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Mortality and survivorship of the quokka (*Setonix brachyurus*) (Macropodidae : Marsupialia) in the northern jarrah forest of Western Australia

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Abstract. The potential for the quokka (*Setonix brachy*urus (Quoy & Gaimard, 1830)), a threatened macropodid marsupial, to increase in abundance following the initiation of predator control was investigated by determining the cause of deaths of radio-collared individuals. Predation was identified as a major cause of death followed by road kills. The non-parametric Kaplan–Meier method modified for staggered entry of individuals was used to estimate survivorship. Although males and females were affected differently by each cause of mortality, their overall survivorship did not differ significantly. Individuals alive at the beginning of the 25-month study had a 61% chance of surviving to the end. This represented an 81% chance of surviving for 1 year. There was no significant difference in survivorship between adults and juveniles. Current rates of adult and juvenile survivorship should allow population recovery, although none has been evident. Pouch young mortality is hypothesised to have inhibited the anticipated quokka population increase since the initiation of predator control. The observed expulsion of pouch young by females when threatened may be a primary predator avoidance strategy.

Introduction

For species that exist as a metapopulation, the extinction of local populations is a natural process and of little concern provided that colonisation and extinction rates are in equilibrium (Harrison 1991). When a metapopulation is in a state of collapse, however, the extinction of each local population is of much greater bearing.

The quokka (*Setonix brachyurus*) is a threatened, macropodid marsupial that is endemic to south-western Australia and that once existed naturally as a classic metapopulation (Hayward 2002; Hayward *et al*. 2003, 2004, 2005). The species suffered a dramatic decline in the 1930s, primarily from predation by the introduced European red fox (*Vulpes vulpes*), and secondarily from habitat alteration and possibly disease (White 1952; Cook 1960; Hayward 2002). This led to the collapse of the metapopulation structure into a non-equilibrium state (as described by Harrison 1991), such that the conservation status of the quokka is now listed as vulnerable according to IUCN criteria (Hayward 2002).

The quokka has been extensively studied on Rottnest Island where the species experiences seasonal mortality over summer (Main 1959), which is attributable to protein starvation from feeding on nutrient-deficient succulents in attempts to derive sufficient moisture to survive through the dry season (Storr 1964). The ecology of the mainland population is very different from that of the Rottnest Island population, being in a more mesic environment and subject to predation pressure from the red fox. This paper estimates survivorship for quokkas from sites within the northern jarrah forest metapopulation and assesses this in light of the recovery of the species.

Methods

General procedures

Quokkas were trapped seasonally at five sites in the northern jarrah forest of Western Australia (Chandler, Rosella Road, Kesners, Hadfield and Victor Road) from spring 1998 until summer 2000–01 using two types of wire mesh cage traps baited with apples or universal bait and set for eight consecutive days (methods and results of this trapping are described in detail in Hayward *et al*. 2003). The northern jarrah forest comprises the northern half of the Jarrah Forest bioregion (Thackway and Cresswell 1995) and encompasses the Darling Plateau from east of Perth to Collie in the south. All but the Victor Road site (a control site)

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were baited monthly with dried meat baits injected with 4.5 mg of sodium monofluoroacetate (1080) poison to control introduced predators. No estimates of fox or cat density were conducted around the quokka sites, although we assume that their density was very low given that baiting seasonally in surrounding areas reduced introduced predator impacts significantly, especially when coupled with perimeter baiting every two months (de Tores 1999).

Captured quokkas were sedated and a radio-transmitter was fitted to 64 (Hayward *et al.* 2004) of an estimated adult population of 84 (Hayward *et al.* 2003). Radio-collars (Biotrack, Institute of Terrestrial Ecology, Wareham, UK) were configured to maximise signal strength and battery life while minimising weight. The collars incorporated movement-sensitive circuitry with a 2.5-h immobile period required to trigger the mortality pulse frequency of ~110 pulses min^{-1}, compared to 55 pulses min^{-1} in 'live' mode.

Breakaway collars were used on juveniles and these employed a perishable rubber collar that stretched with the animal's growth (Hayward *et al.* 2004). Juveniles weighed 0.55 to 1.6 kg for females and 2.5 kg for males (whereupon they were considered adult, after Hayward *et al.* 2003) and were fitted with the expandable collar while they were in the presence of their mother and still suckling (Hayward *et al.* 2004).

Animals were regularly monitored between November 1998 and November 2000, with a particularly intensive period between March 1999 and May 2000 so as to allow direct comparison between the survivorship of animals at each site. This comparative monitoring period occurred when all sites had collared animals and ceased when collar removal began. The location of each collared individual was determined at least monthly and generally more frequently (up to four times per week). This meant that all but two of the dead individuals were found within two days of death.

The cause of death was determined by examining characteristic markings on the carcass (Augee *et al.* 1996). Predation was attributed to the red fox if there was minimal marking on the collar or, if marked, it showed evidence of large canid teeth, if the gut had been eaten or cached in an excavated hole, and if the fur and uneaten remains were cached (Augee *et al.* 1996; de Tores 1999). Predation was attributed to feral cats (*Felis catus*) if there was evidence of bite marks to the back of the skull, which often included the removal of the brain, if the gut remained near the carcass, and if there was no evidence of caching or simple covering of the carcass with debris (Augee *et al.* 1996; de Tores 1999). The western quoll or chuditch (*Dasyurus geoffroii*), although present at each site, was not considered a potential predator of quokkas considering its largely insectivorous diet and it being known to prey only on mammals significantly smaller in size than quokkas (Soderquist and Serena 1994). Dingoes (*Canis lupus dingo*) were not considered as potential predators of the quokka because of their scarcity in the northern jarrah forest (MWH, personal observation; PdeT, unpublished data). Raptor predation was characterised by carcasses being located below trees, when skulls were intact and/or skin peeled back and soft tissue removed (Augee *et al.* 1996). The regular monitoring meant that predation by carpet pythons (*Morelia spilota*) would have been identified by the presence of the collared animal still within the snake (Augee *et al.* 1996). Other evidence of python predation would have been the collar found within a regurgitated pellet containing crushed or fractured bones. Road-killed individuals were located on road verges, had obvious massive trauma and showed no evidence of predation. Carcasses that could not be satisfactorily placed into one of these categories were classed as unknown mortality events.

Survival estimate

The Kaplan–Meier method (product limit estimator) with staggered entry was used to assess survivorship, because the assumptions of the alternative parametric estimators were not always met in this study (Pollock *et al.* 1989*a*; Kendall and Pollock 1992). As trapping was assumed to be unbiased (Hayward *et al.* 2003) and a high proportion of captured individuals were collared (48 of 48 trapped adults and 10 of 23 juveniles were collared: Hayward *et al.* 2004), these individuals were considered a random sample of the population. Other assumptions satisfied were that survival of each individual was independent and that censoring was random (Pollock *et al.* 1989*a*, 1989*b*). Any newly collared animals were assumed to have the same survival rate as those previously collared (Pollock *et al.* 1989*a*).

Survival estimates were derived from 58 animals from the five populations (Hadfield, where 17 of 24 individuals were collared; Kesners, 26 of 26; Chandler, 4 of 7; Victor Road, 10 of 13; and Rosella Road, 1 of 1) and 10 of these were juveniles. An additional eight individuals were excluded from the analyses as their collars ceased transmitting within the recommended seven-day conditioning period (Pollock *et al.* 1989*a*). Two deaths associated with trapping were excluded from the analyses as these would negatively bias the survival estimates (Pollock *et al.* 1989*a*). We don't know whether this conditioning period was of appropriate length or not, but the first death in the collared individuals occurred two months after collaring. Animals whose collar ceased transmitting and whose fate was unknown were censored. Considerable effort was made to locate censored individuals in order to reduce the confidence intervals associated with the survivorship estimates. Although many censored animals were later recaptured (27 recaptured out of 46 censored from 450 individuals at risk) without their collars, they were still classified as censored in the analyses to avoid bias (Pollock *et al.* 1989*b*).

Survival estimates from the Kaplan–Meier method were compared using the log-rank (χ^2) test (Pollock *et al.* 1989*a*). This test assumes that censoring is random but may be violated by a predator killing an animal and simultaneously destroying the transmitter (Pollock *et al.* 1989*a*). Consequently, the most conservative modification of the log-rank test (with a modified variance of the number of deaths) (Pollock *et al.* 1989*a*) was used in this study. The K-sample Mann–Whitney test was used to compare survivorship between sites (Zar 1996). Comparisons between survival estimates at the time of the final sample were conducted using the normal test statistic equation (Pollock *et al.* 1989*a*). The log-rank test compared survival functions in their entirety while the approximation to the normal (Z) test compared the survival curves at the end of the 15-month comparative period. Individual comparisons were not conducted on the Rosella Road site as the only collared animal was censored after 8 months.

Results

Overall survivorship

The 58 collared individuals were monitored over the 25-month study period, during which eight deaths were recorded (Fig. 1). Of the known causes of death, three deaths were attributed to predation and two were road kills (Table 1). Only females were depredated, whereas only males at the Kesners site were killed after being struck by motor vehicles. Despite the existing predator-control program (de Tores 1994, 1999), foxes and cats still preyed on quokkas.

The Kaplan–Meier survivorship estimate for all quokkas for the entire 25-month study was 0.61 (95% confidence intervals (CI) = 0.34–0.87) (Fig. 1). This equates to an annual survivorship of 0.81. This means that an individual alive at the beginning of the study had a 61% chance of surviving for 25 months or an 81% chance of surviving for a year. There was no significant difference between the survival functions between years for all sites combined (November 1998 until October 1999 and November 1999 until October 2000) (Table 2).

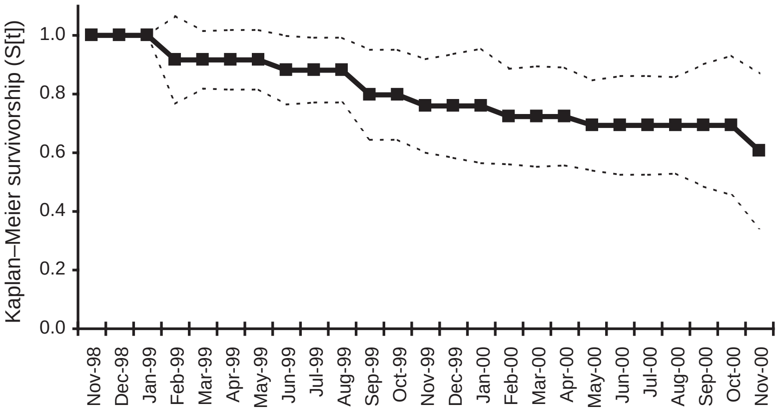

Fig. 1. Kaplan-Meier survivorship plot of quokkas from all sites combined over 25 months beginning 8 November 1998. Confidence limits (95 percentile) are shown as dashed lines.

Comparative period of survivorship (March 1999–May 2000)

Quokkas at each site were intensively monitored over a 15-month comparative period from March 1999 to May 2000. There was no difference between the survival curves of all sites combined (Kruskal–Wallis K-sample test) or for the final survival estimate (Z statistic) (Table 2, Fig. 2).

There was no significant difference between the survival curves or estimates for males and females (Table 2, Fig. 3). Males had a final survival estimate of 0.82 (95% CI = 0.61–1.02), whereas that for females was 0.75 (95% CI = 0.53–0.98). There was also no significant difference between the survival curves and final estimates of adults and juveniles (Fig. 4, Table 2). Adult survivorship was 0.77 (95% CI = 0.59–0.94) during the comparative 15 months, and during that period no collared juveniles died.

Discussion

Survivorship

Overall, quokkas at the study sites had an 81% chance of surviving for 1 year. The similar survivorship values for each sex found in this study is unusual for a sexually dimorphic species like the quokka. Such species generally exhibit lower male survivorship owing to the costs associated with competition for mates, dispersal and increased food demands (see discussion in Owen-Smith 1993). The absence of dispersal in quokkas and similar home-range sizes between the sexes (Hayward *et al.* 2004) may explain the similar survival of the sexes.

The similarity in the survival curves between the sexes and for all sites combined should be interpreted cautiously because of the wide confidence intervals arising from the number of censored animals (Fig. 2). Comparisons between

Table 1. Causes of death of the 58 radio-collared quokkas in the northern jarrah forest
Study site and approximate date of death are also shown

Fate	Males	Females	Study sites (approximate date of death)
Predation by fox	0	2	Hadfield (20.v.1999); Kesners (26.viii.1999)
Predation by cat	0	1	Kesners (16.xii.1999)
Road kill	2	0	Kesners (29.viii.1999, 15.iii.2000)
Unknown	2	1	Hadfield (2.iv.1999); Kesners (1.x.2000); Chandler (27.i.1999)

Table 2. Results of log-rank and normal tests of survivorship
Total number of animals collared in each comparison is shown in parentheses. The Bonferroni correction was applied to the comparisons between sites yielding a significant probability of $P = 0.008$

Comparison	Log-rank test for pairwise comparison/Kruskal–Wallis test for all sites			Z statistic		
	χ^2/H	d.f.	Probability	Z	d.f.	Probability
All sites	1.8711	4	$0.90 > P > 0.75$	2.46	4	$0.75 > P > 0.50$
Males (33) versus females (25)	0.1781	1	$0.75 > P > 0.50$	1.14	1	$0.50 > P > 0.25$
Adults (48) versus immatures (10)	0.9699	1	$0.50 > P > 0.25$	2.61	1	$0.25 > P > 0.10$
Nov. 1998 – Oct. 1999 versus Nov. 1999 – Oct. 2000	0.2849	1	$0.75 > P > 0.50$			

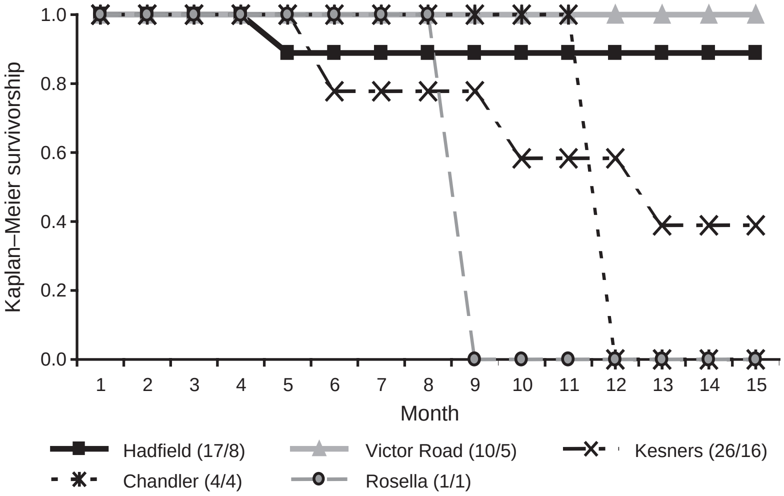

Fig. 2. Survival functions of quokkas at the five sites in the northern jarrah forest between March 1999 and May 2000. The number of collared individuals at each is shown in parentheses followed by the number of censored individuals (collared/censored). The Rosella and Chandler sites were conservatively assumed to have a survival function of 0 and a variance of 1 after all collared animals were censored.

adults and juveniles suffered similar problems and these were compounded by the short lifespan of breakaway collars that were fitted to juveniles (Hayward *et al*. 2004).

Mortality events and the causes of the quokka's decline

Natural deaths for the mainland quokka populations in the past derived from disease, predation, starvation and the direct and indirect effects of fire (Hayward 2002; Hayward *et al*. 2003). Although deaths associated with starvation and fire were not recorded in this study, various forms of predation, and possibly disease, were.

Wild quokkas have been found to be susceptible to infection by *Toxoplasma* parasites (Gibb *et al*. 1966) and *Salmonella* bacteria (Iveson and Hart 1983; Hart *et al*. 1986). Captive quokkas are known to be parasitised by the genera *Progamotaenia* (cestode tapeworms); *Austrostrongylus*, *Breinlia*, *Cloacina*, *Dipetalonema*, *Filaria*, *Microfilaria* (nematode flatworms); and *Entamoeba* and *Toxoplasma* protozoans (Collins 1973). The herpes virus has also caused mortality in captive quokka colonies (Burnet 1970). Post-mortem examination of the least decomposed (an adult female) of the three deaths from this study not attributed to predation or road kill revealed fat reserves, a full stomach and bladder and an absence of obvious internal parasitic cysts, suggesting that disease was not the cause. Although this death occurred in summer, when quokkas may die of dehydration owing to their high water requirements (Main and Yadav 1971), this seems unlikely because water was plentiful at the Chandler site throughout the year owing to the presence of a dam and the animal had a full bladder. The other two quokkas whose cause of death could not be categorised may have succumbed to disease. A recent re-evaluation of the deaths that Cook (1960) attributed to disease indicates that surplus killing by foxes may have been the cause (Short *et al*. 2002). Although it is unlikely that surplus killing by foxes caused the deaths of these three quokkas, it may have been important in the initial decline of the quokka in the 1930s as we find it unlikely that disease was a major factor (Hayward 2002).

The droppings and regurgitated pellets of nocturnal birds of prey, such as the masked owl (*Tyto novaehollandiae*) or

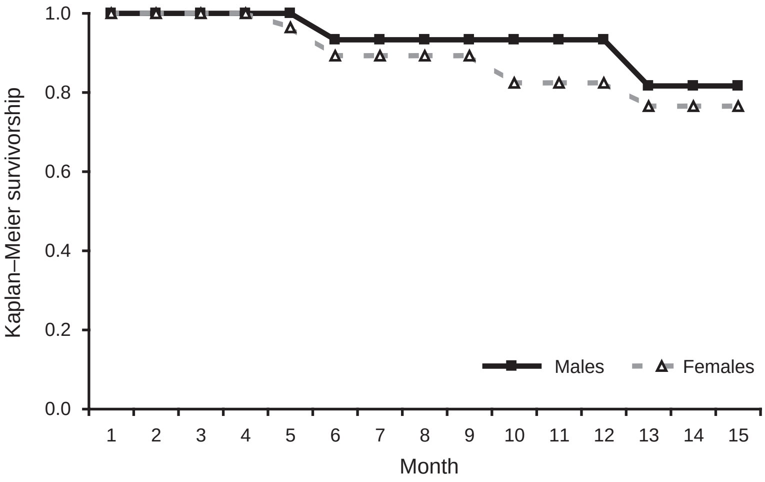

Fig. 3. Survival functions of male and female quokkas in the northern jarrah forest between March 1999 and May 2000.

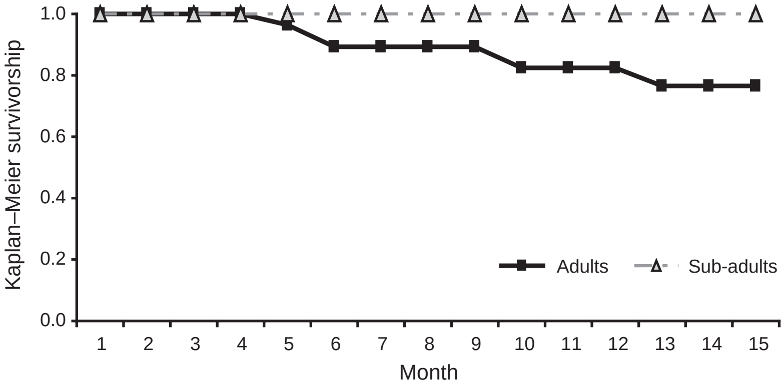

Fig. 4. Survival functions of adult and immature quokkas in the northern jarrah forest between March 1999 and May 2000.

barking owl (*Ninox connivens*), contain quokka bones (Archer and Baynes 1972). Quokka bones were found below a wedge-tail eagle (*Aquila audax*) eyrie on Bald Island (Storr 1965*a*) and ospreys (*Pandion haliaetus*) prey on quokkas on Rottnest Island (Storr 1965*b*). Although this suggests that birds of prey are threats to the quokka, there was no evidence of raptor predation during this study.

The Aboriginal, and later European, inhabitants of the south-west regularly preyed upon quokkas (Gould 1863; Stewart 1936; Whittell 1954; Gardner 1957). The removal of the Noongar people of south-western Australia from a traditional lifestyle has meant that such predation events no longer occur. Despite recent records of humans killing quokkas on Rottnest Island (AAP 1998; Squires 2003), no predation event on quokkas attributable to humans was recorded in this study.

Hunting pressure has been replaced by predation pressure from other introduced placental predators, such as the dingo, European red fox and feral cat. The dingo occurs at such low numbers in the jarrah forest that it is not considered a significant threat to quokkas. The fox and, to a lesser extent, the cat are significant threats to the survival of quokkas (Hayward 2002; Hayward *et al*. 2003) and the only predation events recorded in this study were attributed to these species.

Quokkas may be most susceptible to predation in the wetter months when swamps become inundated and the core home range shifts towards their periphery (Hayward *et al*. 2004). Higher rainfall also results in toxins in the dried meat baits used to control introduced predators leaching out more rapidly, minimising their long-term effectiveness (Fleming and Parker 1991; Saunders *et al*. 2000; Twigg *et al*. 2000). Two predation events occurred in this period and both were attributed to foxes (Table 1). Although these small sample sizes are inconclusive, hunting by foxes may be hindered by dense vegetation in swamps, in contrast to the cat, which may be equally as successful inside the swamps as outside.

In addition to recently arrived predators, other causes of mortality have appeared since European arrival. Today, road kills are one of the most common ways of identifying new quokka sites throughout the mainland and one of the most common sources of quokka mortality (Table 1). Roads and tracks traverse the jarrah forest, delineating forest blocks as management units. Where these cross the preferred habitat of quokkas, in the upper reaches of creek systems (Hayward *et al*. 2005), the potential for road kills exists. Most of these tracks are closed to the general public and are poorly maintained, which limits vehicle speed, such that they are a minimal threat. The high traffic volumes of surfaced roads and the speed that vehicles travel on them provides a more serious threat to wildlife, including quokkas. The Kesners site has a 200-m tributary of the main swamp bisected by a bitumen road, and two individuals were killed crossing to this isolated section of swamp, probably to access the adult females known to inhabit the area (Hayward 2002). Although quokkas in the Kesners swamp are most at risk of road kill, the lower reaches of the Hadfield swamp is also bisected by a large, but unsurfaced, road that carries a high volume of traffic travelling at high speed. Given the impact of road kills on quokka populations, it would be beneficial to incorporate traffic-calming structures and wildlife underpasses into the design of roads that potentially affect quokka swamps.

Reasons for the lack of response to introduced predator control

Female quokkas can produce 1.8–2.0 young per year (Sharman 1955*a*, 1955*b*; Shield 1964) and thus have the potential to produce 17 young over a lifetime (Hayward *et al.* 2003). This high potential fecundity did not result in substantial population increases in the study sites despite the relaxation of predation pressure (Hayward *et al*. 2003). Evidence of the lack of population increases include a paucity of recent museum records (Western Australian Museum, personal communication, in Hayward *et al*. 2003), reports of quokka population declines elsewhere (Maxwell *et al*. 1996), and trapping in the 1970s and early 1990s at several of our study sites that indicated similar, and generally larger, populations previously (Hayward 2002) when compared to now (Hayward *et al*. 2003). There is evidence that the decline is due to the low juvenile recruitment rate because fewer than one in two pouch young survived to independence (Hayward *et al*. 2003). The collaring of juveniles in this study shortly before their permanent departure from the pouch ensured that it was not an early juvenile death that we missed by fitting collars to juveniles after the time they are most at risk (i.e. initial independence).

It seems unlikely that nutrition is the cause of the low recruitment rate, given that populations are considered to be well below carrying capacity (Hayward *et al*. 2003) and nutrition is not considered a limiting factor at these sites (Hayward 2005). Similarly, genetic analysis of quokkas trapped at each of the five sites revealed that they are not inbred or lacking genetic diversity (Alacs 2001).

The behaviour of female quokkas within traps offers a possible explanation, however. When trapped animals became aware of the researcher approaching they generally attempted to escape, during which larger young were often expelled or released from the pouch of females. The pouch young would flounder on the ground and 'hiss' loudly. Whether the young were actually physically expelled by the mother or became dislodged during these violent, evasive movements is unknown but considering the muscular control that female quokkas have over the pouch opening (highlighted when the muscle becomes relaxed during sedation) it seems likely that this is a behavioural response rather than accidental. Pouch young expelled in traps were taped back into the pouch and the 100% survivorship of radio-monitored individuals suggests that trapping was unlikely to have inhibited the population recovery.

If the pouch release is found to be a physical action by the mother then it can be viewed as a useful predator-avoidance strategy. When a female quokka becomes aware of a life-threatening interaction with a predator she may expel her offspring whose subsequent noise attracts the attention of the approaching predator. It seems likely that the predator would take the young in such circumstances. Comparable behaviour has been observed in other marsupials: grey kangaroos expel their pouch young when chased by foxes (Banks 1997), as do swamp wallabies (*Wallabia bicolor*) when chased by dingoes (Robertshaw and Harden 1986). The high proportion of young swamp wallabies in the diet of the dingo were thought to have been consumed after being ejected by the mother (Robertshaw and Harden 1985, 1986).

Management implications

Although almost 8% of quokkas at Kesners were killed by introduced predators, overall the threat to the quokka from predation in the northern jarrah forest appears to have been alleviated. Adult survivorship following fox control is at levels that would allow population increases assuming that pouch young are successfully weaned. That this noticeable population increase has not been apparent to date highlights the likelihood that mortality of pouch young is limiting this increase (Hayward *et al*. 2003). Conservation efforts should continue to focus on all of the extant populations in the northern jarrah forest, except possibly that at the Rosella Road site, which consists of a lone male (Hayward *et al*. 2003). On-going predator control appears crucial because, even with reduced predation intensity, introduced carnivores still cause mortality in already small quokka populations. Additionally, the extent and causes of mortality of juveniles and pouch young are unknown but are likely to explain why the expected population increase has not been observed (Hayward *et al*. 2003). Where roads that carry high traffic volume cut swamps containing extant quokka populations, it would be beneficial to construct traffic-calming devices to slow vehicle speeds, and possibly also to construct wildlife underpasses to facilitate movement between isolated patches but bearing in mind that these can become predator traps (Foster and Humphrey 1995; Clevenger and Waltho 2000).

On the mainland the quokka cannot be managed as one biological entity and it is fundamental that conservation managers utilise its metapopulation structure (Hayward *et al*. 2003, 2004, 2005) during management activities. Local extinction probability has a greater influence on metapopulation persistence time than the rate of colonisation (Etienne and Heesterbeek 2001). Given this, and the minimal likelihood of increasing the colonisation rate between local quokka populations because of the large distances separating them (Hayward *et al*. 2003), we advocate reinstating metapopulation function by continuing control of introduced predators. We also recommend that management be directed at increasing the possibility of colonisation from the existing isolated populations to adjacent, threat-free habitat. Available habitat should be maximised by means of fine-scale, delicate control burns at existing sites and slightly larger burns at sites surrounding extant populations (Hayward *et al*. 2005). In the absence of these management actions, we predict further localised, and eventually regional, extinction of the quokka.

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