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Predicting the occurrence of the quokka, *Setonix brachyurus* (Macropodidae : Marsupialia), in Western Australia's northern jarrah forest

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Abstract. The quokka, *Setonix brachyurus*, is a medium-sized, macropodid marsupial that is endemic to south-western Australia. It has declined markedly in its distribution and abundance since the early 1930s and is listed as vulnerable under IUCN criteria. The presence or absence of quokka populations at 66 sites in the northern jarrah forest of Australia was investigated using generalised linear models (GLM). We hypothesised that fox control and the presence of a mosaic of post-fire seral stages within *Agonis linearifolia* swamp vegetation were important in predicting the presence of quokkas. The number of poison meat baits delivered per hectare, the average number of years since the swamps burnt and the number of post-fire age classes within the swamps (mosaic value) were used as explanatory variables. Two models had substantial support ($\Delta AIC_c < 2$), with the best approximating model including the variables 'baiting' and 'swamp age', and the second-best model including the additional variable 'swamp mosaic value'. The two best models had Akaike weights (weight of evidence as being the best model of the data) of 0.465 and 0.308 respectively. We used an information-theoretic approach and multimodel inference to determine the best approximating model of baiting, swamp age and swamp mosaic, and Akaike weights to assess model fit and to rank variable importance. Baiting had a model average parameter estimate of 98, swamp age 79 and a mosaic of swamp age classes 42, implying that baiting was more than twice as important as the number of swamp ages classes at a site in predicting the occurrence of quokkas. Evidence from our analysis therefore supports previous studies that concluded that continued fox control and the maintenance of a mosaic of early seral stage (<10 years since fire) and long unburnt habitat (>19 years since fire) are essential for its conservation.

Introduction

Mathematical models that describe or predict the presence or absence of flora and fauna are important tools for conservation managers (Buckland and Elston 1993; Catling and Coops 1999; Catling *et al*. 2000; Milsom *et al*. 2000; Kanowski *et al*. 2001; Wintle *et al*. 2005). Mathematical models can provide key insights into threatening processes, critical habitat components and/or the species' ecology. For example, Short (1982) identified the critical habitat requirements of the brush-tailed rock-wallaby, *Petrogale penicillata*, in New South Wales via modelling. The conservation priorities of Mexico have been predicted using mathematical models (Bojorquez-Tapia *et al*. 1995). The impact on the survivorship of African wild dogs, *Lycaon pictus*, following handling for research purposes has also been modelled (Ginsberg *et al*. 1995). Finally, the critical importance of preferred prey species as habitat features of lions, *Panthera leo*, was illustrated via models predicting their diet (Hayward *et al*. 2007).

The quokka, *Setonix brachyurus*, is a medium-sized, macropodid marsupial that is endemic to the south-western corner of Australia (Kitchener 1995; Hayward 2002). Although the Rottnest Island population has been extensively studied, there is no justification for extrapolating their ecological features to the mainland quokkas owing to the vast environmental and ecological differences between the two (Waring 1959; Hayward 2002). Compared to the contiguous Rottnest Island quokka population, those on the mainland occur at low density and in widely separated sites (Hayward *et al*. 2003). Mainland quokkas breed throughout the year, compared with the seasonal reproduction on Rottnest Island (Hayward *et al*. 2003), which is thought to be due to the availability of permanent water and nutritious forage throughout the year on the mainland (Hayward 2005).

The quokka markedly declined in its distribution and abundance in the early 1930s, and this has continued so that today the quokka is listed as vulnerable in accordance with IUCN criteria (Hayward 2002). Increasing evidence from autecological studies into the causes of the decline of the quokka indicate that the decline coincided almost exactly with the arrival and establishment of the European red fox, *Vulpes vulpes*, in the south-

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west of Australia (Hayward 2002). Yet, despite the relaxation of predation pressure following control of introduced predators, there has been no obvious population recovery (Hayward *et al.* 2003). At northern jarrah forest sites, birth rates and survivorship of adult and subadult quokkas were sufficient to allow a population increase (Hayward 2002; Hayward *et al.* 2003); however, there was evidence that a lack of recruitment may have inhibited such a recovery (Hayward *et al.* 2003). Movements also appear sufficient to allow colonisation of adjacent habitat patches; however, no dispersal was observed (Hayward *et al.* 2004). Habitat components (dense vegetation at low heights and floristic diversity) may have inhibited recovery as quokkas are thought to prefer early-seral-stage habitat as part of a mosaic of older age classes (Christensen and Kimber 1975; Hayward 2002). This is probably a result of the high availability of preferred foods soon after fire (Hayward 2005) and the refuge from predation afforded by unburnt patches (Hayward *et al.* 2005*b*). Although these studies have intimated the causes of the quokka's failure to respond to fox control, no definitive answer has been forthcoming, largely owing to the localised extinction of quokka populations at unbaited control sites (Hayward 2002; Hayward *et al.* 2003).

Here we explore two key hypotheses about the ongoing threatening processes affecting the quokka: first, that fox control is essential for the survival of quokka populations, and, second, that specific habitat components within the *Agonis linearifolia* swamps are critical in maintaining quokka populations. These habitat components were the mean time since fire burned the swamp and a value that reflected the number of discrete post-fire age classes present at a site (mosaic value). Specifically, our objectives were to determine the relative importance of fox control, time since fire and the number of swamp age classes in explaining the presence or absence of quokka populations in the northern jarrah forest using an information-theoretic approach via generalised linear models (GLM).

Methods

Determining the presence of the quokka

Surveys were conducted at 66 sites supporting *A. linearifolia* swamp shrublands within the northern jarrah forest (Fig. 1). Study sites were selected from the upper reaches of waterways in the northern jarrah forest and included sites with known quokka populations (10), sites with locally extinct populations (3), sites where quokka road-kills had been reported (4), and sites from the upper reaches of creek systems (51). Throughout the historical range of quokka distribution in the northern jarrah forest (Fig. 1), therefore, the full range of each habitat component was sampled. On the basis of previous work (Hayward 2002), we consider that the samples had minimal bias.

At each site, 10 transects were walked from the edge of the swamp vegetation into the watercourse at the centre of the swamp over a 1-km section. Owing to the relative uniformity of the swamps (Hayward 2002), transects were generally of a similar length (~30–50 m: Hayward *et al.* 2005*c*). The presence of quokkas at a site was determined by obtaining fresh scats within the characteristic runways quokkas create through their preferred, densely vegetated, *Agonis linearifolia* swamp habitat (Hayward 2002; Liddelow undated). Fresh scats located within the quokka runways (15 cm high by 10 cm wide) indicated presence (Hayward *et al.* 2005*c*). These scats are easily discernable from those of other medium-sized mammal species inhabiting the swamps (*Isoodon obesulus, Trichosurus vulpecula* and *Dasyurus geoffroii*) by their macropodid shape and vegetable content. Furthermore, quokkas are the only macropodid in the region that inhabit swamps and are small enough to fit inside the runways so confusion with *Macropus irma* or *M. fuliginosus* is highly unlikely (Hayward *et al.* 2005*c*). The linear relationship between the number of scats detected and the density of quokkas at a site (Hayward *et al.* 2005*c*) suggests that 10 transects accurately determine the presence or absence of quokkas at a site. Although this relationship allows us to estimate the population density of quokkas at a site (Hayward *et al.* 2005*c*), we used this technique solely to determine the presence or absence of quokkas at the site as a more conservative way of modelling the factors that predict quokka presence or absence.

Ecological variables investigated

A 'rule of thumb' exists that says the sample size of the least-represented category divided by 10 represents the maximum number of variables that should be used in generalised and regression models (Harrell 2001). Consequently, we were restricted in the number of explanatory variables we could use. The uncorrelated variables used were the number of dried meat baits delivered per hectare around the swamp since feral predator control began in 1994 (Baiting), the average age of the swamp (Swamp age), and the number of post-fire age classes present at a site (Mosaic value).

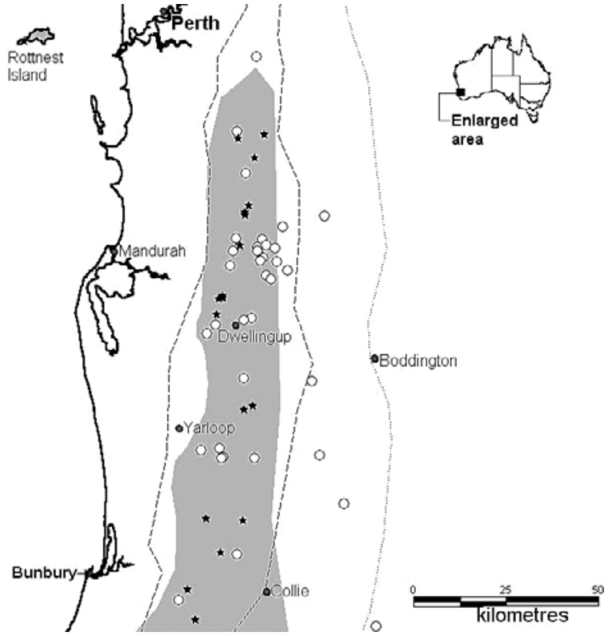

Fig. 1. Location of sites investigated for the presence of quokkas in this study. Quokka populations were found at sites denoted with filled stars whereas sites depicted with open circles showed no evidence of the presence of quokkas. The shaded area represents the distribution of the quokka in the northern jarrah forest in 2000. The dashed line shows the 1000-mm annual rainfall isohyet and the dotted line shows the 700-mm isohyet.

A whole range of potential explanatory variables were previously investigated by data-mining, including aspect, distance from forest edge, distance to nearest disturbance, amount of disturbance nearby, area of ecotonal habitat, total number of distinct habitat units, rainfall, slope, and swamp length (Hayward 2002). This led to hypotheses that could be tested using the three variables used here (Hayward 2002).

Higher levels of baiting in the northern jarrah forest have been shown to result in significant increases in the density of predation-sensitive native fauna (de Tores 1999; Friend and Beecham 2004; Mawson 2004; Morris *et al*. 2004) and reduced densities of foxes (based on sand plot monitoring and calibration using cyanide poison) (de Tores 1999). A range of baiting levels arose owing to variations in the annual frequency of bait delivery within the Western Shield and Operation Foxglove programs, which ranged from an unbaited control region through biannual, quarterly and bimonthly baiting regimes and more frequent and intense baiting at specific sites (e.g. around five known quokka populations) where monthly baiting was implemented (de Tores 1999; Thomson and Algar 2000; Hayward *et al*. 2003).

Swamp age was calculated as the area of each swamp habitat unit at a site multiplied by the average age of that unit and then divided by the total area of swamp (Hayward 2002; Hayward *et al*. 2005*b*). Habitat units were mapped using aerial photography and defined by the time since fire last burned them (Hayward 2002; Hayward *et al*. 2005*b*). This meant that sites with a range of burn ages could be compared with sites with one age class. With age since fire previously identified as a factor affecting quokka presence (Christensen and Kimber 1975), the average swamp age was used to determine whether there was a preference for any particular age class.

Swamp mosaic value was calculated as the number of swamp habitat units found at each site (Hayward 2002; Hayward *et al*. 2005*b*). This was considered as a variable in conjunction with swamp age following the apparent habitat preferences of quokkas for mosaics with >1 habitat type (Hayward 2005; Hayward *et al*. 2005*b*). Data were either log- or arcsine-transformed to achieve normality and heterogeneity of variances.

Generalised linear modelling

We used a binomial distribution (presence/absence) with a logit link function in the information-theoretic GLMs using all possible subsets of the three variables, which resulted in seven possible models. Akaike's information criteria corrected for small sample size (AIC_c) (Akaike 1973, 1974; Hurvich and Tsai 1989) based on the intercept-only model were used to select between candidate models where models with the lowest AIC_c were deemed to be the best models of the set of candidate models considered (Buckland *et al*. 2001; Burnham and Anderson 2001). Models with a ΔAIC_c (calculated by subtracting the AIC_c of the best approximating model from each subsequent model) of less than 2 were classified as having substantial support, while those with a ΔAIC_c greater than 7 had no support (Burnham and Anderson 2001).

Akaike weights were used to show the weight of evidence in favour of a model and this is essentially the weight of evidence that the model is the Kullback–Leibler best model for the data (Burnham and Anderson 2001). Model averaging was used to determine the importance of each modelled explanatory variable in predicting the presence or absence of the quokka (Burnham and Anderson 2001).

Results

Field surveys revealed 32 sites with quokkas present out of the 66 sites sampled. The model that provided the Kulback–Leibler best fit to the data included the baiting and swamp age variables (Akaike weight = 0.465: Table 1). The only other model that received strong support (i.e. $\Delta AIC_c < 2$) included all three variables (baiting, swamp age and mosaic value) and had a ΔAIC_c of 0.82 with an Akaike weight of 0.308 (Table 1). Summing the Akaike weights for these two models showed that they represented a 77.3% confidence set or combined weight of evidence. The only variable that showed a degree of support in the GLM when investigated alone was baiting ($\Delta AIC_c = 2.93$: Table 1) and these three models represented an 88.0% confidence set.

Baiting had a model average value of 98, swamp age had a model average value of 79, and swamp mosaic value had a model average value of 42. This implies that fox control was twice as influential in determining quokka occurrence than a mosaic of age classes at a site.

The number of baits per hectare and the swamp mosaic value showed positive linear relationships with increased likelihood of quokka populations found at increased levels of baiting (Table 2; Fig. 2). The average swamp age variable had a negative linear relationship, with recently burnt areas having the greatest likelihood of quokka presence (Table 2; Fig. 2).

Discussion

Presence/absence modelling can assist in identifying factors that send local populations extinct and the models derived here provide support for earlier hypotheses explaining localised extinction of quokka populations. First, intense control of introduced predators (foxes) is related to the persistence of quokka populations. The number of introduced predator-control baits per hectare is an indirect method of determining the predation pressure on the quokka. Foxes are the only predator likely to be impacted by the current baiting program and fox densities are

Table 1. Model-selection statistics for the presence/absence of quokka populations

The explanatory variables are: the number of dried meat baits delivered to control feral predators (Baiting), the mean number of years since fire burnt each swamp (Swamp age) and the number of swamp age classes within each swamp (Mosaic). The generalised linear models are numbered sequentially from the model with the lowest Akaike information criterion (AIC_c). The number of parameters (K), the ΔAIC_c and the Akaike weights of each model are also shown

Model	K	AIC_c	ΔAIC_c	Akaike weights
1. Baiting + Swamp age	3	69.14	0	0.465
2. Baiting + Swamp age + Mosaic	4	69.96	0.82	0.308
3. Baiting	2	72.07	2.93	0.107
4. Baiting + Mosaic	3	72.23	3.09	0.099
5. Swamp age + Mosaic	3	76.81	7.67	0.010
6. Swamp age	2	77.24	8.10	0.008
7. Mosaic	2	79.04	9.90	0.003

generally lower in areas of high-intensity baiting (de Tores 1999), which can result in positive demographic responses by predation-sensitive prey species (Christensen 1980; Kinnear *et al*. 1988, 1998; Friend 1990; Short *et al*. 2002). Fox impact may occur through predation upon quokkas directly at a swamp or during movements between swamps and may affect both adults and juveniles (Hayward 2002). This result also supports the idea that foxes may have been the major cause of the initial 1930s decline of the quokka (Hayward 2002). Although feral cats, *Felis catus*, have been recorded preying upon quokkas (Hayward *et al*. 2005*a*), the success of quokkas on Rottnest Island where cats are abundant suggests that they are far less of a threat even if they increase in abundance in the jarrah forest via mesopredator release (Courchamp *et al*. 1999; Crooks and Soule 1999; Mitchell and Banks 2005) following a decline in fox abundance. This is probably because each predator has a preferred weight-range of prey that it selectively targets (Hayward and Kerley 2005; Hayward 2006; Hayward *et al*. 2006*a*, 2006*b*) and the quokka is above this range for cats but within the preferred prey weight range of foxes (the critical weight range of Burbidge and McKenzie 1989).

Second, our models support the hypothesis that the presence of quokkas is influenced by two key habitat components: the time since fire (swamp age) and the number of age classes within the swamp (mosaic value: Table 1). Quokkas are more likely to exist at swamps with both young post-fire successional stages and areas with long average ages since fire (Fig. 2). Very few sites possessed only one age class and so the average age value generally reflected a mosaic of habitat units and is therefore heavily influenced by small patches of long-unburnt refugia.

Habitat components have previously been identified as important in sustaining quokka populations owing to the quokka's preference for a mosaic of freshly burnt (<10 years) and long-unburnt areas (Christensen and Kimber 1975; Hayward *et al*. 2003). This preference may reflect a mix of dietary requirements provided by the fresh regrowth that occurs in recently burnt swamps (Hayward 2005), provided that areas within those swamps remain unburnt to provide shelter and refuge from predation (Hayward 2002). This attribute may have arisen to cope with the frequent, patchy, low-intensity fire regime employed by the Noongar aboriginal people of south-western Australia (Wallace 1966; Burrows *et al*. 1995; Ward and Sneeuwjagt 1999). Displacement of Noongars in the 1860s followed by the fire-exclusion policy of the European colonists (Burrows *et al*. 1995; Wilson and Friend 1999) ultimately led to a change of fire regime involving less frequent but more intense fires and, probably, total combustion of swamps. This probably reflected the fire regimes before human arrival in Australia. Upon the return of this fire regime, with European fire-

Table 2. Logistic regression summary and variable coefficients for each variable

Variable	β	s.e.	*P*
Baiting	1.329	0.593	0.025
Swamp mosaic	0.458	0.252	0.069
Swamp age	0.078	0.037	0.034
Constant	–3.067	0.828	<0.001

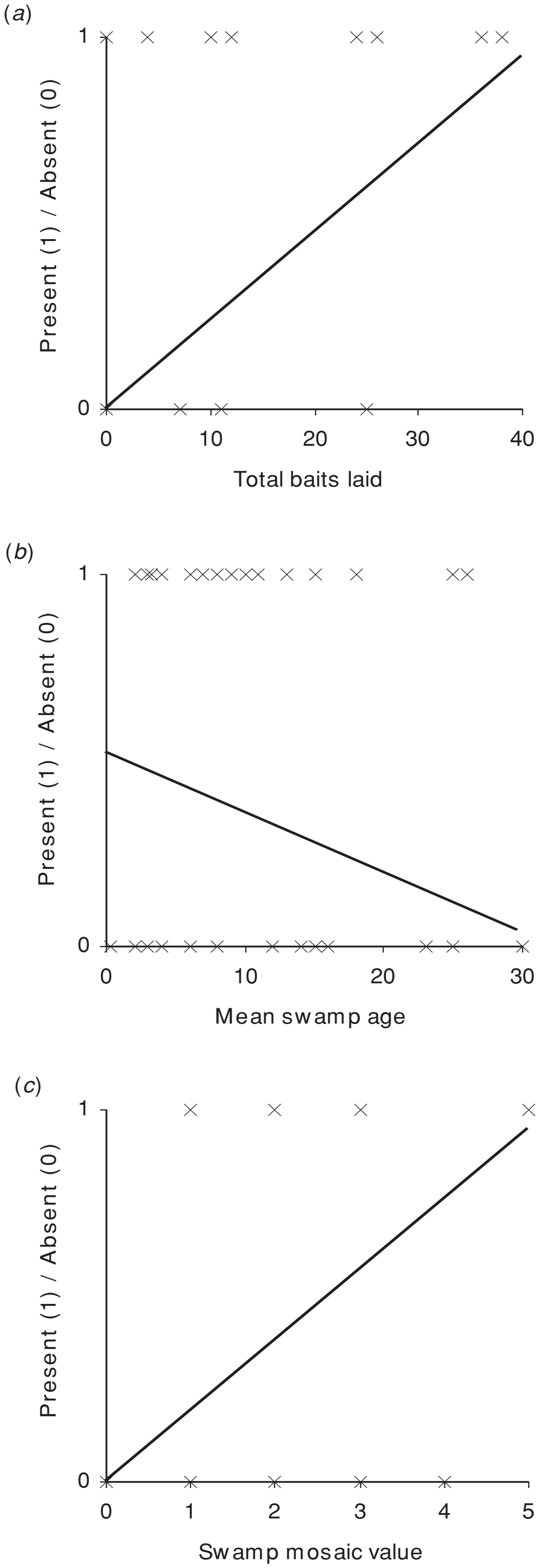

Fig. 2. Plots of individual logistic relationships of each of the variables in the best two generalised linear models (1 and 2): (*a*) baits ha^{-1}, (*b*) swamp age, and (*c*) mosaic of age classes. The *x*-axis of each plot is in the units of measurement of that variable and the *y*-axis is the partial residuals.

exclusion policies, this presumably exposed quokkas to direct mortality and unsustainable predation by the fox, which exacerbated the problems associated with altered fire regimes (Hayward 2002).

The relationship between fox control and the presence of quokkas is of major significance on mainland Australia. Kinnear *et al*. (1988) were among the first to report experimental evidence for the impact of foxes on Australian native fauna, but the validity of such results has been questioned, largely through the inadequacy of experimental controls (Hone 1999). Similar problems were encountered when trying to relate changes in quokka abundance with the impact of predation pressure (Hayward 2002; Hayward *et al*. 2003). Yet this modelling exercise supports the hypothesis that higher levels of fox control are associated with a higher probability of the presence of a quokka population (Hayward 2002; Hayward *et al*. 2003), in conjunction with a mosaic of seral stages within the *Agonis* swamp. Thus, we suggest that the reason for the continued low abundance of quokkas in the northern jarrah forest (Hayward *et al*. 2003) is likely to be a combination of continuing predation pressure, even with existing fox-control measures, and the absence of sufficient suitable swamp habitat supporting a mosaic of seral stages to provide food and predation refuge.

A technique that could separate the causes of local population decline and localised extinction would be a valuable asset for conservation management. The two causes may not be the same (Caughley 1994). For example, the quokka may have declined initially owing to the presence of the fox, but may have been resilient to habitat alteration (e.g. the quokka remains abundant around the tourist infrastructure of Rottnest Island: M. W. Hayward, pers. obs.). Once the species declined, it may have been driven to localised extinction by a combination of predation and an absence of suitable habitat. Knowledge of these two factors would provide conservation managers with a tool to prioritise management actions and more accurately predict their outcomes. We hypothesise that this may be done using presence/absence modelling to identify localised extinction causes and population abundance modelling to distinguish the causes of population declines. This hypothesis can be tested on the quokka because population estimation is possible using the same faecal pellet count methods we have employed here (Hayward *et al*. 2005*c*).

Occupancy models are another technique that could be used to analyse the presence/absence of the quokka. Such models use an information-theoretical approach, similar to that used here, to model the detection probabilities of presence/absence surveys to account for false absence results (MacKenzie 2005). In essence, this is similar to measuring observability in Distance Sampling (Buckland *et al*. 2001). The 10 transects conducted into each surveyed swamp in this study could be considered multiple surveys and therefore allow detection probabilities to be measured. These surveys, however, were conducted 100 m apart and therefore do not reflect the likelihood of detection at the same location. Furthermore, previous research suggests that surveying over a 1-km stretch of swamp accurately predicts population presence/absence and also population density (Hayward *et al*. 2005*c*). The nature of these relationships suggests that if faecal pellets are not found in the swamps then quokkas do not occur there (Hayward *et al*. 2005*c*).

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