

Appendix 45 Forest Restoration – Zoological Society of London Article 2014

Does forest restoration in fragmented landscapes provide habitat for a wide-ranging carnivore?

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Keywords

carnivore; forest; fragmentation; mining; range contraction; re-colonization; restoration; roadkill.

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Editor: Nathalie Pettorelli

Associate Editor: Vincenzo Penteneriani

Received 17 May 2013; accepted 3 February 2014

doi:10.1111/acv.12112

Abstract

The loss of suitable macro- and microhabitats can negatively affect an animal's ability to persist in an area, ultimately leading to range contractions. The western quoll *Dasyurus geoffroii* is a wide-ranging Australian carnivore that has suffered a catastrophic range contraction since European settlement, partly due to landscape fragmentation. Bauxite mining in the jarrah forest of south-western Australia, where western quoll currently persist, disturbs and fragments large areas, potentially reducing habitat available to quolls. We examined macro- and microhabitat use by western quolls in fragmented landscapes containing remnants of unmined jarrah forest and bauxite mine restoration to determine the impacts of this fragmentation on its ecology. Specifically, we aimed to identify the microhabitats required by western quoll for denning and movement and if post-mining restored forests provided these microhabitats. Quolls used restoration of varying ages for denning. They were adaptable in den substrates used, selecting subterranean burrows associated with surface rocks in restoration where preferred substrates used in unmined forest (hollow logs and stumps) were less available. Logs were also an important microhabitat used by quolls to traverse through unmined forest and we recommend more logs are restored post-mining. Our results suggest that post-mining restoration provides a permeable matrix for western quolls, and individuals quickly re-colonize restored areas and use available habitat, particularly for denning. Important microhabitats such as logs, stumps and large hollow-bearing trees are relatively sparse in restored forest. Our study does not explicitly consider the potential effects of this on quoll survival and demography so further studies of breeding success and long-term survival across multiple generations of quoll are recommended. We concluded that forest restoration can be an important strategy in managing fragmented landscapes for wide-ranging species by providing pathways for movement, habitat for re-colonization and improved landscape connectivity for these species.

Introduction

Destruction and fragmentation of habitat are serious threats to global biodiversity (Wilcove *et al.*, 1998) that continue at unsustainable rates in many landscapes due to human pressures for resources (Crooks, 2002). Many mammal species, particularly carnivores with large home ranges and small populations [e.g. mountain lion *Felis concolor* (Crooks, 2002)], are vulnerable to local extinction in fragmented landscapes, with reduced probabilities of occurrence in small, isolated habitat patches (Woodroffe & Ginsberg, 1998). Furthermore, not only is the size of fragments within the landscape important, but also how species perceive and use the intervening matrix, or 'non-habitat' (Rosenblatt *et al.*, 1999; Hobbs, 2005). It has been suggested that there is

a need to enlarge and/or connect fragments of priority habitat using restoration (Dobson, Bradshaw & Baker, 1997), but this may provide little benefit for fauna if the restoration does not meet all the requirements for faunal re-colonization (Craig *et al.*, 2012). Additionally, in some cases, plant community succession within restored areas may take decades, or centuries, before the restored vegetation starts to resemble the original community (Grant, 2003; Craig *et al.*, 2012) and slow-forming microhabitats, such as coarse woody debris and tree hollows, appear (e.g. Kanowski *et al.*, 2003). The suitability of restoration as habitat for fauna may therefore vary depending upon the availability of microhabitats required by particular species (e.g. Martin *et al.*, 2004). Furthermore, how effective restoration is at improving matrix permeability and, hence, con-

nectivity between fragments remains poorly known for many wide-ranging carnivorous mammals.

Understanding the ecology and threats affecting Australia's vulnerable mammal species is a high priority, particularly in fragmented landscapes where risks of decline are highest (e.g. Reed, 2004; McKenzie *et al.*, 2007). The high rate of extinctions and range contractions since European settlement (Short & Smith, 1994) have been highest among ground-dwelling (Johnson, 2006) and medium-sized species (Burbidge & McKenzie, 1989; Johnson & Isaac, 2009) such as the carnivorous western quoll *Dasyurus geoffroi*. It once occurred across ~70% of Australia (Orell & Morris, 1994), but is now restricted to 5% of its former range in part due to loss and fragmentation of habitat (Dunlop & Morris, 2008). The jarrah (*Eucalyptus marginata*) forest in south-western Australia is an important stronghold for western quoll, being the largest contiguous habitat currently inhabited by this species. However, this has become increasingly fragmented due to bauxite mining in the northern jarrah forest since 1963. Resultant patches of complete forest disturbance within natural forest could potentially limit landscape connectivity for quolls, yet no studies have examined the effect of landscape fragmentation, and removal of potentially important habitat due to surface mining, on this wide-ranging species.

We investigated how western quoll respond to efforts to reconnect jarrah forest fragments remaining after bauxite mining using post-mining restoration of the intervening matrix (i.e. restored bauxite mine-pits). We specifically aimed to determine: (1) if quoll populations exist in bauxite mining areas of the northern jarrah forest and at what densities; (2) if quolls select diurnal den sites more frequently in unmined, compared with restored, forest and what substrates they use as den sites; (3) whether restored forests provide the microhabitats required by quolls. We then recommend restoration enhancements to facilitate quoll re-colonization and use of restored forests.

Materials and methods

Study area and species

The study was conducted at Alcoa of Australia's (hereafter Alcoa) Huntly (32°37'S, 116°03'E) and Willowdale (32°53'S, 116°02'E) mines in the northern jarrah forest of south-western Australia (Fig. 1), where c. 600 ha of forest is cleared, mined and restored annually. The climate of the area is Mediterranean, with cool, wet winters and warm, dry summers. Rainfall averages ~1000 mm year⁻¹, with > 75% falling between May and September (Beard, 1990).

The jarrah forest is a dry sclerophyll forest, dominated by two eucalypts, jarrah and marri (*Corymbia calophylla*). Typical mid-storey and understorey species include *Banksia grandis*, *Persoonia longifolia*, *Bosstaea aquifolium* and *Adenanthos barbiger*. The northern jarrah forest has a history of logging, fire and *Phytophthora* dieback that has resulted in a mosaic of forest types, structures and disturbances (Koch, 2007). Bauxite mining is a more recent dis-

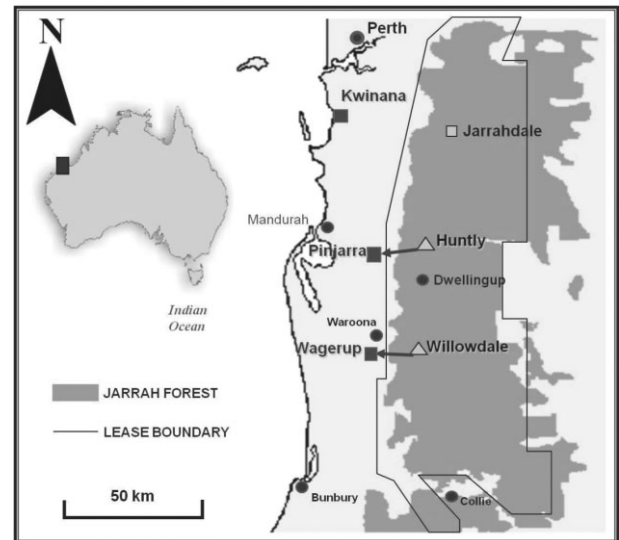


Figure 1 Map of Alcoa's mining lease in the northern jarrah forest of south-western Australia and the location of study sites at Huntly and Willowdale mines.

turbance that causes forest fragmentation and a resultant mosaic of restored forest of varying ages interspersed within remnant patches of unmined forest (Fig. 2). Mine-pits are restored by returning topsoil and seeding between 60 and 100 overstorey, mid-storey and understorey species (see Koch, 2007; Koch & Samsa, 2007). Since 1992, 'habitat piles' comprising piles of logs, stumps and rocks have been returned to restoration to provide habitat for fauna (Nichols & Grant, 2007).

Western quolls are wide ranging: males have a home range of c. 15 km² and females 3–4 km² (Serena & Soderquist, 1989a). Quolls are nocturnal, with a broad diet of invertebrates, mammals, birds and small lizards, and den during the day in hollow logs and ground burrows (Dunlop & Morris, 2008). Quolls have been recorded in nearby unmined forest landscapes (Serena & Soderquist, 1989a; Glen *et al.*, 2009), and although quolls have been recorded in both restored and unmined forest within Alcoa's mine lease (Nichols & Grant, 2007), records have been too infrequent to understand the effects of mining on quolls.

Western quoll trapping

Fourteen trapping sessions (13 at Huntly and 1 at Willowdale) across nine trapping transects (8 at Huntly and 1 at Willowdale) were conducted between June 2009 and December 2010. Trapping transects comprised up to 54 cage traps (220 × 220 × 550 mm, Sheffield Wire Works, Welshpool, WA, Australia) spaced at 200- or 400-m intervals in a variety of habitats along the edge of forest tracks. Traps were baited with chicken and opened for four or five consecutive nights. Trapping networks were not standardized across trapping periods but were designed to survey large parts of mining regions to increase the chance of

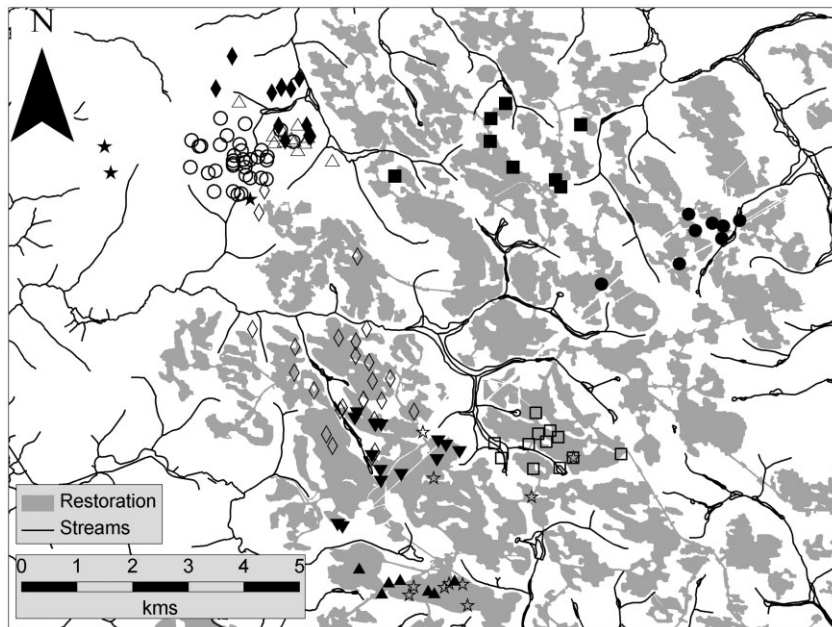


Figure 2 Map of Huntly mine site showing the locations of selected dens of the 11 tracked quolls in relation to the mosaic of restored (in grey) and unmined forest (in white). Dens selected by each of the 11 tracked quolls are shown with a different symbol for each individual quoll.

capturing sufficient animals for radio-tracking and spooling studies. Captured quolls were weighed, sexed, aged, uniquely marked with microchips inserted subcutaneously between the shoulder blades and released at their capture site.

Radio tracking

Radio collars with a two-stage transmitter and mortality mode (Sirtrack, Havelock North, NZ) were attached, via a leather neck collar, to 14 adult quolls: 9 females and 5 males (> 800 g in body weight) trapped at Huntly. Transmitters and collars weighed ~20 g and were < 2.5% of body weight. After transmitter attachment, animals were observed for 15 min for signs of distress, before being released at their capture site. Collared animals were tracked during the day to den locations opportunistically between July 2009 and July 2010, using three element Yagi antennas and R-1000 Telemetry Receivers (Communications Specialists) and the macrohabitat (unmined or restored forest), restoration age (if in restoration) and substrate (log, under stump, under rock pile, hole in ground, under tree, artificial, tree hollow and habitat pile) of each den were recorded. At completion of the telemetry study, all animals were trapped and their transmitters were removed.

Spool and line tracking

Spool and line tracking was used to assess microhabitat use by individual quolls at Huntly because this technique has been successfully used for other quoll species (Jones & Barmuta, 2000; Glen & Dickman, 2006). Trapped quolls selected for spool and line tracking were held throughout the day and provided with food and water. Spools were

attached to the rump with quick-setting viscous glue, the end tied to a nearby tree and the quolls released 1 h after sunset at their capture site. Spools comprised two 220-m-long white nylon thread (Danfield Ltd, Leigh, UK) tied together and wrapped firstly with plastic wrap and then with pharmaceutical sticking plaster (Jones & Barmuta, 2000). Spools weighed ~12 g and were < 2.2% of body weight.

The trail of thread was mapped the following morning. The first 60 m of each spool trail was considered flight behaviour and discarded from analyses. Observations of frequent changes in the direction of spool trails indicated that quoll resumed 'normal' movements within this distance. Microhabitat variables (Table 1) were recorded at 10-m intervals along the spool trails and along random trails of the same length. Random trails originated at the same point as the spool trail and extended in a random direction and were established to quantify microhabitat availability in the area each quoll was spooled. Individual quolls were only spooled once during the study.

Data analyses

Density estimates were calculated using DENSITY 4.3 (Efford, 2008), using spatially explicit capture-recapture (SECR) methods with maximum likelihood where numbers of captures/recaptures were sufficient. Density was also estimated as the total number of individuals captured divided by the total effective trapping area (ETA): the area enclosing the trapping transects with a 1.5-km buffer (half the span of a quoll home range; Serena & Soderquist, 1989a).

'Den range' was calculated for each individual based upon the tracked locations of den sites and using 100% minimum convex polygons in Ranges 7.2.5 (South, Kenward & Walls, 2008; see Serena & Soderquist, 1989a).

Table 1 Microhabitat variables measured along spool and random trails

Attribute	Description
Log travel (m)	Distance travelled along log in previous section of spool trail
Log travel proportion (%)	Log travel distance divided by the total length of spool trail
No. of logs	Number of logs (> 10 cm diameter) travelled on in previous section of spool trail
Cover – QCM (%)	Estimate of % cover using the quadrant cover method (QCM) (Glen, Sutherland & Cruz, 2010). The area within a 1-m horizontal radius of the sampling point was divided into four quadrants using the thread as the centreline. For each quadrant, it was determined if features (vegetation, logs, trees, etc.) lying within would obscure the study animal from potential predators. Each quadrant was given a score of zero (clearly visible from a height of 0.5 m), 10% (partially obscured) or 20% (fully obscured), and a further score of 0, 10 or 20% was assigned based upon visibility from directly above the animal, giving a maximum score of 100% for each sample point.
Shrub height (m)	Maximum height of shrubs (in a 2 × 2 m quadrat set-up using the thread as the centreline)
Tree density	Number of trees (in a 2 × 2 m quadrat set-up using the thread as the centreline)
Log density	Number of logs > 10 cm in diameter (in a 2 × 2 m quadrat set-up using the thread as the centreline)
Tree use and height (m)	Number of trees climbed in previous section of spool trail and a visual estimate for each tree of the maximum height climbed
Litter volume (m ³ ha ⁻¹)	Sum product of measurement of % cover of litter (visually estimated) and average of four random measures of litter depth (in a 2 × 2 m quadrat set-up using the thread as the centreline)

Each variable was measured at 10-m intervals along trails.

Proportions of unmined forest and restoration of varying age classes (0–7 years old, 7–14 years old, 14–21 years old, 21+ years old) within den ranges were calculated using ArcGIS 9.3.1.

Habitat preference associated with dens was tested using paired two sample *t*-tests to compare the proportional use of macrohabitat of actual dens (obtained from radio tracking) to available macrohabitat (in quoll den ranges). General linear models were used to test for significant differences in the relative use of different age classes of restoration by quolls that utilized restoration, with availability for establishing den sites. As too few males were tracked, analyses were conducted on females and all quolls combined.

A log-linear model, a non-parametric technique for analysing relationships between categorical variables, was used to test how the frequencies of commonly used den substrates (logs, under stumps, under rock piles and holes in ground) differed between unmined and restored forest, individual quolls and the interaction between these two factors. The most parsimonious model was selected, based upon backwards stepwise elimination from the full model, using likelihood ratio chi-square tests and the lowest Bayesian information criterion. Other den substrates used, but not included in analyses due to insufficient sample sizes, were under tree, artificial, tree hollow and habitat pile.

We examined differences in overall microhabitat use between spool and random trails on unmined data alone because sample sizes in restored forest were too small ($n = 3$) for meaningful analyses. We first created a similarity matrix between all trails using a Euclidean similarity measure on normalized data and visually represented differences between trails using principal coordinates analysis. We then analysed differences between spool and random trails using a permutational multivariate ANOVA (PERMANOVA) with use (spool vs. random) as a fixed factor and, to account for differences between individual quolls, individual as a random factor. As spool and random trails differed signifi-

cantly (see the Results section), we then analysed each of the seven microhabitat variables individually using a general linear mixed model with the microhabitats as the dependent variables, spool versus random as a fixed factor and individual as a random factor to determine which variables were contributing to the difference.

All univariate statistics were calculated using R 3.0.0 (R Development Core Team, 2011, Vienna, Austria) and Systat 11 (Systat Software, 2004), and assumptions of normality and heterogeneity of variance were met. Multivariate analyses were calculated in PERMANOVA+ for Primer (Primer-E, 2008).

Results

Western quoll density and mortality

In total, 29 individual quoll (17 males and 12 females) were captured on 60 occasions. Densities and trap success varied across seasons and years (Table 2). Fourteen animals were fitted with transmitters, of which three were found dead on the Huntly mine access road with evidence of road trauma. Another micro-chipped individual and two untagged quolls were also found dead from vehicle strikes along this road.

Den use

During the study, 138 den sites were located from 11 tracked animals: 75 in unmined forest and 63 in restoration varying from 2 to 32 years old (Fig. 2). Den site substrates differed significantly between unmined and restored forest ($G_2 = 19.4$, $P < 0.001$). In unmined forest, dens were mostly in hollow logs and ground burrows beneath tree stumps, but these substrates were never used in restored forest where dens were mostly ground burrows, usually associated with rock piles at the surface (Fig. 3). Other dens used in

Table 2 Western quoll *Dasyurus geoffroii* captures, age and sex classes, and population density estimates calculated using maximum likelihood methods in Program DENSITY spatially explicit capture-recapture (SECR) or effective trapping area (ETA) across different seasons and years at Huntly mine

Trapping period	No. of trap nights	Captures			Sex		Age		Density (SECR) (individuals km ⁻²)	Density (ETA) (individuals km ⁻²)
		No. of individual	No. of captures	% trap success	Female	Male	< 1 year	> 1 year		
July 2009	750	4	8	1.1%	3	1	0	4	0.03	
December 2009	808	12	18	2.2%	4	8	8	4	0.29	
April 2010	650	11	23	3.5%	6	5	7	4	0.08	
December 2010	486	4	6	1.2%	2	2	1	3	0.04	
July 2009 (Willowdale)	250	4	5	2.0%	1	3	0	4	0.15	
Total	2944	29	60	2.0%	12	17	14	15		

Willowdale mine area was only trapped on one occasion.

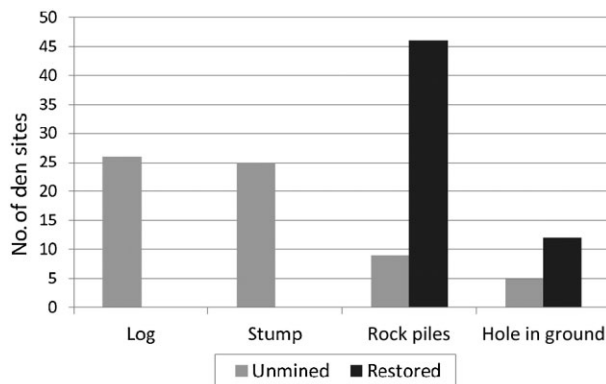


Figure 3 Frequency of diurnal den sites in unmined and restored forest by substrate type.

unmined forest were hollows in marri trees > 60 cm in diameter, including one hollow ~10 m above the ground. In restoration, only one animal used dens associated with habitat piles, and these were both subterranean burrows beneath the piles. Individuals differed significantly in the type of den substrate used ($G_{20} = 33.1$, $P = 0.033$) and there was a significant interaction between individual and macrohabitat ($G_{10} = 28.7$, $P = 0.001$). However, the interaction arose because six individuals denned in both unmined and restored forest, and displayed the den preferences in each forest type described earlier, whereas five individuals were absent from either unmined or restored forest and, therefore, displayed no den preference in the forest type where they were absent, leading to a result with statistical, but no biological, significance. There was no evidence of any spatial autocorrelation in den types selected (Supporting Information Appendix S1).

Both sexes combined, and females alone, used unmined and restored macrohabitats for denning in proportion to their availability ($t_7 = -2.34$, $P = 0.052$ and $t_5 = -1.76$, $P = 0.139$, respectively) (Fig. 4). For animals that used restored forest, use of different restoration ages for denning was proportional to their availability ($F_{3,32} = 0.03$, $P = 0.860$ and $F_{3,24} = 0.09$, $P = 0.763$, respectively).

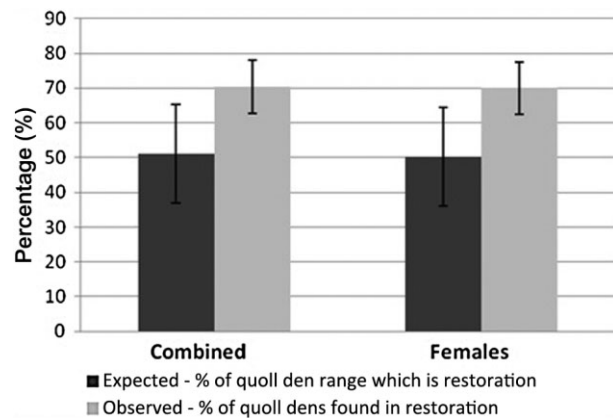


Figure 4 Observed and expected proportional habitat use for denning (\pm SE) in restored forest (combined group; $n = 8$ and females; $n = 6$).

Microhabitat use

At Huntly, 14 individual quoll (4 adult and 1 juvenile female, 2 adult and 7 juvenile males) were spooled, yielding 3420 m of spool trail. Average spool trail length (excluding flight response distance) was 244 ± 28 m (SE). Most activity was recorded on the ground in both unmined (87.5 \pm 2.7 SE %) and restored forest (98.7 \pm 0.9 SE %). Arboreal activity was recorded for three animals in unmined forest (1.3% of total unmined forest trails), who climbed a total of 12 *Banksia grandis* trees (3.10 ± 1.86 SE trees km⁻¹ of trail) to a maximum height of 5 m. Three quolls had spool trails that passed through restoration for a cumulative 60 spool trail points (18% of all spool trail points).

Attributes of spool trails in unmined forest were significantly different from random trails (pseudo- $F_{1,11} = 3.58$, $P = 0.009$) (Fig. 5). Relative to random trails, spool trails had more travel along logs and greater log densities but were not significantly different from random trails in other microhabitats (Table 3).

Discussion

Western quoll population densities (ETA) (0.03–0.09 individuals km⁻²) and trap success (1.1–3.5%) for this study

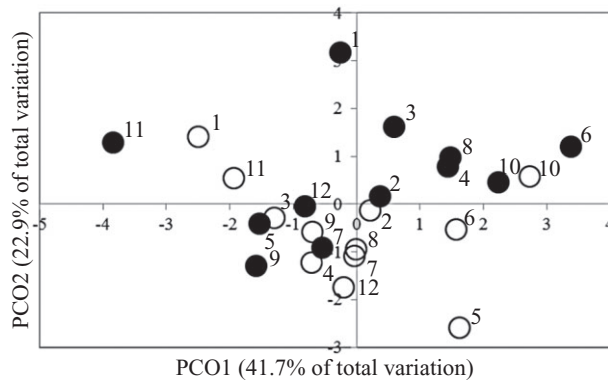


Figure 5 Two-dimensional principal coordinates analysis (PCO) comparing individual quoll spool trails (●) and random trails (○) in unmined forest. Numbers next to each symbol show the quoll and random trails for the 12 individual quolls. Comparisons are based upon seven microhabitat variables averaged from along the length of each spool and random trail. Spool trails differed significantly from random trails.

were variable spatially and temporally, but within the range (0.01–1.2 individuals km⁻²; 1–6%) of other jarrah forest studies in unfragmented landscapes (Morris *et al.*, 2003; A. S. Glen, unpubl. data) and generally higher than those in semiarid zone studies (0.03 individuals km⁻²; 0.3–1.5%) (Rayner *et al.*, 2012). High variability in densities of other wide-ranging carnivores, such as the Andean mountain cat *Leopardus jacobitus* and culpeo *Lycalopex culpaeus* in South America and leopard *Panthera pardus* in Africa, have been attributed to prey distribution, human activity and habitat fragmentation (Walker *et al.*, 2007; Swanepoel *et al.*, 2012). Although there is no evidence that surface mining negatively impacts upon quoll populations based upon densities consistent with unfragmented landscapes, road kill is a potential indirect impact. Significant quoll mortality from vehicle strikes was observed along the mine access road. The widening and sealing of an access road through an eastern quoll *Dasyurus viverrinus* population in Tasmania resulted in high rates of road kill, contributing to its local extinction (Jones & Barmuta, 2000). Road kill has also been implicated in the decline of other medium-sized mammals, such as Florida panther *Felis concolor* (Harris & Gallagher, 1989), European badgers *Meles meles* (Gallagher & Nelson, 1979) and koala *Phascolarctos cinereus* (Dique *et al.*, 2003). Longer term research of quoll survival in mined landscapes is recommended to quantify road kill impacts upon population viability. In the interim, we recommended strategies be implemented to reduce road kill, such as signage of high use areas and changes, and enforcement of, speed limits.

Hollow logs are important den sites for western quoll in the jarrah forest (Serena & Soderquist, 1989a; Dunlop & Morris, 2008). The den sites located in unmined forest in this study were largely in hollow logs and under stumps. The den sites in restored forest were more often located in subterranean burrows, typically under rock piles, so despite the limited number of logs returned to restored forest (3% of log densities in unmined forest: R. A. McGregor, unpubl. data),

individual quolls were adaptable and able to re-colonize restored areas by selecting den sites to utilize available microhabitats. This adaptability in the use of available den substrates is consistent with their broad habitat use across their former range (Johnson & Roff, 1982; Dunlop & Morris, 2008). No avoidance of any age class of restored forest for denning was observed with dens found in every restoration age class, including one in 2-year-old restoration that consisted of bare ground and little vegetation. Another was found in mesh material of a roadside drainage sump. Given the scarcity of suitable logs in restored forests, this study highlights the value of retaining rock at the surface during restoration. However, further study is required to determine if all age cohorts or sexes are equally adaptable in their selection of denning sites in unmined and restored forests. It also remains unclear if there are negative effects of denning in restoration. For example, a mixture of log and subterranean burrow dens may be important for breeding habitat (Serena & Soderquist, 1989b), quoll predator avoidance or thermoregulatory needs. Predation risks may be higher for juveniles born and raised in maternal dens in young restored forests due to their lower structural complexity. Studies of breeding success and long-term survival across multiple generations of quoll are recommended. There was also some overlap in the home ranges of some individuals based upon den use (Fig. 2). Although den selection in unmined forest and restoration was consistent across all individuals irrespective of conspecific overlap, and quolls are essentially solitary animals (Serena & Soderquist, 1989a), further studies would elucidate whether conspecific interactions influence quoll den selection.

Logs were an important microhabitat feature for quolls in unmined forest as has been recorded for spotted-tailed quolls *Dasyurus maculatus* (Jones & Barmuta, 2000; Glen & Dickman, 2006). Traversing logs possibly benefits quolls by increasing hunting efficiency, decreasing predation risk (providing rapid escape routes or shelter) (Jones & Barmuta, 2000; Stokes *et al.*, 2004) or providing a source of prey (skinks, invertebrates, mammals) (Lindenmayer *et al.*, 2002). There were insufficient data to provide us with any indication of what microhabitats quolls prefer in restored forest. However, a small number of quolls (3) were tracked travelling through restored forest where there are relatively limited numbers of logs and this may indicate that logs are used where available but are not a required microhabitat for all individuals. Alternatively, restored forest may be a suitable pathway for travel and access to den sites, but may not be used for foraging and predation due to a lack of suitable logs. The consequences for quolls of lower log densities in restored areas is poorly understood, and more research is required, but given the frequent use of logs by quoll in unmined forest, it is recommended that logs be returned to restored forest in greater number, especially those found to be sufficiently long (> 3.0 m) and wide (> 40 cm) to support a quoll den (R. A. McGregor, unpubl. data).

It is likely that forest clearing for mining has an immediate negative impact upon quoll inhabiting these areas, but quolls are able to rapidly re-colonize restored areas. Some

Table 3 Mean (\pm SE), F and P -values from the mixed models for each microhabitat variable measured along spool and random trails in unmined forest

Variable	Quoll	Random	Quoll versus random	
			$F_{1,11}$	P
Log travel proportion (%)	12.48 \pm 2.75	4.23 \pm 0.76	8.71	0.013
No. of logs	70.6 \pm 11.0	81.9 \pm 10.9	0.90	0.364
Cover – QCM (%)	23.13 \pm 3.12	22.82 \pm 2.50	0.02	0.898
Shrub cover height (m)	0.58 \pm 0.07	0.54 \pm 0.07	0.87	0.372
Tree density (ha^{-1})	1423 \pm 225	1835 \pm 197	2.13	0.172
Log density (ha^{-1})	1749 \pm 254	1174 \pm 168	12.81	0.004
Litter volume ($\text{m}^3 \text{ha}^{-1}$)	63.3 \pm 7.8	81.4 \pm 7.5	2.78	0.110

carnivore species, such as crab-eating fox *Cerdocyon thous* and tayra *Eira barbara*, are also adaptable and little affected by landscape fragmentation and modification (Chiarello, 2000; Lyra-Jorge, Ciochetti & Pivello, 2008), while others, such as jaguar *Panthera onca*, are unable to adapt to landscape modifications and are vulnerable to habitat fragmentation (Lyra-Jorge *et al.*, 2008). It is unclear exactly which traits separate susceptible from adaptable species, but the size of the fragments within the landscape, how a species perceives and uses the intervening matrix (Hobbs, 2005), and matrix permeability (Lyra-Jorge *et al.*, 2008) appear to be important, especially for mammals with large home ranges. Highly permeable matrices connect fragments and permit movements through the landscape, maintaining important activities and processes, such as foraging, mate location and juvenile dispersal, which are essential to the persistence of carnivore populations (Elmhagen & Angerbjörn, 2001).

Although western quolls perceive restored areas as a permeable matrix, this is not the case in the larger region they once inhabited. Large-scale clearing for agriculture, or alternative mining methods that involve little or no restoration, likely result in more isolated habitat patches and reduce matrix permeability, with consequent negative effects on quoll population viability. Low quoll capture rates in the wheatbelt region of Western Australia (Morris *et al.*, 2003; Dunlop & Morris, 2008), where large-scale clearing for agriculture has occurred and remnant patches of woodland are small and isolated, seem to support the hypothesis that quolls have been significantly affected by land clearing and habitat fragmentation (Dunlop & Morris, 2008).

Conclusions

Our findings indicate that post-mining restoration provides a permeable matrix for quolls, which are adaptable and able to re-colonize and use restored areas for denning and movement. Patterns of movement, spatial organization and population densities in restored forest showed no significant differences from quoll populations in nearby unmined forests. Our results suggest that post-mining restoration maintains landscape connectivity. However, further research is needed to better understand quoll survival and quoll–predator interaction in restored forest, in which microhabitats such as logs, stumps and large hollow-bearing trees are relatively scarce.

Wide-ranging carnivores worldwide have suffered high extinction rates and range contractions in recent times due to loss, disturbance and fragmentation of habitat. Identifying critical habitat and restoring this habitat for fauna will increase matrix permeability and maintain connectivity between fragments, ensuring the effective management and conservation of these species in the future.

Acknowledgements

The project approval was conducted under Murdoch University Animal Ethics Committee Permit W2291/09 and Department of Environment and Conservation (DEC) Permit SF007251. Financial support was provided by Alcoa of Australia. Thanks are due to DEC Dwellingup for equipment loans and, specifically, to Al Glen for the advice during project commencement.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. A description of the statistical tests to identify spatial autocorrelation in den substrate selection and the results of those tests.