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Testing multiple pathways for impacts of the non-native Black-headed Weaver *Ploceus melanocephalus* on native birds in the early phase of invasion

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Some, but not all non-native species have strong negative impacts on native species. It is desirable to identify whether a non-native species will have a negative impact at an early stage in the invasion process, while management options such as eradication are still available. Although it may be difficult to detect early impacts of non-native species, this is necessary to ensure that management decisions can be based on case-specific scientific evidence. We investigate the impacts of a non-native bird, the Black-headed Weaver *Ploceus melanocephalus*, at an early stage in its invasion of the Iberian Peninsula. To do this we, a priori, identify potential pathways by which competition for shared resources by Black-headed Weavers could lead to population declines in ecologically similar native species, and generate hypotheses to test for evidence of competition along these pathways. Black-headed Weavers could potentially impact native species by displacing them from nesting habitat, or by locally reducing habitat quality. We did not find evidence for either potential competition pathway, suggesting that Black-headed Weavers do not currently compete with native species. However, it is possible that mechanisms that currently allow coexistence may not operate once Black-headed Weavers reach higher population densities or different habitats.

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

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 to sub-Saharan Africa, and were first recorded in the Iberian Peninsula in the mid-1990s (Matias 2002). Breeding was confirmed in fewer than ten 10km^2 grid cells in the most recent Portuguese and Spanish breeding bird atlases (Marti & de Moral 2003, Equipa Atlas 2008). Black-headed Weavers nest in emergent vegetation (Colias & Colias 1964) and feed their nestlings on large invertebrates collected primarily by gleaning vegetation (Moreau 1960, Fry & Keith 2004), so share resource requirements with native Great Reed Warblers *Acrocephalus arundinaceus* and Eurasian Reed Warblers *A. scirpaceus* (Graveland, 1996, Matias 2002, Cardoso 2008, Leisler & Schulze-Hagen 2011). Black-headed Weavers have been reported behaving aggressively towards both species (Matias 2002). While this could indicate that they are dominant at accessing shared resources, this has not been tested.

At the current stage of invasion we cannot test the influence of Black-headed Weavers on the productivity of native species, so instead focus on detecting behavioural responses to competition. Our approach involves identifying possible pathways by which shared resource requirements could lead to population declines of native species, and generating testable hypotheses for processes along these pathways (Fig. 1). We test each of the following numbered hypotheses. We first test whether resource requirements of Black-headed Weavers overlap with native species (Fig. 1, Hypothesis 1). We speculate that this could have a negative impact on native species if Black-headed Weavers exhibit interspecific territoriality and thereby exclude native species (Fig. 1, Hypotheses 2-4), or locally reduce habitat quality (Fig. 1, Hypotheses 5-6). Both of these could lead to population declines either by forcing native species to nest in sub-optimal habitat (Fig. 1, Hypothesis 7), or by directly reducing the space available for native species. By testing for competition at a range of stages along these pathways we can maximise our ability to detect competition, and have a useful framework for assessing the potential for competitive exclusion.

METHODS

Study sites

Fieldwork was conducted at four sites in western Portugal. Black-headed Weavers have been established at Paul de Tornada (PT, 39.448° N, 9.135° W) and Barroca d'Alva (BA, 38.729° N, 8.899° W) since the mid-1990s (Matias 2002). Uncolonised sites, with similar habitat and within 20km of colonised sites, were selected as controls. These were Lagoa de Óbidos (LO, 39.385° N, 9.210° W) and Lezíria Grande (LG, 38.931° N, 8.964° W). PT and LO are both extensive wetlands, consisting of patchworks of reedbed (dominated by reed *Phragmities australis)* and open water. BA and LG both consist of reed lined ditches crossing a mix of rice and wheat cultivation and pasture. The colonised study sites selected have high population densities of Black-headed Weavers and native *Acrocephalus* warblers, so potentially provide the best data available on the interaction of Black-headed Weavers and native species. Fieldwork was not conducted at other sites colonised by Black-headed Weavers as they either were unsuitable for Reed Warblers and Great Reed Warblers, or were ecologically sensitive sites.

Playback experiment and aggressive interactions

If Black-headed Weavers exhibited interspecific territoriality towards native species we would expect them to initiate aggressive interactions with native species, and possibly also respond to heterospecific song. To test whether Black-headed Weavers initiated aggressive interactions with native species (hypothesis two) all incidents of aggression between Black-headed Weavers and native species observed during fieldwork were recorded. Where possible, the species initiating aggression was noted. A binomial test was used to test whether the proportion of aggressive interactions differed from random expectation.

In order to test hypothesis three we conducted a playback experiment to test the reaction of Black-headed Weavers to conspecific and heterospecific song in May 2012, during the weaver breeding season. Songs of Black-headed Weaver, Great Reed Warbler (from Constantine *et al.* 2006) and Eurasian Reed Warbler (from Roche 1997), as well as a recording of background noise made at night at PT, were played from a portable speaker placed five metres away from Black-headed Weaver nests. The quality of warbler recordings was checked by playing these recordings within conspecific territories, and both elicited a reaction. Each recording was played for five minutes, as Catchpole (1978) found this was sufficient time to elicit a response from Eurasian Reed Warblers. Playback experiments were videoed, and the distance of closest approach by Black-headed Weavers during the playback was estimated to the nearest metre.

The responses of Black-headed Weavers from 16 territories (eight at PT and eight at BA) were tested over a three day period to reduce seasonal variation in individual motivation to respond (Dunn *et al.* 2004, Golabek *et al.* 2012). To minimise the effect of habituation, no more than two recordings were played in each territory in one day, with one recording played in the morning and one in the evening. To further control for habituation, the order in which recordings were played was balanced across the 16 territories.

We modelled the distance of approach (m) by Black-headed Weavers as a function of playback treatment using a generalised linear mixed model, with territory identity as a random effect. Data from both sites were pooled as site identity was not significant when included in the previous model ($t_{44} = 0.521$, $P = 0.605$). Due to convergence issues, the model was fitted using quasi-likelihood, with the mean-variance relationship set so that the variance increased with the mean.

Territory and habitat mapping

We made 12 territory mapping visits to each site between early April and late June 2012 (i.e. from territory establishment to nesting) to record the locations of Black-headed Weaver, Great Reed Warbler and Eurasian Reed Warbler territories. Sites were visited during the morning active period (Robbins 1981), and observations of target species were mapped onto a base map with the aid of a handheld GPS unit. We assigned these observations to territories following Marchant (1983).

We only used observations of singing, fighting or territorial calling birds for determining territory size. Observations were digitised using ArcMap 9.3 (ESRI 2008), and projected onto a Universal Transverse Mercator grid (zone 29N). We calculated the territory centroid by taking the mean of the coordinates of these observations, and delimited territory boundaries by constructing the minimum convex polygon (MCP) that encompassed observations from each territory. Aerial photographs (1 m resolution, Instituto Geográfico Português 2004) were digitised to produce vector maps of reedbed at each site, which were updated based on field observations where there had been large changes in reedbed extent. These maps were used to clip territory MCPs so that they only contained reedbed. We did this so that territories reflected utilisation distributions more closely; areas of open water and agriculture were rarely used by *Acrocephalus* warblers (J.P.B. Grundy pers. obs.), so contributed very little to the resources available to breeding birds.

To test hypothesis four, territory overlap between pairs of species was calculated by dividing the area occupied by both species by the total area occupied by either species. This calculation was performed on a raster grid (~5m resolution), rather than directly on the vector layers, to aid comparison with a null model. The purpose of the null model was to randomly shift the position of each territory, while maintaining the number of territories at each site, observed territory size and restricting territories to be in reedbed. Further details of the null model mechanism are given in Supporting Information Appendix S1. The null model did not restrict intraspecific territory overlap, but overlap of randomly generated conspecific territories was still similar to observed overlap. The null model was run for 1000 iterations, and the overlap between heterospecific territories was calculated in each case, to give a null distribution of overlap values. Competitive exclusion will lead to lower than expected observed values, while selection of similar reedbed habitat will lead to greater observed values than expected. Two-tailed *P*-values were calculated by comparing the observed overlap to quantiles of this null distribution.

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

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

Habitat sampling

Seven territories of each species, corresponding to the minimum number of Great Reed Warbler territories at any one of our study sites, and seven areas of unoccupied reedbed were randomly chosen at each site. At each location habitat variables were measured in one randomly placed 50 x 50 cm quadrat, with the exception of two quadrats being placed in Great Reed Warbler territories because of their larger territory size (Cramp, 1992). In each quadrat, we measured the height (cm) of ten new (current season's growth) and ten old (previous season's growth) reeds, the diameter (mm) of ten new and ten old reeds, the density of new and old reeds (measured by counting all reeds within the quadrat), and the percentage cover of reeds, other emergent vegetation, herbaceous plants, woody plants and grasses (estimated visually). These were selected as habitat variables that had been identified as being important for the target species (Dyrcz 1986, Graveland 1996, Martinez-Vilalta *et al.* 2002, Poulin *et al.* 2002), and considered to capture variation in reedbed habitat. Water depth is also an important influence on Great Reed Warbler nest site selection (Graveland 1998), but management of agricultural ditches caused water levels to fluctuate between days at our study sites, so this variable was not included in analyses.

Differences in habitat between species (hypotheses one) were identified using non-metric multidimensional scaling (NMDS), performed in PRIMER v6 (Clarke & Gorley 2006) based on a Euclidean distance matrix generated from the habitat variables. NMDS allows dissimilarities to be mapped in two dimensions. Stress values assess the fit between distances in the distance matrix and those in two dimensional space. Stress values of less than 0.1 indicate a good fit (Clarke & Warwick 1994); the stress value of 0.08 in this study therefore indicates good fit. We investigated how areas of NMDS space related to different habitat characteristics by modelling the matrix of raw habitat variables as a function of NMDS coordinates using the manylm function in the R package mvabund (Wang *et al.* 2012), and plotting the direction of these relationships. We used *D* (Schoener 1970) to calculate the overlap in habitat associations of the three species. To do this, a kernel density function was used to calculate the density of territories of each species in habitat space. *D* is then calculated as

$$D = 1 - ½(\sum_{ij} |z_{1ij} – z_{2ij}|),$$

where z_{1ij} is the standardised territory density of species one and z_{2ij} is the standardised territory density of species two at point *ij* in environmental space. Full details on the calculation of *D* are given in Broennimann *et al.* (2012). *D* ranges from zero to one, with values closer to one indicating higher overlap. We tested whether the overlap between habitat associations of native species shifted to be less similar to those of Black-headed Weavers at sites where Black-headed Weavers are present (hypotheses seven). To do this, we compared observed values of *D* for the overlap between the densities of territories of native species and Black-headed Weavers at sites where Black-headed Weavers were present to values of *D* generated in 1000 iterations of a null model that randomly allocates observations to groups while maintaining the original number of observations in each group (the identity test, Warren *et al.* 2008).

Having multiple sampling points in Great Reed Warbler territories (due to their larger territory size than other study species) allowed us to test whether variation between territories of the same species was greater than variation within territories. Sampling points within the same Great Reed Warbler territory had more similar habitat characteristics than sampling points in different territories (median Euclidean distance within territories = 77.9, median Euclidean distance between territories = 97.0, Wilcoxon test, $P = 0.076$), justifying the decision to concentrate sampling effort on maximising the number of territories sampled, rather than sampling more points within a territory. Unless otherwise stated, all statistical analyses were performed in R v2.15 (R Development Core Team 2012), with power analyses performed using the package pwr (Champely 2007).

RESULTS

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

Great Reed Warblers occupied less habitat space than the other species (Fig. 2a). Great Reed Warbler territories were characterised by having taller and thicker reeds, although both Eurasian Reed Warblers and Black-headed Weavers also used this habitat (Fig. 2a & d). Black-headed Weaver and Eurasian Reed Warbler territories overlapped in habitat space more than either species overlapped with Great Reed Warblers (Table 1). These results support hypothesis one (Fig. 1).

Is there interspecific territoriality?

Limited support was found for hypotheses two and three (Fig. 1). Aggressive interactions were rarely noted between Black-headed Weavers and native species; in over 120 hours of fieldwork, seven aggressive interactions were observed. In five out of the six occasions where the aggressor was observed, Black-headed Weavers initiated aggression (Binomial test, $P = 0.219$). Black-headed Weavers approached conspecific song ($t_{44}=2.642$, $P = 0.011$, Fig. 3), but not heterospecific song ($t_{44} \leq 1.723$, $P \geq 0.092$, Fig. 3) significantly more than background noise.

Observed territory overlap was never lower than expected if territories were randomly distributed, so no support was found for hypothesis four (Fig. 1). Overlap between Great Reed Warbler and Black-headed Weaver territories was higher than expected if territories were randomly distributed at BA ($\text{Overlap}_{\text{OBS}} = 0.256$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P = 0.01$) but not significantly different than expected at PT ($\text{Overlap}_{\text{OBS}} = 0.011$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P = 0.43$). Overlap between Eurasian Reed Warbler and Black-headed Weaver territories was higher than expected if territories were randomly distributed at both PT ($\text{Overlap}_{\text{OBS}} = 0.046$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P < 0.001$) and BA ($\text{Overlap}_{\text{OBS}} = 0.327$, $\text{Overlap}_{\text{NULL-Median}} = 0$, $P < 0.001$).

Do Black-headed Weavers reduce habitat quality?

No support was found for hypotheses five, six and seven (Fig. 1). Great Reed Warbler territory occupation date did not vary significantly between sites ($F_{1, 10}$ = 1.45, P = 0.256). The distance to the nearest Black-headed Weaver territory did not influence territory occupation date of Great Reed Warblers ($F_{1, 10}$ < 0.01, P = 0.951). This result was robust to measurement error caused by gaps between territory mapping visits, as no significant relationships were observed in any permutation of possible occupation dates.

Both Eurasian Reed Warbler and Great Reed Warbler territories were larger in extensive wetland sites than ditch-crossed sites (Fig. 4). Territory size was not affected by the presence of Black-headed Weavers (Fig. 4).

Neither Eurasian Reed Warbler (D_{OBS} = 0.791, $D_{NULL\text{-}Median}$ = 0.715, P = 0.164, Fig. 2b) nor Great Reed Warbler (D_{OBS} = 0.629, $D_{NULL\text{-}Median}$ = 0.546, P = 0.170, Fig. 2c) territories shifted to be more or less similar to Black-headed Weaver territories at sites where Black-headed Weavers were present.

Power analysis

Non-significant results in the direction expected by our hypotheses were found for the response of Black-headed Weavers to native species' songs, and the proportion of aggressive interactions initiated by Black-headed Weavers. We were only able to detect large effect sizes in these analyses; the former analysis had sufficient power to identify mean approaches of $\geq$ 1.07m as being significantly different from responses to background noise, while the latter analysis would only be significant if all aggressive interactions were initiated by Black-headed Weavers.

DISCUSSION

Evidence for pathways to competition

Whilst there was overlap in the habitat characteristics of territories of Black-headed Weavers and native *Acrocephalus* warblers, we did not find any statistically significant evidence to support the hypothesis that competition by Black-headed Weavers is currently having population impacts on native species. We therefore conclude that at current population densities (0.43 to 0.70 pairs ha^{-1} in our study sites, Sullivan *et al*. in press) Black-headed Weavers are unlikely to have a negative impact on ecologically similar native species.

The habitat characteristics of Eurasian Reed Warbler and Great Reed Warbler territories were similar to those reported in previous studies (Graveland 1996, Leisler & Schulze-Hagen 2011). Great Reed Warblers occupied areas with tall, thick reeds, often associated with the water-facing margin of reedbeds (Graveland, 1998). Eurasian Reed Warblers and Black-headed Weavers occupied these areas, but were also found in areas of reedbed that were encroached by terrestrial vegetation (Fig. 2). Eurasian Reed Warblers were the main species that occupied dense reed, which is often associated with the land-facing margin of reedbeds (Leisler & Schulze-Hagen 2011). Because all three species overlapped in habitat requirements, they are likely to select similar areas of reedbed, which may explain the higher than expected spatial overlap between heterospecific territories at some sites.

The larger size of Eurasian Reed Warbler and Great Reed Warbler territories in extensive reedbeds compared to reed-lined ditches supports previous studies (Dyrcz 1986). Food depletion by Black-headed Weavers could cause native species to increase the size of their territories (Marshall & Cooper 2004), but we did not find any evidence for this.

Although there is anecdotal evidence of Black-headed Weavers displaying aggression towards native species, we found little evidence for this. The results of the playback experiment did not support the hypothesis that Black-headed Weavers respond to native species song. The recordings of Eurasian Reed Warbler and Great Reed Warbler song used in the playback experiment elicit a response from conspecifics, but did not lead to a statistically significant response from Black-headed Weavers. This could be a type II error, as there was a weak tendency for Black-headed Weavers to approach Great Reed Warbler song, but the response was less strong than to conspecific song. It is unlikely that visual stimuli were required to evoke territorial behaviour towards heterospecifics, as aggressive interactions were rarely noted. Additionally, Black-headed Weavers were frequently observed close to native species without being aggressive (J.P.B. Grundy pers. obs.). Therefore, at present there is little support for territorial defence against reed warblers by Black-headed Weavers.

The proximity to Black-headed Weavers did not influence the attractiveness of territories to returning male Great Reed Warblers. Great Reed Warblers are philopatric to their natal site (Bensch & Hasselquist 1991), so have information about the quality of reedbed patches from previous years. The locations of Black-headed Weaver territories are fairly consistent between years (M.J.P. Sullivan unpubl. data), so if they reduced Great Reed Warbler productivity this information would be available to returning Great Reed Warblers. Neither Eurasian Reed Warblers nor Great Reed Warblers shifted into habitat less similar to Black-headed Weavers at sites where Black-headed

Weavers were present. This does not support the hypothesis that Black-headed Weavers affect native *Acrocephalus* warblers by forcing them into sub-optimal habitat.

We did not directly assess whether Black-headed Weavers reduce the productivity of native species. Due to the restricted distribution of Black-headed Weavers, it would be difficult to disentangle the effects of Black-headed Weavers from other variables on the productivity of native species. Black-headed Weavers could reduce the productivity of native species by competing for nestling food, without causing displacement. In fact, any feeding competition from weavers is likely to be diffused to some extent as although female weavers foraged mainly in their territories, males often foraged outside their territories (J.P.B. Grundy, pers. obs.). Directly testing whether Black-headed Weavers affect the productivity of native species would provide compelling evidence for or against competition acting at territory level, but is not feasible at the present stage in the invasion.

We have only explored a limited range of potential impacts by Black-headed Weavers. Although *Acrocephalus* warblers were the most ecologically similar native species, Black-headed Weavers could also compete for reedbed nesting sites with species such as Savi's Warblers *Locustella luscinioides*, and for winter food with a range of native granivorous birds. Aside from competition, Black-headed Weavers could have negative impacts by influencing disease transmission, as they are reservoirs for local haemoparasites (Ventim *et al.* 2012).

The apparent coexistence of Black-headed Weavers and *Acrocephalus* warblers may be due to mechanisms that only operate at low population densities. For example, inter-specific territoriality between *Acrocephalus* warblers motivated by factors other than resource defence (Leisler & Schulze-Hagen 2011) reduces their population densities below the resource carrying capacity (Mikami *et al.* 2004). This could allow Black-headed Weavers to colonise without impacting native species, however, it is possible that shared resources become limiting when Black-headed Weavers reach higher population densities.

Application to other avian invasions

Pathways from resource overlap to population reduction of native species can be constructed for other non-native species, and could be used to assess the risk posed by newly established species. This can be illustrated using work on two established non-native species as examples. Both Ring-necked Parakeets *Psittacula krameri* and European Starlings *Sturnus vulgaris* nest in tree cavities and so could compete for this resource with native hole-nesters in Europe and North America respectively. If they are dominant at accessing tree cavities then they can potentially limit the availability of nest sites for native species, which if sufficiently scarce could limit the population of these species (Newton 1994). Small scale studies have demonstrated that both European Starlings (Weitzel 1988) and Ring-necked Parakeets (Strubbe & Matthysen 2009) can displace native species from nest sites. European Starlings may cause native species to alter the timing of their breeding or to nest in sub-optimal cavities, although Koch *et al.* (2012) found limited evidence for this. While these studies have been performed when the species are widespread, similar studies could have been carried out in the early stages of both invasions and used to inform management decisions. Our knowledge of the impacts of a non-native species will be refined as a species spreads, as large-scale studies that could provide stronger evidence for competition are possible. For example, large scale studies have shown that the population level impacts of both European Starlings and Ring-necked Parakeets are limited at current densities (Koenig 2003, Newson *et al.* 2011).

Challenges with informing management decisions

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

We recommend taking a pragmatic approach to interpreting the results of studies such as this. As well as testing the statistical significance of hypotheses, we suggest looking at the direction of relationships and magnitude of effect that can be detected given statistical power. This allows identification of species that are showing clear early impacts (i.e. statistically significant results to hypothesis testing), horizon scanning for impacts that may later prove to be significant (i.e. non-significant results in the hypothesised direction), and assessment of uncertainty based on the power of statistical tests. Studies such as this can be performed on multiple species, and the results can be compared in order to prioritise management actions. By testing multiple hypotheses along potential pathways to competitive exclusion we have a clear framework for evaluating the potential for competition, allowing the provision of information to aid management decisions early in the invasion process when eradication is feasible.

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Supporting Information

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

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

TABLES

Table 1. Overlap (Schoener’s D) between territories of Reed Warbler, Great Reed Warbler and Black-headed Weaver in habitat space.

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

FIGURE LEGENDS

Figure 1. Potential pathways by which Black-headed Weavers (BHWs) may impact the population of native *Acrocephalus* warblers. Overlapping resource requirements are shown by ovals, processes are shown by rectangles connected by solid arrows. Hypotheses are linked to the relevant process by dashed arrows. Supported hypotheses (see results) are shown in bold.

Figure 2. NMDS ordination of habitat characteristics in target species territories. Stress=0.08. (A) Position of target species territories and unoccupied background reedbed in NMDS space. (B) Position of Reed Warbler territories in NMDS space at sites where Black-headed Weavers were present and absent. (C) Position of Great Reed Warbler territories in NMDS space at sites where Black-headed Weavers were present and absent. (D) Relationship between habitat variables and the NMDS space. Arrows show the direction of relationships between habitat variables and environmental space. Arrow lengths were only selected for presentation purposes. RHn, height of new reeds (cm); Rho, height of old reeds (cm); RDn, diameter of new reeds (mm); RDo, diameter of old reeds (mm); Dn, density of new reeds; Do, density of old reeds; RC, percentage cover of reeds; HC, percentage cover of herbaceous plants; GC, percentage cover of grasses; EC, percentage cover of emergent vegetation excluding reeds; WC, percentage cover of woody vegetation.

Figure 3. Response of male Black-headed Weavers to playback treatments. Mean responses are plotted, with error bars showing the standard error. *P* values show how significant the difference between the response to each treatment was from the response to background noise, and were calculated using a generalised linear mixed model modelling the increased approach as a function of treatment, with territory identity as a random effect. BHW, Black-headed Weaver; GRW, Great Reed Warbler; RW, Reed Warbler.

Figure 4. Mean ± SE territory sizes of (A) Great Reed Warblers and (B) Reed Warblers at the study sites. Extensive wetland sites are plotted with squares; ditch-crossed sites are plotted with circles. Filled shapes denote sites where Black-headed Weavers are present, and unfilled shapes denote sites where they are absent. Letters indicate sites that did not significantly differ (i.e. $P > 0.05$) in post-hoc tests performed on each species.