David B. Lindenmayer, Mason Crane, Megan C. Evans, Martine Maron, Philip Gibbons, Sarah Bekessy, Wade Blanchard (2017) The anatomy of a failed offset. *Biological Conservation*, Vol. 210, Pp 286-292.

DOI: https://doi.org/10.1016/j.biocon.2017.04.022

© 2017. This manuscript version is made available under the CC-BY-NC-ND 4.0 license <u>http://creativecommons.org/licenses/by-nc-nd/4.0/</u>

3 The anatomy of a failed offset

4

1

2

5	David Lindenmayer ^{1, 2} , Mason Crane ^{1, 2} , Megan C. Evans ³ , Martine Maron ³ , Philip Gibbons ² ,
6	Sarah Bekessy ⁴ , and Wade Blanchard ¹

7

¹National Environmental Science Program, Threatened Species Recovery Hub, Fenner

- 9 School of Environment and Society, The Australian National University, Canberra, ACT
- 10 2601, Australia
- ¹¹ ²Fenner School of Environment and Society, The Australian National University, Canberra,
- 12 ACT 2601, Australia
- ¹³ ³School of Earth and Environmental Sciences, The University of Queensland, Brisbane,
- 14 Queensland 4072, Australia
- ⁴School of Global Studies, Social Science and Planning, RMIT University, GPO Box 2476,
- 16 Melbourne 3001, Australia
- 17
- 18 Corresponding author: David Lindenmayer, Fenner School of Environment and Society, 141
- 19 Linnaeus Way, The Australian National University, Canberra, ACT 2601, Australia.
- 20 <u>david.lindenmayer@anu.edu.au</u>
- 21
- 22 Word Count: 7714 words (excluding table and appendices)

23 Abstract

Biodiversity offsetting is widely applied but its effectiveness is rarely assessed. We evaluated 24 the effectiveness of a nest box program intended to offset clearing of hollow-bearing trees 25 associated with a freeway the upgrade in southern Australia. The offset targeted three 26 threatened vertebrates: squirrel glider (Petaurus norfolcensis), brown treecreeper 27 (Climacteris picumnus) and superb parrot (Polytelis swainsonii). Clearing led to the loss of 28 587 tree hollows and the offset was the placement of an equivalent number of nest boxes in 29 nearby woodland (1:1 ratio). Of these, we monitored 324 nest boxes in six sample periods 30 31 between 2010 and 2013, yielding 2485 individual checks of nest boxes. For the three target species, we found: (1) no records of nest box use by the superb parrot, (2) 32 two records of the Brown Treecreeper (0-0.76% of accessible nest boxes used per survey 33 34 period), and (3) seven records of use of nest boxes by the Squirrel Glider (0-2.1% of accessible nest boxes used per survey period). Rates of nest box use by the Superb Parrot and 35 Squirrel Glider were markedly lower than rates of use of hollow-bearing trees observed in 36 other investigations. Low levels of use by target species coupled with the extent of nest box 37 attrition suggest the offset program will not have counterbalanced the loss of the hollow-38 bearing trees. 39 We make suggestions for improving future offset programs including a greater emphasis on: 40 (1) avoiding impacts on hollow-bearing trees; (2) offset effectiveness as a measure of 41 42 compliance; and (3) using realistic offset ratios. 43 Keywords: Nest boxes; cavity-dependent species; south-eastern Australia; tree hollows; 44

45 vegetation clearing; endangered box gum grassy woodland.

46

47

1. Introduction

Biodiversity offsetting is a widely used approach that attempts to mitigate the impacts of human activities on biodiversity (Maron et al. 2016). It involves generating conservation benefits in one area that aim to compensate for the impacts of a given form of development in another area. However, the large and rapidly increasing literature on offsets is highlighting potential problems with offsetting, such as the relatively narrow range of impacts on biodiversity that can be offset (e.g. Gibbons and Lindenmayer 2007; Maron et al. 2015b; Gibbons et al. 2016; Maron et al. 2016).

55 One major deficiency in much of the work on offsets is that their effectiveness is rarely subject to empirical assessment after implementation (Tischew et al. 2010; Bull et al. 56 2013) (but see Pickett et al. 2013)). The loss of some kinds of natural assets can be 57 58 particularly difficult to offset and hence particularly important to evaluate post-hoc. An example is large old trees which can take a long time to develop and which have a range of 59 key characteristics not found in small young trees, small old trees or large young trees 60 (Lindenmayer and Laurance 2016). Cavities or hollows are a critical characteristic of large 61 old trees and they are an important nesting and denning resource for a wide range of species 62 in many ecosystems globally (Fischer and McClelland 1983; Remm and Lohmus 2011). 63 Populations of large old trees with hollows are declining in a wide range of forest, savanna, 64 agricultural and urban environments around the world, often as a result of logging, land 65 66 clearing or other destructive activities (Lindenmayer and Laurance 2016). Offsetting is sometimes used in an attempt to mitigate the effects of the loss of large old trees with 67 hollows, particularly through the establishment of nest boxes to replace the cavity provision 68 69 role of these trees. However, empirical assessments of the efficacy of such offsets programs are lacking, particularly at large spatial scales. 70

Here we address this knowledge gap through a four-year case study of an offset in 71 72 southern New South Wales, south-eastern Australia which entailed the establishment of nest boxes to compensate for losses of natural hollows due to the widening of Australia's most 73 74 heavily used interstate freeway, the Hume Highway. The Hume Highway links the nation's two largest cities (Sydney and Melbourne) and its expansion had multiple ecological impacts. 75 These included removal of habitat for hollow-dependent threatened species listed at the State 76 and National level, clearing of nationally endangered temperate box gum grassy woodland, 77 and removal of hollow-bearing trees (Australian Government Department of the 78 79 Environment, Water, Heritage and the Arts, 2010; NSW Government Department of Planning, 2010). Thousands of trees were cleared as part of the road widening, realignment 80 and construction, including many large old trees that play a range of key ecological roles 81 82 within box gum grassy woodland. One of the most important roles of large old trees is the provision of nesting and denning habitat for an array of cavity-dependent native vertebrates 83 (Manning et al. 2006; Lindenmayer et al. 2016b). Indeed, the loss of hollow bearing trees is 84 85 listed as a key threatening process under the New South Wales Threatened Species Conservation Act (1999) (NSW Office of Environment and Heritage 2007). In addition to the 86 impacts of establishing human infrastructure, populations of large old trees in box gum grassy 87 woodland are threatened by a range of other processes including (among others): livestock 88 grazing (Fischer et al. 2009), secondary salinity (Stirzaker et al. 2002), firewood collection 89 90 (Driscoll et al. 2000), and fire (Crane et al. 2016).

The establishment of nest boxes was one component of a broader biodiversity offset strategy implemented to satisfy legislative requirements under State and National environmental protection laws (Roads and Traffic Authority, 2010). Here, we focus on the nest box component of the offset strategy which was designed to compensate for the loss of tree hollows (Department of Environment and Climate Change Undated) (Department of Planning 2010). The loss of tree hollows was compensated at a ratio of 1:1, resulting in the
establishment of 587 nest boxes. Criteria for the design and installation of nest boxes
emphasized the need to establish a diversity of nest box types characterized by different
entrance sizes and internal volumes, and the need to monitor patterns of nest box use and
occupancy (Department of Environment and Climate Change Undated).

Evaluating the effectiveness of an offset requires an understanding of the baseline or 101 counterfactual scenario against which the outcomes delivered by the offset are judged (Maron 102 et al. 2015b). According to State policy at the time of this development, biodiversity offsets 103 104 implemented in New South Wales "should aim to result in a net improvement in biodiversity over time", and "enhancement of biodiversity in offset areas should be equal to or greater 105 than the loss in biodiversity from the impact site" (Department of Environment and Climate 106 107 Change 2008). This implies that the baseline is the biodiversity value at the impact site before clearing, although in practice, offsetting in New South Wales assumes a decline of 10% on 108 average over an unspecified time horizon (Maron et al. 2015a). The criteria used to guide the 109 installation of the nest boxes (Department of Environment and Climate Change Undated) 110 http://www.environment.nsw.gov.au/biodivoffsets/oehoffsetprincip.htm) states that: 111

112 *To ensure success, nest-boxes must provide suitable habitat until such time that* 113 *retained trees close to the alignment develop nest hollows and cavities to replace those that*

113 retained trees close to the diffiment develop hest honows and cavilies to replace those114 were lost.

From an ecological perspective, this means that the nest boxes must be effective for between 50 and 100 years after installation or until significant new nest hollows develop (Lindenmayer et al. 2009), and presumably provide "suitable habitat" equivalent to the amount and quality of habitat provided by tree hollows prior to clearing. However, research on nest boxes elsewhere in our study region suggest that occupancy of nest boxes by species of conservation concern is generally low (Lindenmayer et al. 2015).

A key part of the offset policy underpinning this project was to establish nest boxes for 121 three threatened taxa known to occur in box gum grassy woodland adjacent to where large 122 old scattered trees were being cleared (Department of Environment and Climate Change 123 2008). These were two birds: the brown treecreeper (*Climacteris picumnus*) and superb parrot 124 (Polytelis swainsonii), and the nocturnal marsupial, the squirrel glider (Petaurus 125 norfolcensis). Design criteria for these nest boxes were specified in various New South Wales 126 127 Government documents including Overton et al. (2013) and Department of Environment and Climate Change (2008). 128

129 Our first question in this investigation was: Are nest boxes an effective offset for clearing of hollow-bearing trees for the three species of conservation concern? There 130 were two components to this evaluation: are the nest boxes used by the target species at rates 131 similar to those expected by the lost tree hollows? And is it likely that the next boxes will 132 remain suitable for the duration that the lost tree hollows would have done? Although pre-133 clearing surveys of the impacted habitat were conducted (Abigroup 2010), these data were 134 not made available to us, and hence the occupancy of the lost tree hollows by the three 135 species of conservation concern (as well as other cavity-dependent fauna) at the impact sites 136 could not be known. To estimate the counterfactual (occupancy of natural tree hollows by the 137 species of conservation concern in the absence of tree clearing), we drew upon data from a 138 range of sources (see Section 2: Methods). At the outset of this investigation, we were 139 doubtful of the efficacy of the establishment of nest boxes as an effective offset. This was 140 because research on nest boxes elsewhere in our study region indicated a paucity of use by 141 species of conservation concern (Lindenmayer et al. 2015). 142

As part of conducting surveys of the nest boxes for the three species of conservation
concern, we also gathered data on nest box use by other cavity-dependent taxa. This enabled
us to address a second question: What are the overall levels of nest box use and by which

species? In answering this question and using data on covariate measures of nest boxes and
site-level characteristics, we also sought to quantify the factors influencing nest box use by
different species of cavity-dependent fauna.

149 **2.** Methods

150 2.1 Study area and kinds of nest boxes installed

Our study area was temperate eucalypt box gum grassy woodland adjacent to the 151 Hume Highway between the towns of Coolac and Holbrook in southern New South Wales. 152 Areas of remnant native woodland and scattered hollow-bearing trees were cleared to 153 154 accommodate the widening of the Hume Highway. The cleared trees were estimated to support 587 hollows and the corresponding offset was the establishment of 587 nest boxes. 155 These were of varying dimensions to offset the loss of a range of types of hollows, although 156 157 the offset did not attempt to compensate for the other habitat values of the trees that were cleared. Of the 587 nest boxes, 263 could not be monitored for occupational health and safety 158 reasons such as being installed very close to the Hume Highway. We monitored the 159 remaining 324 nest boxes between 2010 and 2013 and of these, 83 were designed specifically 160 for squirrel glider, 77 for the brown treecreeper, and 37 for the superb parrot (see Appendix A 161 for design details of each box type). Other kinds of nest boxes monitored were those for bats 162 (62 boxes), the common brushtail possum Trichosurus vulpecula (42 boxes), the common 163 ringtail possum *Pseudocheirus peregrinus* (13 boxes) and large birds (10 boxes). 164 165 We inspected nest boxes in the spring of 2010, 2011, 2012 and 2013 and summer of 2011 and 2012, yielding 2485 individual checks of nest boxes over the four-year duration of 166 the study. During each survey, we recorded both animal presence and other signs of use such 167 168 as scats, hair, feathers and nests. Where there was uncertainty in identifying species from the

169 evidence of nest box use, we sent samples of scats and hair to an expert for formal

identification. In addition to identifying which species used the nest boxes, we also recorded

whether nest boxes were functional (e.g. if they had fallen to the ground) and were thereforecapable of being occupied or indeed in some cases whether the box was still present at all.

173 2.2 Baseline data for the counterfactual scenario and the evaluation of offset

174 effectiveness

The counterfactual scenario for assessing the effectiveness of nest boxes as an offset 175 demanded quantifying the occupancy of natural tree hollows by the three target species of 176 conservation concern in the absence of tree clearing. The absence of pre-clearing survey data 177 from the impacted sites meant that occupancy rates for the brown treecreeper, squirrel glider 178 179 and superb parrot prior to the clearing of hollow-bearing trees and the establishment of the offset was not known. We therefore estimated the counterfactual scenario by drawing on data 180 from a range of other sources. Our first dataset for estimating the counterfactual scenario was 181 182 derived from a matched case-control study of nest trees occupied by the superb parrot in box gum grassy woodland (Crane et al. 2010), including the areas where this investigation was 183 located (Manning 2004; Manning et al. 2013). That study identified 136 occupied nest trees 184 from a sample population of 2857 large old hollow-bearing trees located in 513 50 x 20m 185 plots. These data equate to 4.7% occupancy of trees with natural cavities by the superb parrot 186 during the breeding season for the species. 187

Our second dataset for analyzing the counterfactual scenario was a radio-tracking 188 study of den use by the squirrel glider within box gum grassy woodland in the broader study 189 190 area (Crane et al. 2008; Crane et al. 2010; Crane et al. 2012). That study showed that individuals may use between 2-13 hollow-bearing trees as den and nest sites and swap 191 regularly between these trees from day to day (Crane et al. 2010). The average denning range 192 of the species in our study region (i.e. the area encompassed by the suite of nest trees used by 193 an individual) is 3.6 ha (Crane et al. 2010). Approximately one in every ten of the old, large 194 diameter hollow-bearing trees within a denning range was occupied by the species in a year, 195

although most individuals have a primary and secondary den site used most frequently withother trees used less often (M. Crane, Lindenmayer and Cunningham unpublished data).

To the best of our knowledge, there have been no investigations specifically targeting the rates of occupancy of natural cavities in trees by the brown treecreeper in our study region. Other studies have indicated that the brown treecreeper uses a variety of kinds of hollows for nesting, but primarily exploits dead branches, spouts, tree trunks and fallen logs (Higgins et al. 2001). The species is also known to use nest boxes (Higgins et al. 2001).

For nest boxes to be effective, the species targeted by such programs need to occur in 203 204 the surrounding landscape so that animals can occupy them. Examinations of threatened species profiles developed by the New South Wales Office of Environment and Heritage 205 (2017) confirmed that the offset sites occurred within the known ranges of all three species 206 207 targeted in this study. This corroborated data from our field surveys of the three target species in the region based on spotlighting for arboreal marsupials and point interval counts for birds 208 completed in 2011 and 2013 at 68 long-term field sites within 10 km of where nest boxes had 209 been established (see Lindenmayer et al. 2016a; Lindenmayer et al. 2016c). 210

211 2.3 Estimated costs of the nest box offset program

We compiled information from the New South Wales Roads and Maritime Services on the range of costs (in 2010 Australian dollars) associated with the establishment of the nest box offset program. These included pre-establishment strategic planning, nest box construction, and post-establishment monitoring.

216 **3**.

Data exploration and analyses

217 3.1 Comparison with the counterfactual scenario

218 To answer our first question (<u>Are nest boxes an effective offset for clearing of</u>

219 hollow-bearing trees for the three species of conservation concern?), we compared rates

of use of nest boxes attached to trees by each of the species of conservation concern with the

rates of occupancy of natural hollows in trees from studies outside the areas subject to
clearing for highway upgrading (superb parrot and squirrel glider). Equivalent data for the
brown treecreeper were unavailable. For these comparisons, we included only boxes with an
entrance large enough to permit entry for a given species. Data on the 62 bat boxes (that have
a small entrance) were removed for all three target species of conservation concern. For the
squirrel glider and the superb parrot, we also removed data on the 77 nest boxes designed for
the brown treecreeper.

228 **3.2** Overall patterns of use

229 To answer our second question (What are the overall levels of nest box use and by which species?), we employed Bayesian binary logistic regression modelling to analyse 230 factors influencing nest box use by the following two groups of animals. These groups were: 231 232 (1) mammals (black rat, brush-tailed phascogale, common brushtail possum, common ringtail possum, Gould's wattled bat, house mouse, sugar glider, squirrel glider, yellow-footed 233 antechinus, and unknown glider, unknown possum); and (2) birds (brown treecreeper, 234 common starling, crimson rosella, eastern rosella, grey shrike-thrush, white-throated 235 treecreeper, unknown bird and unknown rosella). We also modelled the five individual 236 species with sufficient presence data to facilitate further analysis (black rat, common 237 brushtail possum, common ringtail possum, yellow-footed antechinus and feral honeybees). 238 To quantify the factors influencing nest box use, we modelled the effects of the 239

following covariates: survey occasion (spring 2010, spring 2011, summer 2011, spring 2012, summer 2012 and spring 2013); number of paddock trees within 500 metres; nest box type (brown treecreeper, squirrel glider, superb parrot, bat, common brushtail possum, common ringtail possum and large bird); the diameter of the tree to which a nest box was attached; dieback score for the tree to which a nest box was attached; and distance to closest major patch of native woodland vegetation. In addition, for an area of 1 ha around each nest box, we measured or calculated values for: the total number of stems in the surrounding vegetation;
number of trees greater than 50cm in height; number of hollow bearing trees greater than
50m; topographic wetness index (TWI); and lithology fertility rating.

The response variable for all analyses was the presence/absence of the species or 249 species group of interest which we modelled using a Bayesian logistic regression with a 250 random effect for site. We chose uninformative but proper priors for the fixed effects 251 components and minimally informative but proper priors for the variance components of our 252 models. Specifically, we used Student t-distributions for the regression parameters to 253 254 minimize the effects of complete separation. We used a default prior for the random effect standard deviation (site). We summarized the logistic regression model parameters by the 255 posterior mean and 95% credible intervals. We conducted the analysis using the brms 256 257 package (Buerkner 2015) in R version 3.2.1 (R Core Team 2015) using the RStudio interface (RStudio Team 2015). 258

259 **4. Results**

4.1 Are nest boxes an effective offset for clearing of hollow-bearing trees for species of conservation concern?

We found limited or no use of nest boxes by the three species of conservation concern 262 targeted by the offsets program, including in the boxes specifically established for them. We 263 recorded no cases of nest box use by the superb parrot, including boxes specifically designed 264 265 for the species (Table 1). This contrasts with the values from the studies by (Manning 2004; Manning et al. 2013) showing that 4.7% of hollow-bearing trees were used as nest sites by 266 the superb parrot (Fig. 1). That is, our results suggested that nest boxes are not a suitable 267 method for offsetting the loss of nest sites for this species. The superb parrot was detected at 268 2% of sites surveyed in 2011 and 13% of sites in 2013 that were located near the offset 269 impact areas. 270

Of all 324 nest boxes observed in this study, seven were used by the squirrel glider 271 across the four-year duration of our study, with the percentage use of nest boxes ranging from 272 zero to 0.6% of nest boxes per survey period (Table 1). Of the 185 nest boxes considered 273 accessible to the squirrel glider, percentage use values ranged from 0% to 2.1% per survey 274 period. Only one of the seven records of nest box use by the squirrel glider was in a box 275 specifically designed for the species. Rates of nest box use were lower than those recorded 276 for old, large diameter hollow-bearing trees within the denning range of a given individual in 277 a comparable survey period (approximately 10%) (Crane et al. 2010) (Crane et al., 278 279 Lindenmayer and Cunningham unpublished data). Other things being equal, to offset the loss of nesting sites for this species, at least five trees with suitable nest boxes are required for 280 every one hollow-bearing tree destroyed. The proportion of long-term sites near the offset 281 282 impact areas in which the squirrel glider was detected ranged from 1% in 2011 to 6% in 2013 (Fig. 1). 283

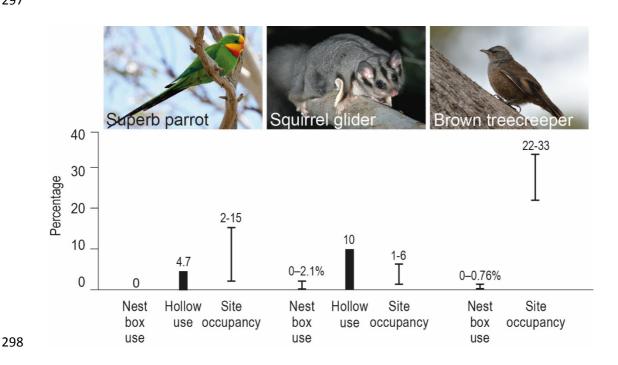
We recorded the brown treecreeper using two nest boxes in one survey period (0.6% of nest boxes in spring 2010; see Table 1). Neither of the two records of the brown treecreeper were from a box designed for the species. After removing nest boxes inaccessible to the brown treecreeper, percentage use values ranged from 0% to 0.76% per survey period. The brown treecreeper was present at 22 and 33% of long-term sites that we surveyed in 2011 and 2013, respectively (Fig. 1).

290

Fig. 1. Percentage rates of nest box use by each of the species of conservation concern
(denoted nest box use), rates of use of large old hollow-bearing trees from studies outside the
areas subject to clearing for highway upgrading (for superb parrot and squirrel glider only)
(denoted hollow use), and the proportion of long-term sites where each of the three target

species had been recorded between 2010 and 2013 (denoted site occupancy). Data on nest 295 box use excludes boxes with an entrance too small to permit entry of a given species. 296

297





4.2 What are the overall levels of use of the nest boxes and by which species? 300

Over the four-year duration of our study and for a given survey period, between 301 44.7% and 65.1% of nest boxes contained an animal or showed signs of use (Table 1). We 302 recorded 17 species occupying the 324 nest boxes, of which four were exotic species: the 303 feral honeybee, black rat, house mouse and common starling. The most commonly recorded 304 305 species were the yellow-footed antechinus, with usage rates varying between survey periods from 12.0-13.7%, the common brushtail possum (11.0-11.4%), feral honeybee (7.0-11.4%), 306 black rat (4.2-13.5%), common ringtail possum ((2.6%-5.7%), and common starling (0.6-307 2.5%) (Table 1). 308

309

Table 1: Percentage of nest boxes where evidence of use was recorded over four years of

311 monitoring. Exotic species are marked with an asterisk*.

Common name	Scientific	2010	2010 2011			2012	
	name						
		Spring	Spring	Summer	Spring	Summer	Spring
Black rat*	Rattus rattus	4.2	13.6	4.3	7.8	10.8	5.1
Brown	Climacteris	0.6	0	0	0	0	0
treecreeper	picumnus						
Brush-tailed	Phascogale	0.3	0	0.6	0.3	0.3	0.7
phascogale	tapoatafa						
Common	Trichosurus	11.5	11.4	11.4	13.1	10.5	11.1
brushtail possum	vulpecula						
Common ringtail	Pseudocheirus	2.6	6.5	4.0	5.9	4.3	5.7
possum	peregrinus						
Common	Sturnus	0.6	2.5	1.9	0.7	1.6	1.4
starling*	vulgaris						
Crimson rosella	Platycercus	1.3	0.6	0.3	0	0	0.7
	elegans						
Eastern rosella	Platycercus	0.3	0.3	0	0	0	0.3
	eximius						
Feral honeybee*	Apis mellifera	7.0	11.7	11.4	7.8	8.2	8.1
Goanna	Varanus varius	0.3	0	0	0.3	0	0
Gould's wattled	Chalinolobus	0.3	0.3	0.3	0	0.7	0
bat	gouldii						
Grey shrike-	Colluricincla	0	0.6	0.3	0	0	0
thrush	harmonica						
House mouse*	Mus musculus	0	1.5	0	0	0.9	0

Marbled gecko	Christinus	0	0.6	0.3	0.3	0	0.3
	marmoratus						
Peron's tree frog	Litoria peronii	0	0	0.3	0.3	0.7	0
Squirrel glider	Petaurus	0.6	0.3	0	0.3	0.7	0.3
	norfolcensis						
Sugar glider	Petaurus	0.9	0.3	0.6	0.9	0.3	0.3
	breviceps						
Unknown animal	Unknown	0	0	0	0.3	0	0
	Animal						
Unknown bird	Unknown Bird	0	0	0	2.3	0.7	0.3
Unknown glider	Unknown	0	0.6	0.6	0.7	0.7	3.0
	Glider						
Unknown	Unknown	0	0	0	1.3	0	0
possum	Possum						
Unknown rosella	Unknown	0	0	0	0.3	0.3	0
	Rosella						
White-throated	Cormobates	0.3	2.2	0.6	1.6	0.3	0.7
treecreeper	leucophaea						
Yellow-footed	Antechinus	13.7	12.0	13.3	13.1	13.1	12.5
antechinus	flavipes						
Any	Any	44.7	65.1	50.3	57.4	54.1	50.5
Number of		313	324	324	305	305	297
boxes surveyed							

312

313 4.3 What factors influenced nest box use?

We constructed Bayesian logistic regression models of the factors influencing the use of nest boxes by the five most commonly recorded species and for which there were

sufficient data to facilitate statistical analyses (the yellow-footed antechinus, common 316 brushtail possum, common ringtail possum, black rat and feral honeybee) (Appendix B). Nest 317 box design was a significant factor in all of the final models with marked, inter-specific 318 differences in the kinds of boxes used by different species (Appendix B). There was a 319 positive effect of the diameter of the tree to which a nest box was attached in the model for 320 the common ringtail possum but a negative effect for the black rat. The models for the 321 yellow-footed antechinus and the feral honeybee contained evidence of a positive relationship 322 between nest box use and the number of stems in the vegetation characterizing the 323 324 surrounding landscape. There also was evidence of season and/or year differences in the proportion of nest boxes used by the common ringtail possum, black rat and feral honeybee. 325 Other significant covariates in the models we constructed included an effect of the 326 327 underlying lithology and topographic wetness of the sites where nest boxes were established (Appendix B). The feral honeybee more often used nest boxes in locations where there was a 328 high value for the topographic wetness index whereas the reverse effect characterized the 329 model for the common ringtail possum (Appendix B). 330

331 4.4 Nest box attrition

Approximately 8.3% (27/324) of nest boxes became ineffective for use during the four years of our study. There were several reasons for nest box failure with the two most prominent being boxes falling from trees (14 boxes), and presumed theft (7 boxes).

335 4.5 Estimated costs of the nest box offset program

The development of a plan for subsequent nest box establishment cost AU\$50,000. The cost of construction was AU\$200 per nest box or a total of AU\$64,800. The cost of installation was AU\$262 per box or AU\$84,888 in total. Monitoring of the 324 nest boxes was completed by The Australian National University under contract with the New South Wales Department of Roads and Maritime Services at a total cost of AU\$64,000 or approximately AU\$197.50 per box for each of six survey periods (or \$33.90 per box per
survey period). That is, the total cost of establishing and monitoring nest boxes under this
offset program was AU\$199,688.

344 **5. Discussion**

The use of offsets in conservation and environmental management is widespread 345 globally (Gibbons et al. 2016; Maron et al. 2016) and is rapidly increasing (Ives and Bekessy 346 2015), but the effectiveness of such an approach has rarely been subject to empirical 347 assessment, particularly after an offset has been implemented (Pickett et al. 2013; May et al. 348 349 2016). We addressed this knowledge gap in the study reported here on the use of nest boxes designed to offset the clearing of hollow bearing trees as part of the widening of a major 350 highway in rural Australia. Our analyses revealed that the nest box strategy examined here 351 352 was not sufficient to offset impacts of development on the availability of nesting sites for at least two of the target species of conservation concern (i.e. squirrel glider, superb parrot), but 353 had greater utility as a method to offset the loss of nesting sites for common species. In the 354 remainder of this paper we further discuss these sobering results. We conclude with 355 suggestions for improving future offset programs. 356

357

5.1 Limited nest box use by target threatened species

The key finding from our empirical study was the relative paucity of records of use of 358 nest boxes by target species of conservation concern (or complete absence in the case of the 359 superb parrot) (Fig. 1). The low rates of use of trees with nest boxes relative to usage patterns 360 of hollow-bearing trees in other investigations in nearby areas, coupled with the occurrence 361 of the three species in the general area where nest boxes were established, has demonstrated 362 that the offset for these animals has largely failed. Our results are similar to those of Le Roux 363 et al. (2016) whose research in the same broad ecological community reported slightly higher 364 overall occupancy rates, but zero occupancy by threatened species (including the superb 365

parrot) and domination of nest boxes by common or exotic species. However, some of our 366 results showing low levels of occupancy for species of conservation concern differ from 367 those of other researchers who have found that nest boxes specifically designed for particular 368 taxa can support populations of those species (Goldingay et al. 2015), including the squirrel 369 glider that was targeted in our study. The reasons for the differences between studies remain 370 unclear. A possible explanation for the differences between studies may have been associated 371 with the quality of work undertaken by private contractors to install nest boxes. In particular, 372 the boxes were often were poorly attached to small diameter trees (so that the mounting 373 374 brackets and the box were unstable). This problem may have not only contributed to reduced levels of occupancy but also contributed to the attrition of more than 8% of the nest boxes 375 over the duration of our study. An additional explanation may be that other studies such as 376 377 that by Goldingay et al. (2015) were undertaken in areas where the abundance of hollowbearing trees was limited and/or the population density of the species greater, and hence rates 378 of nest box occupancy may be expected to be relatively high. The duration of our study was 379 four years and it is possible that we may have achieved high rates of nest box occupancy over 380 a more prolonged period. However, other longer-running studies (Lindenmayer et al., 2015; 381 Crane et al., unpublished data), also have met with limited or no success for the species of 382 conservation concern targeted in this study. Moreover, all of the target species occur within 383 or very close to where the nest boxes were established. Both these factors suggest that a 384 385 longer study may not have met with more success than we have reported here.

386 5.2

5.2 Overall patterns of nest box use and factors influencing use

We found that the most common species of vertebrates using the nest boxes were species that are relatively common in woodland landscapes (the yellow-footed antechinus, common brushtail possum and common ringtail possum) and/or were exotic species (the feral honeybee, black rat and common starling) (Table 1). Statistical models of the factors affecting nest box occupancy for the five most commonly recorded species (see Appendix B) typically included a combination of nest box characteristics, attributes of the site or landscape surrounding where the nest box was located, and environmental features of the location (such as topographic wetness index or underlying lithology). This underscores the importance of factors at multiple scales affecting the probability of nest box occupancy, ranging from those that corresponded to the individual nest box level, to site and landscape level features.

We found no evidence for a positive or negative effect on nest box occupancy of 397 variables such as the number of large old paddock trees in the surrounding landscape nor the 398 399 number of hollow-bearing trees within 50 metres of a nest box (Appendix B). There also was no evidence of significant effects of dieback of trees in the surrounding vegetation on nest 400 box occupancy (Appendix B). The reasons for the lack of influence of these variables remain 401 402 unclear. Paddock trees are often used for nesting and foraging by species such as the squirrel glider and superb parrot (Manning and Lindenmayer 2009; Crane et al. 2012) and at the 403 outset of the project we anticipated this variable may be important for the species in models 404 of nest box occupancy. It is possible that where such trees are prevalent, there is limited need 405 for animals to find shelter in nest boxes. 406

We found that nest boxes were sometimes occupied by species such as the black rat and common starling (Table 1), which are significant vertebrate pests in Australian agricultural landscapes. This has implications for offset policies because of the risks of perverse outcomes such as the potential to create nesting resources for pest species, including those that might compete with target species of conservation concern.

412 5.3 The anatomy of a failed offset and some recommendations for improvement

413 Several factors influenced the outcomes of the offset examined in this study. Whilst 414 the provision of nest boxes was well intentioned, we believe that future offset programs 415 might be more effective if key recommendations, outlined below, are taken into account.

First, the 1:1 offset ratio used to compensate tree hollows with nest boxes was 416 inadequate as it failed to account for the risk of offset failure (Maron et al. 2012; Miller et al. 417 2015; Gibbons et al. 2016). Although the time between impact and the installation of next 418 boxes was minimized (Department of Environment and Climate Change Undated) the low 419 usage rate of nest boxes we observed suggests a high offset ratio would be required to 420 achieve no net loss using this strategy. In the case of the squirrel glider and based on 421 comparable occupancy rates for natural cavities in hollow-bearing trees, multipliers of at least 422 five trees with a suitable nest box will be required to offset every one tree hollow that is 423 424 cleared. That is, there would need to be a substantially larger number of nest boxes installed than the number of hollow-bearing trees lost in a development project to provide a benefit 425 that counterbalances the loss of nesting hollows. However, nest boxes may not replace such 426 427 functions at all for some species like the superb parrot.

The relatively high rate of attrition of nest boxes may well mean that they are 428 rendered non-functional relatively soon after they are installed and hence well before the 429 cavity-provision role of large old trees (which experience a much lower rate of attrition than 430 nest boxes [see (Crane et al. 2016)], can be offset. This was known prior to the establishment 431 of the offset; the nest box criteria developed by the Department of Environment and Climate 432 Change (undated) stated that nest boxes were likely to deteriorate after 5-10 years and needed 433 to be checked twice yearly until cavities develop in trees in the surrounding vegetation 434 435 (typically when trees are 80-120 or more years old). Given this, we strongly suggest that a key part of offset policy must be to conduct due diligence on the likely effectiveness of a 436 given offset approach before it is undertaken. For example, this should include a detailed 437 prior assessment of previous work on the use of nest boxes by particular target species, 438 including they numbers and types of boxes that are occupied (if they are used at all) and 439 hence an appraisal of the likelihood of success (or failure) of such an offset strategy. 440

Until an effective, timely, and lasting offset for tree hollows can be demonstrated as 441 viable, we suggest that hollow-bearing trees should be treated as "red flag" attributes, 442 particularly where they support nesting sites for threatened and uncommon species, and 443 impacts avoided during developments. Where this is not feasible, we suggest that an offset 444 policy should include: (1) combined natural regeneration and/or establishment plantings of 445 restored woodland alongside guaranteed long-term nest box maintenance (i.e. repair or 446 regular replacement over many decades) until new cohorts of hollow-bearing trees are 447 recruited; (2) protection and management of areas containing mature trees that are under 448 449 threat from ongoing land uses; and (3) a suitable multiplier that accounts for the comparative low rate of use of nest boxes relative to occupancy of hollow-bearing trees (see above), 450 together with the long time lag between impact and offset delivery. 451

452 A substantial multiplier on the number of nest boxes required, coupled with a demand for long-term maintenance and regular replacement of nest boxes, means higher costs. 453 Therefore, cost effectiveness analysis should be considered when comparing potential options 454 for offsets. Indeed, the AU\$199,688 expended on the largely unsuccessful nest box offset 455 program examined here was manifestly inadequate given low levels of nest box use by target 456 species and high rates of attrition of nest boxes. An approximation of the cost of making this 457 offset effective is \$12.16 million dollars (in 2010 Australian dollars). This was based on the 458 cost of: (1) monitoring all boxes twice per year for 90 years; (2) the installation of five times 459 460 as many boxes as established in the current study; and (3) the replacement of each nest box three times over a period of 90 years. This cost estimate may seem high, but should be 461 considered in light of the risk of projects being delayed or halted if offset failure is identified 462 during project implementation. A costly example of this is the indefinite delay of a highway 463 widening project in the West of Victoria, driven in part by public backlash due to offset 464 failure (Shyling 2017). 465

It is important to highlight here that the conditions of approval required nest boxes to 466 be installed, but did not stipulate that the nest boxes must be effective (Department of 467 Planning 2010). Despite the ecological failure of the offset and the significant resources 468 invested, the proponent has complied with the relevant condition of approval and is unlikely 469 to be required to remedy the offset. This distinction between offset compliance and offset 470 effectiveness has been previously illustrated by May et al. (2016) and Sudol and Ambrose 471 (2002). At least in Australia, offset effectiveness is not a regulatory requirement unless 472 explicitly stated in conditions of approval. This failure in biodiversity offset governance 473 474 (Maron et al. 2016) has obvious implications for the pursuit of effective and efficient offsetting in practice. The Australian Government has produced a draft policy on outcomes-475 based conditions (Department of the Environment and Energy 2016) but at this stage, the use 476 477 of such conditions it is not mandatory. The global proliferation of offset policies indicates that offsets will continue to be used to compensate for biodiversity impacts resulting from 478 development (Bull et al. 2013; Maron et al. 2016). We therefore argue for: (1) proponents to 479 480 be required to demonstrate offset effectiveness; (2) clear lines of responsibility to be established for offset delivery, monitoring, evaluation and maintenance over the long term; 481 and (3) timely and transparent reporting of offset compliance and effectiveness to the public 482 (Maron et al. 2016; May et al. 2016). The risk, as in the example given in the previous 483 paragraph, is that public backlash will impact on projects, even if the regulatory system fails 484 485 to provide adequate guidance.

In this study, the offset for the clearing of hollow-bearing trees was the establishment of nest boxes. However, large old hollow-bearing trees have a wide range of ecological roles well beyond those of habitat provision for cavity-dependent fauna (Lindenmayer and Laurance 2016). For example, Le Roux et al. (2015) found that multiple small trees could not replicate the habitat provided by individual large trees for 29% of all bird species they observed. Indeed, hollows are but one component of habitat for many species with large old
hollow-bearing trees being important for foraging (e.g. for the squirrel glider (see Crane et al.
2012) and brown treecreeper (reviewed by Higgins et al. 2001). Nest boxes clearly cannot
offset these additional values and a wider range of actions will be needed to compensate for
the losses of these values when large old hollow-bearing trees are cleared.

Finally, the analyses reported here highlight the critical role of both: (1) baseline data 496 (which were not available in this study); and (2) post-implementation monitoring (see also 497 Pickett et al. 2013) for the effective evaluation of offsets. Despite the deficiencies in the 498 499 offset program reported here, it is nevertheless notable that the proponent supported both post-offset establishment monitoring as well as the reporting of the results of that monitoring. 500 Indeed, an important part of offset policy is to rigorously assess the effectiveness of the offset 501 502 with empirical data after it has been implemented. We strongly encourage the publication of outcomes of more offset monitoring programs, irrespective of the results. Indeed, several 503 authors have noted that more is often learned from conservation failures than conservation 504 successes (Redford and Taber 2000) and our hope is that this type of learning will inform the 505 design and role of offsetting into the future. 506

507 6. Acknowledgments

Funding: This work was supported by the New South Wales Roads and Transport 508 Authority (now Roads and Maritime Services). Claire Shepherd assisted with manuscript 509 510 preparation. This study was conducted under animal ethics permits approved by The Australian National University and the New South Wales Office of Environment and 511 Heritage. DL, SB and MM were supported by the National Environment Science Programme 512 513 Threatened Species Recovery Hub. We thank Barbara Triggs for expert analysis of hair and scats collected from nest boxes. Dr Devictor and Dr Lunney made useful comments that 514 improved an earlier version of the manuscript. 515

516 7. References

- Abigroup. 2010. Holbrook Hollow Bearing Tree Report. Terrabyte Services, Wagga,
 Australia.
- Buerkner, P.-C. 2015. brms: Bayesian Regression Models Using Stan. R package version
 0.9.1.
- Bull, J.W., Suttle, K.B., Gordon, A., Singh, N.J., Milner-Gulland, E.J. 2013. Biodiversity
 offsets in theory and practice. Oryx 47, 369–380.
- 523 Crane, M., Lindenmayer, D.B., Cunningham, R.B. 2010. The use of den trees by the squirrel
- 524 glider (Petaurus norfolcensis) in temperate Australian woodlands. Aust. J. Zool. 58, 39-49.
- 525 Crane, M., Lindenmayer, D.B., Cunningham, R.B., Stein, J. 2016. The effect of wildfire on
- ⁵²⁶ "keystone structures", in agricultural landscapes. Austral Ecol. doi:10.1111/aec.12414.
- 527 Crane, M., Montague-Drake, R.M., Cunningham, R.B., Lindenmayer, D.B. 2008. The
- 528 characteristics of den trees used by the Squirrel Glider (Petaurus norfolcensis) in temperate
- 529 Australian woodlands. Wildl. Res. 35, 663-675.
- 530 Crane, M.J., Lindenmayer, D.B., Cunningham, R.B. 2012. Use and characteristics of
- 531 nocturnal habitats of the squirrel glider (*Petaurus norfocensis*) in Australian temperate
- 532 woodlands. Aust. J. Zool. 60, 320-329.
- 533 Department of Environment and Climate Change. 2008. Principles for the Use of
- 534 Biodiversity Offsets in NSW. NSW Department of Environment and Climate Change,
- 535 Hurstville, Sydney.
- 536 Department of Environment and Climate Change. Undated. Hume Highway Duplication Nest
- 537 Box Criteria. Department of Environment and Climate Change, Sydney.
- 538 Department of Planning. 2010. Project approval 08_0138. Area west of Holbrook.
- 539 Department of Planning, Government of NSW, Sydney.

- 540 Department of the Environment and Energy. 2016. Outcomes-based conditions policy and541 guidance.
- 542 Driscoll, D., Milkovits, G., Freudenberger, D. 2000. Impact and use of firewood in Australia.
 543 CSIRO Sustainable Ecosystems Report. CSIRO, Canberra.
- 544 Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K., Forrester, R.I. 2009. Reversing a
- tree regeneration crisis in an endangered ecoregion. Proc. Natl. Acad. Sci. USA 106, 1038610391.
- 547 Fischer, W.C., McClelland, B.R. 1983. Cavity-nesting Bird Bibiography including Related
- 548 Titles on Forest Snags, Fire, Insects, Diseases and Decay. Intermountain Forest and Range
- 549 Experiment Station, Ogden, Utah.
- 550 Gibbons, P., Evans, M.C., Maron, M., Gordon, A., Le Roux, D., von Hase, A., Lindenmayer,
- 551 D.B., Possingham, H.P. 2016. A loss-gain calculator for biodiversity offsets and the
- circumstances in which no net loss is feasible. Conserv. Lett. 9, 252-259.
- Gibbons, P., Lindenmayer, D.B. 2007. Offsets for land clearing: No net loss or the tail
 wagging the dog? Ecol. Manage. Restor. 8, 26-31.
- 555 Goldingay, R.L., Rueegger, N.N., Grimson, M.J., Taylor, B.D. 2015. Specific nest box
- designs can improve habitat restoration for cavity-dependent arboreal mammals. Restor.
- 557 Ecol. 23, 482-490.
- 558 Higgins, P.J., Peter, J.M., Steele, W.K. 2001. Handbook of Australian, New Zealand and
- Antarctic Birds. Volume 5: Tyrant-flycatchers to Chats. Oxford University Press, Melbourne,
 Australia.
- Ives, C.M., Bekessy, S.A. 2015. The ethics of offsetting nature. Front. Ecol. Environ. 13,
 568-573.

- Le Roux, D., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D., Gibbons, P. 2016.
- 564 Effects of entrance size, tree size and landscape context on nest box occupancy:
- 565 Considerations for management and biodiversity offsets. Forest Ecol. Manage. 366, 135-142.
- Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D., Gibbons, P. 2015. Single large
- 567 or several small? Applying biogeographic principles to tree-level conservation and
- 568 biodiversity offsets. Biol. Conserv. 191, 558-566.
- 569 Lindenmayer, D.B., Crane, M., Blanchard, W., Okada, S., Montague-Drake, R. 2015. Do nest
- 570 boxes in restored woodlands promote the conservation of hollow-dependent fauna? Restor.
- 571 Ecol. 24, 244-251.
- 572 Lindenmayer, D.B., Lane, P.W., Barton, P.S., Crane, M., Ikin, K., Michael, D.R., Okada, S.
- 573 2016a. Long-term bird colonization and turnover in restored woodlands. Biodivers. Conserv.
- 574 25, 1587-1603.
- 575 Lindenmayer, D.B., Laurance, W. 2016. The ecology, distribution, conservation and
- 576 management of large old trees. Biol. Rev. doi:10.1111/brv.12290.
- 577 Lindenmayer, D.B., Michael, D., Crane, M., Okada, S., Florance, D., Barton, P., K., I. 2016b.
- 578 Wildlife Conservation in Farm Landscapes. CSIRO Publishing, Melbourne.
- 579 Lindenmayer, D.B., Mortelliti, A., Ikin, K., Pierson, J., Crane, M., Michael, D., Okada, S.
- 580 2016c. The vacant planting: limited influence of habitat restoration on patch colonization
- 581 patterns by arboreal marsupials in south-eastern Australia. Anim. Conserv.
- 582 doi:10.1111/acv.12316.
- 583 Lindenmayer, D.B., Welsh, A., Donnelly, C.F., Crane, M., Michael, D., MacGregor, C.,
- 584 McBurney, L., Montague-Drake, R.M., Gibbons, P. 2009. Are nest boxes a viable alternative
- source of cavities for hollow-dependent animals? Long-term monitoring of nest box
- occupancy, pest use and attrition. Biol. Conserv. 142, 33-42.

- 587 Manning, A.D. 2004. A Multi-scale Study of the Superb Parrot (*Polytelis Swainsonii*):
- Implications for Landscape-scale Ecological Restoration. The Australian National University,Canberra.
- 590 Manning, A.D., Fischer, J., Lindenmayer, D.B. 2006. Scattered trees are keystone structures -
- implications for conservation. Biol. Conserv. 132, 311-321.
- 592 Manning, A.D., Gibbons, P., Fischer, J., Oliver, D.L., Lindenmayer, D.B. 2013. Hollow
- futures? Tree decline, lag effects and hollow-dependent species. Anim. Conserv. 16, 395-403.
- 594 Manning, A.D., Lindenmayer, D.B. 2009. Paddock trees, parrots and agricultural production:
- 595 An urgent need for large-scale, long-term restoration in south-eastern Australia. Ecol.
- 596 Manage. Restor. 10, 126-135.
- Maron, M., Bull, J.W., Evans, M.C., Gordon, A. 2015a. Locking in loss: Baselines of decline
 in Australian biodiversity offset policies. Biol. Conserv. 192, 504-512.
- 599 Maron, M., Gordon, A., Possingham, H.P., Mackey, B.G., Watson, J. 2015b. Stop misuse of
- 600 biodiversity offsets. Nature 523, 401-403.
- Maron, M., Hobbs, R.J., Moilanen, A., Matthews, J.W., Christie, K., Gardner, T.A., Keith,
- D.A., Lindenmayer, D.B., McAlpine, C.A. 2012. Faustian bargains? Restoration realities in
- the context of biodiversity offset policies Biol. Conserv. 155, 141-148.
- Maron, M., Ives, C.D., Kujala, H., Bull, J.W., Maseyk, F.J., Bekessy, S., Gordon, A.,
- Watson, J.E., Lentini, P.E., Gibbons, P., Possingham, H.P., Hobbs, R.J., Keith, D.A., Wintle,
- B.A., Evans, M.C. 2016. Taming a wicked problem: Resolving controversies in biodiversity
- 607 offsetting. BioScience 66, 489-498.
- May, J., Hobbs, R.J., Valentine, L.E. 2016. Are offsets effective? An evaluation of recent
- environmental offsets in Western Australia. Biol. Conserv. 206, 249-257.

- 610 Miller, K.L., Trezise, J.A., Kraus, S., Dripps, K., Evans, M.C., Gibbons, P., Possingham,
- H.P., Maron, M. 2015. The development of the Australian environmental offsets policy:
- From theory to practice. Environ. Conserv. 42, 306-314.
- 613 NSW Office of Environment and Heritage. 2007. Loss of hollow-bearing trees key
- 614 threatening process determination. NSW Scientific Committee final determination.
- NSW Office of Environment and Heritage. 2017. Threatened species profile search.
- 616 http://www.environment.nsw.gov.au/threatenedspeciesapp/
- 617 Overton, J.M., Stephens, R.T.T., Ferrier, S. 2013. Net present biodiversity value and the
- design of biodiversity offsets. Ambio 42, 100-110.
- 619 Pickett, E.J., Stockwell, M.P., Bower, D.S., Garnham, J.I., Pollard, C.J., Clulow, J., Mahony,
- 620 M.J. 2013. Achieving no net loss in habitat offset of a threatened frog required high offset
- ratio and intensive monitoring. Biol. Conserv. 157, 156–162.
- 622 R Core Team. 2015. R: A Language and Environment for Statistical Computing. R
- 623 Foundation for Statistical Computing, Vienna, Austria.
- Redford, K., Taber, A. 2000. Writing the wrongs: developing a safe-fail culture in
- conservation. Conserv Biol 14, 1567-1568.
- Remm, J., Lohmus, A. 2011. Tree cavities in forests The broad distribution pattern of a
- 627 keystone structure for biodiversity. Forest Ecol. Manage. 262, 579-585.
- 628 RStudio Team. 2015. RStudio: Integrated Development for R. RStudio Inc., Boston,
- 629 Massachusetts.
- 630 Shyling, O. 2017. VicRoads confirms Western Highway work suspended. The Wimmera
- 631 Mail-Times. Fairfax Regional Media, http://www.mailtimes.com.au/story/4481972/vicroads-
- 632 confirms-western-highway-work-suspended/.

- 633 Stirzaker, R., Vertessey, R., Sarre, A., editors. 2002. Trees, Water and Salt. An Australian
- 634 Guide to Using Trees for Healthy Catchments and Productive Farms. Joint Venture
- 635 Agroforestry Program, Canberra.
- 636 Sudol, M.F., Ambrose, R.F. 2002. The US Clean Water Act and habitat replacement:
- evaluation of mitigation sites in Orange County, California, USA. Environ. Manage. 30, 727–
- 638 734.
- 639 Tischew, S., Baasch, A., Conrad, M.K., Kirmer, A. 2010. Evaluating restoration success of
- 640 frequently implemented compensation measures: results and demands for control procedures.
- 641 Restor. Ecol. 18, 467-480.