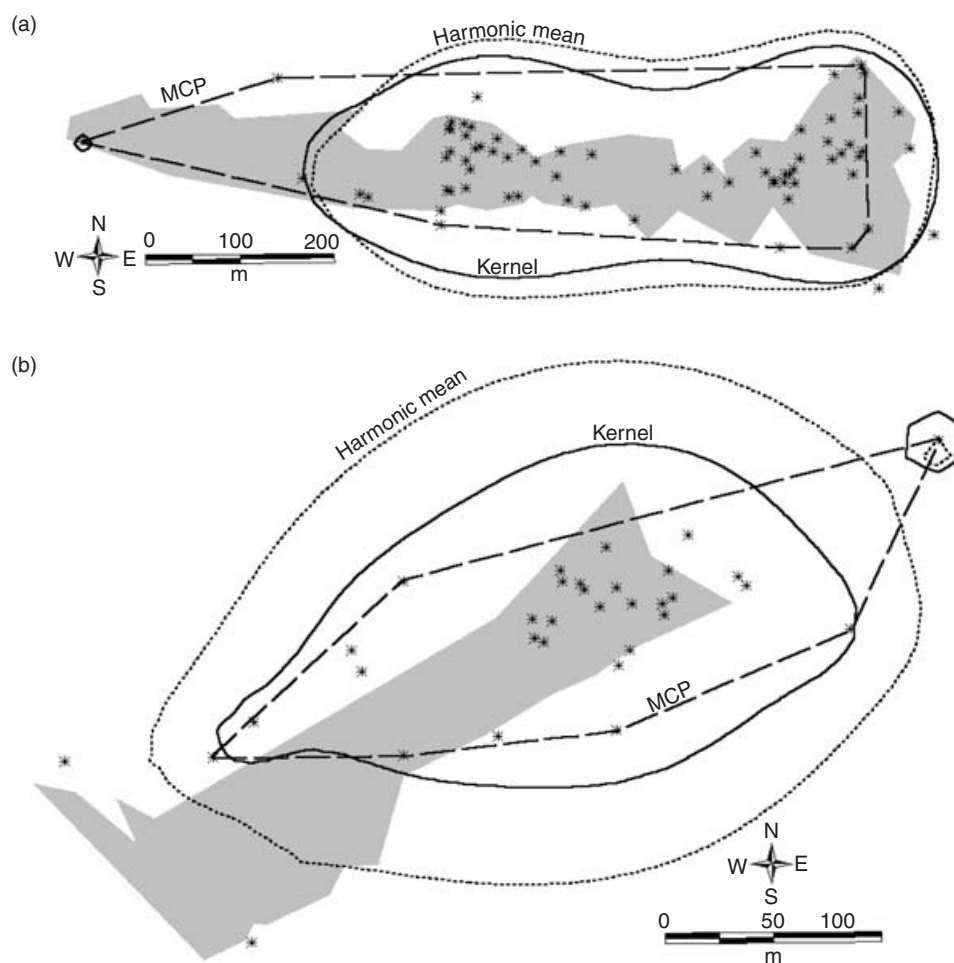
Fig. 4. Comparison between the three estimation methods for: (a) a male quokka *Setonix brachyurus* (VM1) from the Victor Road site; (b) a female quokka (KF11) from the Kesners site; *, individual location fixes; shading, swamp boundary. Circle in top right corner of (b) for all three methods is caused by a discontinuous 95 percentile contour after the two most distant fixes (in the bottom left corner) were excluded. Such discontinuities can indicate multiple range centres or dispersal where a larger number of fixes are involved.

Table 2. Statistical test results on home ranges of quokkas *Setonix brachyurus* estimated by the kernel method. Male–female comparisons use data from home ranges calculated with > 40 fixes, while the remainder use data from home ranges with > 10 fixes. Small sample size precluded doing one large analysis. Two-factor ANOVA with sex and site interactions and ANCOVA on site differences with population density interaction removed could not be conducted owing to inadequate sample size. Bonferroni correction meant that probabilities < 0.007 were classed as significant

Comparison	Test	Interaction probability	Test statistic	Probability
Overall home range				
Females *vs* males	ANCOVA corrected for body mass	0.01	$F_{1,36} = 3.50$	0.069
Diurnal *vs* nocturnal	Repeated measures ANOVA		$F_{1,19} = 4.68$	0.041
Sites[a]	Two factor ANOVA with sex	0.176	$F_{3,58} = 9.41$	< 0.001
Seasons	Two factor ANOVA with sex	0.277	$F_{3,78} = 3.79$	0.013
	Two factor ANOVA with site	0.255	$F_{3,66} = 6.01$	0.263
	Repeated measures ANOVA		$F_{3,19} = 3.93$	0.019
Core home range				
Females *vs* males	ANCOVA corrected for body mass	0.180	$F_{1,19} = 4.35$	0.052
Sites	Two factor ANOVA with sex	0.524	$F_{3,58} = 3.73$	0.019

[a] Rosella Road site excluded owing to presence of only one animal.

home-range sizes hereafter. Accordingly, the mean (± SE) home-range size for quokkas in the northern jarrah forest was 6.39 ± 0.77 ha and the mean core (50%) range size was 1.21 ± 0.12 ha (Table 1). Male home ranges (6.92 ± 1.16 ha) were not significantly larger than those of females (5.91 ± 1.07 ha) when corrected for body mass; however, core ranges of males (1.47 ± 0.18 ha) were significantly larger than those of females (0.97 ± 0.12 ha) (Table 2).

### Home-range differences between the sites

There were significant differences in overall home-range sizes between the sites (Tables 1 & 2) with animals at Hadfield having smaller ranges than all other sites (Scheffe's test: Chandler, $P = 0.0288$; Kesners, $P = 0.0156$; Victor Road, $P < 0.0001$). The core home ranges showed similar results (Table 2) with Hadfield quokkas having significantly smaller ranges than those at Chandler and Kesners (Scheffe's test: $P = 0.0491$ and $P = 0.0282$, respectively). Both entire and core home-range size were significantly negatively related to population density; however, this relationship was stronger for females than males (Fig. 5).

Temporal differences in home-range size

Diurnal home ranges averaged 3.51 ± 0.40 ha and were smaller than nocturnal ranges (5.48 ± 0.90 ha) (Table 1), but these differences were not significant (Table 2). Relative home-range sizes in autumn were significantly larger than in spring (Fig. 6) when sexual differences (Bonferroni/Dunn post hoc test with adjusted significance level of 0.0083: $P = 0.0040$) and site differences (Bonferroni/Dunn post hoc test: $P = 0.0012$) were examined (Table 2). Repeated measures ANOVA of seasonal differences (Table 2) showed autumn home ranges were significantly larger than those of spring (Bonferroni test: $P = 0.0033$).
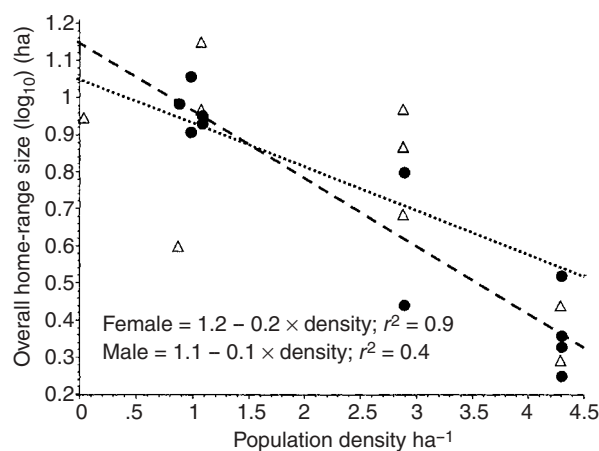
Fig. 5. Regression plot of home-range size of quokkas *Setonix brachyurus* estimated by the kernel method plotting males (open triangles) and females (closed circles) against population density at each site. Male regression line, dotted; female regression line, dashed.

Female = 1.2 − 0.2 × density; r^2 = 0.9
Male = 1.1 − 0.1 × density; r^2 = 0.4
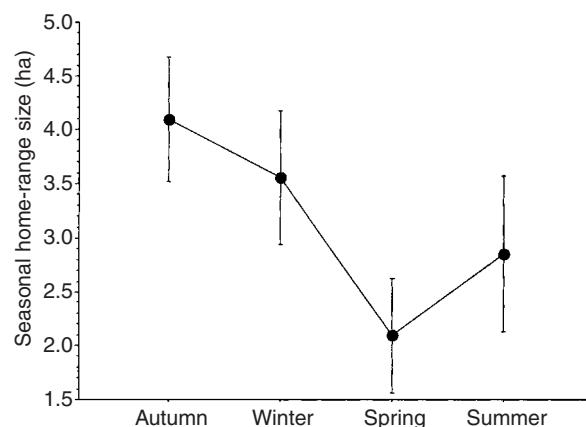
Fig. 6. Variation in relative seasonal home-range size of the quokka *Setonix brachyurus*. Sample sizes are shown in Table 2.

Movements of home-range centres

Using the Gaussian kernel estimate of range centres (Worton, 1989), individual quokkas showed no significant difference in the direction of movements upstream or downstream between the seasons. There was a significant difference in movement patterns across the swamp where quokkas moved toward the edge of the swamp significantly more than toward the centre (Sign test: $n = 24$, $P = 0.041$) between autumn and winter.

Dispersal

Of 50 collared adult quokkas, only one showed any evidence of a shift in home range that may have indicated dispersal, although more likely it was simply a shift in home range. An adult male was initially trapped in the western section of the Chandler swamp and remained there for the following 2 months. He then moved approximately 1 km to the east where he stayed until his collar failed 7 months later. This male made three forays back into his initial home range during the first month after the dispersal but never stayed more than a few days. A week after this dispersal was first observed, a new adult male was trapped in the western section where, radiotelemetry revealed, he took up residence. The new adult male (3.57 kg) was larger than the displaced male (2.98 kg) suggesting a dominance or agonistic encounter may have initiated the movement. No other adults were observed shifting home range and no adult or juvenile moved between swamp systems. Considering the high proportion of individuals collared and the subsequent trapping of individuals that had previously escaped their collars, it is unlikely that dispersal events were missed. Unpopulated *Agonis linearifolia* swamps occur within 600 m of each of the study sites and each of these were surveyed when individuals were censored.

Ten juvenile quokkas were also collared at some stage during this study. Two escaped their breakaway collars and were not seen again. Of the remaining seven males and one female that continued transmitting or were recaptured, only one male (from Hadfield swamp) had moved > 100 m from the natal home range or from where it was first trapped. This individual was later captured 900 m downstream as a sub-adult, but was not trapped in the following five seasonal trapping sessions. All others remained near their original capture location.

DISCUSSION

Home ranges

The absence of sexual differences in home-range size may be explained by the dominance hierarchy created by male quokkas (Packer, 1969; Kitchener, 1972). The dominant male may well have a large home range that encompasses the range of more than one female, but he may also exclude subordinate males from having such large home ranges. In addition, quokkas are sexually size-dimorphic (Hayward,

2002; Hayward *et al.*, 2003) and these features suggest that sexual differences in home-range size should exist with males having larger ranges than females.

Six quokkas on Rottnest Island moved continuously throughout the night before returning to a regular rest site (Kitchener, 1973). Captive quokkas sleep during the day with evening and early morning (generally pre-dawn) peaks in foraging (Packer, 1969). This activity pattern explains why the nocturnal home range of the quokka in the northern jarrah forest was larger than the diurnal range. On the mainland however, any differences are minimized by the diurnal resting behaviour of quokkas, where individuals rested within the swamp during the day near to where they ceased their nocturnal activities as opposed to an actual nest site. The absence of specific diurnal rest sites concurs with the lack of evidence found during specific searches for quokka 'nests' on the mainland (M. Dillon, pers. comm.). Such resting behaviour meant that diurnal ranges were as long as nocturnal ranges but only slightly exceeded the boundary of the *Agonis*-dominated swamp vegetation.

Factors affecting home-range size

Increased population density resulted in reduced home-range size and this is consistent with the hypothesis that the study sites support populations below carrying capacity (Hayward *et al.*, 2003). This suggests that dispersal will only occur once populations attain higher densities. That females exhibit this relationship more markedly than males suggests that males may be more tolerant of other males compared to the tolerance of females to other females; or the dense vegetation may reduce interactions amongst promiscuous males intruding upon adjacent territories while seeking polygynous mating opportunities.

Seasonal relative home-range size is cyclical, peaking in autumn and declining to spring before increasing again (Fig. 6). In the northern jarrah forest, autumn is the peak period of water restriction (Commonwealth Bureau of Meteorology). Available forage is also likely to be scarce at this time, particularly if quokkas are only selecting the freshest available browse (Norbury, Sanson & Lee, 1989). Conversely, spring is at the end of the highest rainfall period when water (and probably fresh plant growth) is abundant and home ranges are smallest. This pattern of seasonal variation in home-range size on the mainland contrasts with that observed on Rottnest Island, where ranges increased in wetter months (Kitchener, 1973). This is probably owing to the restriction of the quokkas to water sources over summer on Rottnest Island where home ranges increase when this restriction is eased in winter, although it may also be an artefact of the small sample size (six) of the Rottnest study.

Seasonal movements in home-range centre

By the beginning of the high rainfall period (winter) each year the swamps are almost completely dry after

6 months with minimal rain (Bureau of Meteorology). Thus, in autumn, quokkas moved to the centre of the swamp probably either searching for water to satisfy their high requirements (Main & Bakker, 1981) or to obtain refuge within the dense vegetation there. While home ranges became central within the swamp, they also covered a larger area at this time as quokkas moved further to obtain sufficient forage and water. The onset of winter rains greatly reduces the amount of dry land available as swamps become inundated and so quokkas moved to the very edge of that vegetation. By doing so quokkas may increase their susceptibility to predation in winter and spring by minimizing their use of refugia.

Dispersal

Only one out of 50 radio-collared adult quokkas showed any evidence of long distance (1 km) range shift or dispersal. Another larger male was captured immediately after this movement and thereafter repeatedly in the same area and it is possible that this new male forced this movement. This supports dominance hierarchy studies (Packer, 1969; Kitchener, 1972), and such behaviour may be the catalyst for dispersal at sites at carrying capacity. Of the other uncollared adults or adults that were collared for only a short time, all were recaptured in the same area as their initial capture. Several individuals were trapped repeatedly from pouched young through to young-at-foot at which time a radio-collar was attached. One juvenile female and seven juvenile males were collared or recaptured from pouch young stage until adulthood. All those individuals stayed within the natal swamp and generally within their natal home range. Only one individual (male) dispersed from its natal home range *c*. 1 km downstream before losing its collar. This occurred at Hadfield swamp, the site with the highest quokka density (Hayward *et al*., 2003). The fact that this site was considered to be below carrying capacity (Hayward *et al*., 2003) may mean that only small, within-patch, dispersal distances are currently necessary to avoid inbreeding. The absence of dispersal at the other mainland sites may also be owing to their low population densities.

Each of the other 58 collared (out of 95 individuals and 62 adults captured) and recaptured individuals persisted within a short distance of their initial capture site. Intensive searches were made of surrounding sites for collared individuals that were censored. Consequently, it is unlikely that dispersal events were missed and not recorded.

Implications for the metapopulation

Given the linear nature of the quokkas preferred riparian habitat, the average home-range size of just over 6 ha roughly equates to *c*. 600 m along the swamp and 100 m across it (Fig. 4). Despite their relatively small home ranges, quokkas are highly mobile and the longest recorded movement was of an adult male that had been trapped for several years at a site and was later found dead beside a road approximately 10 km away (not part of this study) (R. Brazell pers. comm.). Movements of 600 m would allow quokkas to access adjacent swamps either within the same catchment or across a ridge into an adjacent one and movements of 10 km obviously would allow access to more distant patches. That such movements were not observed adds weight to the hypothesis that fundamental metapopulation processes are no longer occurring (Hayward *et al*., 2003), particularly considering genetic analysis suggested a much higher rate of movement between populations historically (Sinclair, 1998) and no recent movements (Alacs, 2001).

There are various explanations for the lack of observed inter-patch movement. First, inter-patch movement will be restored once individual populations reach the carrying capacity of the habitat. Considering the flexibility in home-range size based on the relationship with population density, it may be a long time before inter-patch movements occur. Second, macrohabitat does not seem to be the limiting factor as *Agonis linearifolia* dominated swamps occur widely in the northern jarrah forest (Havel, 1975*a*,*b*) and there is no reason or evidence to suggest that the distances between them have increased, thereby reducing quokka dispersal.

The preference of quokkas for early seral stage habitat (< 10–15 years post-fire) (Christensen & Kimber, 1975; Hayward, 2002) suggests microhabitat factors may also be an important driver of dispersal. Once the habitat reaches the 10- to 15-year post-fire seral stage, quokkas may be forced to disperse as the habitat no longer provides adequate predation refuge and food resources. This issue will be investigated in future studies. This study was conducted during a period of average climatic conditions (Hayward, 2002) so it is unlikely that unusual short-term temperature or rainfall phenomena inhibited inter-patch movement.

Conclusion

The small distances moved by quokkas increase concerns for the persistence of the overall metapopulation. Their restriction to the natal swamp and even natal home range means there is little potential for recolonization of adjacent patches and the threat of genetic problems associated with inbreeding depression is high (Frankham, 1995).

Although the applicability of metapopulation theory to large mammals has been questioned owing to the difficulty in observing inter-patch movements and colonization/extinction events because of their longevity, other mechanisms can be used to identify whether a species does exist as part of a metapopulation (Elmhagen & Angerbjorn, 2001). The absence of inter-patch movements by the quokka seems unlikely to be owing to distances between patches but rather the inhibiting effect of introduced predators (established for 60 years) and possibly an absence of suitable microhabitat patches within dispersal distance (Christensen & Kimber, 1975; Hayward *et al*., 2003). The infrequency of population turnover was probably originally exacerbated

by the specific habitat requirements of the quokka (Christensen & Kimber, 1975), but instead of colonizing new sites, the increased mortality risk of dispersing meant that localized extinction occurred. Thus, although no inter-patch movements were recorded, the quokka does exhibit the features (discrete habitat patches supporting breeding populations and ecological processes, such as growth rates, acting on local and regional scales (Hayward *et al*., 2003)) that characterize metapopulations in large mammals (Elmhagen & Angerbjorn, 2001). Therefore, this study supports the conclusions that the quokka in the northern jarrah forest did originally exist as a classic metapopulation which is now either collapsing or has collapsed (Hayward *et al*., 2003).

The cause(s) of the apparent lack of inter-patch movement remain(s) hypothetical. The existence of populations well below carrying capacity seems the most probable explanation (Hayward *et al*., 2003). Predation pressure may be exacerbating this problem through the maintenance of low population density and by preying upon dispersing individuals. That predation on dispersing individuals was not observed in this study suggests there may have been selection for non-dispersal or philopatry in the quokka since the arrival of the fox into the south-west of Australia in the early 1930s (King & Smith, 1985).

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