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Prescribed burning as a conservation tool for management of habitat for threatened species: the quokka, *Setonix brachyurus*, in the southern forests of Western Australia

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Abstract. Prescribed burning is frequently advocated as a means of managing habitat for threatened species. We studied effects of fire on the quokka (*Setonix brachyurus*), a species currently used as a focal species for planning prescribed burns in the southern forests of Western Australia. We examined (i) the recolonisation of burnt areas; (ii) the refuge value of unburnt vegetation; and (iii) fire prediction variables that may help to guide fire planning to achieve desired habitat management outcomes. We hypothesised that fire regimes promoting vegetation structure and patchiness of burnt and unburnt vegetation would result in more rapid recolonisation of burnt areas by quokkas. Occupancy modelling identified the most important variables for recolonisation as retention of vertical vegetation structure and multiple unburnt patches across >20% of the total area. These outcomes were associated with high surface moisture, low soil dryness and slow fire rates of spread. Intense wildfire resulted in complete loss of vegetation structure and a lack of unburnt patches, which contributed to these areas remaining uncolonised. Burning with high moisture differentials, maximising the effectiveness of edaphic barriers to fire, retaining unburnt vegetation and maintaining vegetation structure were found to be important elements of fire regimes in this region.

Additional keywords: colonisation rates, fire regime, mesic habitats, moisture differential, patchiness, vegetation structure.

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Introduction

The use of prescribed burning to generate heterogeneous environments, often referred to as fire mosaics, is a commonly advocated strategy for biodiversity conservation (Burrows 2008; Penman *et al.* 2011; Di Stefano *et al.* 2013). However, the spatial and temporal characteristics of the fire mosaic needed to facilitate biodiversity conservation in a given region are usually poorly understood (Clarke 2008; Driscoll *et al.* 2010; Haslem *et al.* 2012; Di Stefano *et al.* 2013).

Fire management guidelines developed to promote heterogeneous fire outcomes often encourage the application of fire under conditions most likely to achieve patchiness of burnt and unburnt vegetation, such as the regular application of low intensity fire under moist spring conditions (e.g. Burrows *et al.* 2004; Burrows and McCaw 2013). Under these conditions, forests are expected to burn mildly and vegetation in swamps and creek lines often remains mostly unburnt due to higher levels of moisture than surrounding ecotypes. In this way, more mesic areas that are important for threatened species are afforded more protection from fire (Burrows *et al.* 2004;

Burrows and McCaw 2013). However, with an overall drying trend, the edaphic barrier of moisture is becoming less effective and mesic areas are increasingly vulnerable to fire (IPCC 2007; Williams *et al.* 2009).

Active management of fire is important for the protection and maintenance of habitat for many threatened species in southwestern Australia (e.g. Friend and Wayne 2003; Hayward *et al.* 2005; Brown *et al.* 2009; Valentine *et al.* 2014). Therefore, understanding the role of fire in the ecology of threatened species and embracing opportunities to apply fire to generate genuine conservation outcomes is increasingly important. This is particularly so given the expectations of larger, more frequent and more severe wildfires with a warming and drying climate (IPCC 2007; Cary *et al.* 2012; Driscoll *et al.* 2012). The increasing risk of severe wildfires to human populations has also increased political pressure to undertake prescribed burning for the proactive protection of human life and property (e.g. Boer *et al.* 2009; Keelty 2012). This increases the risk of inappropriate fire regimes threatening ecosystems and species for which ecological knowledge may be lacking.

A species that is currently used as a focal species for management of fire in the southern forests is the quokka *Setonix brachyurus* (Burrows *et al.* 2004). The quokka is a medium-sized macropod that is declared ‘vulnerable’ according to the IUCN (2014), has a wide geographical distribution on the Australian mainland, and is known to be sensitive to fire-regimes. In the northern parts of their distribution, quokkas require dense riparian vegetation for diurnal refuge, they utilise recently burnt vegetation for feeding, and fire is considered necessary to regenerate senescing habitat (Christensen and Kimber 1975; Hayward *et al.* 2005, 2007). In the southern parts of their distribution, quokkas use a diverse range of ecotypes outside of the riparian systems (Bain *et al.* 2015) and favour habitats with complex vegetation structure, low densities of woody debris and fine scale habitat patchiness (Bain *et al.* 2015). These habitat characteristics can be maintained or significantly altered by fire. We hypothesised that fire regimes that maintain or promote vegetation structure, result in patchiness of burnt and unburnt vegetation and reduce woody debris on the forest floor would result in more rapid recolonisation of habitat by quokkas.

The present study investigated the current application of fire in the southern forests of Western Australia and the effect that this has on the quokka. In particular, we were interested in the factors driving recolonisation of areas post fire, the spatial arrangement and refuge value of unburnt vegetation and identification of fire prediction parameters that may help to guide fire management for the conservation of this species. The influence of current fire management practices on other threatened and endemic species that occur with the quokka is also discussed.

Methods

Study area

This study was carried out in the forests between Manjimup and Denmark in south-western Australia (Fig. 1). Vegetation cover in this region is reasonably continuous, with tall forests interspersed with diverse ecotypes such as woodlands, sedge lands, shrub lands, creeks, rivers, wetlands and granite outcrops (Shepherd 2003). Forests in the region are dominated by jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*), karri (*Eucalyptus diversicolor*), red tingle (*Eucalyptus jacksonii*) and yellow tingle (*Eucalyptus guilfoylei*), with some species growing up to 80 m tall. Ecotypes that are occupied by quokkas in this region often have a sedge-dominated understorey and a complex vegetation structure with up to six layers of vegetation (Bain *et al.* 2015).

The region has a Mediterranean-type climate with warm dry summers (November–January) and mild wet winters (June–August). Approximately 85% of the region supports native vegetation with 65% of the area vested as national park for the purpose of conservation (Kile 2013). Prescribed burning is used extensively within this landscape to conserve and promote elements of biodiversity and for fuel reduction to mitigate wildfires and protect human life and private lands (Department of Parks and Wildlife, unpubl. data). Between May 2009 and May 2011, 143 781 ha in the region were subject to prescribed burns and an additional 34 115 ha burnt under wildfire conditions (Department of Parks and Wildlife, unpubl. data).

To evaluate the response of quokkas to fire in this landscape, we measured habitat variables, fire predictor variables and estimated presence of quokkas in 14 treatment areas and in six

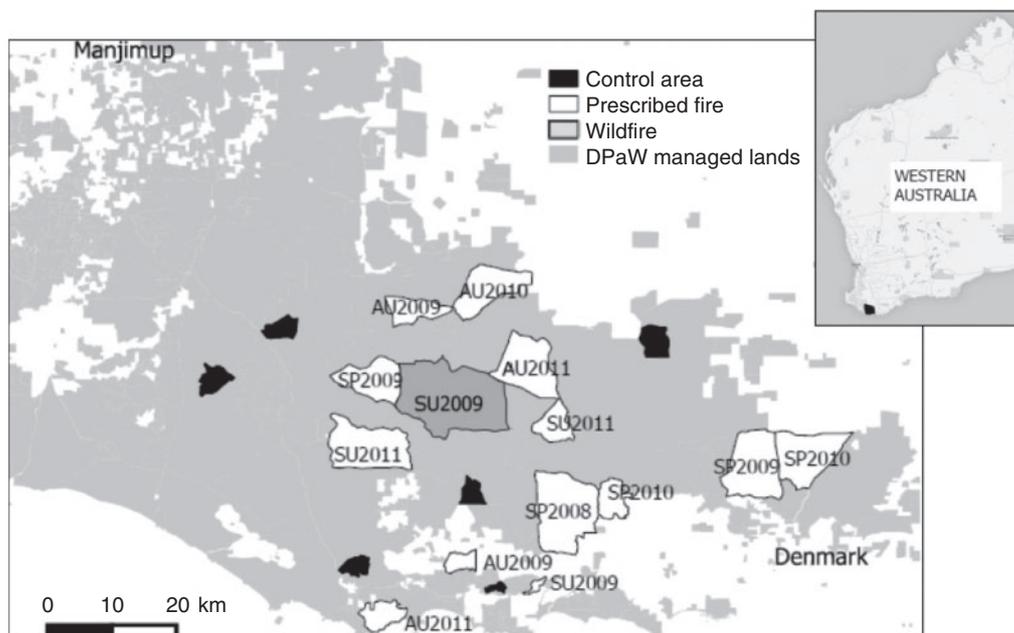


Fig. 1. Location of the study area and treatment areas. Treatment areas were burnt in prescribed burns between May 2009 and May 2011; the dark grey area was burnt by a wildfire before the prescribed burns could be implemented. DPaW, Department of Parks and Wildlife.

control areas for two years before fire and three years following fire. Thirteen of the treatment areas were burnt as planned and covered an aggregated area of 50 965 ha, and the remaining area was burnt in a wildfire before the planned prescribed burn, covering an area of 14 800 ha.

The treatment areas were selected based on: (i) being occupied by quokkas before the fire; (ii) being part of the prescribed burning program; (iii) within relatively flat areas (slopes $<15^\circ$) to negate differences in fire behaviour arising from topography; and (iv) within the same rainfall zone (900–1400 mm annual average rainfall; Pink 2012). All sites that fit these criteria were used in the study. Many of the treatment areas were adjacent to other treatment areas due to the temporal and spatial nature of the burn planning processes in this region. This, combined with large recorded movements of quokkas in this region (up to 10 km per night; Bain 2015), meant that complete independence between areas could not be guaranteed between sample periods. However, independence within sample periods was achieved by timing surveys to coincide with periods where nocturnal movement patterns were smallest and dispersal and emigration–immigration processes were unlikely (Bain 2015). Six control areas were selected that were also occupied by quokkas at the beginning of the study and were matched to the treatment areas in terms of time since last fire, topography and vegetation (Fig. 1).

Factors influencing occupancy and colonisation

Within each treatment and control area six 2-km non-linear transects were walked to assess the presence of quokkas using faecal pellets counts as described in Bain *et al.* (2014). Transects were positioned at least 200 m from the edge of the treatment area boundary, a minimum of 1 km from other transects and targeted all main ecotypes within the area likely to be suitable for quokkas (Bain *et al.* 2015). The presence or absence of fresh faecal pellets was recorded every 100 m along each transect, within 1 m either side of the transect. Data from transects were pooled for each treatment area to obtain area-level encounter histories for occupancy modelling. Fresh faecal pellet groups were geo-referenced using a Global Positioning System (Garmin GPSMAP 62, Garmin, Olathe, KS) in the field and mapped in QGIS.

For each treatment area, post fire variables were recorded that were most likely to affect the favoured habitat characteristics of vegetation structure, low density of woody debris and proximity to vegetation of different age (Bain *et al.* 2015). These included: the proportion of the area unburnt, the proportion of area with crown defoliation (dominant trees), the number, average size and spatial arrangement of unburnt patches, the scorch height, the number of vegetation layers retained following fire and the density of woody debris.

The spatial arrangement of unburnt patches within treatment areas was plotted from a fixed wing aircraft, verified on the ground and then mapped in QGIS. The minimum size of unburnt patches mapped was determined by their visibility from the air. The proportion of area unburnt (%) and the number and average size of unburnt patches (ha) patches were calculated using QGIS tools. The spatial arrangement of unburnt patches was categorised into one of four categories: (i) none present; (ii) isolated unburnt patches separated from other unburnt vegetation by a

distance of >5 km; (iii) unburnt patches separated from other unburnt vegetation by 1–5 km; (iv) two or more clustered unburnt patches within 1 km of each other.

During each site visit, the proportion of area with crown defoliation, defined as complete loss of leaves from the canopy, was measured every 100 m along transects using digital cover estimation techniques (Macfarlane *et al.* 2000, 2007). Scorch height, defined as the height of charring on tree trunks (m), was also measured every 100 m along the transects using a clinometer. The number of vegetation layers that were still living (green) and contributing to the vegetation structure was counted at each of these data points, and the density of woody debris was categorised as low, medium or high following methods in Bain *et al.* (2015). Data from transects were pooled and averaged for each treatment area.

Additional transect-level data were collected to assess post-fire habitat characteristics associated with use of habitat by quokkas. Distance to unburnt vegetation and distance to the edge of the burnt area were calculated in QGIS for each point on transects. The number of unburnt patches within 1 and 5 km of each point and the size of the closest unburnt patches were recorded by overlaying transect points on plots of unburnt patches in QGIS. These data were averaged to obtain the post-fire habitat values for points where quokkas were present or absent.

Fire predictor variables

Fire predictor variables were recorded for each treatment area on the day of ignition and included: surface moisture content, Soil Dryness Index, Fire Danger Index, the rate of spread, time since last fire, season of fire and the size of the fire treatment area. The surface moisture content (SMC) is a measure of the moisture in the top 5–10 mm of leaf litter expressed as a percentage (Sneeuwjagt and Peet 1998). The SMC was measured on the day of burn using a fine fuel moisture meter (Wiltronics Research Pty Ltd, Alfredton, Vic.) at 10 points distributed throughout the treatment area that were considered to contain representative forest vegetation. These points were averaged for each area. Prescribed burning in the southern forest is usually planned when SMCs are between 9 and 22% (Sneeuwjagt and Peet 1998).

Soil Dryness Index (SDI) is used to predict the dryness of soils, deep forest litter, logs and living vegetation based on daily rainfall and an estimate of evapotranspiration derived from maximum temperature. The index estimates the amount of effective rainfall required to restore the soil moisture profile to full capacity and ranges from 0 when soils are saturated to 2000 when soils are extremely dry (Mount 1972; Burrows 1987; Finkele *et al.* 2006). SDI is calculated daily for several sites across the south-west forests (Australian Bureau of Meteorology 2009–2011;). For this study, we used the SDI calculations for a site known locally as Shannon, which is 5 km west of the study area. Prescribed burning in the southern forest is usually planned for when SDI calculations are between 700 and 1200, depending on the season and forest type (Sneeuwjagt and Peet 1998).

Fire Danger Index (FDI) is the predicted maximum rate of spread of a fire based on surface moisture content and wind speed. Calculations assume level topography, 60% crown cover and 5 years of leaf litter accumulation (Sneeuwjagt and Peet 1998) and are calculated daily for jarrah and karri forest types

throughout the fire season by the local Department of Parks and Wildlife (hereafter referred to as ‘Parks and Wildlife’) office. An FDI range is prescribed for each planned burn, which takes into account local variation in topography, crown cover and leaf litter accumulation. Burns are planned for when the calculated FDI is within the prescribed FDI range.

The rate of spread (ROS) is the forward rate of movement of the head fire, expressed in metres per hour. This parameter is calculated in the field by measuring the distance travelled by a fire in 15 min and multiplying this by 4. Rates of spread were documented hourly for each day that the burn was active, at a minimum of four points throughout the burn. Estimates were made by the field officer in charge of the burn and verified by a trained observer from a fixed wing aircraft. These estimates were averaged for the duration of the burn.

Time since last fire (TSF) is the inter-fire period for a particular area expressed in years. This parameter was calculated from digital fire history records maintained by Parks and Wildlife. Seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). The size of the fire treatment area (FSz) was calculated in hectares from a map of each treatment area in QGIS.

Statistical analyses

Prior to analysis, continuous variables were standardised as z-scores following recommendations in MacKenzie *et al.* (2006). Correlation between predictor variables was assessed using Pearson’s residuals, with variables discarded where correlations were >0.6 . Four variables were discarded at this stage in the analysis including: the proportion of area with crown defoliation, the number of vegetation layers, density of woody debris, and the season of burn.

The multiseason occupancy model (MacKenzie *et al.* 2006) was used to estimate the detection probability (p), occupancy rate (ψ) and colonisation probability (γ) using Program MARK (White and Burnham 1999). This model assumes that habitats are closed to changes in occupancy within a season, but allows for colonisation and local extinction between seasons. Temporally replicated transects were treated as occasions.

Three sets of models were developed: one that separated spatial and temporal variation and fire effects in the analysis by focusing on two covariates: treatment (control vs treatment) and time (before vs after the fire). The intent of this analysis was to use the interaction of these covariates to demonstrate a fire effect. Once we had confirmed greater levels of support for models that estimated a fire effect, we developed two sets of models to identify the combination of post fire habitat variables and fire predictor variables that best described detection and colonisation parameters. We used Akaike’s Information Criterion with a small sample size correction (AICc) for model selection and considered models with delta AICc values <2 to have strong support, with preference being given to the most parsimonious model (Quinn and Keough 2002). Akaike weights were calculated for each model to provide an indication of the relative likelihood of the model (Burnham and Anderson 2002). Parametric bootstrap and Pearson chi-square goodness-of-fit tests were used to assess the fit of the models to our data (MacKenzie and Bailey 2004).

To assess patterns in the use of unburnt patches as refuge, analysis of variance was used to evaluate the differences between areas within the treatment areas where quokkas were present following fire and areas where they were not detected. Occupancy was used as the dependent variable and this was considered acceptable given the consistently high estimates of detection probability generated from the multi-season models (Table 1) and the low likelihood of false absences.

Results

Factors influencing occupancy and colonisation probability

The probability of detection and the rate at which quokkas recolonised areas in this study were found to be a function of the interaction between treatment (control v. treatment) and time (pre- vs post-burn) (Table 1, model set 1). Parameter estimates from the strongest model (model weight of 0.83) indicate that the probability of colonisation in treatment areas was highest before fire and three years post fire and that detection probability remained relatively constant (Fig. 2). The probability of colonisation remained constant throughout the study in the control areas and the detection probability followed the same pattern as in the treatment areas (Fig. 2).

The strongest model (model weight of 0.73) described scorch height, the proportion of area unburnt and the size of unburnt pockets as having the strongest influence on colonisation of post-fire habitat by quokkas (Table 1, model set 2). The recolonisation of post fire environments by quokkas was most rapid for areas with scorch heights of less than 10 m (mean $3.4 \text{ m} \pm \text{s.e. } 0.54$), where more than 20% of the area was unburnt (mean $36.9\% \pm \text{s.e. } 3.55$), and unburnt pockets were larger than 36 ha (mean $143.0 \text{ ha} \pm \text{s.e. } 23.94$). These areas were recolonised by quokkas within 12 months (mean $0.4 \text{ years} \pm \text{s.e. } 0.11$), with some areas occupied immediately following fire (Fig. 3). Four areas were burnt with moderate intensity, characterised by higher scorch heights (mean $12.6 \text{ m} \pm \text{s.e. } 0.61$), a lower proportion of area unburnt (mean $20.0\% \pm \text{s.e. } 1.71$), and smaller unburnt pockets (mean $20.1 \text{ ha} \pm \text{s.e. } 2.14$). Quokkas were detected in these areas within an average of 2.4 years ($\pm \text{s.e. } 0.07$; Fig. 3). One treatment area was burnt with high intensity within a wildfire area and post fire conditions included high scorch heights (mean $27.1 \text{ m} \pm \text{s.e. } 1.4$) and no unburnt pockets. Quokkas had still not been detected within this area at the end of this study, 4 years following the fire event.

Refuge value of unburnt vegetation

A total of 87% of unburnt patches occurred in association with creek lines, swamps or granite outcrops. The distance to unburnt vegetation within the fire boundary, the size of the closest unburnt patch and the number of unburnt patches within 1 km had the strongest influence on the activity patterns of quokkas following fire. In particular, for the first year post-fire, all quokkas were detected within 230 m (mean $68.0 \text{ m} \pm \text{s.e. } 10.54$) of unburnt vegetation, were associated with unburnt patches that were larger than 36 ha (mean $175.7 \text{ ha} \pm \text{s.e. } 28.49$) and were within 1 km of at least two unburnt patches (mean $3.4 \pm \text{s.e. } 0.19$). For areas that were mildly burnt, unburnt patches were less important in the second and third years post-fire as shown by greater movements away from these refuges as the surrounding

Table 1. Comparison of fitted models for quokka occupancy, colonisation and detection probability using multiseason occupancy models

Top models presented. $\Delta AICc$ is the difference in AICc from the top ranked model; w is the model weight; k is the number of parameters in the model; GOF is the Pearson chi-square statistic P value, used to provide a measure of model fit: values <0.1 demonstrate lack of fit of models to the data; ψ is the estimated occupancy in the first year of the study; γ is the estimated colonisation probability; p is the detection probability. Post-fire habitat covariates modelled include: treatment (TR), time (t), the proportion of area unburnt (UB), the average size of unburnt patches (SP), the average scorch height (SH), the number of unburnt patches (NP) and their spatial arrangement or clustering (CP). Fire predictor covariates modelled include: SDI, surface moisture content (SMC), Fire Danger Index (FDI), time since last burnt (TSF), fire size (FSz) and rate of spread (ROS)

Model	$\Delta AICc$	w	k	GOF
Model set no. 1. Interactive effects of fire treatment (control vs treatment) and time (pre- vs post-burn) on detection probability				
$\psi(\cdot), p(t, TR), \gamma(t, TR)$	0.00	0.83	6	0.25
$\psi(\cdot), p(TR), \gamma(TR)$	3.48	0.15	4	0.24
$\psi(\cdot), p(t), \gamma(t)$	7.09	0.02	5	0.17
$\psi(\cdot), p(\cdot), \gamma(\cdot)$	30.65	0.00	3	0.00
Model set no. 2. Combinations of fire effect covariates and time (number of years post-fire) that best describe recolonisation parameters				
$\psi(\cdot), p(t), \gamma(SH, UB, SP, t)$	0.00	0.73	7	0.54
$\psi(\cdot), p(t), \gamma(UB, SP, NP, t)$	2.71	0.19	7	0.19
$\psi(\cdot), p(t), \gamma(SH, UB, NP, t)$	4.55	0.07	7	0.14
$\psi(\cdot), p(t), \gamma(SP, NP, CP, t)$	8.86	0.01	7	0.01
$\psi(\cdot), p(t), \gamma(NP, CP, t)$	14.12	0.00	6	0.00
$\psi(\cdot), p(t), \gamma(SH, UB, SP, NP, CP, t)$	29.12	0.00	9	0.00
Model set no. 3. Combinations of fire predictor variables and time (number of years post-fire) that best describe recolonisation parameters				
$\psi(\cdot), p(t), \gamma(SDI, SMC, ROS, t)$	0.00	0.79	7	0.53
$\psi(\cdot), p(t), \gamma(SMC, ROS, t)$	2.67	0.21	6	0.11
$\psi(\cdot), p(t), \gamma(SDI, FDI, TSF, SE, FSz, t)$	22.15	0.00	8	0.03
$\psi(\cdot), p(t), \gamma(SMC, FDI, TSF, SE, FSz, t)$	40.65	0.00	9	0.00
$\psi(\cdot), p(t), \gamma(SDI, SMC, FDI, TSF, SE, FSz, ROS, t)$	121.33	0.00	11	0.00

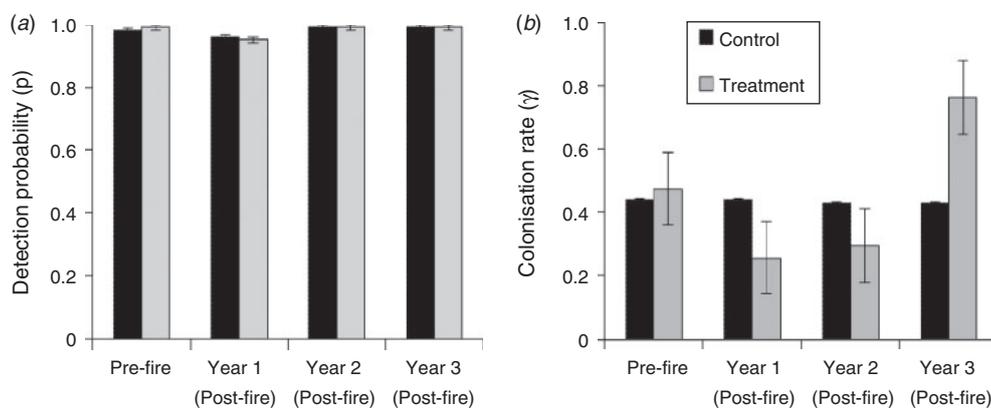


Fig. 2. Estimated detection probability (p) and colonisation rate (γ) for quokkas in treatment areas and control areas in the southern forests of Western Australia: (a) changes in the detection probability over time; and (b) changes in the colonisation rate over time.

vegetation recovered. All quokkas detected in the third year post-fire were still within 1 km of unburnt vegetation (mean 319.4 m \pm s.e. 25.29).

Fire predictor variables

The fire predictor variables best able to predict colonisation probability included surface moisture content, Soil Dryness Index and rate of spread (Table 1, model set 3). Models containing these predictors had a combined model weight of 1.0, and the top model had a weight of 0.79 (Table 1). Areas that at the time of fire had a surface moisture content greater than 11%,

a Soil Dryness Index lower than 800 and a rate of spread less than 50 m h⁻¹ were recolonised by quokkas within 12 months. Quokkas took more than four years to recolonise areas with a surface moisture content of 8%, a Soil Dryness Index of 922 and an average rate of spread of 130 m h⁻¹.

The surface moisture content, average rate of spread and SDI were all closely correlated with the three post fire habitat variables found to be most influential on the time taken by quokkas to recolonise areas following fire (Table 2). Scorch height decreased with increasing surface moisture and increased with increasing rate of spread and SDI. The proportion of area

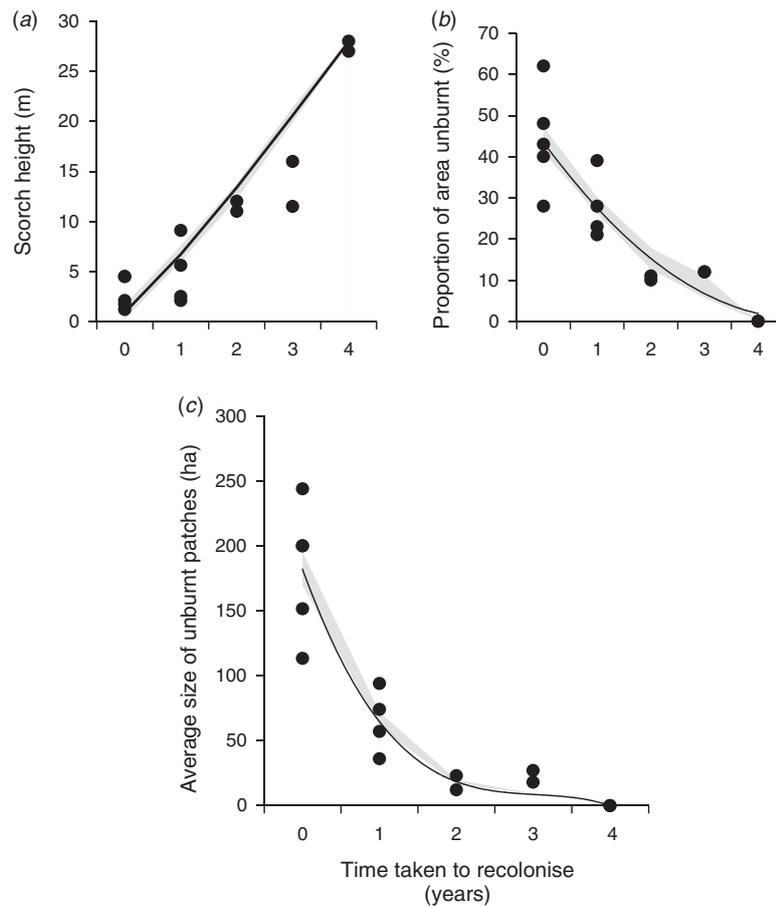


Fig. 3. The effect of fire response variables on the time taken by quokkas to recolonise areas in the southern forest post-fire: (a) fire intensity (scorch height) with a linear trend line fitted; (b) proportion of area unburnt with a polynomial trend line fitted; (c) size of unburnt patches with a polynomial trend line fitted. Points represent site-averaged data and shaded bands represent the upper and lower bounds of the standard errors.

Table 2. Pearson's correlations (R^2) between significant fire predictor variables and post-fire habitat conditions that have the highest influence on recolonisation of habitat by quokkas

Fire predictor variables	Surface moisture content (%)	Average rate of spread (m h^{-1})	Soil Dryness Index
Scorch height	-0.777	0.819	0.605
Proportion of area unburnt (ha)	0.736	-0.803	-0.638
Average size of unburnt patches (ha)	0.603	-0.597	-0.475

unburnt increased with increasing surface moisture and decreased with increasing rate of spread and SDI. The average size of unburnt patches increased with increasing surface moisture and decreased with increasing rate of spread and Soil Dryness Index (Table 2).

Discussion

Factors affecting recolonisation of habitat following fire

In support of our hypothesis, recolonisation of fire-affected areas by quokkas in the southern forest was strongly affected by

the intensity and patchiness of the fire, the presence of unburnt patches that presumably provided refuge during and after the fire event, the structure of vegetation remaining within burnt areas and associated implications for recovery of a complex vegetation structure. In particular, scorch height, the proportion of area unburnt and the size of unburnt patches were identified as measurable post burn habitat variables with the greatest influence on recolonisation of areas by quokkas in this region. Quokkas recolonised post fire habitats within 12 months where scorch heights were less than 10 m and more than 20% of the area remained unburnt, with multiple unburnt patches larger

than 36 ha. These findings are consistent with known habitat requirements of quokkas in this region, including vegetation with a complex structure (at least three layers) and proximity to areas of alternative vegetation age (Bain *et al.* 2015).

Variation in fire intensity is an important source of heterogeneity in fire-affected ecosystems, particularly in relation to the structural complexity of vegetation and the retention of unburnt patches (Bradstock *et al.* 2010; Leonard *et al.* 2014; Robinson *et al.* 2014). Scorch height provides a measure of the average flame height during the fire, which can be an indirect measure of fire intensity and the effect of fire on vertical vegetation structure (Burrows 1997; Gould *et al.* 2007; Clarke 2008). Mid-storey and overstorey species often survive low intensity fires reasonably intact, allowing them to continue to contribute to the ongoing structural diversity of the vegetation (Burrows 1997; Gould *et al.* 2007; Clarke 2008). In addition, edaphic barriers to fire that are created by rock, large logs, discontinuous vegetation and moisture are most effective under these conditions, resulting in a greater patchiness of burnt and unburnt vegetation (Clarke 2002; Penman *et al.* 2007; Leonard *et al.* 2014). Unburnt patches in this study were invariably associated with rocky outcrops or ecotypes with higher levels of moisture such as creek lines and swamps.

In contrast, intense fire behaviour and associated high scorch heights can increase the loss of vertical vegetation structure and increases the time taken for vegetation to return to a complex structure. More intense fires can also overcome edaphic barriers and result in homogeneous fire outcomes over broad spatial scales (Price and Bradstock 2012; Burrows 2013; O'Donnell *et al.* 2014). This was the case within the wildfire-affected area in the present study, where intense fire behaviour resulted in scorch heights greater than 27 m that affected all vegetation layers, removed structural complexity and resulted in all components of the landscape burning, including riparian systems and rock outcrops. Quokkas had yet to recolonise this area at the end of the study, four years following the fire. The collapse of dead mid-storey vegetation in the third year following fire may have contributed to ongoing unsuitable habitat conditions for quokkas in this area, owing to rapid accumulation of woody debris on the forest floor (Bain *et al.* 2015).

Refuge value of unburnt vegetation

Unburnt patches clearly act as a refuge for animals to escape fire, persist in and subsequently recolonise the post-fire landscape, or to assist with post-fire recolonisation from adjoining unburnt areas. In this study, quokkas were recorded in unburnt patches well inside the fire-affected area within a month following fire, suggesting that at least some individuals remained *in situ* during the fire, taking refuge within these patches. The size of these patches and their spatial arrangement relative to other patches or other unburnt vegetation were important determinants of whether they were occupied following fire. Quokkas occupied unburnt patches greater than 36 ha and within 1 km of at least two other unburnt patches. For the first year following fire, 100% of detections were within 230 m of unburnt vegetation. Quokkas were detected further away from unburnt patches in the second and third years following fire, however, all detections remained within 1 km of unburnt patches, which suggests that

the patches were still central to movement patterns as the surrounding vegetation recovered.

The relative importance of unburnt patches as refuge areas is likely to depend on the degree to which they provide resources that are otherwise unavailable within the surrounding burnt area (Penman *et al.* 2007; Robinson *et al.* 2014). The preferential selection by quokkas for unburnt patches greater than 36 ha and within 1 km of at least two other unburnt patches may be related to predator pressure. Increased distance from unburnt vegetation has previously been associated with an increased risk of predation for many small and medium-sized herbivores (Banks 2001; Le Mar and McArthur 2005; Styger *et al.* 2011). Quokkas and other small herbivores tend to forage in proximity to a safe refuge where predators are present, but utilise the burnt areas to take advantage of the greater abundance of forage following fire (Southwell and Jarman 1987; Blumstein *et al.* 2002; Hayward 2002; Archibald and Bond 2004).

In addition, the home-range size of quokkas in this region is large, with core areas of females overlapping substantially but no overlap of core areas for males (Bain 2015). Group fidelity among females and the lack of core range overlap between males are likely to influence the suitability of unburnt patches in terms of their size and ability to meet the space requirements of individuals. This is also likely to affect the viability of sub-populations of quokkas persisting in unburnt patches while surrounding burnt areas are recovering.

The spatial arrangement of refuge patches and their context in the broader fire mosaic is important for maintaining populations over time (Watson *et al.* 2012; Robinson *et al.* 2014). The ability of quokkas and other species to either disperse through the burnt landscape or use refuge patches as 'stepping stones' is important in maintaining habitat connectivity and movement patterns at a landscape scale (Templeton *et al.* 2011; Driscoll *et al.* 2012). The effective provision of refuge patches within burnt areas is particularly important where adjoining areas are planned to be burnt within three years, which is often the case in this region where recently burnt areas offer a low-risk boundary for the implementation of future burns. Cumulative impacts of multiple large areas burnt adjacent to each other and with limited temporal separation are potentially significant where effective refuge areas have not been achieved.

Prescribing for effective refuge within planned burns

The regime and the manner in which prescribed burns are undertaken is important in determining the likely availability of temporary refuge, suitable habitat, and long-term persistence of species in and surrounding fire-affected areas. This is of particular interest given the recent political pressure to increase prescribed burning to protect human life and assets, which has arisen from several large and intense wildfires that have resulted in loss of lives and properties (e.g. Keelty 2012; Price and Bradstock 2012). Although there is a genuine need to protect human life and property from severe wildfires, the simultaneous achievement of ecological outcomes is possible and should not be overlooked.

Prescribing to retain 20% or more of an area unburnt is a common occurrence in the southern forest (e.g. Bain 2009) and the present study has confirmed moisture parameters and field rates of spread that can achieve this. Soil moisture contents

greater than 11%, soil dryness indices lower than 800 and field rates of spread less than 50 m h⁻¹ contributed to mild fire behaviour in forested areas of this region that maximised the retention of vegetation structure, promoted retention of unburnt vegetation due to active edaphic barriers, and resulted in rapid recolonisation of burnt areas by quokkas. The spatial arrangement of the 20% unburnt vegetation is important from both an ecological perspective and from a burn security perspective. Clustered but spatially separated patches are likely to provide the best refuge value for fauna, as long as they meet the minimum size requirements, 36 ha for quokkas, and contribute to habitat connectivity within and between burnt areas. From the perspective of burn security, spatially separated pockets are also less likely to re-ignite under hot dry weather conditions that might allow fire to escape from the secured boundary into adjacent unburnt vegetation.

Prescribing for effective refuge in prescribed burns in a manner that is consistent with the outcomes of this study does not conflict with the current requirements of land managers to meet burn security outcomes and private property protection outcomes and does not increase the risk of severe wildfire in this landscape, particularly where larger unburnt patches occur >1 km from the burn boundary (Gould *et al.* 2007; Department of Parks and Wildlife, unpubl. data (standard operating procedure 24)).

Proactive management of fire to protect taxa and ecosystems sensitive to fire regimes is of increasing importance in the context of climate change, given the expected increase in large scale and intense wildfires and the increasing challenges associated with protecting mesic habitats and their ecological function. Current evidence indicates prescribed burning can create conditions conducive to the persistence and recolonisation of habitat by quokkas in the short term, but it is also clear that some fire regimes can adversely affect quokkas in the short to medium term and may well have long-term implications for habitat connectivity and metapopulation function. This is particularly the case where the spatial and temporal scale of impact is such that animals can no longer safely move between suitable habitat patches.

Quokkas in this area routinely move between 0.5 and 4 km in a night within stable home ranges and have been recorded dispersing more than 14 km to establish new home ranges (Bain 2015), so movement across large distances is possible. However, our results suggest that movement through open habitat is generally avoided, probably as a result of vulnerability to predation and thermoregulation requirements. Large-scale and intense fires reduce the ability of quokkas to move between suitable habitat patches and essentially results in temporary habitat fragmentation. Prescribed burning can also contribute to this habitat fragmentation where multiple large burns are planned in the same area within a short period of time, if effective refuge is not retained.

This study has the potential to contribute to an approach to prescribed burning that allows human protection objectives to be met but also meets the ecological needs of the quokka within burn areas. This also has some application for a range of threatened and endemic species that occur with the quokka. Although the spatial arrangement of refugia may vary, the importance of moisture differentials, maximising the effectiveness of edaphic barriers to fire, retention of unburnt vegetation associated with mesic and rocky habitats and retention of vegetation structure are likely to be common requirements from

a fire regime for other species. This has been demonstrated by other research in the region, which has highlighted that the abundance of the western ringtail possum (*Pseudocheirus occidentalis*) is negatively associated with greater fire intensity and habitat fragmentation arising from loss of tree canopy (Wayne *et al.* 2006). Research in other parts of Australia also supports the notion that the suggested approach to burning may benefit a wider range of species (e.g. Sitters *et al.* 2015a, 2015b).

Use of such explicit ecological criteria during fire planning and implementation may also help to build ecosystem resilience and provide protection to biodiversity values against the increase in homogenising wildfires that are predicted under a drying climate scenario (Flannigan *et al.* 2009; Williams *et al.* 2009; Wilson *et al.* 2010).

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