

1 **Hollow futures? Tree decline, lag effects and hollow-dependent species**

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45 **Short title:** Hollow futures?

46

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48 mortality, tree recruitment.

49

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51 **Abstract**

52 Tree hollows are a critical breeding resource for many organisms globally. Where
53 hollow-bearing trees are in decline, population limitation can be a serious
54 conservation issue. A particular problem in addressing hollow limitation is the long
55 time that hollows take to form. This means there can be a significant lag time between
56 detecting a species' population decline, and arresting the lack of hollows through
57 reducing tree mortality and increasing regeneration. Once underway, declines of
58 hollow-dependent species therefore can be difficult to halt. It is imperative that we
59 identify and anticipate such future problems before they occur, and implement
60 conservation action in advance. In this study, we use a novel application of an
61 established modelling method to explore this issue and illustrate an 'early warning'
62 approach, focusing on a case study of the vulnerable superb parrot (*Polytelis*
63 *swainsonii*) from south-eastern Australia. The species is dependent on hollow-bearing
64 trees for nesting that have a very long generation time (>120 years). Potential nest
65 trees for the superb parrot are on a trajectory of decline. We modelled the future
66 hollow resource for this species under different management scenarios including: (a)
67 business-as-usual – i.e. no further specific conservation action; (b) and (c) waiting
68 until considerable further reductions (90% and 70%) in hollows before implementing
69 conservation actions to replace hollow-bearing trees; and (d) implementing enhanced
70 conservation actions now to redress loss of hollows. We found that all scenarios
71 except (d) 'conservation action now', resulted in substantial declines in potential nest
72 trees, and came at significant opportunity cost in terms of reducing tree mortality and
73 increasing tree regeneration. Delaying conservation action will greatly increase the
74 long-term risk of extinction of hollow-dependent species. Predicting and slowing the
75 decline in available hollows by early by early intervention and restoration

76 management is critical, even if hollow-dependent species populations may appear to

77 be secure in the short-term.

78

79 **Introduction**

80 Tree hollows provide a critical breeding resource for many organisms
81 globally. For example, across Europe, North America, Southern Africa and Australia,
82 18% of birds use hollows for nesting, and 11% are obligate users (Newton, 1994). In
83 situations where tree populations are in decline, the associated reduction in hollow
84 availability has been associated with a decline in hollow-using species (Newton,
85 1994, Gibbons & Lindenmayer, 2002, Marsden & Pilgrim, 2003, Aitken & Martin,
86 2008, Heinsohn *et al.*, 2009).

87 Reversing the decline in hollow-bearing trees population is complicated by
88 ‘lag effects’. These describe the delay between initiation of actions to halt and reverse
89 tree decline, and the time needed for trees to be old and large enough to produce
90 suitable hollows (>120 years) (Manning *et al.*, 2004, Gibbons *et al.*, 2008). Lag
91 effects have serious implications for threatened, hollow-dependent species (Saunders
92 *et al.*, 2003, Maron, 2005), potentially resulting in an extinction debt (Tilman *et al.*,
93 1994), that is, a future commitment to extinction from action (or inaction) now. Delay
94 in beginning tree protection and restoration risks producing increasingly long, hollow-
95 scarce population bottlenecks in the future, due to the long time it takes for hollows to
96 form (Manning *et al.*, 2004, Gibbons *et al.*, 2008). This has direct, long-term
97 implications for populations of hollow-dependent species.

98 Here, we explore the role of lag effects on the availability of potential nest
99 trees of an obligate hollow using species, namely the vulnerable superb parrot
100 (*Polytelis swainsonii*) in south-eastern Australia. A key challenge in planning
101 conservation action for hollow-dependent taxa is to predict which species will be at
102 risk from future hollow scarcity. Population estimates and simple extrapolation of
103 trends based on passive monitoring can sometimes have limited predictive power

104 (Lindenmayer & Likens, 2010). To predict long-term conservation risk, some
105 understanding of ecological processes affecting critical resources that limit
106 populations of a given species is essential. We examined a key ecological process by
107 modelling recruitment and mortality of populations of potential nest trees for the
108 superb parrot. Our aim was to explore the possible risks of delaying conservation
109 actions to protect and restore hollow-bearing trees. We used an established method
110 for modelling scattered tree populations (Gibbons *et al.*, 2008, Fischer *et al.*, 2010,
111 Gibbons *et al.*, 2010), to simulate and predict future hollow scarcity under different
112 conservation scenarios. Our key questions were:

113 (1) What is the effect of current management practices on potential nest trees if these
114 practices continue into the future?

115 (2) What is the effect of delaying tree conservation and restoration actions until
116 potential nest tree populations drop substantially (by 70% to 90% of current levels)?

117 (3) What is the effect of immediately acting to reduce potential nest tree mortality and
118 increase recruitment?

119 Our analysis provides an ‘early warning’ approach that can be adapted to other
120 obligate hollow nesting species.

121

122 **Materials and Methods**

123 *Study species*

124 The superb parrot (weight 130 – 160 g, wingspan 53 – 57 cm, length approximately
125 40 cm), occurs in a restricted range in south-eastern Australia (Webster, 1988,
126 Webster & Ahern, 1992, Higgins, 1999). It nests in hollows in branches and tree
127 trunks, and breeds between September and December (Webster, 1988, Webster &
128 Ahern, 1992, Manning *et al.*, 2004).

129 Across a significant part of its range, the superb parrot breeds in agricultural
130 landscapes with scattered hollow-bearing trees (Manning *et al.*, 2004). These trees are
131 remnants from temperate eucalypt woodlands that have been converted for cultivation
132 and livestock grazing. While the superb parrot persists in these landscapes, the
133 regeneration of the trees on which it depends for nest hollows has largely ceased due
134 to suppression of tree regeneration from livestock grazing, cultivation, exotic plants
135 and other human-induced disturbances (Fischer *et al.*, 2009, Weinberg *et al.*, 2011).
136 Because mortality among existing trees is also high (Ozolins *et al.*, 2001), the number
137 of trees with hollows is declining (Gibbons *et al.*, 2008).

138

139 *Study area*

140 The study area is a major breeding area of the superb parrot, located on the South–
141 West Slopes of New South Wales (33° 25′–35° 18′S; 147° 41′–149° 24′E,
142 approximately 24,740 km²; Manning *et al.* 2004). The vegetation type used by the
143 superb parrot in this region is box-gum grassy woodland dominated by yellow box
144 (*Eucalyptus melliodora*), Blakely’s red gum (*E. blakelyi*) and white box (*E. albens*),
145 often in conjunction with other species such as apple box (*E. bridgesiana*), mealy
146 bundy (*E. nortonii*), red box (*E. polyanthemos*), candlebark (*E. rubida*), brittle gum
147 (*E. mannifera*) and red stringy bark (*E. macrorhyncha*) (Benson, 1991, Benson, 1999,
148 NSW NPWS, 2002). These woodlands once covered an extensive area of south-
149 eastern Australia (Beadle, 1981, Department of Environment and Heritage, 2006).
150 However, over 92% of woodland has been cleared, and what remains is highly
151 modified (Threatened Species Scientific Committee, 2006), mostly consisting of
152 small remnant patches and scattered paddock trees (Gibbons & Boak, 2002, Manning

153 *et al.*, 2004). Consequently, box-gum grassy woodlands are listed as a critically
154 endangered ecological community (Department of Environment and Heritage 2006).

155

156 *Predicting the availability of potential nest trees for the superb parrot*

157 We used a simulation model described by Gibbons *et al.* (2008) and populated it with
158 datasets from within our study area to predict the future availability of potential nest
159 trees for the superb parrot under different conservation scenarios. This simulation
160 model tracks the mean diameter at breast height (DBH) and mean number of trees
161 with hollows in stands through time with recruitment and mortality applied at pre-
162 defined rates. The simulation model is stochastic in the sense that parameters in the
163 model (e.g. tree mortality) can be entered as random values within a range of
164 observed or likely values. The model is then run as many times as there are random
165 values so predictions for any single scenario are calculated as a range of values from
166 multiple runs of the model. The different steps in the simulation modelling and data
167 used to populate each step are described below.

168

169 **1. Populate the simulation model with tree diameter distribution data**

170 The first step was to populate the simulation model with data for existing trees in the
171 study area. We calculated the mean number of trees in 10 cm DBH classes (i.e., 0-10
172 cm, 11-20 cm, etc.) for each tree species and health class (i.e., living or dead), based
173 on data collected at 48 separate 2 ha sites in the agricultural matrix within our study
174 area (the range of diameters recorded in the 48 x 2ha sites was 1cm – 232cm DBH).

175

176 **2. Identify potential nest trees for the superb parrot**

177 Second, we predicted the proportion of trees that are potential nest trees for the superb
 178 parrot. Manning et al. (2004) observed that 98% of 136 nest hollows used by the
 179 superb parrot had a minimum entrance width ≥ 5 cm, so we recorded a tree as a
 180 potential nest tree for the superb parrot if it contained ≥ 1 hollow with an estimated
 181 minimum entrance width ≥ 5 cm. Hollows ≤ 1 m above the ground, in cut stumps and in
 182 fire scars at the base of trees were not recorded.

183 We recorded the presence/absence of hollows with minimum entrance width
 184 ≥ 5 cm, DBH and tree species in all living and dead trees ≥ 5 cm DBH at 513 50m \times
 185 20m plots. These plots were part of a different study than the 48 sites described in
 186 step 1, but were located in the same study region. In these 513 plots, we recorded
 187 2665 living trees (Blakely's red gum, yellow box, white box, red box, mealy bundy
 188 and apple box) and 192 dead trees. We predicted the proportion of living trees that are
 189 potential nest trees for the superb parrot by fitting a Generalised Linear Model (GLM)
 190 with a logit link to these data in which the presence/absence of at least one hollow
 191 potentially suitable for the superb parrot in a tree (p_1) was the (binary) response
 192 variable and DBH and tree species the explanatory variables. This model was:

193

$$194 \text{ logit}(p_1) = -4.1129 + (0.0718 \times \text{DBH}) - 2.3761 \times \text{Species group} \quad \text{Equation 1}$$

195

196 where Species group was a factor with two levels (Species group 1 is white box, red
 197 box, mealy bundy and apple box. Species group 2 is yellow box and Blakely's red
 198 gum). The relationships between DBH and the probability of hollows suitable for the
 199 superb parrot were not significantly different between the tree species in each group.
 200 The area under the Receiver Operating Characteristic curve (AUC) for this model was
 201 0.93 indicating the model had "excellent" discriminating ability (Pearce & Ferrier,

202 2000). The model used for predicting the proportion of dead trees that are potential
203 nest trees for the superb parrot (p_d) was:

204

$$205 \text{ logit}(p_d) = -3.4715 + (0.0809 \times \text{DBH}) \quad \text{Equation 2}$$

206

207 The AUC for this model was 0.83, indicating the model had “good” discriminating
208 ability (Pearce & Ferrier, 2000).

209

210 **3. Recruitment of new potential nest trees over time**

211 To simulate the development of new potential nest trees for the superb parrot over
212 time, we developed a relationship between tree age and DBH for the two groups of
213 tree species used in Equation 1 to predict potential nest trees. However, data on the
214 relationship between age and DBH only exist for one tree species in our study area
215 (yellow box) (Banks, 1997). Using the data in Banks (1997), Fischer *et al.* (2010)
216 derived the following relationship to predict the ages of yellow box trees:

217

$$218 \text{ Age} = 0.019714 \times \pi \times (\text{DBH}_{\text{standardized}}/2)^2 \quad \text{Equation 3}$$

219

220 Where $\text{DBH}_{\text{standardised}}$ is the “yellow box equivalent diameter” for each tree as
221 explained below.” To also predict the ages of trees of other species, we followed the
222 procedure outlined by Fischer *et al.* (2010) and calculated a ‘yellow box equivalent
223 diameter’ for each individual tree of the various other eucalypt species. The procedure
224 assumed that all eucalypt species in our study area follow an identical growth curve
225 relative to their maximum attainable diameter, and have the same approximate life-
226 span as yellow box. DBH values for all tree species were initially standardised to a

227 value between zero and one, as a proportion of the maximum attainable diameter (i.e.
228 the maximum diameter observed in the field). Those values were then multiplied by
229 the maximum diameter observed for yellow box to obtain a ‘yellow box equivalent
230 diameter’. Equation 3 was then used to estimate the ages of these trees. We
231 acknowledge that this procedure is unlikely to give precise age estimates, but it is a
232 pragmatic solution given the paucity of data available for trees in our study area.

233

234 To determine how many new potential nest trees were recruited over time, we: (1)
235 standardized DBH values for each cohort (DBH class) to “yellow box equivalents”,
236 (2) predicted age from DBH for each cohort using Equation 3, (3) added the number
237 of years equivalent to each time-step in the simulation, (4) used the inverse of
238 Equation 3 to predict the DBH of the cohort at the end of this time-step, and (5)
239 converted standardized DBH values back to raw values for each tree species. These
240 final DBH values were then used to predict what proportion of trees will be potential
241 nest trees in the future, using Equation 1 for living trees, or Equation 2 for dead trees.

242

243 The time-step in the simulation model was equivalent to the period between
244 regeneration events (i.e. when new eucalypts become established). The mean age of
245 trees in the smallest DBH classes (0-20cm DBH) recorded at the 48 sites was
246 approximately 5-12 years. We used the most optimistic (shortest) period of 5 years
247 between regeneration events in all scenarios representing business as usual (i.e.
248 current management approaches continue into the future). This means that the model
249 is a ‘best case scenario’ when regeneration is more limited. Gibbons *et al.* (2008)
250 found that the number of scattered trees perpetuated over the long-term is sensitive to
251 the number of trees recruited during each regeneration event. Therefore, for

252 simulations representing business-as-usual, we recruited trees at the mean (\pm SE) rate
253 of 0.02 ± 0.01 per ha for species group 1 (yellow box, Blakely's red gum) and
254 0.22 ± 0.18 per ha for species group 2 (white box, mealy bundy, apple box), which is
255 the mean (\pm SE) number of trees we recorded in the smallest DBH classes (0-20cm
256 DBH) at the 48 sites. These data were entered stochastically. That is, a random value
257 for the number of trees (per ha) recruited every time-step was selected from a normal
258 distribution with a mean (\pm SE) equivalent to the estimates obtained for each tree
259 species group.

260

261 **4. Mortality of trees**

262 We included two sources of mortality in our model. We calculated annual mortality
263 from data collected on changes in the densities of scattered trees between 1964 and
264 1994 within the study area (Cowra 8630 map sheet, Geoscience Australia) (Ozolins *et*
265 *al.*, 2001). The mean (\pm SE) for annual mortality was 0.013 ± 0.005 . Gibbons *et al.*
266 (2008) found that the numbers of scattered trees in these landscapes was highly
267 sensitive to annual mortality, so we populated the simulation model with these data
268 stochastically. For each run of the simulation model, we selected mean annual
269 mortality randomly from a normal distribution with a mean \pm SE of 0.013 ± 0.005 . We
270 also set, at 500, the maximum number of years that trees will remain living or
271 standing, which is based on longevity estimates for yellow box reported by Banks
272 (1997). There were no other data from which this estimate could be derived and
273 Gibbons *et al.* (2008) report that the number of scattered trees is not sensitive to this
274 parameter in simulations of this type.

275

276 **5. Predictions from the simulation model**

277 For each scenario, we predicted the mean ($\pm 95\%$ prediction interval) numbers of
278 potential nest trees for the superb parrot at each time-step, or at the end of each
279 recruitment event, over 100 runs of the simulation model.

280

281 *Simulated Scenarios*

282 We simulated four alternative scenarios for conserving potential nest trees of the
283 superb parrot. We use scenarios because they provide decision-makers with a broad
284 range of management options to consider. Further, we know that persistence of tree
285 hollows is most sensitive to mortality and recruitment (Gibbons et al. 2008), and
286 different scenarios allow us to explore the effects of altering these key parameters. We
287 include one scenario that is no further conservation action (a), and two based on the
288 IUCN criteria for listing species ((b) and (c); IUCN, 2002). We did this because (1)
289 these scenarios relate to the percentage decline in a given population needed to meet
290 the criteria for two IUCN status levels (Critically Endangered and Endangered), and
291 (2) a link between superb parrots populations and nest hollow availability is highly
292 likely in the study area (see Discussion). The final scenario (d) relates to immediate
293 conservation action to improve current levels of mortality and recruitment.

294

295 **(a) No further conservation actions.** Under this scenario, we commenced the
296 simulation using current potential nest tree densities in the agricultural matrix (3.9 per
297 ha), which is, conservatively, half of the mean density of potential nest trees that
298 occurs in relatively unmodified remnants dominated by yellow box and Blakely's red
299 gum (Gibbons *et al.*, 2008). Current rural land management practices are assumed to
300 continue, so no action is taken to increase existing tree landscape-scale tree
301 recruitment or reduce existing tree mortality.

302

303 **(b) Wait until 90% reduction in potential nest trees.** We used the IUCN criterion
304 of a 90% population decline (though not its rate) as a guide to trigger for conservation
305 actions– this would equate to ‘Critically Endangered’ status if considering a species
306 (IUCN, 2002). Under this scenario, we allowed potential nest tree density to drop to
307 0.8 per ha or approximately 10% of pre-clearing levels, before landscape-scale tree
308 recruitment at the rate of one new tree per ha planted every 10 years and reduction of
309 annual tree mortality to half current levels.

310

311 **(c) Wait until 70% reduction in potential nest trees.** We used the IUCN criterion of
312 a 70% reduction (though not the rate) as a guide to trigger conservation actions– this
313 would equate to ‘Endangered’ status if considering a species (IUCN, 2002). Under
314 this scenario, we allowed the potential nest trees density to drop to approximately
315 30% of pre-clearing levels (2.4 per ha), before there was landscape-scale tree
316 recruitment at the rate of one new tree per ha planted every 10 years and reduction of
317 annual tree mortality to half current levels.

318

319 **(d) Implement enhanced conservation actions now.** Under this scenario, we
320 immediately implemented landscape-scale tree recruitment at the rate of one new tree
321 per ha planted every 10 years and reduced of tree mortality to half current levels.

322

323 Scenario (a) represents the most likely (i.e. business-as-usual) scenario.
324 Scenarios (b) and (c) were chosen to represent the implications of waiting until there
325 are further reductions in populations of the superb parrot before triggering a higher
326 threat status and therefore increased conservation efforts. Scenario (d) represents the

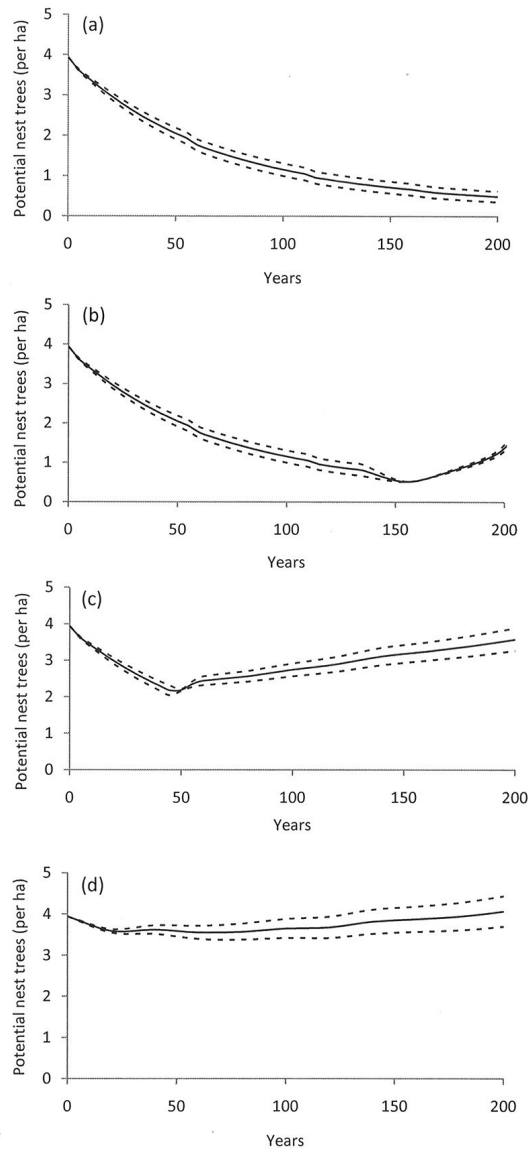
327 case where decline in potential nest trees to date triggers an immediate increase in
328 conservation resources to redress the major factors causing the decline of potential
329 nest trees. This is the least likely scenario.

330

331

332 **Results**

333 **(a) No further conservation actions.** Under this scenario, our modelling indicated
334 that the density of potential nest trees would continue to decline from the current
335 estimate of 3.9 per ha, which is approximately 50% of the original (pre-clearing)
336 estimate (8 per ha), over the 200 year simulation period (Figure 1a). The predicted
337 mean density of potential nest trees declined to 6% of the original (pre-clearing)
338 estimate by the end of the simulation period (200 years).



339

340 **Figure 1. Predicted numbers (mean \pm 95% prediction interval) of potential nest**
 341 **trees (per ha) for the superb parrot over 200 years under scenarios of (a)**
 342 **business-as-usual (no further conservation actions); (b) wait until 90% reduction**
 343 **in potential nest trees before implementing conservation actions; (c) wait until**
 344 **70% reduction in potential nest trees before implementing conservation actions;**
 345 **and (d) implement enhanced conservation actions now.**

346

347 **(b) Wait until 90% reduction in potential nest trees.** Under this scenario, we
 348 waited until a 90% decline in the density of potential nest trees relative to an original

349 (pre-clearing) estimate (8 per ha) before implementing restoration actions. A
350 predicted 90% decline in the mean density of potential nest trees relative to the
351 original (pre-clearing) density occurred after 135 years. After initiation of restoration
352 actions (reducing tree mortality and increasing tree recruitment), the predicted mean
353 density of potential nest trees began to increase (Figure 1b), but reached only 29% of
354 the original (pre-clearing) mean density by the end of the simulation period (200
355 years).

356

357 **(c) Wait until 70% reduction in potential nest trees.** Under this scenario, we waited
358 until a 70% decline in potential nest trees relative to the original (pre-clearing)
359 estimate (8 per ha) before taking action. A predicted 70% decline in mean potential
360 nest trees density relative to original (pre-clearing) density occurred after 40 years.
361 After initiation of restoration actions (reduced tree mortality and increased tree
362 recruitment), the predicted mean density of potential nest trees began to increase
363 (Figure 1c). By 200 years, the mean density of potential nest trees had reached 3.6 per
364 ha, still below the current mean density, and 45% of the original (pre-clearing) mean
365 density.

366

367 **(d) Implement enhanced conservation actions now.** Under this scenario, we
368 immediately initiated restoration actions (reducing tree mortality and increasing tree
369 recruitment). The predicted mean density of potential nest trees remained relatively
370 stable over the simulation period. The predicted mean density of potential nest trees
371 declined from the current mean density of 3.9 per ha to 3.6 per ha at 60 years before
372 increasing to a mean of 4.1 per ha at the end of the simulation period (200 years),
373 which is slightly above the current density (Figure 1d).

374

375 **Discussion**

376 Conservation of hollow-dependent species in woodland and forest is a global issue
377 (Saunders *et al.*, 1982, Newton, 1994, Newton, 1998, Gibbons & Lindenmayer, 2002,
378 Lindenmayer *et al.*, 2011). We have used one species, the superb parrot, to illustrate
379 the universal problem of lag effects in managing potential nest trees of hollow-
380 dependent species. To do this, we examined the effect of different conservation
381 scenarios on potential nest trees for an obligate hollow using species to illustrate the
382 risk associated with lag effects. Our results show that it is essential to anticipate future
383 hollow-limited bottlenecks as a result of long-term tree decline.

384 In three out of four scenarios ((a) to (c)), the number of potential nest trees
385 was predicted to decline substantially. Even where a delayed response eventually took
386 place ((b) and (c)), potential nest trees did not recover to current levels within 200
387 years. Under Scenario (a) (“no further conservation action”), the potential for eventual
388 local extinction of the superb parrot within the study area, as potential nest trees
389 decline to very low densities, is evident. Although scenarios (b) and (c) did eventually
390 begin to reverse the decline in potential nest trees, the risk is that society at that time
391 may not choose, or be able to, act. Furthermore, if our predictions prove to be overly
392 optimistic, e.g. because our models were too conservative (see Material and
393 Methods), or if tree clearing accelerates (see below), the possibilities to act effectively
394 in the future may be severely constrained. The only scenario that resulted in the
395 predicted number of potential nest trees remaining stable over the next 200 years was
396 Scenario (d) (“implement enhanced conservation actions now”). This indicates that
397 immediate action to reduce tree mortality and enhance tree regeneration within the

398 study area will be essential to avoid serious impact on hollow-availability for at least
399 200 years.

400 The mortality of scattered trees where they occur around the world is often
401 increased by the intensification of agricultural production (Manning *et al.*, 2006a). For
402 example, cultivated land expanded by 75% in our study area between the 1960s and
403 1990s (Ozolins *et al.*, 2001). Global food demand is predicted to increase by 70 to
404 100% by 2050 (Godfray *et al.*, 2010). In our study area, the growth of cultivated land
405 is predicted to increase (Zhang *et al.* 2006; Grain Research and Development
406 Corporation 2010). In recent years, the majority of permits issued to clear native
407 vegetation in this region have been associated with either converting pastoral land to
408 cultivation, or introducing technologies (e.g., pivot irrigators, control-traffic farming)
409 to increase productivity in cultivated land. Many of these applications can have a
410 detrimental impact on the superb parrot. For example, in New South Wales over a
411 three-year period from 2008-2011, 114 applications to clear native vegetation
412 (including 85 applications to clear scattered paddock trees) had the superb parrot
413 listed a likely to occur on the site. Of these, 49 applications were within our study
414 area (NSW Office of Environment and Heritage, 2011). Our results clearly
415 demonstrate that any actions that undermine or delay conservation efforts to reduce
416 tree mortality and increased recruitment (i.e. Scenario (d)) should be avoided.

417 Artificial nest boxes have been suggested as a possible approach to overcome
418 hollow scarcity (McComb & Noble, 1981, Twedt & Henne-Kerr, 2001). However,
419 recent monitoring of 3200 nest boxes placed along a major four-lane highway that
420 crosses superb parrot breeding areas, has not found a single breeding event in these
421 artificial structures (D. Lindenmayer *et al.*, unpublished data). It is also not clear that
422 nest boxes could be placed in sufficient numbers, at a landscape scale, and be

423 maintained continuously for the recovery periods indicated by this study. Current
424 knowledge suggests that the maintenance and perpetuation of hollow-bearing trees is
425 the most plausible solution for the conservation of the superb parrot.

426 In interpreting all scenarios, we assumed a positive relationship between the
427 density of potential nest trees and populations of the superb parrot. This relationship is
428 widely reported for hollow-dependent birds (Newton, 1994, Gibbons & Lindenmayer,
429 2002, Marsden & Pilgrim, 2003, Murphy *et al.*, 2003, Saunders *et al.*, 2003, Heinsohn
430 *et al.*, 2009), and has been shown experimentally (Brawn & Balda, 1988, Aitken &
431 Martin, 2008). However, the level at which hollow availability limits populations of
432 the superb parrot is unknown. As with other hollow-dependent species, this will vary
433 spatially, and in relation tree and hollow availability and competition from other
434 species (Newton, 1998, Manning *et al.*, 2004).

435 It has been postulated in a study of potential nest trees in roadside vegetation
436 that hollows were unlikely to be limiting for the superb parrot (Davey & Purchase,
437 2004). It is highly unlikely such a conclusion (which is speculative only) could validly
438 be extrapolated to the trees in the agricultural matrix that we modelled. This is
439 because: (1) Roadside vegetation is among the most undisturbed native vegetation in
440 this part of Australia (van der Ree & Bennett, 2001) and empirical research within the
441 study areas has shown considerable differences in tree density between travelling
442 stock reserves and adjacent paddocks (Lentini *et al.* 2011). Lentini *et al.* (2011,
443 unpublished data) found that travelling stock reserves has on average 90.7 stems per
444 ha (± 25.85) compared to 5.6 stems per ha (± 1.51) in adjacent paddocks. Furthermore,
445 exotic 4.1 (± 1.49), wheat 2.2 (± 0.43), canola 1.6 (± 0.53), and Lucerne or clover
446 paddocks 1.5 (± 0.37) had even fewer stems per ha. As such land uses are the majority
447 in landscapes used by the superb parrots, this has profound implications for the

448 relative amount of hollows available (see below), and process-based prediction of
449 population sustainability. (2) There is greater level of threat from clearing, spray drift
450 and fertilizers to trees in the agricultural matrix (Manning & Fischer, 2010) compared
451 to trees in roadsides. (3) Roadsides represent a small proportion of the landscape
452 compared to the agricultural matrix (the area we have modelled) where the majority
453 of superb parrots occur (Manning *et al.*, 2006b). Scattered trees and small remnants
454 (<1ha) of the agricultural matrix represent 54% of the total area remaining of this
455 woodland (Gibbons and Boak 2002). (4) Hollow availability in box-gum grassy
456 woodland with very low tree densities (< 6 per stems ha over 15cm DBH), supports
457 very low numbers of hollows potentially suitable for superb parrots (11 hollows over
458 5cm diameter per ha) compared to low density (6 – 10 stems per ha and 31 hollows),
459 medium density (11 – 50 stems and 74 hollows per ha, and high density (51 – 100
460 stems and 111 hollows per ha) (L. Rayner, unpublished data). Low density scattered
461 trees are typical of the landscapes occupied by the superb parrot in the study area.
462 Manning *et al.* (2004) found most (60%) of superb parrot nest trees in the study area
463 were surrounded by only 1 – 5 trees within 50 metres. Manning *et al.* (2006b) found
464 most superb parrots occurred where there was low density woodland. Therefore, we
465 believe that it is reasonable to assume that as tree populations continue to decline in
466 the agricultural matrix (as we have predicted), hollow availability will further limit
467 the population size of the superb parrot (see Newton 1994; Newton 1998). Critically,
468 it is the inexorable trend observed in our modelling that should be of serious concern
469 to conservation decision-makers. Failure to identify and respond appropriately to lag
470 effects in restoration of nest hollows will place many dependent species at increased
471 risk of extinction in the future. The predicted effects of lag times on tree hollow-
472 dependent species are now beginning to be documented (e.g. Saunders *et al.*, 2003,

473 Maron, 2005). Not only does waiting to act increase extinction risk and reduces future
474 response options, but it is also likely to cost more (i.e., more trees will need to be
475 regenerated) and potentially will be less successful due to synergistic processes
476 affecting small populations such as inbreeding and stochastic events (Lindenmayer &
477 Fischer, 2006). Our novel application of an established modelling method provides an
478 early warning approach that conservation managers can use to identify species at risk
479 from longer-term ecological trends so that they can initiate vigorous conservation
480 measures now. Without such approaches, there is a serious risk that species facing
481 future bottlenecks in key resources, such as those dependent on hollows, will always
482 be disadvantaged by classification systems that assign conservation threat level based
483 on past population trends.

484

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489

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