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1 **Running head:** *Investigating impacts of non-native species*

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.

26 **Keywords:** Invasive species, risk assessment, competition, coexistence, *Acrocephalus* warblers

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31 Non-native species are major drivers of avian biodiversity loss (Clavero *et al.* 2009). While some of
32 the most severe impacts have been caused by introduced mammalian predators (Blackburn *et al.*
33 2004, Hilton and Cuthbert 2010), exotic birds can impact native species through a number of
34 mechanisms, such as predation, hybridisation and transmission of disease (Kumschick & Nentwig
35 2010). Although rarely demonstrated, non-native birds have also been suspected of competing with
36 native species (Blackburn *et al.* 2009). For example, the establishment of the Common Myna
37 *Acridotheres tristis* in Australia was followed by a decline in the abundance of a number of native
38 bird species (Garrock *et al.* 2012). Whether species compete depends on the degree to which niche
39 differences result in one species limiting their own population more than the populations of other
40 species (Chesson 2000, Adler *et al.* 2007), the degree of asymmetry in the competitive weights of
41 species (Adler *et al.* 2007), and the presence of other mechanisms such as predation that limit the
42 population of one species more than others (Griswold & Lounibos 2005). Competitive exclusion is
43 likely when species share similar resource requirements (Ieronymidou *et al.* 2012), and one species
44 is either dominant at accessing those resources, or has a faster reproduction rate (Chesson 2000,
45 Adler *et al.* 2010).

46 It is desirable to identify whether a non-native species will compete with native species early in the
47 invasion process, while the non-native species has a restricted distribution and eradication remains
48 feasible (Lodge *et al.* 2006). However, it is easier to evaluate impacts when an invasion is advanced,
49 as more data are available, allowing competition to be identified with more confidence (Wiens 1989).
50 This leads to a trade-off between early risk assessment and the strength of evidence for
51 demonstrating the existence of an impact. While this has motivated researchers and policy makers
52 to suggest that lack of scientific certainty should not preclude control of non-native species (UNEP
53 1992, Sixth Conference of the Parties Convention on Biological Diversity 2002, Edelaar & Tella 2012),
54 eradication is costly and poses animal welfare issues (Defra 2003), leading to recognition that it is
55 desirable to have an evidence base to prioritise and justify management actions (Defra 2003, EEA
56 2010). Thus there is need to use scientific evidence collected early in the invasion process to aid
57 management decisions. This is especially pressing in the Iberian Peninsula, where the number of
58 non-native birds species recorded breeding has increased rapidly since the late 1980s (Matias 2002).

59 We assess the evidence for competition between the recently established Black-headed Weaver
60 *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 10km² 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 *Phragmites 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 (m²) 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 (Dyrzc 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 `manyglm` 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

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

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

226 **RESULTS**

227 **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

234 **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 ($\text{Overlap}_{\text{OBS}} = 0.256$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P = 0.01$) but not significantly different than expected
245 at PT ($\text{Overlap}_{\text{OBS}} = 0.011$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P = 0.43$). Overlap between Eurasian Reed Warbler
246 and Black-headed Weaver territories was higher than expected if territories were randomly
247 distributed at both PT ($\text{Overlap}_{\text{OBS}} = 0.046$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P < 0.001$) and BA ($\text{Overlap}_{\text{OBS}} = 0.327$,
248 $\text{Overlap}_{\text{NULL-Median}} = 0$, $P < 0.001$).

249

250 **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 $\geq 1.07m$ 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 (Dyrz 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 *luscinoides*, 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.

385

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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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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 \pm 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.