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1	Title								
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15 Abstract

16 Conserving biodiversity in production forest landscapes with on-going resource extraction, such 17 as mining and logging, is challenging. Habitat restoration is a strategy that is increasingly used to 18 ameliorate impacts to biodiversity in such landscapes. However, restored forest may have limited 19 value for species that require slow-developing microhabitats, such as tree hollows and logs, and 20 the role that restored forest can play in maintaining populations of these species in production 21 forest landscapes is poorly understood. We examined this issue by assessing the suitability of 22 post-mining restored jarrah (*Eucalyptus marginata*) forest as bat roosting habitat in a production 23 landscape in south-western Australia. We used radio telemetry to track Gould's long-eared bats 24 (Nyctophilus gouldi) and southern forest bats (Vespadelus regulus) to diurnal roosts during both 25 the maternity and mating seasons. No bats were tracked to a roost in restored forest despite one-26 third of bats traveling through, or above, restored forest from capture to roosting locations. Both 27 N. gouldi and V. regulus preferentially roosted in large (>60cm DBH), mature trees in mid to late 28 stages of decay. Absence of roosts, and suitable roost trees, in young (<40 years old) restored 29 jarrah forest indicated that restored forest is poor roosting habitat in the short term, compared to 30 remnant forest, where bats selected mature roost trees (~150-200 years old). Our study suggests 31 that habitat restoration in production forest landscapes is unlikely to play a significant role in 32 conserving populations of species requiring slow-developing microhabitats, for decades if not 33 centuries. Retaining and managing forest remnants would be a more effective strategy to 34 conserve populations of these species.

35

36 Key words

37 Nyctophilus gouldi, Vespadelus regulus, forest restoration, tree hollows, mining

38 1. Introduction

39 Conserving global biodiversity is becoming increasingly challenging as humans continually alter 40 the Earth's habitats, leading to numerous species extinctions (Bradshaw, 2012; Fonseca, 2009). 41 In production landscapes, those used for anthropogenic purposes such as mining and logging, 42 conserving biodiversity provides many challenges but habitat restoration has recently emerged as 43 a potential tool to slow, or prevent biodiversity loss in these landscapes (Suding, 2011; Young, 44 2000). While many studies have examined the role habitat restoration can play in conserving 45 biodiversity in production landscapes, few have examined the relative importance of restored and 46 remnant forest, and the interaction between them (e.g., Craig et al., 2012). Yet understanding the 47 role that both habitats play in conserving biodiversity across production forest landscapes is 48 likely to be critical for species relying on microhabitats that are slow to develop in restored areas, 49 such as tree hollows and logs (Vesk et al., 2008).

50

51 Forest-dwelling bats are one group that may rely heavily on remnant forests in production 52 landscapes as they require tree hollows for roosting. Tree-hollow roosts are critical for forest-53 dwelling bats as they buffer daily and long-term microclimates, reducing the energetic costs of 54 thermoregulating, (e.g., Sedgeley, 2001), facilitate predator evasion (e.g., Fenton et al., 1994), 55 support social relationships (e.g., Lewis, 1995), and are necessary for rearing young (e.g., Law 56 and Chidel, 2007). Roosting habitat for forest-dwelling bats typically comprises multiple 57 roosting structures within an area as many bat species exhibit roost site fidelity, switching 58 between a pool of suitable roosts in close spatial proximity (Threlfall et al., 2013; Webala et al., 59 2010). As restored forest is unlikely to provide roosting habitat in the short-term (Vesk et al., 60 2008), this requirement for multiple roosts suggests forest-dwelling bats may require the

61 retention of relatively large areas of remnant forest to persist in production landscapes.

62 Considerable research has focused on roosting preferences of forest-dwelling bats in timber-

63 managed landscapes and those re-vegetated after agricultural use (e.g., Elmore et al., 2004; Law

64 et al., 2011) but we know of no studies specifically examining roosting preferences in post-

65 mining landscapes. Consequently, the reliance of forest-dwelling bats on remnant forest for

66 roosting remains poorly understood in these production landscapes.

67

68 Forest-dwelling bats typically roost in large, mature trees but exhibit intra and interspecific 69 variations in roosting preferences (Broders and Forbes, 2004; Goldingay and Stevens, 2009; 70 Kalcounis-Ruppell et al., 2005; Vonhof and Gwilliam, 2007). Roosting preferences can differ at 71 multiple spatial scales: 'roost', a roosting structure such as a tree (Threlfall et al., 2013; Vonhof 72 and Gwilliam, 2007); 'site', the vegetation immediately surrounding the roost (Broders and 73 Forbes, 2004; Lumsden et al., 2002a; Perry et al., 2007); and 'landscape', the habitat(s) 74 surrounding the roost (Broders et al., 2006; Lumsden et al., 2002b; Pauli et al., 2015). Males and 75 non-breeding female forest bats are generally less selective in roosting requirements than 76 reproductive females at all three spatial scales. Reproductive females tend to select larger roost 77 trees than non-breeding females (Lumsden et al., 2002a; Threlfall et al., 2013) and maternity 78 roosts are typically farther from foraging sites than male roosts (e.g., Lumsden et al., 2002b). Bat 79 species exhibiting flexibility in roosting requirements may roost under decorticating bark or 80 within trunk fissures while more conservative species may be restricted to roosting in hollows 81 (e.g., Law et al., 2011). Understanding roost preferences at multiple spatial scales and across 82 seasons within a restored production landscape is imperative for ensuring effective conservation 83 and management of habitat for bat populations.

84

85 In production forest landscapes where excavating fauna (e.g., woodpeckers) are absent, such as 86 Australia, the natural formation of hollows can occur very slowly (Whitford, 2002), potentially 87 limiting roosting structures available to forest-dwelling bats in restored forest. To determine the 88 relative importance of restored and remnant forest as roosting habitat, we radio-tracked two bat 89 species (Gould's long-eared bat Nyctophilus gouldi (Tomes 1858); and southern forest bat 90 Vespadelus regulus (Thomas 1906)) within a restored production landscape in the northern jarrah 91 (Eucalyptus marginata) forest of south-western Australia. Parts of the northern jarrah forest have 92 been mined for bauxite for over forty years with >15000 ha already mined and ~ 600 ha of forest 93 still annually cleared, mined, and restored (Koch, 2007a). Mine restoration aims to return a fully-94 functioning jarrah forest ecosystem and restored sites are similar floristically to remnant, i.e., 95 unmined, forest but lack the large, mature trees (Koch and Hobbs, 2007) typically preferred by 96 forest-dwelling bats as roost sites. Furthermore, with only one study examining bat roosting 97 preferences during the mating season in a timber-harvested landscape of the southern jarrah 98 forest (Webala et al., 2010), bat roosting preferences in restored production landscapes of the 99 jarrah forest remain inadequately known.

100

We aimed to assess bat roosting preferences across a restored production landscape by
determining: (i) species specific bat roosting preferences at three spatial (roost, site and
landscape) and two temporal (mating and maternity seasons) scales; and (ii) the relative
availability of suitable roosts in restored and remnant unmined forest. We predicted bats would
preferentially roost in large, mature trees (Kalcounis-Ruppell et al., 2005; Webala et al., 2010)
that were in intermediate stages of decay (Broders and Forbes, 2004; Vonhof and Gwilliam,

2007) and situated in relatively open sites with low canopy cover (e.g., Elmore et al., 2004) and
that roosting sites would be absent in restored forests due to the absence of large, mature trees
(Law et al., 2011; Taylor and Savva, 1988). From roosting studies of the conspecifics, or
congenerics, elsewhere in Australia we predicted *N. gouldi* would be more flexible in roosting
requirements than *V. regulus* (Lunney et al., 1988; Webala et al., 2010) and that males and nonbreeding females would have more flexible roosting requirements than reproductive females
(Law and Anderson, 2000; Threlfall et al., 2013).

114

115 **2. Materials and methods**

116 2.1 Study area

117 The study was conducted at Huntly minesite (32°36' S, 116°07' E), operated by Alcoa of 118 Australia (hereafter Alcoa), located ~90 km SSE of Perth, Western Australia. Huntly has a 119 Mediterranean climate with cool, wet winters and warm, dry summers. Annual rainfall for 120 Dwellingup, ~10 km S of Huntly, is 1237 mm, with >75% falling between May and September. 121 Mean minimum and maximum temperatures vary from 5 to 15 °C in July to 15 to 30 °C in 122 February. The original vegetation at Huntly was jarrah forest, a dry sclerophyll forest whose 123 overstory is dominated by two eucalypts, jarrah and marri (Corymbia calophylla), but with some 124 blackbutt (*E. patens*) and bullich (*E. megacarpa*) in gullies. Midstory species include sheoak 125 (Allocasuarina fraseriana) and bull banksia (Banksia grandis) while common understory species 126 include Bossiaea aquifolium, Lasiopetalum floribundum and X. preissii (Koch, 2007b). Post-127 mining, Huntly minesite is a mosaic of unmined and restored forest of various ages (Figure 1). 128 Of 300-400 plant species found in unmined forest, >75% are returned to restored forests, 129 although restored sites are more homogenous floristically across the landscape than unmined,

forest (Koch, 2007b). Young (<15 years) unburnt restored forest typically has a two-tiered
vegetation structure with a jarrah and marri overstory and a thick senescent *Acacia* understory
(Grant, 2006). For further details on mining and restoration processes, see Koch (2007a).

134 2.2 Field methods

135 Bats were trapped and tracked during maternity (31 October to 9 December 2011, when bats give 136 birth and rear their young) and mating (30 January to 17 March 2012, when female bats are in 137 estrous and mating occurs) seasons. Bats were trapped for two to five hours from sunset using harp traps (Two-Bank 4.2 m²; Ausbat Research Equipment) at five separate waterholes within 138 139 unmined forest (Figure 1) although the close proximity of two sets of waterholes meant we 140 effectively surveyed three general trapping areas (Figure 1). Trapping attempts within restored 141 forest failed to capture many, if any, bats, so we trapped bats at waterholes to capture sufficient 142 numbers for meaningful analyses. Position-sensitive radio transmitters (0.27 or 0.31 g for N. 143 gouldi and 0.22 g for V. regulus; model LB2X, Holohil Systems) were attached dorsally to 9 144 female and 12 male N. gouldi and ventrally (Bullen and McKenzie, 2001) to 11 female and 11 145 male V. regulus (Table 1) and weighed <5% of bat body mass (Aldridge and Brigham, 1988), 146 except for one V. regulus. Diurnal roost sites were located by tracking, on foot, individual bats 147 from the day following capture until transmitters dropped off or batteries failed (N. gouldi range 148 1-6 days; V. regulus range 1-5), using three element hand-held Yagi antennas and R-1000 149 Telemetry Receivers (Communications Specialists). Due to logistic constraints we could only 150 track 4 to 6 bats simultaneously. Transmitter signals may bounce off surrounding trees making it 151 difficult to pinpoint exact signal locations but we spent considerable time at each potential roost 152 tree, varying signal frequency and intensity from multiple locations around the tree so we are

153 confident we correctly identified all roost trees, whose location we then recorded using a GPS.
154 We only estimated roost height as jarrah and marri hollows are difficult to detect from the
155 ground and numbers of visible hollows correlate poorly with true hollow numbers (Stojanovic et
156 al., 2012; Whitford, 2002).

157

To determine bat roosting preferences at the roost scale we compared roost trees with available 158 159 trees. We identified one available tree for every roost tree by selecting the nearest tree (≥ 20 cm 160 DBH) to random points between 50 and 100 m in random directions from each roost tree 161 (adapted from Webala et al., 2010). As all bats roosted in unmined forest, we ensured each 162 available tree was also in unmined forest. For each roost and available tree we recorded tree 163 species and measured tree height and diameter breast height over bark (DBH) and estimated tree 164 health using five ordinal variables based on Whitford (2002): snag class (1 =all live tree, 2 =165 <30% dead, 3 = >30% dead, 4 = 100% dead); dead branch order (DBO: from 1 where terminal 166 dead branch is a twig to 9 where terminal dead branch is the trunk); crown senescence (from 1 167 for a crown with no senescence to 9 where no crown remains); bark cover (1 = none; 2 = <10%;168 3 = 10-25%; 4 = >25%); and presence/extent of a fire scar (1 = no visible scar; 2 = small scar; 3 169 = large scar).

170

To determine bat roosting preferences at the site scale we compared vegetation structure
surrounding roost and available trees by centring a 5 x 5 m plot on each tree. We measured,
using a tree vertex, canopy height (average of five tallest overstory plants <10 m from plot),
height difference (difference between roost/available tree height and canopy height) and average
heights of, and distances to, five nearest overstory plants (≥20 cm DBH) from roost/available

trees. For canopy cover we digital photographs, with a camera positioned at breast height on a tripod and pointed directly up at the canopy, and used gap fraction analysis to calculate canopy cover (Macfarlane et al., 2007). We took photographs at the four corners of the plot and averaged these values for an overall plot canopy cover value. We also visually estimated percent (to the nearest 5%) cover of litter, logs, ground vegetation (< 0.75 m) and shrub vegetation (0.75 to 5 m) within each plot.

182

183 To determine bat roosting preferences at the landscape scale we randomly identified an equal 184 number of locations (65) as roost locations within unmined forest (<3 km from each trapping 185 area) using GIS (ArcMap 10.1, ESRI, Redlands, CA, USA). For roost and random locations we 186 calculated 12 variables derived from GIS spatial layers: elevation, slope $(1 = \langle 3^{\circ}, 2 = 3 \cdot 5^{\circ}, 3 =$ 187 $6-7^{\circ}, 4 = 8-9^{\circ}, 5 = 10-11^{\circ}, 6 = 12-14^{\circ}, 7 = 15-17^{\circ}, \text{ and } 8 = \ge 18^{\circ}$; number of years since last fire; 188 distance to nearest restored mine-pit edge; distance to nearest stream; distance to nearest 189 track/road; area of unmined forest within three radii (250 m, 1000 m, and 3000 m); and length of 190 restored mine-pit edge within three radii (250 m, 1000 m, and 3000 m). We initially calculated 191 area and length values for five radii that incorporated the range of distances bats travelled 192 between trapping and first roosting site both in this study (250 m, 500 m, 1000 m, 1500 m, 3000 193 m; Table 1). As 250 m was correlated with 500 m and 1500 m with both 1000 m and 3000 m (all 194 Pearson >0.70) we retained 250 m, 1000 m and 3000 m as the final three radii. In addition, we 195 also quantified, for individual bats, the number of times the straight-line travel path travelled 196 between trapping and first roosting sites (in all but three cases, all in the mating season, this was 197 the roost recorded the day immediately following capture) crossed over restored forest, roost site 198 fidelity, and distances travelled between roost trees.

199

200 To determine the suitability of restored forest as bat roosting habitat we compared vegetation 201 structure at roost sites with vegetation structure within 56 restored sites, from a concurrent bat 202 study (Burgar, 2014). Alcoa has adapted their seeding mix to reduce eucalypt densities in recent 203 years, categorising restored sites as desirable or dense (500 to 2500 or >2500 eucalypt stems ha⁻¹ 204 respectively) based on nine month monitoring data (Grant, 2006). To capture differences in 205 eucalypt densities over time we sampled eight sites each from the following restored forest types: 206 0 to 4 years desirable, 5 to 9 years desirable, 5 to 9 years dense, 10 to 14 years desirable, 10 to 14 207 years dense, >15 years desirable, and >15 years dense. We measured vegetation structure in five 208 5×5 m plots within each site following the same methodology as for roost/available trees, 209 except for canopy cover we took only one photograph at the centre of each plot, and measured 210 the same variables except for height difference and average heights of, and distances to, the five 211 nearest overstory plants. We averaged measurements over the five plots for an overall site value. 212

213 2.3 Statistical analyses

214 All covariates were scaled, standardized around 0 with standard deviation of 1, prior to analysis. 215 To determine if bats chose specific trees for roosting we compared overall characteristics of roost 216 to available trees. We removed three non-eucalypt trees (two sheoak and one bull banksia) from 217 analyses as eucalypts are the predominant canopy trees and the only ones used in restoration. We 218 removed DBO (highly correlated with crown senescence: r = 0.84), before constructing a 219 Euclidean resemblance matrix of remaining scaled roost tree variables (DBH, height, snag class, 220 crown senescence, bark cover and fire scar) for each bat species. We ran an ANOVA to test for 221 differences in overall characteristics between the three eucalypt tree species (bullich, jarrah, and

222 marri); there were no differences for either N. gouldi ($F_{2,58} = 1.40$, P = 0.180) or V. regulus ($F_{3,62}$ 223 = 0.92, P = 0.494), so we pooled eucalypts for all analyses. To determine bat roosting 224 preferences at site and landscape scales, we compared overall vegetation structure and landscape 225 variables, respectively, of roost to available/random sites and included all roost and 226 available/random sites in the analyses. No site scale variables were highly correlated (all r < r227 0.80) so we retained all nine site variables for multivariate analyses but, at the landscape scale, 228 we excluded distance to restored forest, which was highly correlated with length of edge 229 perimeter within 250 m (r = -0.91). We then constructed Euclidean resemblance matrices for 230 each of the nine scaled site variables and 11 remaining scaled landscape variables. We used 231 permutational multivariate analyses of variance (PERMANOVA) at each scale (roost, site and 232 landscape) to test for differences between roosts of each bat species and random/available 233 characteristics with the relevant resemblance matrices as dependent variables against a three 234 level categorical fixed factor (N. gouldi, V. regulus and random/available) and individual bat as a 235 random factor. We used the Adonis function, over 9999 permutations, in R vegan package 236 (Oksanen et al., 2012).

237

To identify whether individual variables were related to bat roost preferences at roost, site and landscape scales we ran Gaussian generalized linear mixed models, at each scale separately, using R lmerTest package (Kuznetsova et al., 2014) for each bat species. Although we measured a "paired" available/random for each roost we had no reason to assume individual bats were associated with a paired available/random so tested each bat group (male, female, maternity and mating) against all available/random trees. Thus, each roost, site or landscape variable was the dependent variable with categorical fixed factors of sex (male, female, and available/random) or season (maternity, mating, and available/random), with individual bat as a random factor. We specified available/random as the reference level so model parameters are in relation to the available/random category. Small sample sizes precluded us from analyzing further interactions (e.g., sex by season). Due to the number of tests conducted only those with P < 0.01 are presented and discussed, although all are provided in the Appendix (*N. gouldi*: Tables A.1 & A.2, *V. regulus*: Tables A.1 & A.3).

251

252 To determine the suitability of restored forest as roosting habitat, we compared vegetation 253 structure at roost sites with restored sites. We constructed a Euclidean resemblance matrix of six 254 site vegetation variables (scaled) collected at both roost and restored sites (canopy height and 255 canopy, shrub, ground, litter and log cover). There were no significant differences in tree density 256 between Alcoa's desirable and dense categories (5 to 9 year old restoration $t_{14} = 1.40 P = 0.184$; 257 10 to 14 year old restoration $t_{14} = -0.35$, P = 0.786; >15 year old restoration $t_{14} = -0.84$, P =258 0.416) so we grouped desirable and dense sites within each restored forest age group and 259 considered forest type as a fixed factor with five levels: roost (36) and restored forest of ages 0 to 260 4 (8), 5 to 9 (16), 10 to 14 (16), and >15 (16) years. To test for multivariate differences in site 261 characteristics between forest types we ran PERMANOVAs with the resemblance matrix of site 262 variables as the dependent factor and forest type as the fixed factor. We used the Adonis 263 function, over 9999 permutations, in R vegan package (Oksanen et al., 2012). To identify how 264 individual structural variables differed between roost sites and restored sites we ran separate 265 generalized linear models for each of the seven vegetation structure variables with forest type as 266 the explanatory variable. To account for lack of independence of individual bats with multiple

roost sites, we averaged vegetation structure values across individual bats to give a single valuefor each bat.

269

For intra and interspecific comparisons of roost site fidelity we ran Welch's two sample *t*-tests to compare between bat species and two-factor ANOVAs to compare within species (i.e., between sexes, seasons and their interaction), testing significant results with Tukey's post-hoc tests. All statistical analyses were performed in R (R Core Team, 2013).

274

275 **3. Results**

276 3.1 Radio-tracking

Of 43 bats affixed with transmitters, three transmitters attached to *N. gouldi* and four attached to *V. regulus* either failed, or bats could not be located, while the remaining 36 bats were tracked to
59 different roost trees for a total of 101 fixes (i.e. one bat tracked to the same roost three times
counted as three fixes but only one roost tree) of which 46 were for *N. gouldi* and 55 for *V. regulus* (Table 1).

282

283 *3.2 Roost scale roost preferences*

All bats roosted in trees in unmined forest (Figure 1). Bats roosted predominantly in jarrah (N =

43) but also in marri (N = 6), bullich (N = 7), sheoak (N = 2) and one bull banksia. Both N.

286 gouldi and V. regulus roosted in jarrah and marri but only N. gouldi roosted in sheoak and

287 banksia while only *V. regulus* roosted in bullich (Table 1). While we could not pinpoint exact

288 roost locations within trees, we made general observations, surmising that most roosts were

hollows (54 of 62 roosts) in the top half of trees (≥ 10 m above the ground). Exceptions to hollow

roosting were observed during the mating season with one *N. gouldi* male roosting 5.7 m above the ground in foliage of a bull banksia, one *V. regulus* male roosting 1.5 m above the ground in a trunk fissure of a dead jarrah, and one female *V. regulus* roosting 0.8 m above the ground in a hollow in a fallen branch.

294

295 Overall, eucalypt tree characteristics differed between available, N. gouldi roost and V. regulus 296 roost trees ($F_{2,124} = 7.25$, P < 0.001) N. gouldi preferred roost trees in greater stages of decay 297 (snag class, mating season P = 0.003, both sexes P < 0.010: DBO and crown senescence, all P < 0.010298 0.01) than available trees (Figure 2). Female N. gouldi and all N. gouldi during the maternity 299 season preferred roost trees with significantly larger DBHs (both P < 0.001) than available trees 300 (Figure 2). Female V. regulus, and V. regulus during the mating season, preferred roost trees in 301 greater stages of decay (mating season, DBO and crown senescence P < 0.001: female, snag 302 class P = 0.002, DBO P = 0.006 and crown senescence P < 0.001; Figure 2) than available trees 303 (Figure 2). During the mating season all V. regulus preferred trees with larger DBHs (P < 0.001). 304

305 *3.3 Site scale roost preferences*

At the site scale, overall vegetation structure differed between available, *N. gouldi* roost, and *V. regulus* roost sites ($F_{2,125} = 1.93$, P = 0.030). *N. gouldi* males preferred roost sites with more log cover than available sites (P = 0.005; Figure 3). Female *V. regulus*, and all *V. regulus* during the mating season, also preferred roost sites with more log cover (female, P = 0.003: mating, P = 0.010) than available sites. All *V. regulus* during the maternity season preferred roost sites with less shrub cover than available sites (P = 0.007, Figure 3).

313 *3.4 Landscape scale roost preferences*

314 Overall landscape scale characteristics differed between random, N. gouldi roost, and V. regulus 315 roost locations ($F_{2,127} = 5.34$, P = 0.001). Univariate analyses found that female N. gouldi 316 selected roosts at higher elevations (P = 0.003), on ground with flatter slopes (P = 0.007), farther 317 from both streams (P = 0.002) and tracks (P = 0.004), and surrounded by less unmined forest <3000 m (P = 0.002), than random locations (Figure 4). During the maternity season, N. gouldi 318 319 selected roosts on ground with flatter slopes (P = 0.001) while, in the mating season, roosts were 320 further from tracks (P = 0.005) and with more unmined forest within 3000 m (P = 0.002) than 321 random locations.

322

323 All V. regulus selected roosts with more restoration edge within 3000 m than random locations 324 (male, female, and maternity P < 0.010, mating P = 0.009; Figure 5). Female V. regulus also 325 preferred more recently burnt roost locations (P = 0.010), surrounded by less unmined forest 326 within 1000 m (P < 0.001) and more restoration edge at all three spatial scales (250 m P = 0.002, 327 1000 m and 3000 m P < 0.001), than random locations. Male V. regulus and all V. regulus during 328 the mating season preferred roost locations at lower elevations than random locations (male P <329 0.001, mating P = 0.006). Also during the mating season V. regulus preferred roosts with less 330 unmined forest within 1000 m than random locations (P = 0.009). During the maternity season 331 V. regulus selected roost locations with less unmined forest (all P < 0.001) and more restoration 332 edge (250 m P = 0.002, 1000 and 3000 m P < 0.001) than random locations, at all three spatial 333 scales.



Overall vegetation structure differed significantly between roost sites and restored sites ($F_{1,90}$ = 46.18, P < 0.001), although restored forest became structurally more similar to roosts as it matured. Univariate analyses revealed vegetation structure was significantly different between roost sites and restored sites for all structural variables (Figure A1; canopy height $F_{4,87}$ = 226.50, P < 0.001; canopy cover $F_{4,87}$ = 58.07, P < 0.001; shrub cover $F_{4,87}$ = 8.23, P < 0.001; ground cover $F_{4,87}$ = 6.47, P = 0.001; log cover $F_{4,87}$ = 18.93, P < 0.001; and litter cover $F_{4,87}$ = 95.14, P342 < 0.001).

343

344 3.6 Roost site fidelity

345 Of the 36 bats tracked, eight were only tracked to one diurnal roost for one day before the 346 transmitter fell off or we could not locate the bat. Of those bats tracked for multiple days, 70% 347 switched roosts after the first day. During the maternity season, all three female N. gouldi and 348 four female V. regulus switched roosts after the first day, compared to only one of three male V. 349 regulus. During the mating season, all three male and five female N. gouldi switched roosts after 350 the first day. In contrast, only one female V. regulus switched roosts after the first day; two 351 females did not change roosts during the tracking period (four and five days) while one female 352 switched roosts between the second and third day. Only one male V. regulus was tracked for 353 multiple days during the mating season and it did not change roosts. There was no difference in distances between roosts between sexes or seasons for either N. gouldi (sex, $F_{1,9} = 2.88$, P =354 355 0.124: season $F_{1,9} = 1.75$, P = 0.218) or V. regulus (sex, $F_{1,7} = 0.07$, P = 0.804: season $F_{1,7} = 0.07$ 356 1.07, P = 0.336) or the interaction between the two for V. regulus ($F_{1,7} = 0.34$, P = 0.578). Small 357 sample sizes meant we could not test the interaction for N. gouldi. N. gouldi travelled farther 358 between subsequent roosts (i.e., roost to roost distances) than V. regulus (218 ± 51 m and 88 ± 21 359 m, respectively; $t_{15} = 2.35$, P = 0.033; Table 1). Considering straight-line flight paths from 360 capture to first roosting site, 13 bats (36%) potentially travelled through restored forest to reach 361 their first diurnal roost.

362

363 **4. Discussion**

364 Faunal recolonization of restored forest may be relatively quick for some species, such as the 365 pygmy possum *Cercatetus concinnus*, but take decades or centuries for others, such as the skink 366 *Egernia napoleonis* (Craig et al., 2012). This was the first study to examine the roosting 367 preferences of bats across a restored production landscape and our results indicate that these bat 368 species require slow-developing microhabitats, not yet present in restored forest. Absence of 369 roosts, suitable roost trees and suitable roost sites in young restored jarrah forest suggests that 370 restored forest <40 years of age is poor roosting habitat, compared to unmined forest, for both N. 371 gouldi and V. regulus.

372

373 4.1 Roost trees characteristics consistent with trees having maximum number of hollows 374 Like other studies, we found that forest-dwelling bats generally prefer roosting in large, mature 375 trees with some intra and interspecific preferences (e.g., Lumsden et al., 2002a; Vonhof and 376 Gwilliam, 2007). In concordance with predictions, and similar to previous findings (Threlfall et 377 al., 2013; Webala et al., 2010), both N. gouldi and V. regulus selected eucalypt roost trees based 378 on tree size and decay stage, preferring larger and more senescent roost trees. Regardless of sex 379 or species, bats selected roost trees in mid-decay stages, consistent with sexual preferences of 380 North American Myotis species (Broders and Forbes, 2004). Contrary to our predictions, female 381 V. regulus and N. gouldi had similar roost tree preferences but during the maternity season V.

regulus were considerably more flexible in roost selection than *N. gouldi*. Hollow occurrence
and abundance increases in eucalypts as DBH and senescence increases (Rayner et al., 2014)
with jarrah and marri hollow abundance peaking in trees with intermediate levels of DBO and
crown senescence (Whitford, 2002). Tree characteristics preferred by both *N. gouldi* and *V. regulus* likely correspond to jarrah and marri trees with the most hollows.

387

388 N. gouldi and V. regulus collectively selected jarrah and marri trees that were ~ 60 and 80 cm 389 DBH, respectively, slightly smaller than mating season roost trees in the southern jarrah forest 390 (Webala et al., 2010) but substantially larger than trees in restored forest (~24 cm DBH in 15 391 year old restored forest; Burgar, 2014). Trees selected for roosting are estimated to be ~150-200 392 years old and contain one or more hollows (Whitford, 2002). By ~60 years old both jarrah and 393 marri trees are estimated to contain at least one hollow with a slit entrance of 20 mm (Whitford, 394 2002). As bats roost in hollows with entrances only slighter larger than themselves (e.g., 395 Goldingay, 2009; Tidemann and Flavel, 1987) bats may not be as restricted by hollow size, and 396 tree age, as many other hollow-dependent fauna, at least during the mating season. Small 397 hollows are less likely to be used during the maternity season as maternity colonies may number 398 \geq 50 females, in addition to their young (Law and Anderson, 2000; Vonhof and Gwilliam, 2007). 399 Studies of maternity colony sizes for jarrah forest bat species suggest colonies of 10-19 N. gouldi 400 adults (Lunney et al., 1988; Threlfall et al., 2013) and 25-66 V. regulus adults (Taylor and Savva, 401 1988; Tidemann and Flavel, 1987). N. gouldi's preference for roost trees almost twice as large in 402 the maternity season, compared to the mating season, is consistent with studies of N. gouldi in 403 suburban eastern Australia (Threlfall et al., 2013) and emphasizes the importance of moderate 404 sized hollows for bats during the maternity season.

405

406	Bats generally prefer relatively open roost sites with lower levels of surrounding vegetation
407	cover than available sites (e.g., Elmore et al., 2004; Webala et al., 2010), but contrary to
408	predictions and research from the southern jarrah forest (Webala et al., 2010), we did not find
409	bats preferentially roosting in relatively open sites with low canopy cover. However, we did find
410	that, during the maternity season, V. regulus preferred roosts with less shrub cover, compared to
411	available sites. In North America Lasiuris borealis roost sites have also been associated with low
412	understory cover and this has been attributed to increased plant growth from reduced shading by
413	midstory and/or small overstory trees in these sites (Perry et al., 2007). It is possible that this is a
414	correlative association for V. regulus as well. The preference by female V. regulus for roosts in
415	more recently burnt forests, compared to available sites, and the fact that all bats roosted in
416	unmined forest which is regularly subjected to prescribed fires, is consistent with research in
417	North America, where forest bat communities are generally resilient to fires (Buchalski et al.,
418	2013; Lacki et al., 2009). While fires only likely cause formation of 10% of hollows (Whitford,
419	2002), fires may assist in hollow formation where limbs have already been broken (Lacki et al.,
420	2009; Whitford, 2002). The preference for more log cover at roost sites, compared to available
421	sites, by male N. gouldi, female V. regulus and all V. regulus during the mating season suggests
422	these bats may select roosting sites close to foraging opportunities as coarse woody debris
423	contains a rich invertebrate fauna (Horn and Hanula, 2008; Koch et al., 2010), including orders
424	consumed by both bat species (Burgar et al., 2014). We acknowledge this is speculative and
425	suggest future research evaluates the value of coarse woody debris as habitat for prey species of
426	jarrah forest bats.

428 *4.2 Suitability of the restored landscape as roosting habitat*

429 We trapped bats at five locations during both maternity and mating seasons and no bats were 430 observed roosting in restored forest. This was despite >35% of bats presumably travelling 431 adjacent to, or through, restored forest to reach roosting sites from trapping locations. 432 Concordant with our predictions, roosting sites were lacking within restored forests due to the 433 absence of roosting structures, i.e., hollow bearing trees, and this is likely driving roost 434 preferences at the landscape level. A concurrent study investigating bat box use in the northern 435 jarrah forest suggests that some bat species are capable of roosting in restored forest when roost 436 structures are available (Burgar, 2014). Our findings are consistent with bat roosting research in 437 production landscapes elsewhere in Australia where tracked bats were always found roosting in 438 remnant forest, either avoiding regrowth or selecting retained mature trees for roosting (Law et 439 al., 2011; Webala et al., 2010). In timber-harvested landscapes, N. gouldi roosted in forests 440 logged within 10-25 years, albeit in large trees retained during harvesting (Webala et al., 2010) 441 whereas V. regulus avoided roosting in regrowth, preferring mature forest (Taylor and Savva, 442 1988; Webala et al., 2010). In south-eastern Australia the congeneric V. pumilus preferred 443 roosting in mature forest when available, but was capable of roosting in remnant, regrowth and 444 eucalypt plantation forest when mature forest was absent (Law and Anderson, 2000). Restored 445 jarrah forest is a relatively young (<40 years), developing ecosystem and once hollows form it is 446 anticipated restored areas will provide roosting habitat for bats. In the meantime, it is important 447 to both retain patches of mature trees during mining and manage these patches through 448 sustainable harvesting and fire management practices to ensure sufficient habitat for bats is 449 retained across the landscape.

451 A meta-analysis of North American bat research found that hollow roosting bats selected trees 452 that were closer to the nearest water source than available trees (Kalcounis-Ruppell et al., 2005), 453 which may suggest bats select roosts based on proximity to optimal foraging habitats (e.g., 454 Broders et al., 2006). However, reproductive females that consume large quantities of insects 455 each night (e.g., Kalka and Kalko, 2006) have to balance their energetic needs with roosting 456 requirements as suitable maternity roosts may not be near highly profitable foraging areas (e.g., 457 Pauli et al., 2015). In eastern Australia, bat maternity roosts were typically farther from foraging 458 sites than male roosts (Lumsden et al., 2002b) as we indirectly found in our study. As stream 459 zones are generally excluded from mining, streams are absent from restored forest, occurring 460 instead in unmined forests. The selection of sites that were further from optimal foraging habitat 461 (i.e., tracks and streams) for N. gouldi females and all N. gouldi during the mating season may 462 explain why these bats preferred roost sites with more log cover than available sites; they 463 compensated by selecting roosting sites where more prey was potentially available. We also 464 found female V. regulus and all V. regulus during the maternity season preferentially roosted in 465 locations with less surrounding unmined forest and more restoration edge, regardless of spatial 466 scale, than available locations. Edges may provide foraging opportunities, orientation clues and 467 established routes that decrease commuting time to foraging grounds, and provide shelter from 468 wind and/or predators (Verboom and Huitema, 1997). Our results suggest that foraging resources 469 may influence roosting preferences by V. regulus, as V. regulus seems to prefer a mosaic forest 470 landscape comprising unmined and restored forest of various ages. Similarly, in North America 471 Mytois sodalis selected maternity roosts in areas with high local forest cover within broader 472 landscapes with low forest cover (Pauli et al., 2015). A landscape-scale bat roosting study 473 concluded that multiple species of UK bat likely benefited from a network of forest patches

across a landscape where woodland cover was reduced (Boughey et al., 2011). While it is
encouraging that *V. regulus* exploited roosting structures close to restored forest, the percentage
of unmined forest surrounding roosts still never fell below 60% at the 250 m scale. Future
studies are needed to identify the minimum amount of remnant forest surrounding roosts that
bats can tolerate.

479

480 *4.3 Roost site fidelity*

481 Roost switching, by both N. gouldi and V. regulus, while maintaining fidelity to a roosting area 482 suggests roost availability in the northern jarrah forest may not be limiting in unmined forest. 483 Many bat species frequently switch roosts while maintaining fidelity to an area (e.g., Lacki et al., 484 2009; Law et al., 2011), a beneficial behavior that increases familiarity with several roosts of 485 potentially different microclimates and lowers both predation risk and ectoparasite loads (Lewis, 486 1995). Mine-pits, typically 10-20 ha in size (Grant, 2006), potentially encompass entire roosting 487 areas given that N. gouldi and V. regulus travelled an average of 218 and 88 m between roosts, 488 respectively. Assuming bats travelled within a circular area, distances travelled equate to 15 and 489 2 ha roosting area for N. gouldi and V. regulus, respectively. These distances were substantially 490 shorter than in the southern jarrah forest (Webala et al., 2010), but similar to distances in south-491 eastern Australia for N. gouldi (e.g., Lunney et al., 1988; Threlfall et al., 2013). Retention of 492 mature forest should aim to capture enough roost trees to ensure roost area fidelity is maintained. 493 Additionally, mature forest patches interspersed across the landscape would best cater to both 494 intra and interspecific landscape scale roost requirements. Similar to the southern jarrah forest 495 (Webala et al., 2010), retention of roosting habitat at low elevations will benefit V. regulus while 496 retaining roosting habitat on relatively flat ground, which tends to be high in the landscape in the

497 jarrah forest, will benefit *N. gouldi*. We suggest future research be designed specifically from the
498 landscape perspective to elucidate minimum roosting areas for bats within restored landscapes
499 and causal mechanisms influencing roost fidelity requirements.

500

501 **5. Conclusions**

502 The lack of roosting in restored forest underscores the importance of remnant mature forest 503 patches in conserving and maintaining bat populations across production landscapes. Bats' 504 resilience and adaptability generally make them tolerant to disturbance (Arnett, 2003) and, while 505 affected by habitat destruction such as the loss of canopy trees, their vagility reduces the 506 immediate impact of habitat loss for many species (Fenton et al., 1998). During our study neither 507 species was found roosting in restored forest of any age (all <40 years old at Huntly minesite), 508 despite having relatively flexible roosting preferences and the occurrence of N. gouldi in bat 509 boxes within restored forest. While records of bats roosting in regrowth in other studies are 510 encouraging (Law and Anderson, 2000; Lumsden et al., 2002b), the general avoidance of 511 restored forest as roosting habitat in our study, and of regrowth elsewhere (Law et al., 2011; 512 Webala et al., 2010), reinforces the importance of remnant forest to the conservation of bat 513 populations in production landscapes. Our study suggests that restored forest is unlikely to 514 contribute significantly to the conservation of species requiring slow-developing microhabitats in 515 production forest landscapes as these microhabitats will be lacking in restored forest for decades, 516 or even centuries. These species will be best conserved in production landscapes by retaining 517 suitably sized forest remnants and ensuring these remnants are managed effectively to maintain 518 the microhabitats these species require.

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- 526
- 527

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666

668	Figure Captions
669	Figure 1: a) The location of 5 bat trapping sites (diamonds), adjacent to waterholes within Huntly
670	minesite. Restored forest is denoted by grey while unmined forest is white. Black lines denote
671	roads while grey lines denote streams. Roost trees selected by N. gouldi females (black stars), N.
672	gouldi males (grey stars), V. regulus females (black circles) and V. regulus males (grey circles)
673	are shown for b) Sites 1 and 5; c) Sites 2 and 3; and d) Site 4.
674	
675	Figure 2: Boxplots showing significant ($P \le 0.01$) roost scale preferences by sex, season and
676	available roosts for <i>N. gouldi</i> (DBH, snag class, dead branch order and crown senescence) and <i>V</i> .
677	regulus (snag class, dead branch order and crown senescence).
678	
679	Figure 3: Boxplot showing the significant ($P \le 0.01$) site scale preference by sex, season and
680	available roosts for N. gouldi (log cover) and V. regulus (shrub and log cover).
681	
682	Figure 4: Boxplots showing significant ($P \le 0.01$) landscape scale preferences for <i>N. gouldi</i> by
683	sex, season and available roosts (elevation, slope, distance to stream, distance to track and the
684	amount of unmined forest within 3000 m).
685	
686	Figure 5: Boxplots showing significant ($P \le 0.01$) landscape scale preferences for <i>V. regulus</i> by
687	sex, season and available roosts (elevation, time since fire, the amount of unmined forest within
688	250 m, 1000 m, and 3000 m, and the length of restored forest edge perimeter within 250 m, 1000
689	m and 3000 m).

- 691 Figure A.1: Vegetation structure across the restored landscape in south-western Australia. We
- 692 compared vegetation structure between roost sites (n=36) and each age group of restored forest
- 693 sites (0-4 n=8, 5-9 n=16, R 10-14 n=16, R >15 n= 16) using linear models; * indicates a
- 694 significant difference at P < 0.05. All linear models were significant at the P < 0.05.

Tables

Table 1: Radio-tracking results for N. gouldi and V. regulus, by season and sex, tracked between October 2011 and March 2012. Roost tree species and
jarrah (J), marri (M) and other (O), comprising sheoak and bull banksia for N. gouldi and bullich for V. regulus.

			No.	No. never	Total No. of roosts	Dist. to first roost	Dist. btwn roosts	Roost tree species		ecies
Species	Season	Sex	fitted	located	located	$(m) \pm SE$	$(m) \pm SE$	J	Μ	Ο
N. gouldi	Maternity	Female	5	1	7	931 ± 182	341 ± 86	7		
		Male	3	0	3	1232 ± 138	*	3		
	Mating	Female	7	1	11	1831 ± 290	200 ± 77	8	1	2
		Male	6	1	9	705 ± 135	83 ± 59	8		1
V. regulus	Maternity	Female	6	1	8	526 ± 115	83 ± 25	5	1	2
		Male	4	1	4	198 ± 55	6*		2	2
	Mating	Female	5	1	6	628 ± 91	113 ± 80	5		1
	-	Male	7	1	11	685 ± 225	100 ± 42	7	2	2

*During the maternity season no male N. gouldi and only one male V. regulus were tracked to multiple roosts

Figures









Figure 2





Figure 3





Figure 4



Figure 5



