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# Bat habitat use in logged jarrah eucalypt forests of south-western Australia

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## Summary

**1.** Ecologically sustainable forest management is being implemented to address the competing demands of timber production and conservation, but its effectiveness is poorly understood. Bats play key roles in forest ecosystems and are sensitive to timber harvesting, so are potential indicators of whether management is successfully achieving biodiversity conservation in production forests.

**2.** We evaluated logging impacts in jarrah eucalypt forests of south-western Australia by examining insectivorous bat activity, feeding buzzes and insect biomass at four sites in each of recently logged forest, young regrowth and old regrowth.

**3.** Forest tracks supported higher overall activity and higher feeding activity than off-track sites, but activity was similar on-track irrespective of logging history. However, off-track activity in old regrowth was significantly higher than in either young regrowth or recently logged forest.

**4.** *Vespadelus regulus* and *Nyctophilus* spp. were more active in old regrowth than other logging histories. Similarly, *V. regulus*, *Nyctophilus* spp., *Chalinolobus gouldii*, *Chalinolobus morio* and *Falsistrellus mackenziei* activity was significantly greater on- than off-tracks, but activity was similar on-track across logging histories.

**5.** Increased understorey clutter was the strongest predictor of reduced bat activity in off-track sites. Reduced clutter and roost availability most probably explained greater activity in old regrowth forest. Neither insect biomass nor interactive effects of clutter and insect biomass significantly affected bat activity.

**6.** *Synthesis and applications*. Tracks provided internal linear edges within cluttered forests allowing bat species to use such areas for foraging. However, our results suggest that the retention of unlogged areas within logged forests is likely to be the most effective strategy in many forest ecosystems for conserving bat populations and achieving ecologically sustainable forest management for this group.

**Key-words:** bat activity, clutter, eucalypt forest, logging, regrowth, track

## Introduction

Forest logging is a major threat to global biodiversity (Sala *et al.* 2000) and a growing demand for timber means logging rates are increasing (Perry, Ram & Hart 2008). Consequently, there is a drive to develop forest timber harvesting strategies that maintain biodiversity alongside timber extraction. Attempts are, therefore, being made to integrate conservation into production forests according to ecologically sustainable forest management principles such as the maintenance of stand structural complexity and landscape connectivity and heterogeneity (Lindenmayer & Franklin 2002).

Forest bats are one group with great potential for assessing the effectiveness of ecologically sustainable forest management because they are typically sensitive to logging impacts and play key ecological roles in forest ecosystems, indirectly affecting other forest biota (Clarke, Rostant & Racey 2005). Although there are many ways in which logging affects forest bats (Hutson, Mickleburgh & Racey 2001), reductions in the quantity and suitability of foraging habitat, food resources or roosting sites are likely to be major impacts (e.g. Brigham *et al.* 1997; Forkner *et al.* 2006; Peters, Malcolm & Zimmerman 2006).

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Reductions in the quantity and suitability of foraging habitat usually result from changes to forest structure post-logging. These changes can result directly from logging, through removal of large trees, or indirectly as logged forests regenerate with a different structure from unlogged forest. Typically, logging regrowth is denser than unlogged forest, making it less suitable for many foraging bats, among other species (Law & Chidel 2001; Patriquin & Barclay 2003). Secondly, logged forests are usually traversed by flyways (tracks, including roads and trails), which allow bats to access and use forest that is otherwise too cluttered (Adams, Law & French 2009). Thirdly, logging can directly reduce food resources, such as moths and beetles, which depend on dead wood and large trees as habitat (Forkner *et al.* 2006; Summerville & Crist 2008). Lastly, logging can reduce the quantity and suitability of roosting sites. While forest bats roost in a variety of locations, the most severely affected are species requiring late successional features, such as peeling bark and tree hollows (Brigham *et al.* 1997; Law & Anderson 2000).

Jarrah eucalypt forests are dry sclerophyll forests restricted to south-western Australia that have been logged for over 100 years. Ecologically sustainable forest management was first introduced in 1985, with strategies designed to maintain biodiversity including selective logging, and retention of 12 habitat or potential habitat trees per hectare together with unlogged buffers within logged areas and around riparian zones (Conservation Commission of Western Australia 2004). While logging effects on other fauna have been examined (e.g. Craig & Roberts 2005), it is unknown whether ecologically sustainable forest management is maintaining bat populations in production forests. Our study examined how jarrah forest logging affects bats through both changes in vegetation structure and prey populations. We hypothesized that the bat community does not differentiate forest habitats on the basis of logging history. However, at the species level, different species were expected to respond differently according to their ecomorphology and echolocation call attributes. For instance, we predicted that *Nyctophilus* species activity would be higher in forest away from tracks (off-track) than along forest tracks (on-track) given the species' low aspect ratio and wing loadings. Specifically, we tested the hypothesis that logging history had no influence on bat activity, including foraging, and that bat activity was positively correlated with prey availability. Additionally, we hypothesized that tracks exhibited higher bat activity than off-track sites due to reduced vegetation clutter.

## Materials and methods

### STUDY SITE

The study area, located in south-western Australia (Fig. 1), has a Mediterranean climate. At the nearest weather station, temperatures in the coldest and hottest months average 9·6 and 20·3 °C, while annual rainfall is 1011·8 mm with > 70% falling between May and September (http://www.bom.gov.au/climate/averages/tables/

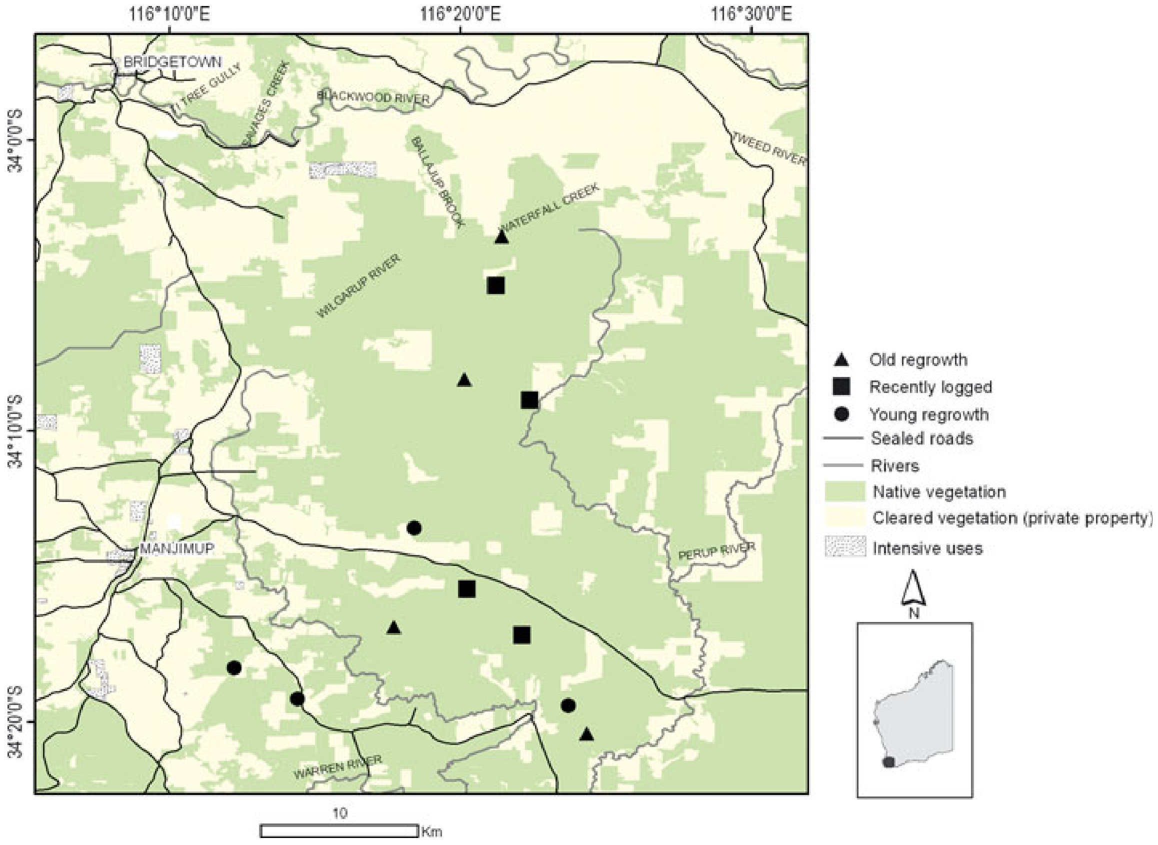

**Fig. 1.** Map showing the spatial arrangement of sampling sites. Inset shows the study area location within Western Australia.

cw_009573.shtml). Vegetation in the study area is jarrah forest, which has an overstorey dominated by jarrah (*Eucalyptus marginata* Donn. ex. Smith) and marri (*Corymbia calophylla* K.D. Hill and L.A.S. Johnson).

### LOGGING HISTORY

Since new logging prescriptions were adopted in 1985, three types of forest can be identified: gap, shelterwood and buffer. Gaps involve removal of the overstorey to release and promote jarrah and marri growth from seedlings, ground coppice and small saplings. Maximum gap size is 10 ha and about 95% of tree basal area (the cross-sectional area of all trees 1·3 m above the ground) is removed with four habitat trees (those containing hollows suitable for fauna) and eight potential habitat trees retained per ha. By contrast, shelterwoods involve the retention of 40–60% of tree basal area to provide seed for regeneration. Finally, buffers are retained between gaps, around riparian areas and along major roads. These buffers are considered unlogged although they were probably lightly logged once after 1945.

### EXPERIMENTAL DESIGN

We employed a two-factor orthogonal experimental design including three logging histories: recently logged forest (< 6 years post-logging), young regrowth (12–30 years post-logging) and old regrowth (>30 years post-logging); and two detector locations (on-track and off-track). Old regrowth contained forest attributes similar to unlogged forest, such as abundant hollow-bearing trees, but unlogged forest could not be included because < 5 ha of jarrah forest has never been logged (Conservation Commission of Western Australia 2004).

Sampling was done at 12 sites that were previously logged, four sites for each logging history. Tracks are a universal feature of logged forests and consist of linear passageways ranging from 1 to 6 m wide and include forest trails and small roads that were unsealed (dirt or crushed stone). Bat activity and vegetation structure were assessed both on-track and off-track at each site, and insect abundance was sampled off-track only. We did not sample activity in riparian zones because they are not logged and so do not provide appropriate controls for studying logging impacts (Law, Anderson & Chidel 1998). Bats typically travel 1–10 km per night (e.g. Lumsden, Bennett & Silins 2002), so sites were > 3 km apart to minimize pseudoreplication and interspersed with respect to logging history (Fig. 1).

### BAT SAMPLING

Bat activity was recorded using Anabat SD1 Bat Detectors (Titley Electronics, Ballina, Australia) mounted 1 m above ground and oriented 40° above horizontal to reduce sound attenuation by understorey vegetation. On-track detectors were set on the sides of, and parallel to, tracks, whereas off-track detectors were placed > 20 m from tracks and oriented away from them. To minimize bat call attenuation from vegetation at off-track sites, detectors were pointed towards small gaps (Law & Chidel 2002).

One site from each logging history was surveyed at both on- and off-track locations in November and December 2007 and 2008 (i.e. six detectors per night). Sampling was carried out during these months because bats breed at this time and so their resource requirements are highest. Each location was sampled for bat activity for two 2-night periods, totalling eight detector nights per site (four on-track and four off-track). All sites were sampled once before any sites were re-sampled. Sampling lasted from dusk to dawn with activity quantified as 'bat passes' (Fenton *et al.* 1998), defined as sequences of two or more distinct call pulses separated from the next set of pulses by > 5 s (Law, Anderson & Chidel 1998). To compare habitat use, bat activity was indexed as the number of passes per night within each site/location. Additionally, feeding buzzes associated with prey attacks were identified and recorded as numbers of feeding buzzes per night at each site/location. To account for variations in bat activity due to temperature, we recorded minimum air temperature using thermometers near off-track detectors. We did not sample on nights with rain or a full moon (Erkert 1982).

### BAT CALL ANALYSIS

Calls were extracted using CFCread© software (C. Corben/Titley Electronics) and identified using Analook version 6 (C. Corben; http://www.hoarybat.com) by comparing call variables (e.g. frequency, pulse duration) with regional call libraries (e.g. Pennay, Law & Reinhold 2004). Due to geographic call variation, we collected reference calls from seven of the nine species known from the region and obtained recordings of the two remaining species from C. Corben (as above). Calls of three species, *Nyctophilus major*, *Nyctophilus gouldi* and *Nyctophilus geoffroyi* are indistinguishable (Pennay, Law & Reinhold 2004), so we lumped them as *Nyctophilus* spp.

### INSECT ABUNDANCE ESTIMATES

We assessed insect prey availability using Australian Entomological Supplies funnel and bucket (diameter 26 cm) light traps with 12 V–8 W battery powered ultra violet lights (URL: http://www.entosupplies.com.au/). During the same months as bat activity, but on alternate nights to bat sampling to avoid confounding bat activity with increased insect activity around light traps (Adams, Law & French 2005), one light trap was placed on the ground in a clear open area (no vegetation cover) near off-track locations at all 12 sites from dusk to dawn for two different nights at each site. Minimum air temperatures were recorded near each trap.

Samples were sorted to order and wet biomass recorded. Dry biomass was estimated using the equation, Dry biomass = 0·0461*Wet biomass + 4·7024, derived from trials and subsamples. To obtain proxies for overall species abundance, given sorting and identification time limitations, individuals of Lepidoptera and Coleoptera, were classified by size and specimens > 1 cm body length identified to morphospecies.

### VEGETATION STRUCTURE

We assessed vegetation clutter at all bat sampling locations in February and March 2008 using two 10-m radius circular plots centred on bat sampling points. While vegetation sampling was done 3 months after bat sampling, the summer drought in these evergreen forests means that vegetation would have changed negligibly, if at all, since bat sampling. Within these plots, clutter (i.e. vegetation; Fenton 1990) in four strata [upper (≥ 15 m), midstorey (5–15 m), shrub (0·75 cm–5 m) and groundlayer stratum (0–0·75 cm)] was estimated as 1 (0–5%), 2 (5–25%), 3 (26–50%), 4 (51–75%) or 5 (≥ 75%) (Law & Chidel 2002). Because stratum height, and height differences between the two uppermost strata, can affect bat activity (Brown, Nelson & Cherry 1997), each stratum score was multiplied by its height to estimate clutter volume (Law & Chidel 2002). For instance, regrowth eucalypts often have extensive branching up their trunks, so multiplying that stratum cover by its height provides an index of clutter volume.

### STATISTICAL ANALYSES

Prior to analyses, all data were transformed [$\ln (x + 1)$] if they were not normally distributed or heteroscedastic. Nonparametric tests were applied when transformations were unsuccessful in rendering data normal and homeoscedasctic. All means are presented ± SE. Two-way multivariate ANOVAS were used to test for differences in understorey and overstorey clutter indices between logging histories and track positions, with clutter indices as dependent variables. Differences between logging histories and track positions in overall and individual species bat activity, and feeding activity, were tested for both years using repeated measures ANOVAS with one within-factor (year) and two between-factors (logging history and detector position). *Post hoc* Tukey tests were performed to check for significant treatment differences (Day & Quinn 1989). Feeding buzzes were not analysed for five species because $< 1\%$ of passes by both *Tadarida australis* and *Mormopterus* species 4 were feeding buzzes, while *Nyctophilus* spp. may not use echolocation calls for detecting prey, but rather use passive listening (Grant 1991). *Mormopterus* is undergoing taxonomic revision, with *Mormopterus* species 4 representing an undescribed species equivalent to *Mormopterus* species 4 population 'O' in Adams *et al.* (1988).

Differences in insect biomass and abundance between logging histories and years were analysed using repeated measures ANOVAS with one within-factor (year) and one between-factor (logging history). Only orders represented by $> 50$ individuals were analysed individually. As insect activity was sampled at off-track locations only, insect abundance and biomass were compared with off-track bat activity only. To test if total dry insect biomass and insect abundance influenced bat activity, we conducted multiple regressions with total dry insect biomass and dry Lepidoptera biomass as independent variables, as these were the only insect variables that varied between logging histories, and overall or individual species bat activity as dependent variables. These data were analysed using STATISTICA 7.0 (Statsoft, Inc., USA). Where non-significant interactions were detected in repeated measures ANOVAS, the models were repeated without non-significant interactions using mixed model analyses in SPSS 17.0 (SPSS, USA).

To analyse relationships between vegetation clutter and bat activity, we first examined correlations between clutter indices for each strata. Ground, shrub and midstorey indices were highly correlated ($0·82 < r < 0·86$, $P < 0·001$), but none were correlated with overstorey clutter. Thus, in analyses, the three understorey indices were summed. Resulting understorey and overstorey clutter indices were then included in multiple regression analyses to test influences of vegetation clutter on bat activity, with individual bat species and overall bat activity as dependent variables. We used generalized estimating equations (SPSS 17.0) to determine the effects of vegetation clutter, insect biomass and their interaction on bat activity. Generalized estimating equations are extensions of Generalized Linear Models used to model correlated data, and they fit marginal models, where relationships between response and predictor variables are modelled separately from correlations between observations within each experimental or sampling unit (Diggle, Liang & Zeger 1994). For generalized estimating equations, each site or year was considered a cluster within which correlated data could occur and an independent correlation structure was used.

## Results

### VEGETATION CLUTTER

Both overstorey ($F_{2,19} = 5·973$; $P = 0·010$) and understorey ($F_{2,19} = 10·392$; $P = 0·001$) indices differed significantly between logging histories. Understorey indices did not differ between logged forest and young regrowth ($P > 0·05$), but both were higher than old regrowth ($P < 0·05$). Overstorey indices of all logging histories were different ($P < 0·05$), with young regrowth the most cluttered and old regrowth the least cluttered (Fig. 2). Both understorey ($F_{1,20} = 39·26$; $P < 0·001$) and overstorey ($F_{1,20} = 4·717$; $P = 0·045$) indices were different between on-track and off-track locations, with more clutter off-track. Overstorey indices differed more at off-track than on-track locations, resulting in a significant logging history by detector position interaction ($F_{2,19} = 0·80$; $P = 0·002$).

### BAT ACTIVITY RESPONSES TO LOGGING

We recorded 12 213 bat passes from nine species, 6110 in 2007 and 6103 in 2008, but 21% of recordings were unidentifiable and thus excluded. Of the remainder, 1·8% were unassignable to either *Chalinolobus gouldii* or *Mormopterus* species 4 and were included for total bat passes, but not for either species.

Although minimum air temperatures were lower in 2008 than 2007 ($F_{1,42} = 27·23$, $P < 0·001$), neither overall nor

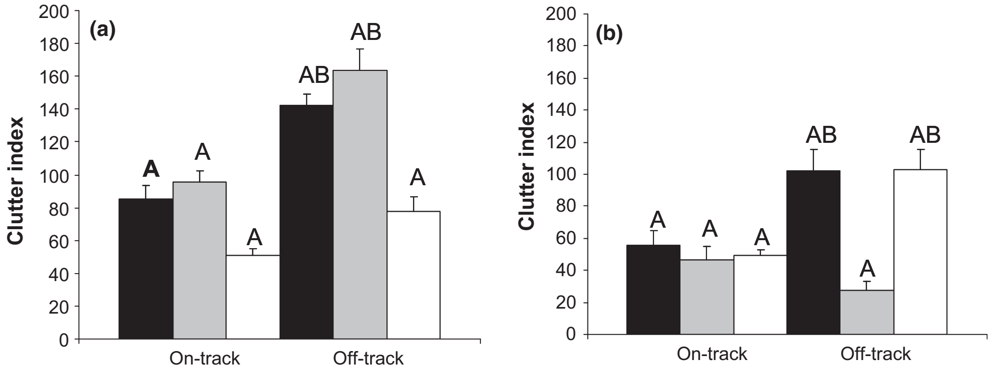

**Fig. 2.** Differences in vegetation clutter indices (untransformed mean ± SE) in three logging histories (young regrowth = black, logged forest = grey and old regrowth = white), on-track and off-track for (a) understorey and (b) overstorey. Different letters denote significant differences at $P < 0·05$.

individual species bat activity was correlated with minimum air temperature ($P > 0·05$), so we interpreted logging impacts on bat activity independently of temperature. When data were pooled across years for both on- and off-track locations, old regrowth had more bat passes than young regrowth ($P = 0·004$) and logged forest ($P = 0·012$) with no difference between the last two logging histories ($P = 0·957$; Table 1; Fig. 3). There was also a significant logging history by year interaction due to logged forest recording more bat passes than young regrowth in 2007, but fewer in 2008. However, this does not change our interpretations of logging impacts because bat activity in both these logging histories was significantly lower than old regrowth in both years.

Differences in activity between logging histories only occurred off-track, with similar activity levels occurring on-tracks across logging histories ($P > 0·05$), resulting in a significant logging history by detector position interaction (Table 1). There was more activity off-track ($P < 0·001$) in old regrowth than either young regrowth or logged forest, which did not differ from each other ($P = 0·996$).

At the species level, logging history significantly influenced two species, *Vespadelus regulus* and *Nyctophilus* spp.. *Vespadelus regulus* used old regrowth forest more ($P < 0·01$) than either young regrowth or logged forest (Table 1). *Nyctophilus* spp. also used old regrowth more than either young regrowth ($P < 0·05$) or logged forest ($P < 0·01$), but there was a significant logging history by year interaction. In 2007, *Nyctophilus* spp. activity did not differ between logging histories, while in 2008 activity was higher in both young and old regrowth compared to logged forest.

### FORAGING ACTIVITY RESPONSES TO LOGGING

We recorded 614 feeding buzzes (235 in 2007 and 379 in 2008) with *V. regulus*, *C. gouldii*, *F. mckenziei* and *C. morio* contributing over 99% of all feeding buzzes. Individual species feeding

**Table 1.** *F*-values from repeated measures ANOVAs for effects of logging history and detector position on bat activity, with year as within-factor and logging history and detector position as between-factors. Significant results are denoted by asterisks after models were rerun without non-significant interactions and only significant interactions are shown

| Species | Logging history (LH) ($F_{2,34}$) | Detector position (DP) ($F_{1,34}$) | Year (Y) ($F_{1,34}$) | LH × DP ($F_{2,34}$) | LH × Y ($F_{2,34}$) | DP × Y ($F_{1,34}$) | LH × DP × Y ($F_{2,34}$) |
|---|---|---|---|---|---|---|---|
| Overall bat activity | 14·54*** | 137·22*** | 0·002 | 8·09** | 3·36** | | |
| *Chalinolobus gouldii* | 0·17 | 15·43*** | 0·45 | | | | |
| *Chalinolobus morio* | 2·14 | 141·79*** | 0·00 | | | | |
| *Falsistrellus mackenziei* | 1·74 | 27·00*** | 0·22 | | | | |
| *Mormopterus* species 4 | 0·20 | 0·46 | 0·46 | | | | |
| *Nyctophilus* spp. | 13·64*** | 28·67*** | 0·64 | | 4·09* | | |
| *Tadarida australis* | 1·06 | 0·11 | 11·72** | | 3·73* | | |
| *Vespadelus regulus* | 15·34*** | 27·33*** | 0·08 | | | | |

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

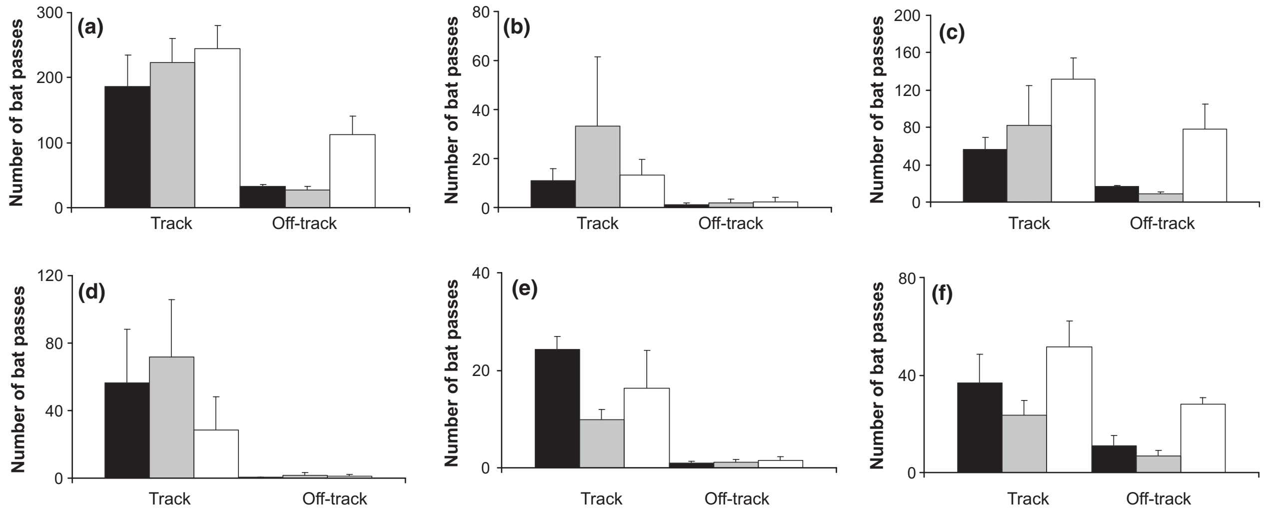

**Fig. 3.** Differences in bat activity (passes per night: untransformed mean ± SE) in three logging histories (same key as Fig. 2) in on-track and off-track positions for (a) overall bat activity, (b) *Chalinolobus gouldi*, (c) *Vespadelus regulus*, (d) *Falsistrellus mackenziei*, (e) *Chalinolobus morio* and (f) *Nyctophilus* spp. Note that *y*-axis values vary among species.

buzzes were not correlated with minimum air temperature ($P > 0{\cdot}05$), so we assessed logging impacts on feeding buzzes independently of temperature.

Overall numbers of feeding buzzes differed significantly among logging histories (Fig. 4; Table 2) with more buzzes in old regrowth than either young regrowth ($P < 0{\cdot}01$) or logged forest ($P < 0{\cdot}05$) and no difference between the latter two ($P = 0{\cdot}173$). *Vespadelus regulus* was the only species where feeding buzzes differed between logging histories, with more buzzes recorded in old regrowth and logged forest ($P > 0{\cdot}05$) than young regrowth ($P < 0{\cdot}01$) (Fig. 4; Table 2). Feeding buzzes also differed significantly between detector positions, with greatest foraging activity on-track (Fig. 3; Table 2) and all four species analysed showing more feeding buzzes on-track (Fig. 4; Table 2). There were significant detector position by year interactions for *C. morio* and *F. mackenziei* as both species recorded significantly more feeding buzzes on-track in 2008 than 2007.

**Table 2.** *F*-values from repeated measures anovas for effects of logging history and detector position on bat feeding buzzes, with year as within-factor, and logging history and detector position as between-factors. Significant results are denoted by asterisks and interactions are not presented as all were non-significant

| Species | Logging history ($F_{2,16}$) | Detector position ($F_{1,16}$) | Year ($F_{1,16}$) |
|---|---|---|---|
| Overall feeding activity | 7·38** | 79·55*** | 2·10** |
| *Chalinolobus gouldii* | 0·08 | 23·03*** | 0·16 |
| *Chalinolobus morio* | 2·48 | 39·38*** | 4·81* |
| *Falsistrellus mackenziei* | 0·47 | 20·45*** | 3·52 |
| *Vespadelus regulus* | 12·80*** | 41·31*** | 4·49* |

$^*P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$.

BAT ACTIVITY AND VEGETATION CLUTTER

Vegetation clutter indices explained significant amounts of the variation in the number of overall bat passes in 2007 (adjusted $R^2 = 0{\cdot}51$, $P < 0{\cdot}001$) and 2008 (adjusted $R^2 = 0{\cdot}53$, $P < 0{\cdot}001$), as well as in numbers of *V. regulus*, *C. morio* and *Nyctophilus* spp. passes in both years. Increasing understorey clutter was negatively correlated with overall bat activity ($t_{19} = -4{\cdot}81$ and $-4{\cdot}47$, $P < 0{\cdot}001$), as well as *V. regulus* ($t_{19} = -4{\cdot}57$ and $-5{\cdot}49$, $P < 0{\cdot}001$), *C. morio* ($t_{19} = -3{\cdot}22$ and $-2{\cdot}39$, $P < 0{\cdot}01$ and $P < 0{\cdot}05$) and *Nyctophilus* spp. ($t_{19} = -5{\cdot}24$ and $-5{\cdot}69$, $P < 0{\cdot}001$) activity. Overstorey clutter was not significantly correlated with either overall or individual species activity.

Vegetation clutter indices were significantly correlated with feeding buzzes in both 2007 (adjusted $R^2 = 0{\cdot}39$, $P < 0{\cdot}01$) and 2008 (adjusted $R^2 = 0{\cdot}51$, $P < 0{\cdot}001$) with increasing overstorey and understorey clutter negatively related to overall feeding buzzes in 2007 ($t_{19} = -3{\cdot}21$; $P < 0{\cdot}01$ and $t_{19} = -2{\cdot}33$; $P < 0{\cdot}05$, respectively) and 2008 ($t_{19} = -4{\cdot}47$; $P < 0{\cdot}01$ and $t_{19} = -2{\cdot}07$; $P = 0{\cdot}05$). *Chalinolobus gouldii*, *C. morio* and *V. regulus* feeding buzzes were significantly negatively related to vegetation clutter in both years.

LOGGING HISTORY, INSECT BIOMASS AND BAT ACTIVITY

We collected *c.* 8900 insects, with Lepidoptera, Coleoptera and Diptera comprising 86% of trapped individuals. Logging history significantly influenced total dry insect and dry Lepidoptera biomass, with old regrowth recording significantly higher biomasses than other logging histories (Table 3). Conversely, logging history had no influence on either biomass

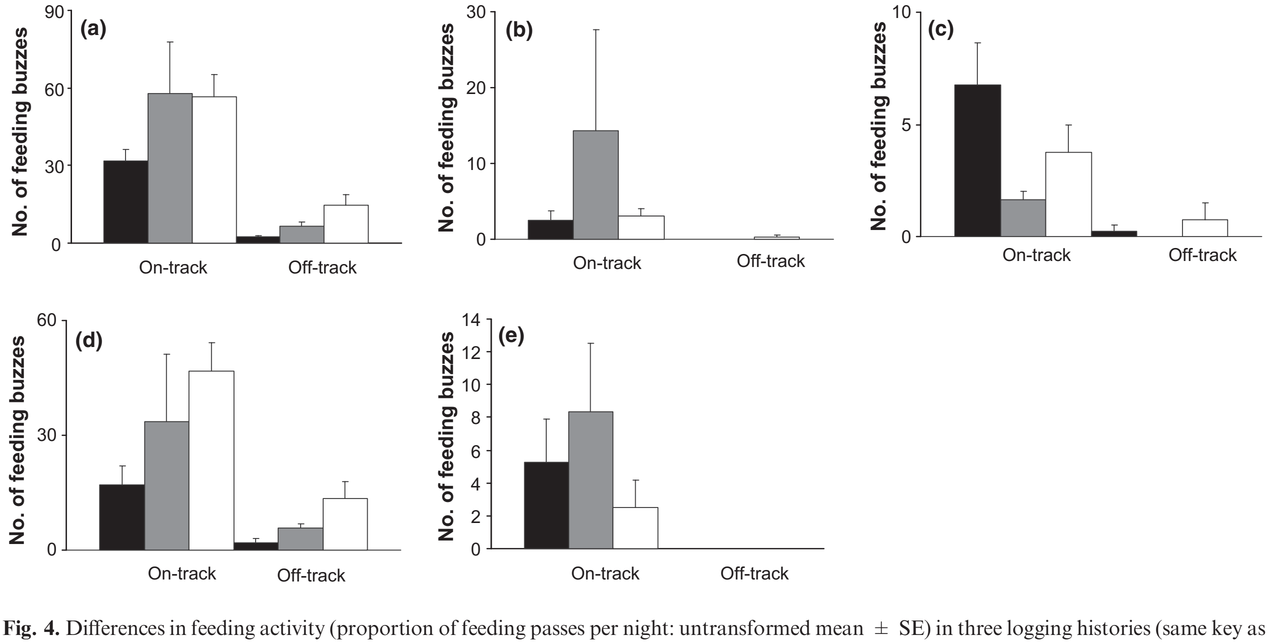

**Fig. 4.** Differences in feeding activity (proportion of feeding passes per night: untransformed mean ± SE) in three logging histories (same key as Fig. 2), on-track and off-track for (a) overall feeding buzzes; (b) *Chalinolobus gouldi*; (c) *Chalinolobus morio*; (d) *Vespadelus regulus*; (e) *Falsistrellus mackenziei*. Note that *y*-axis values vary among species.

**Table 3.** Results of repeated measures ANOVA for effect of logging history on insect dry biomass, with year as within-factor, and logging history as between-factor. Significant results are denoted by asterisks and interactions are not presented as all were non-significant

| | Logging history ($F_{2,37}$) | Year ($F_{1,37}$) |
|---|---|---|
| Total dry insect biomass | 3·39* | 1·30 |
| Lepidoptera | 4·23* | 7·50** |
| Coleoptera | 1·22 | 1·47 |
| Diptera | 0·47 | 0·46 |
| Hymenoptera | 2·01 | 3·93 |
| Blattodea | 1·26 | 0·05 |
| Mantodea | 1·13 | 1·47 |
| Hemiptera | 1·32 | 3·65 |
| Trichoptera | 0·93 | 0·09 |

*$P < 0·05$; **$P < 0·01$.

of other insect orders, total abundance or abundances of individual orders. Neither total dry insect nor dry Lepidoptera biomass explained significant amounts of variation in overall bat passes in 2007 (adjusted $R^2 = 0·07$, $P = 0·180$) or 2008 (adjusted $R^2 = 0·04$, $P = 0·273$), or numbers of passes of individual bat species. There was no significant interactive effect between vegetation clutter and either total dry insect or dry Lepidoptera biomass on overall bat activity. There was also no significant interaction effect of vegetation clutter and either total dry insect or dry Lepidoptera biomass on individual species activity.

## Discussion

This is the first study to relate bat and insect activity to logging history. We found old regrowth forests supported greater bat and insect activity, but lower vegetation clutter, than either young regrowth or recently logged forest. Forest tracks across all logging histories provided important habitat for most bat species. Although tracks were a small proportion of forest landscapes, they facilitated access and use of otherwise inaccessible young regrowth and have the potential to reduce logging impacts on bats.

### METHODOLOGICAL LIMITATIONS

We sampled bat activity using Anabat detectors which have biases in their effectiveness, as not all species are detected equally. Some, such as *Nyctophilus* spp., that emit low amplitude calls which attenuate rapidly (Neuweiler 1989), may be under-represented in detector-based surveys (e.g. Barclay 1999). Furthermore, bat detectors do not measure abundance but activity, so that our conclusions on relative habitat use should be supported by population studies (e.g. on marked individuals). Additionally, vegetation can affect detection ranges, but we minimized this effect by facing detectors into forest gaps or along tracks (Law & Chidel 2002; Patriquin & Barclay 2003). Lastly, we used light traps to sample insect prey, but their efficacy varies between taxa (Bowden 1982), sampling only taxa attracted to light. Thus, our results represent a portion of the overall insect community available to bats.

### IMPACT OF LOGGING ON ACTIVITY OF BATS

Overall bat activity and feeding buzzes were 47% and 45% higher in old regrowth than young regrowth and logged forest, respectively, suggesting that bats foraged more in old regrowth sites. This result was driven by *Vespadelus regulus* and *Nyctophilus* spp. activity, as these species dominated the community. *Nyctophilus* spp. was only affected by logging history in 2008, although why their response differed between years is unknown. Previous studies have demonstrated lower bat activity in cluttered regrowth forest compared with more open, unlogged forests (e.g. Brown, Nelson & Cherry 1997; Menzel *et al.* 2002). Indeed, a negative relationship with understorey clutter was the most consistent predictor of total bat activity in our study, indicating that low bat activity in young regrowth and logged forest was probably related to high understorey clutter at these sites, which probably both interferes with ultrasonic signals and reduces access to prey items (Rainho, Augusto & Palmeirim 2010).

One major finding was that on-track locations had similar activity levels and feeding buzzes across logging histories, suggesting tracks provide suitable commuting and foraging habitat for bats within logged forests. This is consistent with data from eastern Australia, where similar bat activity levels were reported on tracks through regrowth and old growth (Law & Chidel 2002; Lloyd, Law & Goldingay 2006). Tracks cutting through young regrowth create internal edges, allowing bats greater access to sections of young regrowth forest. Although tracks represented a small portion of the landscape (*c.* 1%), which limits the area that bats can access, the high number of feeding buzzes on-tracks, compared to off-track sites, in young regrowth suggests that tracks were important in making sections of otherwise unsuitable habitat available for foraging. Our results add to studies demonstrating that tracks traversing logged forests are used by many bat species (Law & Chidel 2002; Lloyd, Law & Goldingay 2006) and emphasize the importance of linear elements, including tracks (e.g. Menzel *et al.* 2002; Adams, Law & French 2009), hedgerows (Walsh & Harris 1996), riparian creeklines (Lloyd, Law & Goldingay 2006) and coupe edges after logging (Morris, Miller & Kalcounis-Rüppell 2010), to bats. Furthermore, some radiotracking studies have demonstrated that some species roost and forage in regrowth forest (e.g. Law & Anderson 2000).

We found that neither insect biomass nor the interaction effects of vegetation clutter and insect biomass significantly affected bat activity. This suggests that food availability, at least in terms of sampled insect biomass, did not affect bat activity over the range of vegetation clutter sampled. This contrasts with studies which found positive correlations between bat activity and insect abundance (e.g. Hayes 1997) or correlations only where vegetation was relatively open (Adams, Law & French 2009). However, these studies are not directly comparable as they either did not consider temperature as a factor influencing bat and insect activity, or sampled insect abundance using light traps concurrently with bat sampling (Adams, Law & French 2005). Adams, Law & French (2005) sampled insects on- and off-tracks whereas we only sampled off-tracks and so vegetation may have been too cluttered for bats to exhibit higher activity where insects were more common. Thus, although our study indicated that food resources did not explain differences in bat activity, it is unclear whether this lack of agreement with other studies is real or due to methodological differences.

In addition to lower clutter, many bats preferentially roost in mature forests with abundant hollow-bearing trees (e.g. Kalcounis-Rüppell, Psyllakis & Brigham 2005), which could explain high bat activity in old regrowth forest in this study. Furthermore, many temperate tree-roosting bats switch roosts often (e.g. Willis & Brigham 2004) and bats typically roost in different trees within the same general area (e.g. Brigham *et al.* 1997; Cryan, Bogan & Yanega 2001). A concurrent radiotelemetry study revealed that bats preferred roosting in older forest (Webala *et al.* 2010), therefore, although bats may take advantage of greater foraging opportunities at off-track sites in old regrowth, many bat species also roost there (Kunz & Lumsden 2003).

### IMPACTS OF LOGGING ON INDIVIDUAL SPECIES

Different bat species respond differently to logging and resulting changes in vegetation structure (e.g. Law & Chidel 2001), depending on morphology and plasticity in foraging behaviour (Bullen & McKenzie 2001). Species with low aspect ratios are more manoeuvrable than those with high aspect ratios, which forage exclusively in open habitats because they cannot negotiate cluttered habitats (Humes, Hayes & Collopy 1999). With differing aspect ratios among jarrah forest bats, we recorded a range of responses to logging. Logging history significantly affected *V. regulus* and *Nyctophilus* spp. activity, with activity for both greater in old regrowth than other logging histories. Law & Chidel (2001) reported similar findings for *V. regulus* in New South Wales, Australia, with highest activity in unlogged forests. With a moderate aspect ratio (Fullard *et al.* 1991), and relatively high flight speeds, *V. regulus* is a clutter-sensitive species which cannot forage efficiently in highly cluttered regrowth. Indeed, the understorey clutter index explained significant amounts of variation in *V. regulus* activity, suggesting that clutter negatively affected its off-track activity. Conversely, *V. regulus* activity on-tracks did not differ among logging histories, underscoring the importance of tracks as an ameliorative measure in regrowth forest for less manoeuvrable species (Law & Chidel 2002).

Our finding of highest *Nyctophilus* spp. activity in old regrowth in 2008 contrasts with Law & Chidel (2001, 2002) who reported similar *N. gouldi* activity in cluttered regrowth and unlogged forest. *Nyctophilus* species have low aspect ratios and wing loadings, lower than other species in south-western Australia, allowing slow flight and high manoeuvrability (Fullard *et al.* 1991) so they should be the most clutter-tolerant species. Thus, activity was expected to be higher off-track, compared with on-track locations, not lower as we found. This most parsimonious explanation is that post-logging jarrah forest regrowth is more cluttered than the forests studied in New South Wales. High *Nyctophilus* activity on-track, nonetheless, supports previous observations that such 'clutter-tolerant' bats are not confined to cluttered areas for foraging, but routinely use open habitats as well (e.g. Schnitzler & Kalko 2001).

As predicted from ecomorphology, larger species (*C. morio*, *C. gouldii*, *F. mackenziei*) generally avoided regrowth and were more active on-tracks. With high aspect ratios and wing loadings, *Tadarida australis* and *Mormopterus* species 4 are the most clutter-sensitive south-western Australian bats (Fullard *et al.* 1991), and probably avoided clutter by only utilizing open areas. These fast-flying molossids were recorded infrequently on-track and most probably flew above the canopy. However, as ground-based Anabat detectors can readily pick up molossid calls from above the canopy (Herr & Klomp 1997), we suggest that these bats occur in low numbers at our forest sites.

### SYNTHESIS AND APPLICATIONS

We found that old regrowth provided better quality habitat than other logging histories, leading to higher overall and foraging bat activity. Conversely, young regrowth forest recorded the least bat activity and appeared to provide less suitable habitat for many bat species. Since 1985, logging practices in jarrah eucalypt forests have changed to employ selective logging methods as a more ecologically sustainable operation. Current management practices seek to achieve overstorey structural diversity at operational and landscape scales through the establishment of formal and informal reserves and retention of habitat elements in harvesting operations (Conservation Commission of Western Australia 2004). Our study demonstrated that tracks have some potential in ameliorating logging impacts on bats. However, unlogged buffers, compared to forest tracks, constitute a much greater proportion of the jarrah forest landscape, and appeared better at ameliorating logging impacts on bats. Unlogged buffers provided multiple roosting opportunities for bats because they contained higher densities of hollow-bearing trees than post-logging forests (Webala *et al.* 2010) and also provided forests with low or moderate clutter that appeared to be high quality foraging habitat. With *c.* 39% of the study area permanently closed to logging, these measures should increase the availability of open spaces and edges required by many foraging bat species (Law & Chidel 2002), as well as provide roost trees (Lunney *et al.* 1988; Brigham *et al.* 1997). However, the amount of unlogged area that needs to be retained for bat population persistence requires further research. In summary, we believe that the retention of unlogged areas within logged landscapes provides the best solution to maintaining bat populations in production forests and is likely to be the most important strategy in achieving ecologically sustainable forest management for bats in many forest ecosystems.

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