

HABITAT USE OF THE QUOKKA, *SETONIX BRACHYURUS* (MACROPODIDAE: MARSUPIALIA), IN THE NORTHERN JARRAH FOREST OF AUSTRALIA

MATT W. HAYWARD,* PAUL J. DE TORES, AND PETER B. BANKS

Department of Conservation and Land Management, Dwellingup Research Centre, Banksiadale Road, Dwellingup, Western Australia 6213, Australia (MWH)

School of Biological, Earth and Environmental Science, University of New South Wales, Sydney, New South Wales 2052, Australia (MWH, PBB)

Department of Conservation and Land Management, Wildlife Research Centre, P.O. Box 51 Wanneroo, Western Australia 6946, Australia (MWH, PJdT)

Present address of MWH: Terrestrial Ecology Research Unit, Nelson Mandela Metropolitan University, P. O. Box 77000, Port Elizabeth, 6031, Eastern Cape, South Africa

Habitat use of quokka (*Setonix brachyurus*) in the northern jarrah forest of Western Australia was determined by monitoring movements of 58 quokkas over 2 years in 5 local populations. Quokkas were largely restricted to *Agonis* swamps that occur patchily throughout the jarrah forest. Within swamps, they are habitat specialists, preferring early seral stages that have been burned within the previous 10 years. This preference derives from a combination of dietary requirements and refuge from predation. As swamps mature they become suboptimal, forcing quokkas to colonize new patches. Since the collapse of the metapopulation following the introduction of the European red fox (*Vulpes vulpes*) in the 1930s, quokkas have been forced to remain at a site because predation inhibits dispersal.

Key words: Australia, fire regimes, habitat mosaic, metapopulation, quokka, seral stage, *Setonix brachyurus*

The quokka (*Setonix brachyurus*, Quoy and Gaimard, 1830) is a small (2.5- to 4.5-kg), herbivorous, macropodid marsupial that, like many other medium-sized mammals in Australia (Burbidge and McKenzie 1989; Lunney 2001; Lunney and Leary 1988; Morton 1990), has faced widespread decline and extinction (Hilton-Taylor 2000). Quokka distribution has been reduced by almost 50% since the arrival of the European red fox (*Vulpes vulpes*) to the region in the 1930s (Hayward 2002).

Quokkas originally formed a classic metapopulation (Hanski and Gilpin 1991). Local populations were probably restricted to swamp shrublands that occupy broad, flat, upper reaches of creek systems from which individuals occasionally mixed with adjacent populations (Hayward et al. 2003). This metapopulation structure is thought to be in a state of collapse with localized extinction rate exceeding colonization rate (Hayward et al. 2003). Thus, it is imperative to identify and protect remaining habitat used by the quokka.

Herein, we report on the habitat preferences and requirements of the quokka at mainland sites in the northern jarrah

forest of Western Australia and assess the implications of these on the metapopulation dynamics and conservation of the species. We hypothesize that specific habitat requirements of the quokka may be further inhibiting population growth (Hayward et al. 2003).

MATERIALS AND METHODS

Our study area was the mesic southwestern corner of Western Australia (Fig. 1) and comprised the northern one-half of the jarrah forest bioregion (Thackway and Cresswell 1995). This region occurs on the Darling Plateau east of Perth, south to Collie, and is bounded to the east by the agricultural wheatbelt (from 31°54'S, 115°51'E to 33°32'S, 116°34'E). The region supports tall, open and closed *Eucalyptus* forest in the uplands and heath on the coastal plain. Annual rainfall ranges from 700 to 1,400 mm.

Digitally imaged aerial photographs of the study area (Western Australian Department of Land Administration–Panairama, Perth, Australia) were imported into a geographic information system (GIS; MapInfo Professional Version 5.5, MapInfo Corporation Inc., Troy, New York) and referenced to known locations (<1-m accuracy). Maps of the habitats at 5 sites (shown as 1–5 on Fig. 1) were created and described based on structural, floristic, and other habitat characteristics (Hayward 2002). Field surveys were undertaken to confirm these habitat units.

We differentiated habitat units based on floristics by using TWINSPLAN (Hill 1979; Oksanen and Minchin 1997). Microhabitats

* Correspondent: hayers111@aol.com

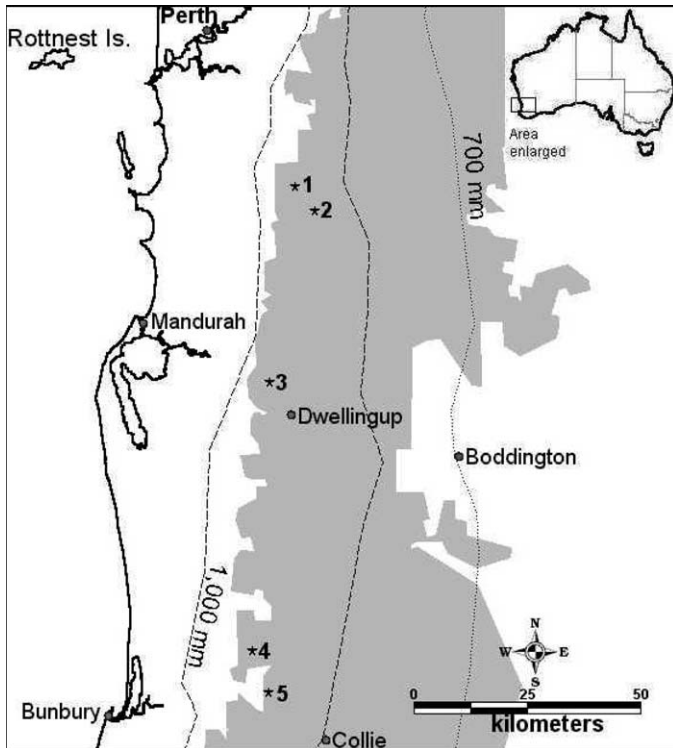


FIG. 1.—Study region and study sites (numbered 1–5) southeast of Perth, Western Australia. The shaded section illustrates the extent of jarrah-marri forest and the 700-mm (dotted line) and 1,000-mm (dashed line) rainfall isohyets are shown.

within *Agonis* swamp shrubland habitat type were described based on the features they had acquired since they last burned, such as species richness, vegetation density, and leaf litter depth, rather than with TWINSpan (Hayward 2002). These microhabitat units were statistically differentiated by analysis of variance (ANOVA) of the factor scores that had been identified with principal component factor analysis (Hayward 2002) in the Statview computer program (SAS Institute Inc., Cary, North Carolina). The area covered by each habitat unit at each site was calculated with MapInfo GIS software (MapInfo Corporation Inc.).

Macrohabitats were defined as swamp (consisting of *Agonis* swamp shrublands, bulch swamp forest, and paperbark swamp habitat types) and forest (all forest habitat types) habitat. *Agonis* swamp shrublands are tall, closed shrublands dominated by *A. linearifolia*, with *Leptospermum tetraquetrum*, *Gahnia decomposita*, and *Astartea fascicularis* in the sedge-dominated understory (Hayward 2002). Bulch swamp forests occur as small fragments within the swamps and are dominated by a canopy of *Eucalyptus megacarpa* with an understory of *Agonis linearifolia*, *Hypocalymna cordifolium*, and *Boronia molloyiae* (Hayward 2002). Paperbark swamp consists of small, species-rich pockets within the *Agonis* swamp dominated by swamp paperbark (*Melaleuca raphiophylla*). Surrounding the swamp is an ecotone bulch (*E. megacarpa*)–blackbutt (*E. patens*) open forest with a shrub understory of *Bossiaea aquifolium*, *Mirbelia dilatata*, and *Thomasia* sp., which becomes typical jarrah (*E. marginata*)–marri (*Corymbia calophylla*) open forest on the slopes and ridge tops (Hayward 2002).

Five sites in the northern jarrah forest that supported small populations of quokkas were trapped to derive mark–recapture population estimates (Hayward et al. 2003) and obtain individuals to radiocollar (Hayward et al. 2004). At each site, 30 wire cage traps were placed inside the swamp and 30 were placed 50–100 m outside

the swamp. These were set for 8 consecutive days at each site during each season (Hayward et al. 2003).

Between November 1998 and November 2000, 58 quokkas (33 males and 25 females) were fitted with radiocollars and 26 of these were tracked long enough to obtain stable home-range estimates. Tracking locations of collared individuals were determined at least 1 day apart to reduce the effects of autocorrelation (Swihart and Slade 1985). Incremental area analysis (Kenward and Hodder 1992) showed that >40 radiolocation fixes were required to determine each home range (Hayward et al. 2004). Triangulation using the Locate II computer program (Nams 1990) was used to determine the position of collared individuals. Only location fixes with error ellipses (a measure of accuracy) of <1 ha were used in the analyses after a preliminary study found that such ellipses were within 15 m of the actual location of the transmitter (Hayward et al. 2004). Nocturnal tracking locations were made from 30 min after sunset to 30 min before sunrise.

The area of each habitat type within 200 m of swamps at each site was analyzed with Ranges V computer program (Kenward and Hodder 1992). Availability of each habitat unit was quantified as proportion of total area encompassed by the 95 percentile kernel estimate (Kenward and Hodder 1992) of home range.

Macrohabitat use was calculated by comparing the location of newly trapped individuals in either swamp or forest habitats by using chi-square tests with equal use of both expected, and ANOVA was used to test for daily and seasonal differences. Specific preference for each microhabitat unit was determined with the Jacobs index (Jacobs 1974) by using Ranges V (Kenward and Hodder 1992) based on radiotelemetry locations of collared individuals. The Jacobs index (*D*) is a derivation of the electivity index (Ivlev 1961), which is independent of the relative abundance of the habitat type (Krebs 1989). The value of *D* is calculated as

$$D = \frac{r - p}{r + p - 2rp}, \quad (1)$$

where *r* is the proportion of microhabitat type in a quokka's home range and *p* is the proportion of locational fixes occurring within that habitat type (Jacobs 1974). Jacobs index values range from +1 (maximum preference) to –1 (maximum avoidance) with values near zero indicating use of a habitat type in proportion to that habitat's availability within the home range (Jacobs 1974). Each habitat unit was preferred or avoided if the mean value of the Jacobs index was significantly different from zero according to single group *t*-tests (Palomares et al. 2001). Habitat units that showed no variation in Jacobs index (i.e., those always –1) were not tested with *t*-tests but were considered as being significantly avoided.

Because each site supported different *Agonis* swamp seral stages, direct comparison between the habitat preferences of individuals was impossible. Consequently, we grouped swamp seral stages into 3 categories according to their fire history: young (<10 years postfire), intermediate (10–19 years postfire), and mature (>19 years postfire) seral stages. Young *Agonis* swamp has the highest floristic richness and vegetation density (Hayward 2002). This declines in intermediate seral stages until only 3 species remain in mature seral stages (Hayward 2002). At least 2 of these groupings occurred at each site except 1 and it was excluded from analysis. Two sites had all 3 habitat groupings. The median habitat preferences of individual quokkas were taken to provide an overall indicator of habitat preference within swamp habitats.

The project was approved by CALM Science Ethics Committee. Trapping permits were issued by CALM (license number SF002928). Procedures used followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

TABLE 1.—Availability (%) of major habitat types and estimates of quokka populations at each site (1–5) along with number of individuals collared and number that had sufficient fixes to derive accurate home-range estimates. Jolly–Seber population estimates are from Hayward et al. 2003.

Habitat type	Site				
	1	2	3	4	5
Total area (ha)	206	231	100	209	83
<i>Agonis linearifolia</i> swamp	6.34	4.84	9.80	3.14	8.68
Recent (<5 years since fire)	0	0	0	0	4.04
5–9 years since fire	0	0	0	1.62	0
10–14 years since fire	2.54	4.84	7.47	0	0.61
15–19 years since fire	0	0	0	1.30	2.20
20–24 years since fire	3.80	0	2.10	0.08	0.35
>25 years since fire	0	0	0.23	0.14	1.58
Blackbutt (<i>Eucalyptus patens</i>) open forest	2.01	0	1.23	0	1.41
Bullich (<i>E. megacarpa</i>) swamp forest	0	0.74	1.78	0.49	0
Bullich–blackbutt open forest	0	13.06	6.81	5.25	0
Jarra (<i>E. marginata</i>)–marri (<i>Corymbia callophylla</i>) open forest	58.88	64.64	53.81	79.04	75.22
Other	32.77	16.72	26.57	12.08	14.69
Estimated population size ($\bar{X} \pm SE$)	1	10 \pm 0	36 \pm 6	29 \pm 5	9 \pm 1
Total number collared	1	6	23	17	11
Number of individuals with accurate home-range estimates	1	3	9	7	6

RESULTS

The dominant habitat type at all sites was jarrah–marri open forest ($66\% \pm 5\%$; $\bar{X} \pm SE$ throughout) with smaller areas of bullich–blackbutt open forest ($5\% \pm 3\%$; Table 1). *Agonis* swamp habitat made up $7\% \pm 2\%$ of the total available habitat (Table 1). The dominant swamp vegetation reflected the fire history of each site with the youngest habitat age classes occurring at site 5 (47% of recently burned *Agonis*) and site 4 (45% 5–9 years old; Table 1). *Agonis* swamp shrubland burned 10–14 years ago was the most common ($39\% \pm 16\%$) and widespread swamp habitat type, occurring at 4 of the 5 sites. Small pockets of older swamp habitat units were scattered across each site (Table 1).

Quokka home range (6.4 ± 0.8 ha), calculated by using fixes determined by radiotelemetry and trapping (Hayward et al. 2004), was primarily centered on the swamp vegetation, with significantly lesser amounts in surrounding forest vegetation ($F = 6.85$, $d.f. = 1, 120$, $P = 0.01$; Fig. 2). The majority of telemetry fixes during daylight hours were within the swamp compared to outside ($\chi^2 = 6.93$, $d.f. = 1$, $P = 0.008$; Fig. 2). No significant difference was found in use of forest and swamp macrohabitat throughout the year (ANOVA, $F = 0.13$, $d.f. = 3, 174$, $P = 0.94$; Fig. 2). At all sites, there were significantly more captures of new quokkas inside swamps (67) than outside (14; $\chi^2 = 30.68$, $d.f. = 1$, $P < 0.001$).

Recently burned areas of *Agonis* swamp shrubland were significantly preferred by quokkas ($t = 4.817$, $d.f. = 19$, $P < 0.001$; Fig. 3). In contrast, intermediate and mature categories

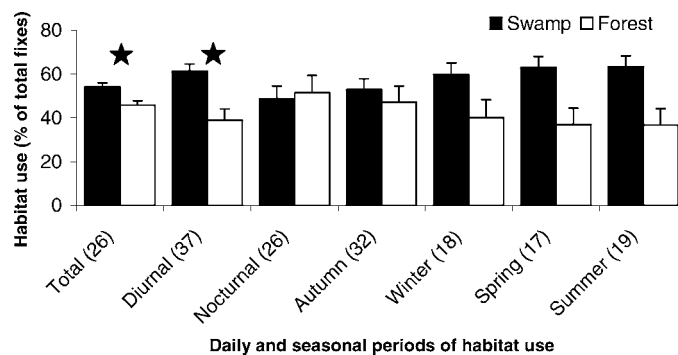


FIG. 2.—Daily and seasonal macrohabitat use by quokkas in *Agonis* swamps in southwestern Australia. Values are means ± 1 SE of percentage of habitat used based on home ranges of quokkas determined by radiotelemetry. Sample size is shown in parentheses and relates to total number of home ranges (and hence habitat-use assessments) that reached an incremental area asymptote overall and seasonally (Hayward et al. 2004). Stars indicate significant differences between swamp and forest habitats.

were used nonselectively by quokkas (intermediate $t = 0.469$, $d.f. = 50$, $P = 0.641$; mature $t = 0.302$, $d.f. = 46$, $P = 0.764$; Fig. 3).

Overall swamp habitat preferences also were analyzed by calculating the median of the preference rank of each habitat unit at each site (Fig. 4). The most favored habitats were the early seral stages of the swamps. As swamps aged, there was a decrease in habitat preference to 19 years postfire, whereupon the swamps became increasingly preferred again to the level of 5- to 9-year postfire seral stages. All forest habitat types were avoided (Hayward 2002).

DISCUSSION

Although quokkas in the northern jarrah forest show a distinct preference for *Agonis* swamp shrubland habitat types, they also exhibit a more specific preference for early

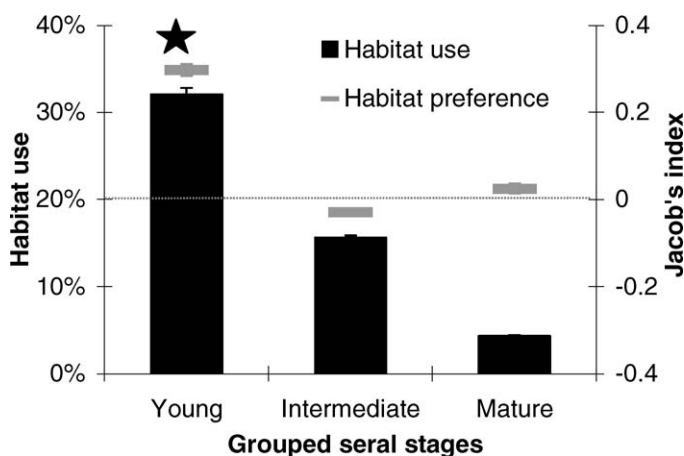


FIG. 3.—Quokka microhabitat use and preferences in southwestern Australia. Seral stages of *Agonis* swamp microhabitat are grouped into 3 categories based on time since fire. Values are mean $\pm SE$ Jacob's index scores relate to habitat preference (positive values) or avoidance (negative values). Star indicates a significant preference.

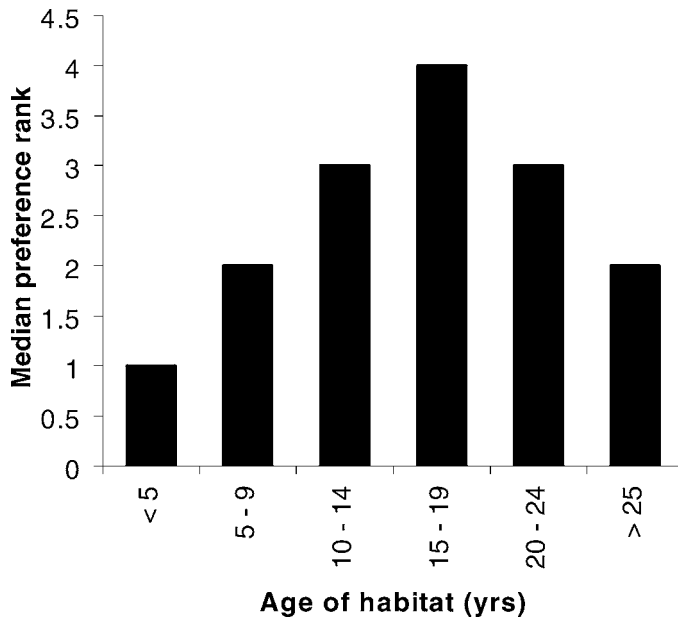


FIG. 4.—Overall median preference rank ($\pm SE$) for swamp habitat for quokkas in *Agonis* swamps for all sites combined. A rank of 1 represents the most preferred swamp habitat. Overall median rank was calculated after preferences for each swamp habitat unit by each individual were determined. Ages of habitats are expressed as years after fire and differ from the categories in Fig. 3 to allow a more detailed examination of seral stage preferences.

seral stages therein. This explains earlier observations that quokkas were observed foraging within a burned swamp less than 3 months after fire, reached peaks of abundance in swamps that were burned less than 12 years previously, and then deserted the habitat after 15 years (Christensen and Kimber 1975). Quokkas often were located diurnally in recently burned areas of site 5 within a year of fire, before increasing their nocturnal use after 2 years. Numerous other macropodids also prefer early seral stages (Christensen 1980; Denny 1985; Lundie-Jenkins 1993; Southwell and Jarman 1987; Underwood and Christensen 1981). This is probably related to the high nitrogen levels of new foliage.

Preference for higher nutrient content typical of the new growth is known in large macropods in southeastern Australia (Catling and Burt 1995). Plants growing within the swamp also show consistent protein and water content throughout the year compared to the fluctuating contents in plant species surrounding the swamp (Storr 1964).

The specific habitat preferences of quokkas may have evolved to enable them to cope with the frequent, low-intensity fire regimes implemented by Australian Aborigines (Ward and Sneeuwjagt 1999). Aborigines used fire to hunt the quokka by burning the swamp and spearing animals as they fled the flames (Gardner 1957; Gould 1863). However, whether Aborigines burned the swamps at a frequency that coincided with peaks in quokka abundance or whether quokka abundance peaked in accordance with the Aboriginal hunting regimes is unknown. Directly igniting the swamp contrasts with modern-day low-intensity control burns that generally burn the swamp edges

without penetrating the swamp. This leads to a reduction in swamp vegetation without creating a mosaic of seral stages.

Over the past 20 years, prescribed burns, and to a lesser extent, wildfires, within the northern jarrah forest, appear to have established a pattern whereby low-intensity fires are often stopped when they encounter swamp vegetation. This different burning pattern within the swamps over the past 20 years may be due to the historical fire regimes and length of control burn rotation compared to the more frequent burning that is preferred in the jarrah forest today (Burrows et al. 1995). Early swamp seral stages provide abundant fresh foliage within reach of foraging quokkas, in addition to dense vegetation for refuge (Hayward 2002). Intermediate and older age classes become taller (less forage is within reach), less species rich, and gradually structurally more open, thereby providing less refuge (Hayward 2002).

Quokkas on Rottnest Island exhibit a capacity to rapidly respond to habitat changes arising after fire. A major fire on the island in 1956 altered the vegetation composition and structure (Pen and Green 1983), which was exacerbated by overgrazing by quokkas (Storr 1963). Despite this, the quokka population has increased (Pen and Green 1983). Clearly, the quokka is able to cope with habitat change.

The quokka's need for dense, swampy vegetation also may have a physiological basis (Kitchener 1972, 1981). Quokkas on Rottnest Island take refuge during hot days beneath the sedge *Gahnia trifida*, which receives much lower radiant heat loads than other vegetation on the island (Kitchener 1972). However, *Gahnia* is reasonably common in the *Agonis* swamp shrublands and so an absence of shelter is not considered to be a limiting factor to mainland quokka populations. Moreover, quokkas have the ability to survive much greater temperatures than those they are likely to face in the wild (Bartholomew 1954). A more likely physiological reason for the macrohabitat preferences of the quokka is that quokkas have relatively high water requirements (Main and Bakker 1981; Main and Yadav 1971), which necessitates close proximity to freshwater throughout the year.

It is important to remember that the quokka may not be restricted to densely vegetated areas on the mainland (Christensen et al. 1985) because these areas are most favorable to it; rather, they may be the habitat least "favored" by the apparent agent of the quokka's decline (Caughley and Gunn 1996), the red fox. In this case, the swamps are probably acting as a refuge for quokkas from fox predation.

This limitation of habitat use in response to increased threat of predation is not uncommon. At present the rufous hare-wallaby (*Lagorchestes hirsutus*) is rarely detected >120 m from densely vegetated *Triodia pungens* habitat, whereas before the arrival of introduced predators it inhabited far more open areas (Lundie-Jenkins 1993). Altered habitat use in the presence of predators has been shown experimentally to occur in the South America rodent *Octodon degus* (Lagos et al. 1995), rabbits (*Oryctolagus cuniculus*), and eastern gray kangaroos (*Macropus giganteus*) in Australia (Banks 2001; Banks et al. 1999). Altered habitat use in the presence of feral predators may reduce the carrying capacity of a site (Kinnear et al. 2002).

The fact that 4 of the 5 sites in the northern jarrah forest where quokkas still exist possess a mosaic of burned areas within the swamp (Table 1) also is relevant. Quokkas feed within recently burned swamps but may not become resident there for at least a year (Christensen and Kimber 1975). Yet, considering the short recorded movements of quokkas (Hayward et al. 2004), they are likely to require refuge habitat in close proximity (<100 m) to these foraging areas. Thus, the persistence of older, unburned habitat within recently burned swamps is important.

Although many species with formerly continuous distributions are being turned into metapopulations by habitat fragmentation (Hanski and Gilpin 1991), this is not the case for the quokka, which existed in naturally fragmented habitats. Virtually all historical reports (Gould 1863; White 1952) link the quokka to areas of dense vegetation (either swamps and thickets in forest or coastal shrublands), and these discreet patches provided habitat for populations within a greater metapopulation (Hayward et al. 2003). The quokka is increasingly restricted to such discreet habitat patches because dispersal between patches no longer occurs (Hayward et al. 2003).

These *Agonis* swamps have never been contiguous linear stretches of habitat along watercourses because changes in vegetational floristics and structure occur as topography changes from the broad, shallow upper reaches of creek systems to the steeper-sided valleys of larger waterways downstream (Havel 1975; Heddle et al. 1980). Despite increasing urbanization, mining, and forestry, *Agonis* swamps remain common in the northern jarrah forest; thus, macrohabitat availability is not limiting the population growth of quokka. Although quokkas historically traveled through these less-favored forest habitat types during dispersal, this no longer occurs (Hayward et al. 2004). This may be a function of strong selective pressure for philopatry after the arrival of the red fox (Hayward 2002). Predation by foxes is likely to have led to dispersal, creating demographic “sinks” for the population (Soulé and Gilpin 1991) until dispersal effectively ceased. Quokkas’ clear preference for discrete patches of habitat and the ephemeral suitability of these patches is consistent with metapopulation theory (Hayward et al. 2003).

The quokkas’ preference for early seral stage habitat in the northern jarrah forest, the indication that the habitat breadth of the quokka may have declined after an increase in predation pressure from introduced predators (Hayward 2002), and the lack of dispersal (Hayward et al. 2004) add to concerns about the persistence of the overall metapopulation. The quokkas’ preference for early seral stage habitat (<10 years since fire) means that the turnover rate of local populations is likely always to have been high, with quokkas emigrating from, or not surviving in, older swamps. Nevertheless, it is unlikely that the *Agonis* swamp habitat types could be considered as a sink habitat (Pulliam 1988). Rather, it is a habitat that at young ages provides for a source population. Then, as this habitat ages, it tends toward a population sink. With greater restriction to discrete, ephemeral habitat patches and less movement between patches (Hayward et al. 2004), it is likely that the collapse of the metapopulation, suggested previously through small population

sizes (Hayward et al. 2003) and philopatry (Hayward et al. 2004), is imminent or has already occurred.

This research suggests specific options for managing habitat for the quokka. We recommend planned controlled or hazard-reduction burning regimes on a 5- to 10-year rotation (or more frequently to mirror Aboriginal burning regimes) to facilitate the conservation of the quokka. These fires should be patchy, to ensure that a fine-scale mosaic of refuge and foraging habitat is available for surviving quokkas, and small at extant sites to minimize direct mortality. Nearby swamps could be burned on a larger scale but at the same recommended frequency to increase their attractiveness if dispersal occurs once extant sites attain high densities. Continued fox control and monitoring is also fundamental.

ACKNOWLEDGMENTS

This project was funded by the Department of Conservation and Land Management and additional fox baiting was funded by Alcoa World Alumina Australia Ltd. MWH was funded by an Australian Postgraduate Award. MWH thanks the friends and family who assisted in the field and I. Abbott, M. Williams, J. Hayward, E. Jefferys, J. Taylor, K. Ross, and anonymous reviewers for providing valuable comments on this paper.

LITERATURE CITED

- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BANKS, P. B. 2001. Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour* 61:1013–1021.
- BANKS, P. B., I. HUME, AND O. CROWE. 1999. Behavioural, morphological and dietary response of rabbits to predation risk from foxes. *Oikos* 85:247–256.
- BARTHOLOMEW, G. A. 1954. Temperature regulation in the macropod marsupial, *Setonix brachyurus*. *Australian Journal of Science* 6:26–40.
- BURBIDGE, A. A., AND N. L. MCKENZIE. 1989. Patterns in the modern decline of Western Australia’s vertebrate fauna: causes and conservation implications. *Biological Conservation* 50:143–198.
- BURROWS, N. D., B. WARD, AND A. D. ROBINSON. 1995. Jarrah forest fire history from stem analysis and anthropological evidence. *Australian Forestry* 58:7–16.
- CATLING, P. C., AND R. J. BURT. 1995. Studies of the ground-dwelling mammals of eucalypt forests in south-eastern New South Wales: the effect of habitat variables on distribution and abundance. *Wildlife Research* 22:271–288.
- CAUGHLEY, G., AND A. GUNN. 1996. Conservation biology in theory and practice. Blackwell Science, Carlton, Australia.
- CHRISTENSEN, P. E. S. 1980. The biology of *Bettongia penicillata* Gray, 1837, and *Macropus eugenii* (Desmarest, 1817) in relation to fire. *Forests Department of Western Australia* 91:1–90.
- CHRISTENSEN, P. E. S., A. ANNELS, G. LIDDELOW, AND P. SKINNER. 1985. Vertebrate fauna in the southern forests of Western Australia. *Forests Department of Western Australia* 94:1–88.
- CHRISTENSEN, P. E. S., AND P. C. KIMBER. 1975. Effect of prescribed burning on the flora and fauna of south-western Australian forests. *Proceedings of the Ecological Society of Australia* 9:85–106.
- DENNY, M. 1985. The red kangaroo and the arid environment. Pp. 55–57 in *The kangaroo keepers* (H. J. Lavery, ed.). University of Queensland Press, Brisbane, Australia.

- GARDNER, C. A. 1957. The fire factor in relation to the vegetation of Western Australia. *Western Australian Naturalist* 5:166–173.
- GOULD, J. 1863. The mammals of Australia. Vol. 1. Published by the author, Bedford Square, London, England, United Kingdom.
- HANSKI, I., AND M. GILPIN. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3–16.
- HAVEL, J. J. 1975. Site-vegetation mapping in the northern jarrah forest (Darling Range). 1. Definition of site-vegetation types. *Forests Department Bulletin* 86.
- HAYWARD, M. W. 2002. The ecology of the quokka (*Setonix brachyurus*) (Macropodidae: Marsupialia) in the northern jarrah forest of Australia. Ph.D. dissertation, University of New South Wales, Sydney, Australia.
- HAYWARD, M. W., P. J. DE TORES, M. L. AUGEE, B. J. FOX, AND P. B. BANKS. 2004. Home range and movements of the quokka *Setonix brachyurus* (Macropodidae: Marsupialia), and its impact on the viability of the metapopulation on the Australian mainland. *Journal of Zoology (London)* 263:1–10.
- HAYWARD, M. W., P. J. DE TORES, M. J. DILLON, AND B. J. FOX. 2003. Local population structure of a naturally occurring metapopulation of the quokka (*Setonix brachyurus* Macropodidae: Marsupialia). *Biological Conservation* 110:343–355.
- HEDDLE, E. M., O. W. LONERAGAN, AND J. J. HAVEL. 1980. Vegetation complexes of the Darling system, Western Australia. Pp. 1–72 in *Atlas of natural resources, Darling system, Western Australia*. Department of Conservation and Environment, Perth, Australia.
- HILL, M. O. 1979. TWINSPLAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York.
- HILTON-TAYLOR, C. (COMPILER). 2000. 2000 IUCN red list of threatened species. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.
- JACOBS, J. 1974. Quantitative measurement of food selection—a modification of the forage ratio and Ivlev's electivity index. *Oecologia* 14:413–417.
- KENWARD, R. E., AND K. H. HODDER. 1992. Ranges V—an analysis system for biological location data. Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, United Kingdom.
- KINNEAR, J. E., N. R. SUMNER, AND M. L. ONUS. 2002. The red fox in Australia—an exotic predator turned biocontrol agent. *Biological Conservation* 108:335–359.
- KITCHENER, D. J. 1972. The importance of shelter to the quokka, *Setonix brachyurus* (Marsupialia), on Rottnest Island. *Australian Journal of Zoology* 20:281–299.
- KITCHENER, D. J. 1981. Factors influencing selection of shelter by individual quokkas, *Setonix brachyurus* (Marsupialia), during hot summer days on Rottnest Island. *Australian Journal of Zoology* 29:875–884.
- KREBS, C. J. 1989. *Ecological methodology*. Harper Collins Inc., New York.
- LAGOS, V. O., L. C. CONTRERAS, P. L. MESERVE, J. R. GUTIERREZ, AND F. M. JAKSIC. 1995. Effects of predation risk on space use by small mammals: a field experiment with a neotropical rodent. *Oikos* 74: 259–264.
- LUNDIE-JENKINS, G. 1993. Ecology of the rufous hare-wallaby, *Lagorchestes hirsutus* Gould (Marsupialia: Macropodidae), in the Tanami Desert, Northern Territory. I. Patterns of habitat use. *Wildlife Research* 20:457–476.
- LUNNEY, D. 2001. Causes of the extinction of native mammals of the western division of New South Wales: an ecological interpretation of the nineteenth century historical record. *Rangeland Journal* 23: 44–70.
- LUNNEY, D., AND T. LEARY. 1988. Effect of European man on fauna in the south-east of New South Wales. *Australian Journal of Ecology* 25:100–116.
- MAIN, A. R., AND H. R. BAKKER. 1981. Adaptation of macropod marsupials to aridity. Pp. 1491–1520 in *Ecological biogeography of Australia* (A. Keast, ed.). Dr. W. Junk, The Hague, Netherlands.
- MAIN, A. R., AND M. YADAV. 1971. Conservation of macropods in reserves in Western Australia. *Biological Conservation* 3:123–133.
- MORTON, S. R. 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* 16:201–213.
- NAMS, V. O. 1990. *Locate II user's guide*. Pacer Computer Software, Truro, Canada.
- OKSANEN, J., AND P. R. MINCHIN. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *Journal of Vegetation Science* 8:447–454.
- PALOMARES, F., M. DELIBES, E. REVILLA, J. CALZADA, AND J. M. FEDRIANI. 2001. Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. *Wildlife Monographs* 148:1–36.
- PEN, L. J. AND J. W. GREEN. 1983. Botanical exploration and vegetational changes on Rottnest Island. *Journal of the Royal Society of Western Australia* 66:20–24.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- SOULÉ, M. E., AND M. E. GILPIN. 1991. The theory of wildlife corridor capability. Pp. 3–8 in *Nature conservation 2: the role of corridors* (D. A. Saunders and R. J. Hobbs, eds.). Surrey Beatty & Sons, Sydney, Australia.
- SOUTHWELL, C. J., AND P. J. JARMAN. 1987. Macropod studies at Wallaby Creek III. The effect of fire on pasture utilisation by macropodids and cattle. *Australian Wildlife Research* 14: 117–124.
- STORR, G. M. 1963. Some factors inducing change in the vegetation of Rottnest Island. *Western Australian Naturalist* 9:15–22.
- STORR, G. M. 1964. The environment of the quokka (*Setonix brachyurus*) in the Darling Range, Western Australia. *Journal of the Royal Society of Western Australia* 47:1–2.
- SWIHART, R. K., AND N. A. SLADE. 1985. Testing for independence of observations in animal movements. *Ecology* 66:1176–1184.
- THACKWAY, R. M., AND I. D. CRESSWELL. 1995. An interim biogeographic regionalisation for Australia: a framework for setting priorities in the national reserves system cooperative program. Vol. 4. Australian Nature Conservation Agency, Canberra, Australia.
- UNDERWOOD, R. J., AND P. E. S. CHRISTENSEN. 1981. Forest fire management in Western Australia. *Western Australian Forests Department, Special Focus* 1:1–34.
- WARD, D. J., AND R. SNEEUWJAGT. 1999. Aboriginal fire: its relevance to present day management of the jarrah forest of south-western Australia. Pp. 54–55 in *Proceedings of 'Bushfire 99' Conference*, April 1999, Albany, Australia.
- WHITE, S. R. 1952. The occurrence of the quokka in the south-west. *Western Australian Naturalist* 3:101–103.

Submitted 20 November 2003. Accepted 2 December 2004.

Associate Editor was Ronald D. Gettinger.