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2   **Testing multiple pathways for impacts of the non-native Black-headed**

3   **Weaver *Ploceus melanocephalus* on native birds in the early phase of**

4   **invasion**

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12   Some, but not all non-native species have strong negative impacts on native species. It is desirable to

13   identify whether a non-native species will have a negative impact at an early stage in the invasion

14   process, while management options such as eradication are still available. Although it may be

15   difficult to detect early impacts of non-native species, this is necessary to ensure that management

16   decisions can be based on case-specific scientific evidence. We investigate the impacts of a non-

17   native bird, the Black-headed Weaver *Ploceus melanocephalus*, at an early stage in its invasion of the

18   Iberian Peninsula. To do this we, a priori, identify potential pathways by which competition for

19   shared resources by Black-headed Weavers could lead to population declines in ecologically similar

20   native species, and generate hypotheses to test for evidence of competition along these pathways.

21   Black-headed Weavers could potentially impact native species by displacing them from nesting

22   habitat, or by locally reducing habitat quality. We did not find evidence for either potential

23   competition pathway, suggesting that Black-headed Weavers do not currently compete with native

24   species. However, it is possible that mechanisms that currently allow coexistence may not operate

25   once Black-headed Weavers reach higher population densities or different habitats.

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Non-native species are major drivers of avian biodiversity loss (Clavero *et al.* 2009). While some of the most severe impacts have been caused by introduced mammalian predators (Blackburn *et al.* 2004, Hilton and Cuthbert 2010), exotic birds can impact native species through a number of mechanisms, such as predation, hybridisation and transmission of disease (Kumschick & Nentwig 2010). Although rarely demonstrated, non-native birds have also been suspected of competing with native species (Blackburn *et al.* 2009). For example, the establishment of the Common Myna *Acridotheres tristis* in Australia was followed by a decline in the abundance of a number of native bird species (Grarock *et al.* 2012). Whether species compete depends on the degree to which niche differences result in one species limiting their own population more than the populations of other species (Chesson 2000, Adler *et al.* 2007), the degree of asymmetry in the competitive weights of species (Adler *et al.* 2007), and the presence of other mechanisms such as predation that limit the population of one species more than others (Griswold & Lounibos 2005). Competitive exclusion is likely when species share similar resource requirements (Ieronymidou *et al.* 2012), and one species is either dominant at accessing those resources, or has a faster reproduction rate (Chesson 2000, Adler *et al.* 2010).

It is desirable to identify whether a non-native species will compete with native species early in the invasion process, while the non-native species has a restricted distribution and eradication remains feasible (Lodge *et al.* 2006). However, it is easier to evaluate impacts when an invasion is advanced, as more data are available, allowing competition to be identified with more confidence (Wiens 1989). This leads to a trade-off between early risk assessment and the strength of evidence for demonstrating the existence of an impact. While this has motivated researchers and policy makers to suggest that lack of scientific certainty should not preclude control of non-native species (UNEP 1992, Sixth Conference of the Parties Convention on Biological Diversity 2002, Edelaar & Tella 2012), eradication is costly and poses animal welfare issues (Defra 2003), leading to recognition that it is desirable to have an evidence base to prioritise and justify management actions (Defra 2003, EEA 2010). Thus there is need to use scientific evidence collected early in the invasion process to aid management decisions. This is especially pressing in the Iberian Peninsula, where the number of non-native birds species recorded breeding has increased rapidly since the late 1980s (Matias 2002).

We assess the evidence for competition between the recently established Black-headed Weaver *Ploceus melanocephalus* and two ecologically similar native birds. Black-headed Weavers are native

61   to sub-Saharan Africa, and were first recorded in the Iberian Peninsula in the mid-1990s (Matias

62   2002). Breeding was confirmed in fewer than ten 10km^2 grid cells in the most recent Portuguese and

63   Spanish breeding bird atlases (Marti & de Moral 2003, Equipa Atlas 2008). Black-headed Weavers

64   nest in emergent vegetation (Colias & Colias 1964) and feed their nestlings on large invertebrates

65   collected primarily by gleaning vegetation (Moreau 1960, Fry & Keith 2004), so share resource

66   requirements with native Great Reed Warblers *Acrocephalus arundinaceus* and Eurasian Reed

67   Warblers *A. scirpaceus* (Graveland, 1996, Matias 2002, Cardoso 2008, Leisler & Schulze-Hagen 2011).

68   Black-headed Weavers have been reported behaving aggressively towards both species (Matias

69   2002). While this could indicate that they are dominant at accessing shared resources, this has not

70   been tested.

71   At the current stage of invasion we cannot test the influence of Black-headed Weavers on the

72   productivity of native species, so instead focus on detecting behavioural responses to competition.

73   Our approach involves identifying possible pathways by which shared resource requirements could

74   lead to population declines of native species, and generating testable hypotheses for processes

75   along these pathways (Fig. 1). We test each of the following numbered hypotheses. We first test

76   whether resource requirements of Black-headed Weavers overlap with native species (Fig. 1,

77   Hypothesis 1). We speculate that this could have a negative impact on native species if Black-headed

78   Weavers exhibit interspecific territoriality and thereby exclude native species (Fig. 1, Hypotheses 2-

79   4), or locally reduce habitat quality (Fig. 1, Hypotheses 5-6). Both of these could lead to population

80   declines either by forcing native species to nest in sub-optimal habitat (Fig. 1, Hypothesis 7), or by

81   directly reducing the space available for native species. By testing for competition at a range of

82   stages along these pathways we can maximise our ability to detect competition, and have a useful

83   framework for assessing the potential for competitive exclusion.

84

85   **METHODS**

86   **Study sites**

87   Fieldwork was conducted at four sites in western Portugal. Black-headed Weavers have been

88   established at Paul de Tornada (PT, 39.448° N, 9.135° W) and Barroca d'Alva (BA, 38.729° N, 8.899°

89   W) since the mid-1990s (Matias 2002). Uncolonised sites, with similar habitat and within 20km of

90   colonised sites, were selected as controls. These were Lagoa de Óbidos (LO, 39.385° N, 9.210° W)

91   and Lezíria Grande (LG, 38.931° N, 8.964° W). PT and LO are both extensive wetlands, consisting of

92   patchworks of reedbed (dominated by reed *Phragmities australis)* and open water. BA and LG both

93   consist of reed lined ditches crossing a mix of rice and wheat cultivation and pasture. The colonised

94   study sites selected have high population densities of Black-headed Weavers and native

95   *Acrocephalus* warblers, so potentially provide the best data available on the interaction of Black-

96   headed Weavers and native species. Fieldwork was not conducted at other sites colonised by Black-

97   headed Weavers as they either were unsuitable for Reed Warblers and Great Reed Warblers, or

98   were ecologically sensitive sites.

99   **Playback experiment and aggressive interactions**

100   If Black-headed Weavers exhibited interspecific territoriality towards native species we would expect

101   them to initiate aggressive interactions with native species, and possibly also respond to

102   heterospecific song. To test whether Black-headed Weavers initiated aggressive interactions with

103   native species (hypothesis two) all incidents of aggression between Black-headed Weavers and

104   native species observed during fieldwork were recorded. Where possible, the species initiating

105   aggression was noted. A binomial test was used to test whether the proportion of aggressive

106   interactions differed from random expectation.

107   In order to test hypothesis three we conducted a playback experiment to test the reaction of Black-

108   headed Weavers to conspecific and heterospecific song in May 2012, during the weaver breeding

109   season. Songs of Black-headed Weaver, Great Reed Warbler (from Constantine *et al.* 2006) and

110   Eurasian Reed Warbler (from Roche 1997), as well as a recording of background noise made at night

111   at PT, were played from a portable speaker placed five metres away from Black-headed Weaver

112   nests. The quality of warbler recordings was checked by playing these recordings within conspecific

113   territories, and both elicited a reaction. Each recording was played for five minutes, as Catchpole

114   (1978) found this was sufficient time to elicit a response from Eurasian Reed Warblers. Playback

115   experiments were videoed, and the distance of closest approach by Black-headed Weavers during

116   the playback was estimated to the nearest metre.

117   The responses of Black-headed Weavers from 16 territories (eight at PT and eight at BA) were tested

118   over a three day period to reduce seasonal variation in individual motivation to respond (Dunn *et al.*

119   2004, Golabek *et al.* 2012). To minimise the effect of habituation, no more than two recordings were

120   played in each territory in one day, with one recording played in the morning and one in the evening.

121   To further control for habituation, the order in which recordings were played was balanced across

122   the 16 territories.

123   We modelled the distance of approach (m) by Black-headed Weavers as a function of playback

124   treatment using a generalised linear mixed model, with territory identity as a random effect. Data

125 from both sites were pooled as site identity was not significant when included in the previous model

126 (t_{44} = 0.521, P = 0.605). Due to convergence issues, the model was fitted using quasi-likelihood, with

127 the mean-variance relationship set so that the variance increased with the mean.

128

129 **Territory and habitat mapping**

130 We made 12 territory mapping visits to each site between early April and late June 2012 (i.e. from

131 territory establishment to nesting) to record the locations of Black-headed Weaver, Great Reed

132 Warbler and Eurasian Reed Warbler territories. Sites were visited during the morning active period

133 (Robbins 1981), and observations of target species were mapped onto a base map with the aid of a

134 handheld GPS unit. We assigned these observations to territories following Marchant (1983).

135 We only used observations of singing, fighting or territorial calling birds for determining territory size.

136 Observations were digitised using ArcMap 9.3 (ESRI 2008), and projected onto a Universal

137 Transverse Mercator grid (zone 29N). We calculated the territory centroid by taking the mean of the

138 coordinates of these observations, and delimited territory boundaries by constructing the minimum

139 convex polygon (MCP) that encompassed observations from each territory. Aerial photographs (1 m

140 resolution, Instituto Geográfico Português 2004) were digitised to produce vector maps of reedbed

141 at each site, which were updated based on field observations where there had been large changes in

142 reedbed extent. These maps were used to clip territory MCPs so that they only contained reedbed.

143 We did this so that territories reflected utilisation distributions more closely; areas of open water

144 and agriculture were rarely used by *Acrocephalus* warblers (J.P.B. Grundy pers. obs.), so contributed

145 very little to the resources available to breeding birds.

146 To test hypothesis four, territory overlap between pairs of species was calculated by dividing the

147 area occupied by both species by the total area occupied by either species. This calculation was

148 performed on a raster grid (~5m resolution), rather than directly on the vector layers, to aid

149 comparison with a null model. The purpose of the null model was to randomly shift the position of

150 each territory, while maintaining the number of territories at each site, observed territory size and

151 restricting territories to be in reedbed. Further details of the null model mechanism are given in

152 Supporting Information Appendix S1. The null model did not restrict intraspecific territory overlap,

153 but overlap of randomly generated conspecific territories was still similar to observed overlap. The

154 null model was run for 1000 iterations, and the overlap between heterospecific territories was

155 calculated in each case, to give a null distribution of overlap values. Competitive exclusion will lead

156 to lower than expected observed values, while selection of similar reedbed habitat will lead to

157 greater observed values than expected. Two-tailed *P*-values were calculated by comparing the
158 observed overlap to quantiles of this null distribution.

159 We recorded the date of first occupancy of each territory by Great Reed Warblers as this relates to
160 the male's assessment of territory quality (Bensch & Hasselquist 1991). This allowed us to test
161 hypothesis five, as the earliest occupied territories should also be the highest quality ones. We
162 restricted this analysis to Great Reed Warblers as previous studies have shown that the order of
163 territory occupancy relates to territory quality (Bensch & Hasselquist 1991), while it is unknown
164 whether the same holds for Eurasian Reed Warblers. The distance (m) between the centroid of
165 Great Reed Warbler and Black-headed Weaver territories was calculated, and its natural logarithm
166 used to model the date of first occupancy of each territory. As the availability of territories at
167 different distances to Black-headed Weavers varied between sites, site was also included in the
168 model. Territories were not visited every day (median interval between visits = 5.5 days), so a bird
169 may have arrived several days before the recorded occupation date. We tested the sensitivity of our
170 analysis to this measurement error by randomly selecting the date of occupation from the pool of
171 possible dates, and re-running the analysis with 1000 repetitions.

172 We calculated the size (m^2) of reedbed-clipped MCPs. Some passerines have larger territories when
173 food availability is low (Marshall & Cooper 2004), so food depletion by Black-headed Weavers may
174 cause native species to have larger territories (hypothesis six). Territory size of Eurasian and Great
175 Reed Warblers was modelled as a function of site using a generalised linear model with a gamma
176 distribution to account for the positive mean-variance relationship, with post-hoc Tukey tests
177 performed using the R package multcomp (Hothorn *et al.* 2008).

178 **Habitat sampling**

179 Seven territories of each species, corresponding to the minimum number of Great Reed Warbler
180 territories at any one of our study sites, and seven areas of unoccupied reedbed were randomly
181 chosen at each site. At each location habitat variables were measured in one randomly placed 50 x
182 50 cm quadrat, with the exception of two quadrats being placed in Great Reed Warbler territories
183 because of their larger territory size (Cramp, 1992). In each quadrat, we measured the height (cm) of
184 ten new (current season's growth) and ten old (previous season's growth) reeds, the diameter (mm)
185 of ten new and ten old reeds, the density of new and old reeds (measured by counting all reeds
186 within the quadrat), and the percentage cover of reeds, other emergent vegetation, herbaceous
187 plants, woody plants and grasses (estimated visually). These were selected as habitat variables that
188 had been identified as being important for the target species (Dyrcz 1986, Graveland 1996,

189   Martinez-Vilalta *et al.* 2002, Poulin *et al.* 2002), and considered to capture variation in reedbed

190   habitat. Water depth is also an important influence on Great Reed Warbler nest site selection

191   (Graveland 1998), but management of agricultural ditches caused water levels to fluctuate between

192   days at our study sites, so this variable was not included in analyses.

193   Differences in habitat between species (hypotheses one) were identified using non-metric

194   multidimensional scaling (NMDS), performed in PRIMER v6 (Clarke & Gorley 2006) based on a

195   Euclidean distance matrix generated from the habitat variables. NMDS allows dissimilarities to be

196   mapped in two dimensions. Stress values assess the fit between distances in the distance matrix and

197   those in two dimensional space. Stress values of less than 0.1 indicate a good fit (Clarke & Warwick

198   1994); the stress value of 0.08 in this study therefore indicates good fit. We investigated how areas

199   of NMDS space related to different habitat characteristics by modelling the matrix of raw habitat

200   variables as a function of NMDS coordinates using the manylm function in the R package mvabund

201   (Wang *et al.* 2012), and plotting the direction of these relationships. We used D (Schoener 1970) to

202   calculate the overlap in habitat associations of the three species. To do this, a kernel density

203   function was used to calculate the density of territories of each species in habitat space. D is then

204   calculated as

205    $D = 1 - \frac{1}{2}(\sum_{ij} |z_{1ij} - z_{2ij}|)$,

206   where z_{1ij} is the standardised territory density of species one and z_{2ij} is the standardised territory

207   density of species two at point ij in environmental space. Full details on the calculation of D are given

208   in Broennimann *et al.* (2012). D ranges from zero to one, with values closer to one indicating higher

209   overlap. We tested whether the overlap between habitat associations of native species shifted to be

210   less similar to those of Black-headed Weavers at sites where Black-headed Weavers are present

211   (hypotheses seven). To do this, we compared observed values of D for the overlap between the

212   densities of territories of native species and Black-headed Weavers at sites where Black-headed

213   Weavers were present to values of D generated in 1000 iterations of a null model that randomly

214   allocates observations to groups while maintaining the original number of observations in each

215   group (the identity test, Warren *et al.* 2008).

216   Having multiple sampling points in Great Reed Warbler territories (due to their larger territory size

217   than other study species) allowed us to test whether variation between territories of the same

218   species was greater than variation within territories. Sampling points within the same Great Reed

219   Warbler territory had more similar habitat characteristics than sampling points in different

220   territories (median Euclidean distance within territories = 77.9, median Euclidean distance between

221 territories = 97.0, Wilcoxon test, P = 0.076), justifying the decision to concentrate sampling effort on

222 maximising the number of territories sampled, rather than sampling more points within a territory.

223 Unless otherwise stated, all statistical analyses were performed in R v2.15 (R Development Core

224 Team 2012), with power analyses performed using the package pwr (Champely 2007).

225

RESULTS

Do native and non-native species use similar nesting habitat?

228 Great Reed Warblers occupied less habitat space than the other species (Fig. 2a). Great Reed

229 Warbler territories were characterised by having taller and thicker reeds, although both Eurasian

230 Reed Warblers and Black-headed Weavers also used this habitat (Fig. 2a & d). Black-headed Weaver

231 and Eurasian Reed Warbler territories overlapped in habitat space more than either species

232 overlapped with Great Reed Warblers (Table 1). These results support hypothesis one (Fig. 1).

233

Is there interspecific territoriality?

235 Limited support was found for hypotheses two and three (Fig. 1). Aggressive interactions were rarely

236 noted between Black-headed Weavers and native species; in over 120 hours of fieldwork, seven

237 aggressive interactions were observed. In five out of the six occasions where the aggressor was

238 observed, Black-headed Weavers initiated aggression (Binomial test, P = 0.219). Black-headed

239 Weavers approached conspecific song (t_{44}=2.642, P = 0.011, Fig. 3), but not heterospecific song ($t_{44} \leq$

240 1.723, $P \geq$ 0.092, Fig. 3) significantly more than background noise.

241 Observed territory overlap was never lower than expected if territories were randomly distributed,

242 so no support was found for hypothesis four (Fig. 1). Overlap between Great Reed Warbler and

243 Black-headed Weaver territories was higher than expected if territories were randomly distributed

244 at BA (Overlap$_{OBS}$ = 0.256, Overlap$_{NULL-Median}$ = 0, P = 0.01) but not significantly different than expected

245 at PT (Overlap$_{OBS}$ = 0.011, Overlap$_{NULL-Median}$ = 0, P = 0.43). Overlap between Eurasian Reed Warbler

246 and Black-headed Weaver territories was higher than expected if territories were randomly

247 distributed at both PT (Overlap$_{OBS}$ = 0.046, Overlap$_{NULL-Median}$ = 0, P < 0.001) and BA (Overlap$_{OBS}$ = 0.327,

248 Overlap$_{NULL-Median}$ = 0, P < 0.001).

249

Do Black-headed Weavers reduce habitat quality?

251 No support was found for hypotheses five, six and seven (Fig. 1). Great Reed Warbler territory

252 occupation date did not vary significantly between sites ($F_{1, 10} = 1.45$, $P = 0.256$). The distance to the

253 nearest Black-headed Weaver territory did not influence territory occupation date of Great Reed

254 Warblers ($F_{1, 10} < 0.01$, $P = 0.951$). This result was robust to measurement error caused by gaps

255 between territory mapping visits, as no significant relationships were observed in any permutation

256 of possible occupation dates.

257 Both Eurasian Reed Warbler and Great Reed Warbler territories were larger in extensive wetland

258 sites than ditch-crossed sites (Fig. 4). Territory size was not affected by the presence of Black-headed

259 Weavers (Fig. 4).

260 Neither Eurasian Reed Warbler ($D_{OBS} = 0.791$, $D_{NULL-Median} = 0.715$, $P = 0.164$, Fig. 2b) nor Great Reed

261 Warbler ($D_{OBS} = 0.629$, $D_{NULL-Median} = 0.546$, $P = 0.170$, Fig. 2c) territories shifted to be more or less

262 similar to Black-headed Weaver territories at sites where Black-headed Weavers were present.

263

264 **Power analysis**

265 Non-significant results in the direction expected by our hypotheses were found for the response of

266 Black-headed Weavers to native species' songs, and the proportion of aggressive interactions

267 initiated by Black-headed Weavers. We were only able to detect large effect sizes in these analyses;

268 the former analysis had sufficient power to identify mean approaches of ≥ 1.07m as being

269 significantly different from responses to background noise, while the latter analysis would only be

270 significant if all aggressive interactions were initiated by Black-headed Weavers.

271

272 **DISCUSSION**

273 **Evidence for pathways to competition**

274 Whilst there was overlap in the habitat characteristics of territories of Black-headed Weavers and

275 native *Acrocephalus* warblers, we did not find any statistically significant evidence to support the

276 hypothesis that competition by Black-headed Weavers is currently having population impacts on

277 native species. We therefore conclude that at current population densities (0.43 to 0.70 pairs ha^{-1} in

278 our study sites, Sullivan *et al*. in press) Black-headed Weavers are unlikely to have a negative impact

279 on ecologically similar native species.

280 The habitat characteristics of Eurasian Reed Warbler and Great Reed Warbler territories were similar

281 to those reported in previous studies (Graveland 1996, Leisler & Schulze-Hagen 2011). Great Reed

282 Warblers occupied areas with tall, thick reeds, often associated with the water-facing margin of

283 reedbeds (Graveland, 1998). Eurasian Reed Warblers and Black-headed Weavers occupied these

284 areas, but were also found in areas of reedbed that were encroached by terrestrial vegetation (Fig.

285 2). Eurasian Reed Warblers were the main species that occupied dense reed, which is often

286 associated with the land-facing margin of reedbeds (Leisler & Schulze-Hagen 2011). Because all three

287 species overlapped in habitat requirements, they are likely to select similar areas of reedbed, which

288 may explain the higher than expected spatial overlap between heterospecific territories at some

289 sites.

290 The larger size of Eurasian Reed Warbler and Great Reed Warbler territories in extensive reedbeds

291 compared to reed-lined ditches supports previous studies (Dyrcz 1986). Food depletion by Black-

292 headed Weavers could cause native species to increase the size of their territories (Marshall &

293 Cooper 2004), but we did not find any evidence for this.

294 Although there is anecdotal evidence of Black-headed Weavers displaying aggression towards native

295 species, we found little evidence for this. The results of the playback experiment did not support the

296 hypothesis that Black-headed Weavers respond to native species song. The recordings of Eurasian

297 Reed Warbler and Great Reed Warbler song used in the playback experiment elicit a response from

298 conspecifics, but did not lead to a statistically significant response from Black-headed Weavers. This

299 could be a type II error, as there was a weak tendency for Black-headed Weavers to approach Great

300 Reed Warbler song, but the response was less strong than to conspecific song. It is unlikely that

301 visual stimuli were required to evoke territorial behaviour towards heterospecifics, as aggressive

302 interactions were rarely noted. Additionally, Black-headed Weavers were frequently observed close

303 to native species without being aggressive (J.P.B. Grundy pers. obs.). Therefore, at present there is

304 little support for territorial defence against reed warblers by Black-headed Weavers.

305 The proximity to Black-headed Weavers did not influence the attractiveness of territories to

306 returning male Great Reed Warblers. Great Reed Warblers are philopatric to their natal site (Bensch

307 & Hasselquist 1991), so have information about the quality of reedbed patches from previous years.

308 The locations of Black-headed Weaver territories are fairly consistent between years (M.J.P. Sullivan

309 unpubl. data), so if they reduced Great Reed Warbler productivity this information would be

310 available to returning Great Reed Warblers. Neither Eurasian Reed Warblers nor Great Reed

311 Warblers shifted into habitat less similar to Black-headed Weavers at sites where Black-headed

312 Weavers were present. This does not support the hypothesis that Black-headed Weavers affect

313 native *Acrocephalus* warblers by forcing them into sub-optimal habitat.

314 We did not directly assess whether Black-headed Weavers reduce the productivity of native species.

315 Due to the restricted distribution of Black-headed Weavers, it would be difficult to disentangle the

316 effects of Black-headed Weavers from other variables on the productivity of native species. Black-

317 headed Weavers could reduce the productivity of native species by competing for nestling food,

318 without causing displacement. In fact, any feeding competition from weavers is likely to be diffused

319 to some extent as although female weavers foraged mainly in their territories, males often foraged

320 outside their territories (J.P.B. Grundy, pers. obs.). Directly testing whether Black-headed Weavers

321 affect the productivity of native species would provide compelling evidence for or against

322 competition acting at territory level, but is not feasible at the present stage in the invasion.

323 We have only explored a limited range of potential impacts by Black-headed Weavers. Although

324 *Acrocephalus* warblers were the most ecologically similar native species, Black-headed Weavers

325 could also compete for reedbed nesting sites with species such as Savi's Warblers *Locustella*

326 *luscinioides*, and for winter food with a range of native granivorous birds. Aside from competition,

327 Black-headed Weavers could have negative impacts by influencing disease transmission, as they are

328 reservoirs for local haemoparasites (Ventim *et al.* 2012).

329 The apparent coexistence of Black-headed Weavers and *Acrocephalus* warblers may be due to

330 mechanisms that only operate at low population densities. For example, inter-specific territoriality

331 between *Acrocephalus* warblers motivated by factors other than resource defence (Leisler &

332 Schulze-Hagen 2011) reduces their population densities below the resource carrying capacity

333 (Mikami *et al.* 2004). This could allow Black-headed Weavers to colonise without impacting native

334 species, however, it is possible that shared resources become limiting when Black-headed Weavers

335 reach higher population densities.

336

337 **Application to other avian invasions**

338 Pathways from resource overlap to population reduction of native species can be constructed for

339 other non-native species, and could be used to assess the risk posed by newly established species.

340 This can be illustrated using work on two established non-native species as examples. Both Ring-

341 necked Parakeets *Psittacula krameri* and European Starlings *Sturnus vulgaris* nest in tree cavities and

342 so could compete for this resource with native hole-nesters in Europe and North America

343 respectively. If they are dominant at accessing tree cavities then they can potentially limit the

344 availability of nest sites for native species, which if sufficiently scarce could limit the population of
345 these species (Newton 1994). Small scale studies have demonstrated that both European Starlings
346 (Weitzel 1988) and Ring-necked Parakeets (Strubbe & Matthysen 2009) can displace native species
347 from nest sites. European Starlings may cause native species to alter the timing of their breeding or
348 to nest in sub-optimal cavities, although Koch *et al.* (2012) found limited evidence for this. While
349 these studies have been performed when the species are widespread, similar studies could have
350 been carried out in the early stages of both invasions and used to inform management decisions.
351 Our knowledge of the impacts of a non-native species will be refined as a species spreads, as large-
352 scale studies that could provide stronger evidence for competition are possible. For example, large
353 scale studies have shown that the population level impacts of both European Starlings and Ring-
354 necked Parakeets are limited at current densities (Koenig 2003, Newson *et al.* 2011).

355

356 **Challenges with informing management decisions**

357 Information on the potential impacts of non-native species is often limited to anecdotal reports,
358 making risk assessment challenging (Strubbe *et al.* 2011). While some researchers argue for a
359 precautionary, zero tolerance approach to non-native species (Edelaar & Tella 2012), others consider
360 that management actions should relate to the amount of evidence that a non-native species has a
361 negative impact (Bauer & Woog 2011). There is a trade-off between statistical power and timely
362 intervention when investigating the impacts of non-native species. For instance, the individual
363 statistical tests used in this study had low statistical power, so would only have been able to detect
364 impacts with large effect sizes. For example, tendencies for Black-headed Weavers to initiate
365 aggression and approach Great Reed Warbler song may have been non-significant due to low
366 statistical power rather than due to the absence of an effect. The failure to find evidence for
367 negative impacts early in an invasion should not be interpreted as conclusive evidence of absence of
368 negative impacts, due to the risk of type II errors, and the fact that coexistence at low population
369 densities may not persist at high population densities. Repeating this study when Black-headed
370 Weavers are more widespread, and hence with a larger sample size, may allow the detection of
371 small impacts that could not be detected in this study. However, eradication becomes increasingly
372 difficult as a species spreads (Lodge *et al.* 2006), so studies that investigate the early impact of non-
373 native species are important.

374 We recommend taking a pragmatic approach to interpreting the results of studies such as this. As
375 well as testing the statistical significance of hypotheses, we suggest looking at the direction of

376 relationships and magnitude of effect that can be detected given statistical power. This allows

377 identification of species that are showing clear early impacts (i.e. statistically significant results to

378 hypothesis testing), horizon scanning for impacts that may later prove to be significant (i.e. non-

379 significant results in the hypothesised direction), and assessment of uncertainty based on the power

380 of statistical tests. Studies such as this can be performed on multiple species, and the results can be

381 compared in order to prioritise management actions. By testing multiple hypotheses along potential

382 pathways to competitive exclusion we have a clear framework for evaluating the potential for

383 competition, allowing the provision of information to aid management decisions early in the

384 invasion process when eradication is feasible.

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393 **REFERENCES**

394 Adler, P. B., Ellner, S. P. & Levine, J. M. 2010. Coexistence of perennial plants: an embarrassment of
395 niches. Ecol. Lett.,13: 1019-1029.
396 Adler, P. B., HilleRisLambers, J. & Levine, J. M. 2007. A niche for neutrality. Ecol. Lett.,10: 95-104.
397 Bauer, H.-G. & Woog, F. 2011. On the 'invasiveness' of non-native bird species. Ibis,153: 204-206.
398 Bensch, S. & Hasselquist, D. 1991. Territory Infidelity in the Polygynous Great Reed Warbler
399 Acrocephalus arundinaceus: The Effect of Variation in Territory Attractiveness. J. Anim.
400 Ecol.,60: 857-871.
401 Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. & Gaston, K. J. 2004. Avian extinction and
402 mammalian introductions on oceanic islands. Science,305: 1955-1958.
403 Blackburn, T. M., Lockwood, J. L. & Cassey, P. 2009. Avian Invasions: The Ecology and Evolution on
404 Exotic Birds, Oxford: Oxford University Press.
405 Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G.,
406 Thuiller, W., Fortin, M. J., Randin, C., Zimmermann, N. E., Graham, C. H. & Guisan, A. 2012.
407 Measuring ecological niche overlap from occurrence and spatial environmental data. Global
408 Ecol. Biogeogr.,21: 481-497.
409 Cardoso, H. 2008. Ploceus melanocephalus. In Atlas das Aves Nidificantes em Portugal. (ed. Equipa
410 Atlas), pp. 540-541. Lisbon: ICNB.
411 Catchpole, C. K. 1972. A comparative study of territory in the Reed warbler (Acrocephalus scirpaceus)
412 and Sedge warbler (A. schoenobaenus). J. Zool., lond.,166: 213-231.
413 Catchpole, C. K. 1978. Interspecific territorialism and competition in Acrocephalus warblers as
414 revealed by playback experiments in areas of sympatry and allopatry. Anim. Behav.,26:
415 1072-1080.

416 Champely, S. 2007. pwr: Basic functions for power analysis. R package version 1.1.
417 Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annu. Rev. Ecol. Syst.,31: 343-
418   366.
419 Clavero, M., Brotons, L., Pons, P. & Sol, D. 2009. Prominent role of invasive species in avian
420   biodiversity loss. Biol. Conserv.,142: 2043-2049.
421 Clarke, K.R. & Gorley, R.N. 2006. PRIMER v6: User Manual/Tutorial. Plymouth: PRIMER-E.
422 Clarke, K.R. & Warwick, R.M. 1994. Change in marine communities: an approach to statistical
423   analysis and interpretation. Plymouth: Plymouth Marine Laboratory.
424 Constantine, M., van den Berg, A. B. & Robb, M. 2006.The Sound Approach to Birding: A guide to
425   understanding bird sound, Poole: The Sound Approach.
426 Cramp, S. (ed.) 1992. The Birds of the Western Palearctic, Vol. 6. Oxford: Oxford University Press.
427 Defra. 2003. Review of non-native species policy: Report of the working group. London: Department
428   for Environment, Food and Rural Affairs.
429 Dunn, M., Copelston, M. & Workman, L. 2004. Trade-offs and seasonal variation in territorial
430   defence and predator evasion in the European Robin Erithacus rubecula. Ibis,146: 77-84.
431 Dyrcz, A. 1986. Factors affecting facultative polygyny and breeding results in the Great Reed Warbler
432   (Acrocephalus arundinaceus). J. Ornithol.,127: 447-461.
433 Edelaar, P. I. M. & Tella, J. L. 2012. Managing non-native species: don't wait until their impacts are
434   proven. Ibis,154: 635-637.
435 EEA. 2010. Towards an early warning and information system for invasive alien species (IAS)
436   threatening biodiversity in Europe. In EEA Technical report.Vol. 5/2010. Luxembourg:
437   European Environment Agency.
438 Equipa Atlas (2008) Atlas das Aves Nidificantes em Portugal (1999-2005), Lisbon: Instituto da
439   Conservacao da Natureza e da Biodiversivade, Sociedade Portuguesa para o Estudo das
440   Aves, Parque Natural da Madeira e Secretaria Regional do Ambiente e do Mar.
441 ESRI. 2008. ArcGIS Desktop. Environmental Systems Research Institute.
442 Fry, C. H. & Keith, S. (eds.) 2004. The Birds of Africa, London: Christopher Helm.
443 Golabek, K. A., Ridley, A. R. & Radford, A. N. 2012. Food availability affects strength of seasonal
444   territorial behaviour in a cooperatively breeding bird. Anim. Behav.,83: 613-619.
445 Grarock, K., Tidemann, C. R., Wood, J. & Lindenmayer, D. B. 2012. Is It Benign or Is It a Pariah?
446   Empirical Evidence for the Impact of the Common Myna (Acridotheres tristis) on Australian
447   Birds. PLoS ONE,7.
448 Graveland, J. 1996. The decline of an aquatic songbird: The Great Reed Warbler Acrocephalus
449   arundinaceus in the Netherlands. Limosa,69: 85-96.
450 Graveland, J. 1998. Reed die-back, water level management and the decline of the great reed
451   warbler Acrocephalus arundinaceus in the Netherlands. Ardea,86: 187-202.
452 Griswold, M. W. & Lounibos, L. P. 2005. Does differential predation permit invasive and native
453   mosquito larvae to coexist in Florida? Ecol. Entomol.,30: 122-127.
454 Hilton, G. M. & Cuthbert, R. J. 2010. The catastrophic impact of invasive mammalian predators on
455   birds of the UK Overseas Territories: a review and synthesis. Ibis,152: 443-458.
456 Hothorn, T., Bretz, F. & Westfall, P. 2008. Simultaneous Inference in General Parametric Models.
457   Biometrical J.,50: 346-363.
458 Ieronymidou, C., Collar, N. J. & Dolman, P. M. 2012. Endemic Cyprus Warbler Sylvia melanothorax
459   and colonizing Sardinian Warbler Sylvia melanocephala show different habitat associations.
460   Ibis, 154, 248-259.
461 Instituto Geográfico Português. 2004. AirPhoto 2004. Lisbon.
462 Koch, A. J., Martin, K. & Aitken, K. E. H. 2012. The relationship between introduced European
463   Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British
464   Columbia, Canada. Ibis,154: 590-600.
465 Koenig, W. D. 2003. European Starlings and Their Effect on Native Cavity-Nesting Birds. Conserv.
466   Biol.,17: 1134-1140.

467   Kumschick, S. & Nentwig, W. 2010. Some alien birds have as severe an impact as the most effectual
468   alien mammals in Europe. Biol. Conserv.,143: 2757-2762.
469   Leisler, B. & Schulze-Hagen, K. 2011. The Reed Warblers: Diversity in a uniform bird family, Utrecht:
470   KNNV Publishing.
471   Lodge, D. M., Williams, S., MacIsaac, H. J., Hayes, K. R., Leung, B., Reichard, S., Mack, R. N., Moyle, P.
472   B., Smith, M., Andow, D. A., Carlton, J. T. & McMichael, A. 2006. Biological invasions:
473   Recommendations for US policy and management. Ecol. Appl.,16: 2035-2054.
474   Marchant, J. H. 1983.BTO Common Birds Census Instructions, Thetford: BTO.
475   Marshall, M. R. & Cooper, R. J. 2004. Territory size of a migratory songbird in response to caterpillar
476   density and foliage structure. Ecology,85: 432-445.
477   Marti, R. & de Moral, J. C. (eds.) 2003. Atlas de las Aves Reproductoras de Espana, Madrid: Dirección
478   General de Conservación de la Naturaleza-Sociedad Española de Ornithología.
479   Martinez-Vilalta, J., Bertolero, A., Bigas, D., Paquet, J.-Y. & Martinez-Vilalta, A. 2002. Habitat
480   selection of the passerine community nesting at the Ebro delta reed-beds (NE Spain): some
481   management implications. Wetlands,22: 318-325.
482   Matias, R. 2002. Aves exóticas que nidificam em Portugal continental, Lisbon: ICNB.
483   Mikami, O. K., Kohda, M. & Kawata, M. 2004. A new hypothesis for species coexistence: male-male
484   repulsion promotes coexistence of competing species. Popul. Ecol.,46: 213-217.
485   Moreau, R. E. 1960. Conspectus and classification of the Ploceine weaver-birds. Ibis,102: 298-321.
486   Newson, S. E., Johnston, A., Parrott, D. & Leech, D. I. 2011. Evaluating the population-level impact of
487   an invasive species, Ring-necked Parakeet Psittacula krameri, on native avifauna. Ibis,153:
488   509-516.
489   Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds - a review. Biol.
490   Conserv.,70: 265-276.
491   Poulin, B., Lefebvre, G. & Mauchamp, A. 2002. Habitat requirements of passerines and reedbed
492   management in southern France. Biol. Conserv.,107: 315-325.
493   R Development Core Team. 2012. R: A language and environment for statistical computing. Vienna:
494   R Foundation for Statistical Computing.
495   Robbins, C. S. 1981. Effect of time of day on bird activity. In Ralph, C.J. & Scott, J.M. Estimating
496   Numbers of Terrestrial Birds. Lanham, USA: Cooper Square Press.
497   Roche, J.-C. 1997.The Bird Songs and Calls of Britain and Europe, Mens: Sittelle.
498   Schoener, T. W. 1970. Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats. Ecology,51:
499   408-418.
500   Sixth Conference of the Parties Convention on Biological Diversity. 2002. Sixth Ordinary Meeting of
501   the Conference of the Parties to the Convention on Biological Diversity. The Hague,
502   Netherlands.
503   Strubbe, D. & Matthysen, E. 2009. Experimental evidence for nest-site competition between invasive
504   ring-necked parakeets (Psittacula krameri) and native nuthatches (Sitta europaea). Biol.
505   Conserv.,142: 1588-1594.
506   Strubbe, D., Shwartz, A. & Chiron, F. 2011. Concerns regarding the scientific evidence informing
507   impact risk assessment and management recommendations for invasive birds. Biol.
508   Conserv.,144: 2112-2118.
509   Sullivan, M.J.P., Grundy, J. & Franco, A.M.A. In press. Assessing the impacts of the non-native Black-
510   headed Weaver on native *Acrocephalus* warblers. Ibis.
511   Unep. 1992. Rio Declaration on Enviornment and Development. United Nations Environment
512   Programme.
513   Ventim, R., Mendes, L., Ramos, J., Cardoso, H. & Pérez-Tris, J. 2012. Local haemoparasites in
514   introduced wetland passerines. J. Ornithol., 153: 1253-1259.
515   Wang, Y., Naumann, U., Wright, S. T. & Warton, D. I. 2012. mvabund– an R package for model-based
516   analysis of multivariate abundance data. Methods Ecol. Evol.,3: 471-474.

517 Warren, D. L., Glor, R. E. & Turelli, M. 2008. Environmental niche equivalency versus conservatism:
518   quantitative approaches to niche evolution. Evolution,62: 2868-2883.
519 Weitzel, N. H. 1988. Nest-Site Competition between the European Starling and Native Breeding Birds
520   in Northwestern Nevada. The Condor,90: 515-517.
521 Wiens, J. A. 1989.The Ecology of Bird Communities, Cambridge: Cambridge University Press.

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524 **Supporting Information**

525 Additional Supporting Information may be found in the online version of this article:

526   **Appendix S1.** Details of the method used to generate simulated territories.

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529 the corresponding author for the article.

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548 **TABLES**

549 **Table 1.**Overlap (Schoener's D) between territories of Reed Warbler, Great Reed Warbler and Black-

550 headed Weaver in habitat space.

	Black-headed Weaver	Great Reed Warbler
Reed Warbler	0.725	0.527
Great Reed Warbler	0.544	

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569   **FIGURE LEGENDS**

570   **Figure 1.** Potential pathways by which Black-headed Weavers (BHWs) may impact the population of

571   native *Acrocephalus* warblers. Overlapping resource requirements are shown by ovals, processes are

572   shown by rectangles connected by solid arrows. Hypotheses are linked to the relevant process by

573   dashed arrows. Supported hypotheses (see results) are shown in bold.

574

575   **Figure 2.** NMDS ordination of habitat characteristics in target species territories. Stress=0.08. (A)

576   Position of target species territories and unoccupied background reedbed in NMDS space. (B)

577   Position of Reed Warbler territories in NMDS space at sites where Black-headed Weavers were

578   present and absent. (C) Position of Great Reed Warbler territories in NMDS space at sites where

579   Black-headed Weavers were present and absent. (D) Relationship between habitat variables and the

580   NMDS space. Arrows show the direction of relationships between habitat variables and

581   environmental space. Arrow lengths were only selected for presentation purposes. RHn, height of

582   new reeds (cm); Rho, height of old reeds (cm); RDn, diameter of new reeds (mm); RDo, diameter of

583   old reeds (mm); Dn, density of new reeds; Do, density of old reeds; RC, percentage cover of reeds;

584   HC, percentage cover of herbaceous plants; GC, percentage cover of grasses; EC, percentage cover of

585   emergent vegetation excluding reeds; WC, percentage cover of woody vegetation.

586

587   **Figure 3.** Response of male Black-headed Weavers to playback treatments. Mean responses are

588   plotted, with error bars showing the standard error. *P* values show how significant the difference

589   between the response to each treatment was from the response to background noise, and were

590   calculated using a generalised linear mixed model modelling the increased approach as a function of

591   treatment, with territory identity as a random effect. BHW, Black-headed Weaver; GRW, Great Reed

592   Warbler; RW, Reed Warbler.

593

594 **Figure 4.** Mean ± SE territory sizes of (A) Great Reed Warblers and (B) Reed Warblers at the study

595 sites. Extensive wetland sites are plotted with squares; ditch-crossed sites are plotted with circles.

596 Filled shapes denote sites where Black-headed Weavers are present, and unfilled shapes denote

597 sites where they are absent. Letters indicate sites that did not significantly differ (i.e. $P > 0.05$) in

598 post-hoc tests performed on each species.