

Designing for conservation outcomes: The value of remnant habitat for reptiles on ski runs in subalpine landscapes

Chloe F. SATO ^{a*}, Jeff T. WOOD ^a, Mellesa SCHRODER ^b, Damian R. MICHAEL ^a, William S. OSBORNE ^c, Ken GREEN ^b and David B. LINDENMAYER ^{a, d}

^a Fenner School of Environment and Society,
The Australian National University,
Canberra, ACT, 0200,
Australia

^b Snowy Mountains Region,
National Parks and Wildlife Service,
PO Box 2228,
Jindabyne, NSW 2627,
Australia

^c Institute for Applied Ecology,
University of Canberra,
Canberra, ACT, Australia

^d ARC Centre of Excellence for Environmental Decisions,
The Australian National University,
Canberra, ACT 0200,
Australia

Email: chloe.sato@anu.edu.au; Phone: +612 6125 8696; Fax: +612 6125 0757
jeff.wood@anu.edu.au
mel.schroder@environment.nsw.gov.au
damian.michael@anu.edu.au
will.osborne@canberra.edu.au
kenneth.green@environment.nsw.gov.au
david.lindenmayer@anu.edu.au

* Corresponding author

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Abstract

Subalpine ecosystems are centres of endemism that are important for biodiversity. However, these areas are under threat from the creation, expansion and continued modification of ski runs, activities that have largely negative effects on wildlife. Despite this threat, research on the impacts of ski runs is limited for reptiles - particularly regarding the value of remnant vegetation retained on ski runs. Here we quantify the effects of habitat loss and fragmentation (i.e., patch size, patch isolation and edge effects) on the abundance of a common subalpine lizard and on thermal regimes (a key determinant of lizard distribution) in an Australian ski resort. The number of lizards observed differed significantly with habitat type (ski runs vs. forested areas) and patch isolation, but not patch size. In addition, the edges of patches supported more lizards than any other habitat type. These patterns of lizard distribution can be explained, in part, by the differing thermal regimes in each habitat. Ski runs had significantly higher ground surface temperatures than any other habitat type, precluding their use for a considerable proportion of the activity period of a lizard. In comparison, edges were characterised by lower temperatures than ski runs, but higher temperatures than the core of forested areas, potentially providing a favourable environment for thermoregulation. Based on our results, we conclude that although modified ski runs have a negative effect on lizards, patches of remnant vegetation retained on ski runs are of value for reptiles and their conservation could help mitigate the negative effects of habitat loss caused by ski run creation.

Keywords Edge effects; Habitat loss; Habitat fragmentation; Lizard; Metapopulation theory; Skink; Thermal regime

Introduction

Habitat loss and fragmentation are primary drivers of biodiversity loss worldwide (Fahrig 2003; Lindenmayer and Fischer 2006). In subalpine landscapes, substantial habitat loss and fragmentation occurs through the construction and expansion of ski resort
30 infrastructure (WWF 2005). The expansion of ski resorts, and modifications undertaken within existing resort boundaries, are a concern as subalpine areas are sensitive but highly biodiverse environments that support many endemic species and communities (Martin 2013; Nagy and Grabherr 2009). Thus, significant disturbance to subalpine areas, coupled with the impacts of climate change (see Spehn et al. 2010; Whetton et al. 1996), may result in the loss
35 of many species from these environments (WWF 2005).

Ski-related disturbances - chiefly associated with ski runs - have largely negative effects on wildlife (Laiolo and Rolando 2005; Negro et al. 2013; Sato et al. 2013a). Ski runs may be particularly detrimental landscape features for wildlife because structural complexity is extremely simplified in these areas. During the construction and annual maintenance of ski
40 runs, native vegetation is cleared, rocks and logs are removed, and slopes are graded to create a smooth skiing surface (Behan 1983; Burt and Rice 2009; Hadley and Wilson 2004; Ries 1996). As a direct or indirect result of these changes, animals inhabiting or dispersing across disturbed ski areas are more susceptible to predation (Martin and Lopez 1999; Sato et al. 2014) and may have to travel greater distances than counterparts in undisturbed habitat to
45 access food, shelter or thermoregulatory resources (Amo et al. 2007). Thus, the continuing creation, expansion, and maintenance of ski runs represent a considerable threat to subalpine reptiles by preventing individuals from dispersing freely throughout the landscape, impeding population connectivity and persistence. However, ski-run networks worldwide often
50 incorporate small-to-large patches of relatively intact forest on, or between, ski runs (Hadley and Wilson 2004; JGR 2010; PBPL 2002; Strong et al. 2002). These vegetated patches may

be capable of supporting populations of lizards (Bell and Donnelly 2006 and references therein), or alternatively, could be suitable “stepping stones” (Bennett and Saunders 2010; Lindenmayer and Fischer 2006) allowing for movements of reptiles between otherwise disconnected areas of continuous forest in ski resorts. As far as we are aware, the value of these vegetated patches on ski runs for reptiles - or other wildlife - in disturbed subalpine landscapes has not been investigated.

In this paper, we use a detailed case study of a common, generalist reptile species - southern grass skink (*Pseudemoia entrecasteauxii*) - to test critical theories and predictions about the effects of habitat loss and fragmentation in a novel landscape context. Specifically, we investigated whether 1) forest loss; 2) patch size; 3) patch isolation; and 4) increased availability of edge habitat affect patterns of lizard abundance in a modified subalpine landscape.

First, we postulated that forest loss associated with ski run construction would have a negative effect on lizard abundance. Cleared habitats tend to support fewer lizards in a variety of ecosystem types (e.g., forests, D'Cruze and Kumar 2011; agricultural areas, Driscoll 2004; plantations, Fischer et al. 2005; subalpine environments, Sato et al. 2013b), and we expected to observe the same pattern in our study system (i.e., greatly reduced abundances of individuals in the cleared, grassy ski-run matrix compared to forested areas). Second, we postulated that large forested patches would support more lizards than smaller forested patches, which is an implicit assumption of metapopulation theory (Gaggiotti and Hanski 2004). This is because large patches offer a greater abundance of exploitable resources for lizards (assuming uniform habitat quality; Gaggiotti and Hanski 2004; Lindenmayer and Fischer 2006; Michael et al. 2008), and thus have a greater potential carrying capacity than small patches. Third, we postulated that isolated habitat patches on ski runs, far from continuous habitat, would support fewer lizards than less isolated patches. In

Australia, lizards such as *P. entrecasteauxii* tend to be dispersal limited (tens of metres; see Clobert et al. 1994; James 1991) and also infrequently use ski runs (Sato et al. 2013b). Combined, these factors are likely to reduce rates of immigration of *P. entrecasteauxii* to isolated patches compared with less isolated patches (Moilanen and Hanski 1998), leading to local population size reductions and eventually localised population extinctions (Eriksson et al. 2014). Finally, we postulated that lizards would be more abundant in edge habitats than the core of forested areas. The altered microclimatic conditions (e.g., increased light penetration that subsequently alters thermal regimes) available in edge habitats may benefit lizards (see Rubio and Simonetti 2011; Schlaepfer and Gavin 2001), encouraging increased use of these habitats. This is particularly the case for basking heliotherms such as *P. entrecasteauxii* (Green and Osborne 2012) that are constrained by highly variable environmental conditions at high elevations (Huang and Tu 2008).

In addition to addressing the four postulates above, we investigated a key potential driver, thermal regimes, which may contribute to the observed patterns of lizard distribution in subalpine ski resorts. Thermal regimes are an important determinant of reptile distribution worldwide (Diaz 1991; Huang et al. 2006) because sufficient warmth and solar radiation is required by these animals to assimilate energy for foraging and reproduction (Avery 1979; Martin et al. 2003). Previously, Sato et al. (2014) found that reduced structural complexity on ski runs can significantly alter thermal regimes, potentially influencing habitat selection and consequently the distribution of lizards. Based on those results, and given that structural complexity and insolation can vary dramatically across grass-forest ecotones (Burt and Rice 2009; Laiolo and Rolando 2005; Shine et al. 2002), we hypothesized that habitat fragmentation would alter the thermal regimes of matrix and patch habitats, and that lizard distribution patterns across these habitats would reflect avoidance of unfavourable thermal environments. Habitats that are too hot may present immediate risks to survival (Spellerberg

1972), and habitats that are too cold may limit opportunities for energy assimilation (Martin and Lopez 1999).

Methods

105 Study species and area

The most abundant lizard species detected in our study area, *P. entrecasteauxii*, occurs commonly in the Australian alpine-subalpine region (Green and Osborne 2012) but has a wider distribution across south-eastern Australia (Wilson and Swan 2008). The species is a small (mean adult snout-vent length = 51.5 mm; mean adult mass = 3.0 g; C. Sato, unpublished data), diurnally-active heliotherm (Green and Osborne 2012) that can tolerate a wide range of body temperatures ($T_{\min} = 2.2\text{-}2.8^{\circ}\text{C}$, $T_{\max} = 41.9\text{-}42.5^{\circ}\text{C}$; Spellerberg 1972). The species occurs in a wide range of habitat types found in ski resorts, particularly where woody debris is plentiful (Michael and Lindenmayer 2010; Sato et al. 2013b), but tends to avoid highly modified ski runs covered with exotic grass (Sato et al. 2013b). While there is no specific information regarding the dispersal ability and home-range size of this species, studies investigating similar-sized lizards in Australia and elsewhere suggest dispersal capability is limited (<20 m; see James 1991; Melville and Swain 1999; Sumner et al. 2001) and home ranges are relatively small (<500 m²; see Clobert et al. 1994; Olsson and Shine 2003; Turner et al. 1969).

120 We conducted surveys for *P. entrecasteauxii* at Thredbo ski resort (36°30'S 148°18'E; Fig. 1a) in Kosciuszko National Park, south-eastern Australia. In this region, during summer, the mean daily solar exposure ranges from 21.4 MJm⁻² to 25.8 MJm⁻² and the mean maximum temperature ranges from 19.1°C to 21.3°C (BOM 2014). During winter, the mean minimum temperatures range from -2.4°C to -3.8°C (BOM 2014). Annual precipitation is

125 >2000 mm per year, with summers drier than winters (Green and Osborne 2012). The study area is covered with snow typically from mid-June to October.

We selected survey sites ($n = 33$) on south-facing slopes, varying in elevation from 1400 m to 1785 m. Across this range, vegetation communities in continuous forest and remnant native vegetation on ski runs intergrade from *Eucalyptus delegatensis*-*E.*

130 *dalrympleana* (alpine ash-mountain gum) dominated forest on the lower slopes to *E. niphophila* (snow gum) dominated forests at higher altitudes. The understorey and ground layer of these sites vary in composition but generally have a dense cover including shrubs such as *Bossiaea foliosa* (leafy bossiaea), *Cassinia uncata* (sticky cassinia), *Hovea montana* (mountain hovea) and *Olearia phlogopappa* (dusty daisy-bush); herbs such as (*Acaena*
135 *novaezelandiae* (bidgee widgee), *Asperula gunnii* (mountain woodruff) and *Stellaria pungens* (prickly starwort); and grasses such as *Poa fawcettiae* (smooth blue snowgrass) and *Poa costiniana* (bog snow-grass); as well as considerable amounts of litter.

Field sites located in the centre of ski runs were dominated by exotic grasses, predominantly *Agrostis capillaris* (browntop bent) and *Festuca rubra* (red fescue). These
140 sites all were subject to the same seasonal management practices (slashing and mowing during summer, and winter slope grooming).

Figure 1 approximately here#

145 Sampling design and lizard surveys

To test our first hypothesis regarding effects of habitat type on lizard abundance, we conducted reptile surveys at a series of ‘patch’ sites ($n = 19$), ‘control’ sites ($n = 7$) and ‘matrix’ sites ($n = 7$) across the south facing slopes of Thredbo ski resort. We located ‘patch’ sites in forested remnants surrounded entirely by highly modified, exotic grass ski runs;

150 'control' sites in tracts of continuous, subalpine forest (>9 ha) showing minimal signs of
disturbance; and 'matrix' sites in the centre of groomed ski runs cleared of native vegetation
and rehabilitated with exotic grasses.

When selecting patch sites, we applied a strict set of criteria so that we could test the
effects of size and isolation (i.e., Postulate 2 and Postulate 3) on lizard abundance. We chose
155 patches according to two size classes: small (<450 m²) or large (>500 m²); and two isolation
classes based on distance to large (>9 ha) tracts of minimally disturbed, subalpine forest: near
(<25 m to forest) or isolated (>35 m to forest). We based these cut-offs for size and isolation
on the natural history of lizards of similar body size (see James 1991; Melville and Swain
1999; Sumner et al. 2001; Turner et al. 1969). We also ensured sites were separated from one
160 another by ≥ 20 m to maximise the chances that observations of lizards were independent.
Using these selection criteria, we established five replicates of small, near patches; five
replicates of small, isolated patches; five replicates of large, isolated patches; and four
replicates of large, near patches. More replicates of large, near patches were unavailable
because of limitations in the spatial availability of remnant vegetation meeting our criteria.
165 Given the strict set of criteria we applied in selecting sites, the constraints of site availability
were such that there was little scope for randomization of site selection.

Within each site (i.e., patch, control or matrix), we established a series of 6 x 10 m
survey plots to standardise the area surveyed at each site (Fig 1b). For patch sites, we scaled
the number of survey plots to the total size of the patch. Accordingly, we surveyed three plots
170 in very large patches (>1600 m²), two plots in large patches (540-1400 m²), and one plot in
small patches (290-420 m²). We located plots in these patches ≥ 5 m from the edge of the
nearest ski run and ≥ 10 m from one another, along a transect that roughly bisected the patch
(Fig. 1). For very small patches (<90 m²), we surveyed the entire area. Control and matrix
sites far exceeded the size of our largest patch (i.e. >3500 m²), so we established the

175 maximum number of survey plots ($n = 3$) in these areas, ensuring that they were separated
from one another by ≥ 10 m.

Finally, to test our fourth postulate regarding the effect of edge availability on lizard
abundance, we surveyed edge habitats at each patch site. The edge between the vegetated
patches and surrounding exotic grass matrix was hard (*sensu* Forman 1995; see Appendix 1)
180 and microhabitat conditions differed noticeably between forest and exotic-grass ski run (C.
Sato, personal observation). We defined edge habitat as the area extending 2 m into a patch
and 3 m into the exotic-grass ski run (Fig. 1b). We used this ‘definition’ of an edge based on
observations of differences in abiotic characteristics; light penetration decreased markedly
within 2 m of the edge of a patch, and beyond this appeared less variable. This edge
185 definition also allowed us to maximise consistency in the size of plot surveyed between edge
habitats and core habitats. Thus, at each patch site, we surveyed one edge plot (5 x 12 m),
unless islands were very small (< 90 m²), in which case we surveyed the entire edge habitat
around the patch.

We conducted reptile surveys during three periods (10 January - 6 February 2011, 10
190 February - 11 March 2012, and 29 November 2012 - 20 January 2013). At each survey plot,
we conducted non-destructive, time- and area-constrained (10 min/60 m²) active searches (a
standard survey technique for diurnally active, terrestrial heliotherms; Manning et al. 2013;
Michael et al. 2012; Sato et al. 2013b). This method involved systematically moving through
a plot searching for lizards around vegetation, rocks, logs, and litter. We recorded all
195 observations of lizards during 10-minute survey periods. At each plot, we completed nine
repeat surveys across three survey periods (i.e., three days per survey period, and three survey
periods across two field seasons, thus a total of 90 minutes at each site). To maximise
chances of detecting lizards, we conducted surveys only on calm, partly sunny to sunny days.
Moreover, we randomised the timing of visits to sites to survey ‘morning’ (0730-1200;

200 Australian Eastern Standard Time [AEST]) and ‘afternoon’ (1200-1600 AEST) periods to
avoid detectability issues associated with temporal variation in lizard numbers.

Thermal environments

To investigate the effects of habitat fragmentation on thermal regimes, and the effects
205 of thermal environment on lizard distribution patterns, we used temperature loggers
(Thermochron i-Buttons, Thermodata Pty Ltd, QLD, Australia; diameter, 17.4 mm; height,
5.9 mm) to record ground surface temperatures. At each plot within ‘isolated’ patches, we
deployed two temperature loggers - one on the eastern side of the plot and one on the western
side of the plot - to capture the spatial variation in ground surface temperatures available to
210 lizards over their active period (see Tracy and Christian 1986). For edge plots, we placed two
temperature loggers at the interface between the vegetated patch and exotic grass matrix. For
control and matrix sites, we placed two temperature loggers in the central plot – one on the
eastern side and one on the western side. We ensured that all loggers were in contact with the
ground (secured in place with a tent peg) and partially covered by grasses or litter to prevent
215 exposure to lengthy periods of direct sunlight.

We programmed all loggers to record temperature every 30 minutes and left the
loggers *in situ* from 1 December to 31 December 2012 – the month of our field season
representing median long-term average temperatures for the study area (BOM 2014). After
this time, we collected all loggers for analysis.

220

Statistical analysis

To explore the effects of fragmentation on the number of lizards observed, we fitted
Hierarchical Generalised Linear Models (HGLMs; Lee et al. 2006) assuming a quasi-Poisson
distribution with a log link function for the response and a gamma distribution with a log link

225 function for the random component. We fitted two models for lizard observations. We
included the number of lizards observed per survey period as the response variable, and ‘Plot’
nested within ‘Site’ as random effects. Additionally, in both models we included ‘Survey
Period’ as a fixed effect, to determine whether the numbers of lizards observed differed
230 between survey periods. We focused our first model on the effect of disturbance (i.e., habitat
loss) on the number of lizard observations (Postulate 1), including ‘Habitat Type’ (i.e.,
matrix, patch or control) as a fixed effect. We then excluded matrix sites from further
analyses of lizard observations because we detected few individuals in the matrix ($n = 6$
individuals across all sites and surveys), and the inclusion of these sites in the HGLMs
masked the effects of other variables of interest (e.g., patch size and patch isolation). For the
235 second HGLM, we used the three habitat fragmentation attributes identified in our
hypotheses as fixed effects: patch size, patch isolation and edge effects (‘Forest Location’)
(Postulates 2 - 4). Arguably, differing densities of lizards observed in edge and core habitats
of patches could be due to the increased difficulty in detecting lizards in densely vegetated
core areas compared with comparatively more open edge habitats. Thus, to determine
240 whether rates of detection differed between edge and core habitats, we fitted N-mixture
models for abundance (Royle 2004) assuming a Poisson distribution for the latent abundance
using ‘unmarked’ package (Fiske and Chandler 2011) implemented in R (R Core Team
2013).

To analyse temperature data, we included temperature readings taken between 0500
245 and 1830 from all sites, when lizards were likely to be active. For these readings, we
calculated the mean, absolute maximum, absolute minimum, and range of ground surface
temperatures recorded at each data logger over the 31-day period that loggers were deployed.
We then used linear mixed models (Harville 1977) to determine whether there were
significant differences in the thermal environments of sites. We included ‘Habitat Type’,

250 'Patch Size', and 'Forest Location' (i.e., edge vs. core habitat) as fixed effects, and 'Logger
Position' (i.e., eastern or western side of plot) and 'Plot' nested within 'Site' as random
effects to account for spatial correlation. We included temperature measures (mean, absolute
maximum, absolute minimum, and range of ground surface temperatures) as the response
variables.

255 For temperature data, we also investigated the length of time that ground surface
temperatures fell outside the critical body temperature thresholds of *P. entrecasteauxii* (an
absolute critical minimum of 2.2°C and an absolute critical maximum of 42.5°C; see
Spellerberg 1972). Beyond these temperature limits, lizard locomotion is impaired, and
consequently individuals lose the ability to escape from conditions that may lead to their
260 death (Spellerberg 1972). Lizards exposed to ground surface temperatures outside their
critical thermal thresholds for more than a few minutes cannot forage for food, escape
predation attempts, or endure physiological stresses (Spellerberg 1972).

In summary, we quantified the total number of hours that ground surface temperatures
exceeded the absolute critical maximum body temperature, and fell below the absolute
265 critical minimum body temperature, of *P. entrecasteauxii* as a proportion of the total number
of hours available for lizard activity (434 hours across 31 days). We then fitted a quasi-
binomial HGLM to investigate whether the calculated proportion of hours differed between
'Habitat Types' (i.e., matrix, patch and control), which was a fixed effect. To account for the
spatial structure, we included 'Plot' nested within 'Site' as random effects. We used GenStat
270 16 (VSN International Ltd) for all statistical computation.

Results

Effects of fragmentation

Across the three survey periods, we recorded 543 *P. entrecasteauxii* observations. We
275 detected most of these individuals in patches ($n = 365$) and undisturbed forest ($n = 172$). We
observed few *P. entrecasteauxii* in the matrix (i.e., centre of ski runs; $n = 6$). There was no
difference in the number of lizards observed between survey periods ($\chi^2_2 = 2.395, P = 0.302$).

The number of *P. entrecasteauxii* observations differed between habitat types ($\chi^2_2 =$
30.38, $P < 0.001$; Fig. 2a), with fewer *P. entrecasteauxii* recorded in the matrix. After we
280 excluded matrix sites from the analysis, we found that patch size did not influence the
number of lizards observed ($\chi^2_1 = 2.806, P = 0.246$), but that forest location did. More lizards
were observed in edge plots than core plots ($\chi^2_1 = 38.55, P < 0.001$), and more lizards were
observed in the edges of vegetated patches near continuous forest than in the edges of patches
far from continuous forest, or in the core of any site ($\chi^2_1 = 4.105, P = 0.04$; Fig. 2b). We
285 found no difference in detection rates of lizards between edge and core habitats ($P=0.45$).

#Figure 2 approximately here#

Thermal environments

290 We found an interaction between Habitat Type and Forest Location (i.e., edge vs. core
habitat) for all measures of ground surface temperature (mean, maximum, minimum, and
range; $P < 0.001$ for all measures; Table 1). Matrix sites had higher mean, maximum and
range of ground surface temperatures than the edge or core of patches, or controls ($P < 0.001$
for all measures; Table 1). Additionally, the edges of patches had higher mean, maximum and
295 range of ground temperatures compared with core habitats (Table 1). Conversely, matrix sites
had lower minimum ground surface temperatures compared to patches or controls ($P < 0.001$;
Table 1).

Table 1 approximately here#

300

The length of time that ground temperatures exceeded the critical maximum body temperatures of lizards (42.5°C; see Spellerberg 1972) also varied with Habitat Type and Forest Location. Matrix sites had longer periods when ground surface temperatures exceeded the critical maximum body temperatures of lizards compared with either patches or controls (matrix: $0.74 \pm 0.21 \text{h day}^{-1}$; patch: $0.17 \pm 0.07 \text{h day}^{-1}$; control: $0.03 \pm 0.02 \text{h day}^{-1}$; $\chi_2^2 = 20.28$, $P < 0.001$; Fig. 3a,c). In terms of edge effects, the ground surface temperature of edge plots exceeded the critical maximum body temperature of lizards for longer periods than core plots, but not as long a period as matrix sites (edge: $0.44 \pm 0.16 \text{h day}^{-1}$, core: $0.01 \pm 0.01 \text{h day}^{-1}$, matrix: $0.74 \pm 0.21 \text{h day}^{-1}$; $\chi_1^2 = 5.81$, $P = 0.016$; Fig. 3b).

310

The length of time that ground temperatures fell below the critical minimum body temperatures of lizards (2.2°C; see Spellerberg 1972) did not differ among Habitat Type ($\chi_2^2 = 0.8849$, $P = 0.642$) or Forest Location ($\chi_1^2 = 0.4796$, $P = 0.489$).

#Figure 3 approximately here#

315

Discussion

Despite the considerable threat that habitat degradation poses to reptile populations (Todd et al. 2010), research investigating effects of ski run construction on reptiles has been limited (Sato et al. 2013a), particularly regarding how fragmentation affects reptile distributions and whether this may be driven by alterations to thermal environments. We found that both thermal environments and lizard abundance were affected by fragmentation. Maximum and mean ground temperatures were higher in the matrix (i.e., the centre of exotic grass ski runs), and exceeded the critical maximum body temperature of lizards for longer

periods, than in forested areas (patches or controls). Similarly, edge habitats were warmer
325 than core habitats of forested areas. Observations of lizards appeared to correspond with these
thermal gradients; we observed lizards infrequently in the matrix, but recorded them in
remnant forested patches on ski-run networks (supporting Postulate 1). We detected more
lizards at the edges of patches near controls (i.e., continuous forest) than at the edges of
patches far from controls, or in the core of any forested area (supporting Postulate 3 and
330 substantiating Postulate 4). Patch size did not appear to influence lizard abundance (refuting
Postulate 2).

Based on our findings, we argue that the creation of ski runs, through the removal of
large tracts of native vegetation and structural habitat features, has a negative effect on lizard
distributions (see also Sato et al. 2013b). This effect is likely due to the limited structural
335 complexity available on ski runs, which in turn limits available resources for basking, shelter
from predators, or refugia from extreme ground surface temperatures (Sato et al. 2014; Fig.
3). Without these resources, the immediate and long-term survival of lizards in these areas
could be greatly reduced. However, retaining remnant patches on these ski runs may, in part,
mitigate the negative effects of habitat loss on lizard populations. Regardless of patch size,
340 remnant patches are capable of supporting lizards in similar densities to undisturbed forest
(Fig. 2). Thus, remnant patches are important design features in ski resorts that may facilitate
the persistence of lizards in modified subalpine landscapes.

One reason for the similarities in lizard densities between undisturbed forest and
remnant vegetation patches is the increased availability of edge habitat for lizards occupying
345 remnant patches. Edge habitats provide benefits to fragmented lizard populations through
altered microclimates (e.g., increased sunlight, decreased humidity, higher temperatures; see
Collinge 1996). The altered microclimatic conditions allow lizards at high elevations to
maximise thermoregulatory opportunities and energy assimilation (Angilletta 2001; Huang et

al. 2013) in an environment where conditions are extreme and highly variable (Carrascal and
350 Diaz 1989; Huang and Tu 2008). Our results strongly suggest that lizards may be selecting
edge habitats over all other available habitats; it was in the edges of remnant patches where
we observed the highest number of *P. entrecasteauxii* across all habitat types (Fig. 2). This
selection is likely due to the optimal thermal qualities of these environments. Edges are
warmer than core habitats but cooler than exotic grass ski runs, providing lizards with
355 increased thermoregulatory opportunities.

Edges also may provide preferred habitat for lizards because, in addition to improved
thermal conditions, refuges from predators are close to basking sites. The proximity of
refuges may increase the probability of escaping a predator (Greene 1988; Martin and Lopez
1999), and also can result in improved body condition (and consequently fitness) when
360 compared with conspecifics that travel greater distances to find shelter (Amo et al. 2007).
Thus, the combination of favourable thermal regimes and proximity to shelter sites provided
by vegetated patches on ski runs could offer lizards suitable environments for extended
periods of 'risk-minimised' basking. While we did not quantify the influence of interacting
factors such as predation risk and structural complexity on lizard habitat choices, this would
365 be an interesting avenue of future research that could further explain the patterns of lizard
distribution in subalpine environments affected by ski resort developments.

Despite the benefits derived from edge habitats in remnant patches, the degree to
which edges of remnant patches, and the remnant patches themselves, can mitigate the
negative effects of initial habitat loss on lizard populations is likely to be highly dependent
370 upon the isolation of those patches. Patch isolation is likely to influence the abundance and
ultimately the probability of local population extinction of reptiles. This is because the matrix
remains largely unused by lizards due to a combination of extreme thermal conditions and
increased rates of predation (Sato et al. 2014). Hence, as vegetated patches become more

isolated from continuous forest (i.e., as individual ski runs are widened or entire ski-run
375 networks are expanded), it is likely that dispersal will be restricted or potentially prohibited
altogether, as in other ecosystems (Dixo and Metzger 2009; Munguia-Vega et al. 2013). The
further lizards must travel across inhospitable, exotic grass ski runs to reach vegetated
patches, the more likely they will be preyed upon (Sato et al. 2014), suffer from heat stress
due to extreme thermal conditions (Spellerberg 1972), or progressively lose body condition if
380 multiple movements occur across a season (Amo et al. 2007). As a consequence, rates of
immigration and colonization to more isolated patches will be reduced, preventing boosts to
local populations and increasing extinction risk (Gaggiotti and Hanski 2004). While lizards
were not absent from isolated patches in our study, the abundance of lizards was reduced in
these areas, even in the edge habitats of these patches, compared with less isolated patches.
385 Hence, lizards may be unwilling or incapable of frequently crossing ski runs.

Implications for management

First and foremost, we argue that it is essential, wherever possible, to retain
undisturbed native vegetation and other elements of structural complexity (such as rocks and
390 logs) to facilitate the persistence of lizards in disturbed subalpine environments. However,
retention of structural complexity on ski runs often directly compromises the safety of skiers
and snowboarders (Kelsall and Finch 1996), so it is not always possible to conserve structural
complexity. In such cases, we contend that careful design and management of ski runs, in a
way that decreases isolation of suitable habitat patches, will assist the continued dispersal of
395 lizards between habitat patches, thus reducing landscape-scale extinction risk. The distances
between vegetated patches on ski runs and continuous forest can be minimised in several
ways. First, for narrow ski runs (<20 m), buffering the edges of runs with native vegetation
(e.g., low heath species that are unlikely to impede skier activity) will reduce the width of the

exotic grass matrix. Heath vegetation should provide sufficient structural complexity to
400 attenuate extreme ground surface temperatures, and potentially provide sufficient cover to
reduce rates of predation on lizards crossing ski runs (Sato et al. 2014). Second, for wide
exotic grass ski runs (>40 m), the distances between forested areas could be minimised
through planting patches of native forest species on the runs (in addition to buffering ski run
edges with native vegetation). Such plantings would break up the extent of the exotic grass
405 matrix, potentially allowing lizards to inhabit the new patches, or to use them as ‘stepping
stones’ to larger patches of forest (Bennett and Saunders 2010; Lindenmayer and Fischer
2006). Finally, connections between suitable habitat patches could be restored by re-
introducing structural habitat features onto ski runs such as semi-submerged rocks or timber,
similar in design to the wildlife crossings used for the threatened *Burramys parvus* (mountain
410 pygmy possum; Mansergh and Scotts 1989), which may need to be relocated before each
winter. However, the efficacy of wildlife crossings for reptiles needs to be investigated before
broad-scale implementation across ski resorts.

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Table 1 Mean, maximum, minimum and range of temperatures recorded (with average standard errors of differences; ‘S.E.D’) in the matrix (M), edges of patches (EP), core of patches (CP) and controls (F)

	Temperature Measure (°C)			
	Mean	Maximum	Minimum	Range
Plot Type				
M	22.4	37.6	5.4	32.2
EP	17.4	31.8	6.2	25.6
CP	13.8	21.0	6.7	14.3
F	14.5	24.0	6.4	17.7
S.E.D	0.70	1.93	0.36	1.96
Wald Statistic	$\chi^2=76.80^*$	$\chi^2=66.32^*$	$\chi^2=21.54^*$	$\chi^2=71.49^*$

425

Wald statistic provided for interaction between *Habitat Type* and *Forest Location* (Location)

* $P < 0.001$

430 **Fig. 1** a) Map of the study region within Kosciuszko National Park (“K.N.P”). The “★” represents Thredbo ski resort. b) Schematic diagram of survey design for forested patches on ski runs. White boxes indicate core plots, hatched boxes indicate edge plots

435 **Fig. 2** Estimated mean number of *P. entrecasteauxii* observations (\pm SE) in: a) three habitat types: control, patch and matrix; and b) the edge and core of near patches, far patches and the core of undisturbed forest (controls). All estimates are given on the natural scale

440 **Fig. 3** Estimated mean proportion of time (\pm SE) that ground surface temperatures exceeded the critical maximum body temperature (T_b) of lizards in three habitat types: a) control, patch and matrix; and b) core habitat, edge habitat and matrix; c) Mean (\pm SE) absolute maximum ground surface temperatures ($^{\circ}$ C) recorded in matrix sites, patches (edge and core), and controls across 31 days, during lizard activity periods. The dashed horizontal line represents the absolute critical maximum body temperature of *P. entrecasteauxii* recorded by Spellerberg (1972)

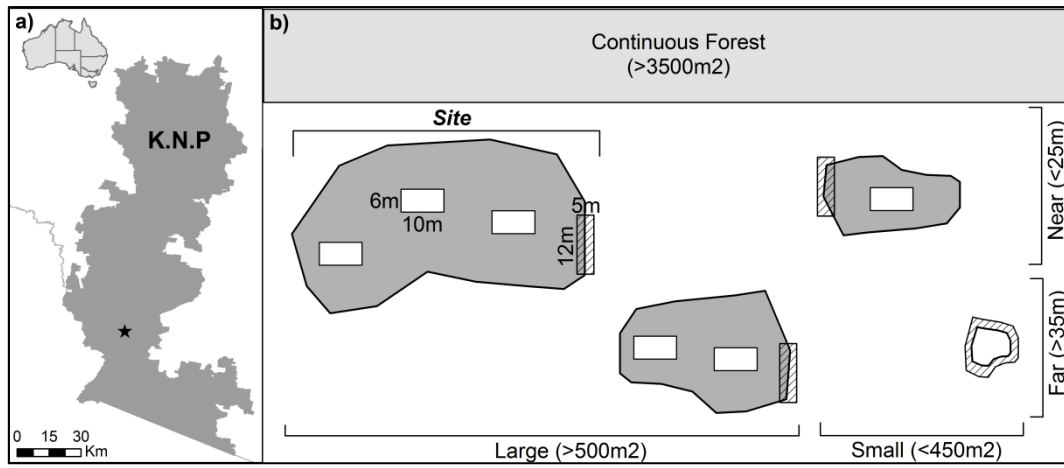


Figure 1.

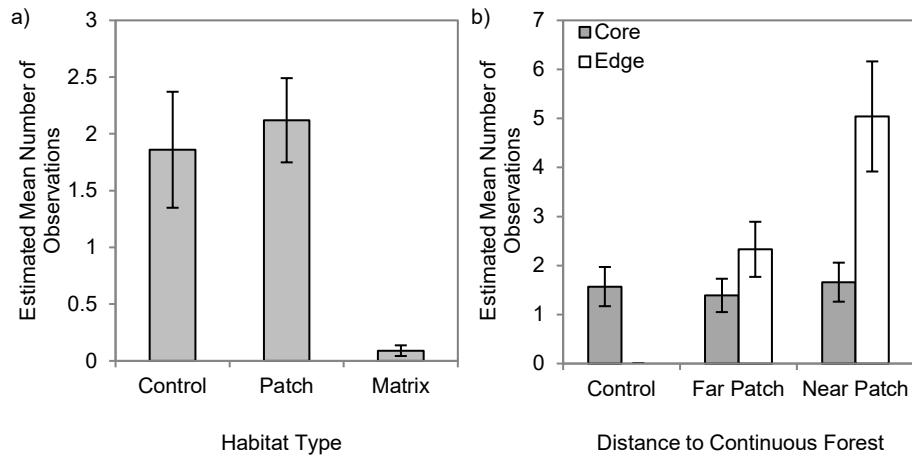
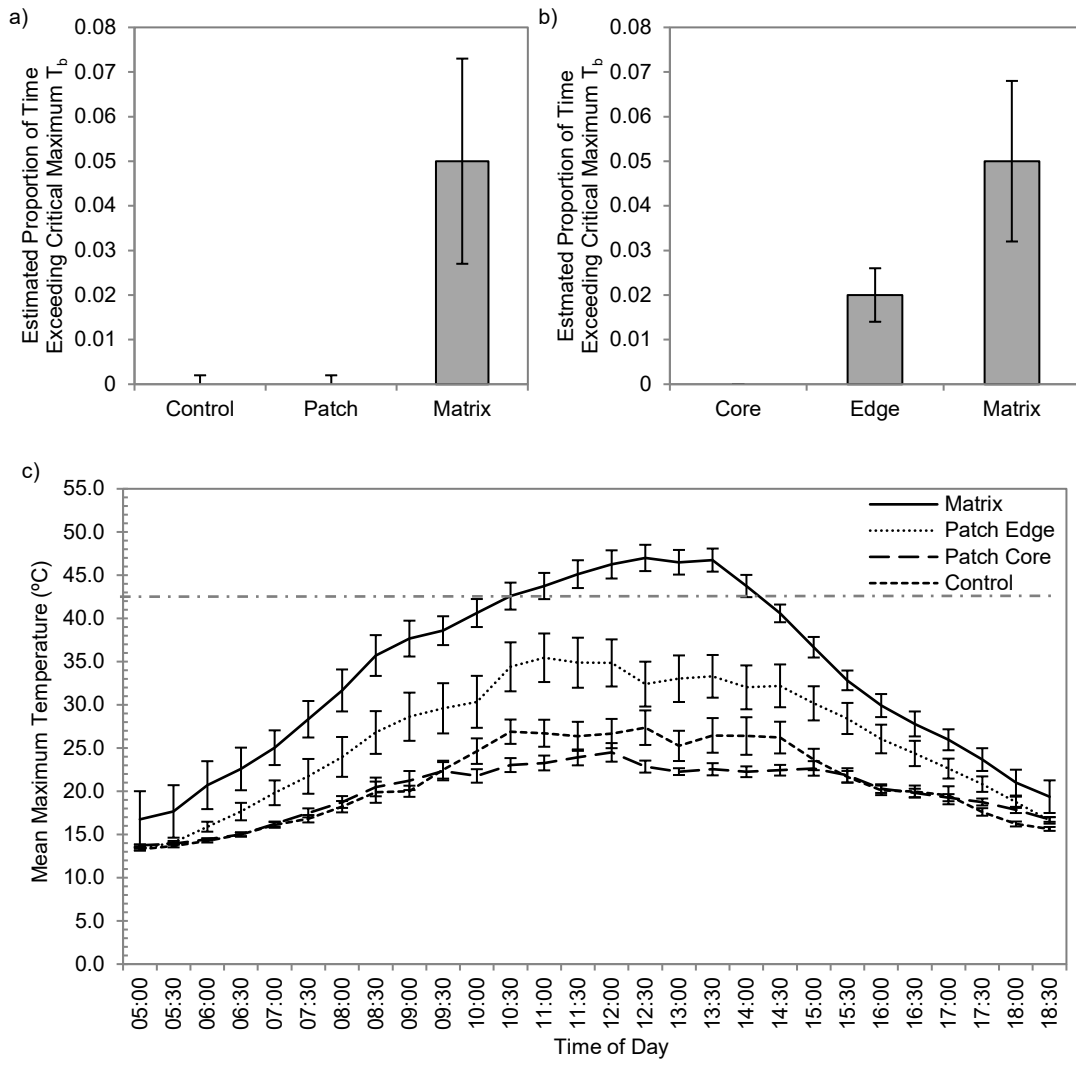


Figure 2.



450

Figure 3.

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Appendix 1. Example of a vegetated patch with hard edges on an exotic grass ski run at Thredbo ski resort.

