**The empty temporal niche: breeding phenology differs between coexisting native
and invasive birds**

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ABSTRACT

Invasive species face new environmental conditions in their areas of introduction. A correct timing of reproduction is crucial for the successful adjustment of individuals to their environments, yet the temporal aspects of the niche are a neglected subject in the study of biological invasions. When introduced, exotic species could successfully invade new habitats by making use of ecological opportunities, e.g. empty temporal Eltonian niches. Specifically, they may achieve this via conservatism of their native reproductive phenology and/or via plasticity in their reproductive timing. Here we compare the reproductive phenology of a marshland passerine community composed of five successfully established tropical exotic species and twelve coexisting Mediterranean native species along four consecutive years. Both groups showed large differences in their phenology, with exotics reproducing along more months and later in the year than natives. One exotic species even breeds only in late summer and early autumn, when virtually all natives have ceased breeding and when overall bird abundance as well as primary production in cultivated areas (rice fields) were highest. Nonetheless, estimates of population sizes and juvenile survival rates in the study area suggest that late breeding is not maladaptive but instead highly successful. The striking difference in reproductive timing suggests that the exotics may be taking advantage of a vacant Eltonian temporal niche, possibly generated by high resource availability in human-transformed habitats (rice fields and other croplands) in the study area. This study highlights the need to also consider the temporal aspects of the niche when studying invasions.

Keywords: timing of reproduction, temporal niche, biological invasions, Grinnellian and Eltonian niche, niche conservatism, weaver.

INTRODUCTION

The adjustment of species to new environments is a central topic in ecology, evolution and conservation biology (Parmesan 2006; Williams 2008). Exotic species provide unique opportunities to assess how species face novel biotic and abiotic conditions and shift or conserve their niches (Sax et al. 2005; Lockwood et al. 2007; Blackburn et al. 2009; Larson et al. 2010). Two niche components have been clearly recognized: Grinnellian niches describe the species' responses to the non-interacting environmental variables (e.g. climate) that influence their large-scale geographical distribution; and Eltonian niches describe the functional role and biotic interactions of species (Soberón 2007).

When exotic species are confronted with novel environments to which they need to adjust, they may either keep their niche (niche conservatism) or they may change it (i.e. niche plasticity), and that is true for both the Grinnellian and Eltonian niche. Recent studies have highlighted that many invasive species conserve their Grinnellian niche in their invaded ranges (Wiens et al. 2010; Strubbe et al. 2013), so that Grinnellian niche conservatism has been recognized as the most likely scenario for most bird invaders in Europe (Strubbe et al. 2013). However, Sol et al. (2002) suggested that behavioural flexibility can be important by providing individuals with the ability to expand or change their foraging habits and successfully invade novel environments, representing a change in Eltonian niches. On the other hand, the opposite result (Eltonian niche conservatism and Grinnellian niche shift) has been found in an invasive arthropod, the signal crayfish *Pacifastacus leniusculus* (Larson et al. 2010), so more studies are called for.

Studies on plants have pointed out the importance of differences in the temporal segregation of the niches of species to understand some successful invasions

(Wolkovich and Cleland 2010), for example because separation in time reduces (competitive) interaction. For other organisms, such as birds, the timing of reproduction of exotic species in their novel environments has been a topic of some historic interest (Baker and Ranson 1938). To maintain viable populations, exotic birds must rapidly adjust to novel environmental conditions (e.g. climate, photoperiod, resources and/or competitors; Blackburn et al. 2009) in the areas of introduction. When introduced, some individuals/species tend to maintain their former reproductive timing (conservatism) whereas others completely change their breeding time (plasticity) (Baker and Ranson 1938). As examples of change, House sparrows, *Passer domesticus*, reproduced continuously during establishment in North America and New Zealand whereas native European sparrows breed seasonally (Hengeveld 1994). At the population level, Rufous-collared Sparrows, *Zonotrichia capensis*, changed from continuous breeding in their native populations in Colombia to seasonal breeding (up to autumn) in an introduced population in the USA (Miller 1965); and several passerines introduced in New Zealand have increased the length of their breeding season relative to the United Kingdom (Evans et al. 2005). However, the role of phenology when studying Eltonian niche overlap (including niche conservatism and niche expansion) mediated via resource competition has been poorly explored in animal invasion biology.

Here we compare the reproductive timing of an entire community of established exotic birds of tropical origin with that of the native, temperate bird community using the same habitats, and explore the importance of this temporal niche axis for establishment success. The timing of reproduction is one of the major life history traits involved in the adaptation of birds to their environments (Lack 1968; Murton and Westwood 1977). Birds show dramatic seasonal reorganizations in physiology (e.g. gonadal development), behaviour (e.g. song, courtship) and morphology (e.g. plumage)

linked to reproduction (Murton and Westwood 1977). Photoperiodic signal is the main driver regulating the timing of reproduction in birds (Dawson et al. 2001; Hahn and MacDougall-Shackleton 2008), although circannual programming is also known to be important (Helm et al. 2009; Visser et al. 2010). As individuals should reproduce at the right time to maximize their fitness (Martin 1987; Daan et al. 1988; Thomas et al. 2001; Sanz et al. 2003), typically when food availability is maximal, additional cues such as temperature, rainfall, or social factors can fine-tune the timing of reproduction to local conditions (Hahn et al. 1997; Ball and Ketterson 2008; Hau et al. 2008). Thus, differences in timing of reproduction are common between and within species (Hahn et al. 1997), showing typical geographical patterns. For example, in temperate zones, seasonal changes in the environment are highly predictable and most temperate birds breed in spring and early summer, coinciding with the peak of food availability (Cramp and Simmons 1977). In many of those temperate habitats, early breeding is theoretically advantageous because of the higher renesting possibilities and also because fledgling survival and recruitment generally decline with the progression of the breeding season (Lack 1968; Daan et al. 1988; Price et al. 1998; but see Penteriani et al. 2014). On the contrary, postponing reproduction should be disadvantageous if this entails competition for food with migrant or wintering individuals or if ecosystem production (i.e. food resources) decreases with the advancing of the season, potentially leading to partial or total reproductive failure. In contrast, related to the less seasonal climate, tropical birds show a wider range of breeding strategies, from seasonal to opportunistic and continuous breeding (Hau et al. 2008). In general, timing of reproduction among tropical birds is expected to be wider and more asynchronous at the population level than among temperate birds (Hau et al. 2008).

Establishment success depends on the invader's ability to fit the ecological characteristics of the recipient community. Competition can be an important factor precluding biological invasions (Sol et al. 2012a; Hernández-Brito et al. 2014) such that exotic species which are functionally different from those already present in the community are more likely to become invaders than species having to face competition with natives (formally called the empty niche, the invasion window or the opportunity window hypotheses; Catford et al. 2009). With respect to timing, invaders may then benefit from a potential Eltonian niche opportunity when having a different timing of reproduction compared to native species if this results in a reduction in competition (i.e. ecological release; Levin 2003). However, establishing species may also be selected to be ecologically similar to the native ones, since this is what the environment dictates. With respect to timing, this then predicts that exotic species should have a reproductive timing that is similar to that of the native species (e.g. adjusting the timing of reproduction to the periods of maximum food availability).

Here we explore (i) whether successful avian invaders originating from tropical areas synchronize their reproductive timing in their new environment to that of the native temperate species, to match conditions that would presumably maximize food availability and fitness (i.e. invaders are selected to be similar to natives), or (ii) whether they may avoid competition with natives in temperate areas by utilizing ecological opportunities occurring at different times of the year (i.e. invaders are selected to be different from natives). Secondly, by comparing the reproductive timing of the tropical invaders in their novel temperate range with that in their native tropical ranges we explore whether these matches or changes in reproductive timing are due to niche flexibility (as might be predicted by the greater flexibility and variation in reproductive timing in tropical birds, Hau et al. 2008), or by niche conservatism (Strubbe et al. 2013).

In order to answer these questions we compared the timing of reproduction of a successfully established and spreading community of exotic passerines in southern Spain (Sanz-Aguilar et al. 2014) with that of sympatric native species. We also compared this with the temporal abundance of birds and ecosystem primary production in the study area as proxies of potential competition between exotic and native breeding and migrant birds.

METHODS

The study area is composed of marshes surrounded by crops (mainly rice and maize crops) in the lower Guadalquivir valley (southern Spain, 36°56'51"N 6°21'31"O). The climate is sub-humid Mediterranean with coastal influence, characterized by wet, mild winters and dry, hot summers (García-Novo and Marín 2005). The study area is situated next to one of the largest and most important wetland systems in Europe, Doñana, a hotspot of avian diversity and key stopover site for hundreds of thousands of birds during spring and autumn migration (García-Novo and Marín 2005).

Bird abundance data: Monthly variation in local abundance of passerine birds from March to November was estimated from the number of birds captured per mist-net session and month from 2008 to 2010 at the fixed capture station "Guadaira River", placed in a representative reed bed mixed with some scattered shrubs and small trees. Capture effort by session was kept constant (217 meters of mist-nets and 4.5-5 hours of duration of sessions) during the period considered and regular mist-netting was disrupted during winter (December to February).

Primary production data: Monthly variation in abundance of food resources for passerines around the capture station (1 km radius, approx. 315 ha) and for the whole area of rice fields was approximated using data on mean primary production extracted from satellite images with a spatial resolution of 1 km and a monthly temporal

resolution extending from April 2008 to December 2012. We used the Terra/MODIS Gross Primary Production (GPP) product (MOD17A2), which is a cumulative composite of GPP values based on the radiation-use efficiency concept (Heinsch et al. 2003).

Reproductive phenology data: From January 2009 to December 2012, three well-trained ornithologists devoted on average three days per week to locate and capture exotic and sympatric native birds all around the study area. Each worker independently searched for and caught passerines (both exotic and native) with mist nets around wetlands and unharvested rice and maize crops throughout the year. Birds were ringed with an individually-numbered aluminium ring. For each captured individual we recorded ring number, species, age and sex (when distinguishable by plumage or biometry) and presence of a brood patch (codes 2 “well defined”, 3 “veined and red” and 4 “wrinkled”, see details in the EURING exchange code 2000, available at: http://www.euring.org/data_and_codes/euring_code_list/euring2000%2Bcodev112.pdf).

Female passerine birds lose abdominal down within a few days of egg-laying, and the vascularisation in the brood patch for incubation is a reliable indicator of reproductive activity (Bailey 1952). Thus, the examination of brood patch condition is a useful technique to establish breeding status. Note that this data set is independent from the bird abundance data because data on the reproductive status of the birds captured at the “Guadaira River” are not available. There was, however, a large temporal overlap (48 months) between both data sets.

Since all established exotics in the area are passerine birds, we restrict ourselves to this group only (native non-passerines can have very different ecologies and phenologies). The entire community of passerines breeding in the study area was sampled for this study (Table A.1, Appendix 1), thus including for analyses five exotic

passerines (common waxbill *Estrilda astrild*, black-rumped waxbill *E. troglodytes*, yellow-crowned bishop *Euplectes afer*, black-headed weaver *Ploceus melanocephalus*, and red avadavat *Amandava amandava*) and twelve native passerines (great reed warbler *Acrocephalus arundinaceus*, Eurasian reed warbler *A. scirpaceus*, European goldfinch *Carduelis carduelis*, European greenfinch *C. chloris*, Cetti's warbler *Cettia cetti*, streaked fantail warbler *Cisticola juncidis*, Savi's warbler *Locustella luscinioides*, common nightingale *Luscinia megarhynchos*, house sparrow, Spanish sparrow *Passer hispaniolensis*, European penduline tit *Remiz pendulinus*, and European serin *Serinus serinus*). Among the exotics, the common waxbill, the yellow-crowned bishop and the black-headed weaver are very abundant in the study area, while black-rumped waxbill and red avadavat are present in low numbers (Sanz-Aguilar et al. 2014).

Waxbills, bishops and weavers are native to tropical and southern Africa and avadavats to tropical Asia; all of them have very large native ranges and highly variable timing of reproduction (Figure 1; Fry et al. 2004; Rasmussen et al. 2005; Clement et al. 2010). All the exotic species considered here are granivorous outside the breeding season. Among natives, some species are granivorous outside the breeding season (e.g. *Passer* sp.) whereas others are insectivorous (e.g. *Acrocephalus* sp.) (Table A.1, Appendix 1). However, all the exotic and native species in the sampled avian community feed their offspring with (at least some) insects, thus largely exploiting similar feeding resources during the breeding season (Cramp and Simmons 1977; Fry et al. 2004; Rasmussen et al. 2005; Clement et al. 2010). They also largely share the same habitats: all exotics are dependent on wetland and other damp vegetations in their native range, and most natives are also found in such vegetations during the breeding season (especially *Acrocephalus*, *Cettia*, *Locustella*, *Luscinia*, and *Remiz*). See further detailed information on species characteristics in Table A.1 (Appendix 1).

As a first test for differences in timing of reproduction we compared the monthly percentages of native and exotic species that were detected breeding with chi-square tests. Then, we compared the monthly proportions of exotic and native females breeding of each species. These percentages were approximated as the monthly number of females with a brood patch divided by the total number of adults captured. We used this approximation because some species are sexually monomorphic and birds without brood patch cannot be reliably sexed.

We tested for differences in timing of reproduction between native and exotic birds by means of Generalized Additive Models (GAM; Zuur et al. 2009). Our dependent variable was the presence (or absence) of a brood patch (logit-link function and binomial error distribution) among captured adult birds. Explanatory variables were species status (native or exotic, two-level factor), time (months) and their interaction. Time was included as a smoother to allow for non-linear temporal trends in the proportion of females with a brood patch. Species identity and year were also included as fixed factors in the models; species identity to account for interspecific differences in brood patch presence and in sample size (entering species identity as a random effect precluded model convergence probably because of unbalanced sample sizes) and year to control for potential interannual differences in the proportion of reproducing adults. For the analyses, we discarded data for those species and months in which < 10 adult individuals were captured and for which estimates were deemed too unreliable. The importance of the explanatory variables was assessed using AICc (Burnham and Anderson 2002).

Finally, we assessed the relationships between monthly primary production, bird abundance at the fixed capture station “Guadaira River” and phenology of reproduction

within the lower Guadalquivir valley with Pearson's product-moment correlations, given the normal distribution of variables.

Origin and phenology of exotics in their native areas: The introduction in Spain of the exotic passerines considered here stems from the international trade of cage birds (Carrete and Tella 2008). We therefore used the CITES trade data base (<http://www.cites.org/eng/resources/trade.shtml>) to identify the countries of origin for those birds exported to Spain and Portugal (the latter being very close to the study area and having the same exotic bird community, Sanz-Aguilar et al. 2014), and to quantify their relative importance in numbers of individuals exported. Data on the phenology of the exotics in their native tropical ranges were taken from Fry et al. (2004). This analysis is restricted to the three species for which we have a good estimate of their reproductive season in the novel, temperate range.

RESULTS

Reproductive timing of exotics versus natives

We captured 14,185 birds (6,132 natives and 8,053 exotics) during the study period, of which 875 native and 466 exotic individuals had an active brood patch (Table A.2, Appendix 1). Both native and exotic species began reproduction in April. However, the proportion of native species reproducing was higher from April to July whereas for the exotic species this was higher from July to October (Figure 2A). We found statistically significant differences between the monthly proportion of exotic and native species in October ($\chi^2=4.29$, d.f.=1, $p=0.04$) and November ($\chi^2=4.44$, d.f. =1, $p=0.04$).

Results from the modelling procedure highly support that the temporal trend in the proportion of reproducing individuals (females with brood patch) differed between native and exotic species, as shown by the very large difference in AICc between the

model including the interaction between time and species status compared to the model without it ($\Delta AICc = 130.9$, Table A.3 Appendix 1). The proportion of reproducing individuals per species from September to November was much higher in exotics than in natives (Figure 2B). Although only low numbers of individuals with an active brood patch were caught, breeding in November was exclusive to exotic species (Figure 2, 3). *Euplectes afer* was only detected breeding during late summer and fall (from July to November) and not a single male was caught with breeding plumage in spring (authors' unpublished data).

These differences in reproductive months translate into differences in the length of the breeding seasons. For the exotic species with most data, *Estrilda astrild* was detected with active brood patches during 8 months, *Ploceus melanocephalus* during 7 months and *Euplectes afer* during 5 months (Figure 3). In contrast, native species reproduced for a maximum of only 4 months (Figure 3), with the exception of *Acrocephalus scirpaceus* which was also detected breeding during 7 months (Figure 3).

Reproductive timing of exotics versus timing of resource production and local bird abundance

Local relative bird abundance increased from winter to spring, reaching peak values in the second half of the year (from July onwards, Figure 4A), coinciding with those months when more exotics than natives are breeding and also with the months of maximum mean primary production in rice fields (Table 1, Figure 2A, Figure 4B). At the community level, breeding of exotic species correlated more with primary production in rice fields, whereas that of native species correlated more with primary production in the natural vegetation around the Guadaira River capture station (Table 1, Figure 2A, Figure 4B). At the individual level, breeding of both exotic and native birds

correlated significantly with the primary production at the Guadaira River (Table 1, Figure 2B, Figure 4B).

Reproductive timing in the invasive range versus the native range

CITES trade data indicate that our exotic passerines: bishops, weavers and waxbills were imported from six, three and seven different African countries, respectively (Table 2). The yellow-crowned bishops and Black-headed weaver were mainly imported from Senegal (86% and 96% of birds, respectively; Table 2) and the Common waxbill from Guinea (70%; Table 2). A comparison between the reproductive timing in our study area and that of the most important countries of origin show that the timing is identical for the black-headed weaver (Figure 1). The Yellow-crowned weaver starts a bit earlier in its native range, but likewise breeds predominantly late in the year (Figure 1). For the Common waxbill there is no data from its main native origins and very little data from neighboring countries (Figure 1). However, as in our study area, it shows a very long breeding in several native countries, including in South Africa which has the most similar (absolute) latitude and climate (Figure 1).

DISCUSSION

Introduced bird species represent an invaluable opportunity to advance our understanding of the roles of ecology, phenotypic plasticity and/or evolutionary responses to new environmental conditions (Evans et al. 2005; Sax et al. 2005; Lockwood et al. 2007; Blackburn et al. 2009). Mostly geographical and climatic components of Grinnellian niches have been used to predict invasion success over a broad range of organisms (Peterson 2003; Strubbe et al. 2013). However, the temporal component of the Eltonian niche (i.e. phenology) has been recently recognized as an important factor in determining the invasion success of plants (Wolkovich and Cleland 2010). In fact, many plant invasions have benefited from a vacant Eltonian phenological

niche, a longer growing or flowering period (i.e., greater niche breadth), and a greater phenological plasticity (Wolkovich and Cleland 2010). Here, we suggest that a similar segregation in phenology seems to contribute to the establishment success of other taxa such as birds. Our data show that the exotic passerines studied here generally breed for more months and later in the year than native species, when overall bird abundance as well as primary production in cultivated areas (rice fields) were highest. This timing of reproduction seems to be comparable to that in their areas of origin, suggesting a conservatism of the temporal niche.

The timing of reproduction of native passerines observed in our study area is similar to that reported for our study species across Mediterranean habitats (Cramp and Simmons 1977), supporting our use of the proportion of adults with a brood patch as a reasonable approximation of reproductive phenology. In contrast, the later breeding of the exotic species studied here is rather surprising, and is only approximated by the Reed warbler. Breeding that is restricted to summer and autumn is in the Yellow-crowned bishop and most likely in the Avadavat (no breeding individuals were detected in spring in this study and in central Spain the species breed from July to December; Molina and Bermejo 2003) is not shown by any native passerine species in the area. This begs the question of why invasives breed later than natives. An obvious candidate explanation is that of a phenological niche opportunity.

Resource availability in novel habitats is critical to ensure survival and reproduction. Resources can be gained either via competition with native species or by exploiting underutilized Eltonian niche opportunities (Tilman 2004; Blackburn et al. 2009; Sol et al. 2012a). Hernández-Brito et al. (2014) found that in the invasive ring-necked parakeet *Psittacula krameri* its more aggressive behaviour helps it to invade new ranges when competing with native species over food and nesting sites. However,

there is little evidence for competition among native and invasive birds (Blackburn et al. 2009). For example, Grundy et al. (2014) failed to detect competition (or impacts) of invasive Black-headed weavers (also included in our study) on two native, ecologically similar species (*Acrocephalus arundinaceus* and *A. scirpaceus*, both also included here) in a nearby study area. In contrast, high phenotypic plasticity (i.e. behavioural flexibility; Sol et al. 2002, 2012b), as well as a superior ability to exploit ecological opportunities in human-modified habitats (Sol et al. 2012a), have been observed among successful invaders. Moreover, there is evidence indicating that communities are not saturated, and that potential niches remain available (Blackburn and Duncan 2001; Sax et al. 2005). Therefore, even though the exotic passerines share the same habitats as the natives (marshes and damp vegetations) and have similar resource requirements during breeding (invertebrates), on balance it seems that the exotics did not just establish by outcompeting native species.

In the study area, exotic invasive birds breed later than native species. Although large numbers of northern European birds stop-over during late summer and fall (Figure 4A), marshes (García-Novo and Marín 2005) and rice fields (Figure 3B) are highly productive at those times, still providing large amounts of seeds and insects for those species breeding late. The exotic passerines established in the study area are year-round residents with a generalist diet (adults consume both insects and seeds) and therefore do not face the same restrictions related to the timing of migration (e.g. moulting after breeding but before migration) as some native migratory species (Table A.1., Appendix 1), or related to resource use (as some strictly insectivorous species, Table A.1., Appendix 1; Murton and Westwood 1977). Additionally, the exotics studied here can benefit from a higher use of resources derived from human activities (Sol et al. 2012a): they can consume abundant seeds at crops and rice fields for self-maintenance whereas

they feed their offspring with insects. This generalist diet may confer exotic birds an advantage over the strictly insectivorous native species in the study area. In fact, breeding of native birds both when using the proportion of species and the proportion of individuals better matched with primary production in natural areas (i.e. Guadaira River), whereas reproduction of exotic birds at the species level better matched with primary production in cultivated areas (i.e. rice fields). When using the proportion of individuals breeding, exotic birds also matched with primary production in natural areas. This result suggests that a large part of the exotics in the study area breed when food abundance is maximum in native vegetations but that some individuals protract their breeding period and/or that some individuals only breed late in the season (Miller 1965) when non-native vegetations are more productive, such that for the species the reproductive seasons are longer and more correlated to productivity in cultivated habitat.

One possibility that needs to be discussed is that the exotic birds breed late but that this in fact is detrimental, i.e. that exotics are displaying a maladaptive reproductive phenology. However, the invasive species studied here have growing and spreading populations, indicating successful reproduction and survival even if they are breeding late in the season (Sanz-Aguilar et al. 2014). Actually, bishops do not breed in spring at all but are the most abundant exotic species in the study area (Sanz-Aguilar et al. 2014). Detailed data on Black-headed weavers confirmed that the species reproduced successfully in late September: of the chicks fledged in late summer/early autumn at least 20% survived to the next breeding season (unpublished data), showing similar mean first-year survival of fledglings produced all along the breeding season (0.22: Sanz-Aguilar et al. 2014). Unfortunately, comparable data on other species are lacking and further work involving marking and recapture of fledglings and breeders at different

times of the breeding season is needed to fully understand the fitness consequences of differential phenologies.

We observed a relatively good fit between the reproductive timing of the exotics in their novel temperate range and that in their inferred native tropical range. The Black-headed weaver showed a perfect match, whereas the Yellow-crowned weaver starts a bit earlier in its native range. While it is difficult to ascertain why this may be, rice cultivation starts earlier in Senegal than in Spain and is more protracted (pers. obs.), and this may explain the longer breeding season. For the Common waxbills we do not have reliable data on reproductive phenology of its native origins. These came from a larger number of countries along the African continent (Table 2), representing a number of different subspecies (Fry et al. 2004). Waxbills in our study area bred for more months than any other species, consistent with their wider likely native origins and/or nearly continuous reproduction in some native countries (Table 2). Overall, the exotics in our study area showed strong similarities between the reproductive phenology in their native areas and in the novel invasive area, suggesting a conservatism of the temporal niche (Vellend et al. 2007; Visser et al. 2010; Wiens et al. 2010).

Overall then, the human-made combination of crop lands next to natural wetlands has created a novel Eltonian niche that allows breeding later in the year for those species that can utilise this niche. Native birds apparently have not capitalised upon this novel temporal Eltonian niche. This vacant temporal niche seems to have enabled certain exotic birds to invade this native bird community. The successful invaders in the study area have similar resource requirements as the native birds (i.e. invaders are selected to be ecologically similar in resource use), but they also may have pre-adapted reproductive timing that better matches the novel temporal niche (i.e. invaders are selected to be ecologically different in time). The absence of migration and

their diet switch from insects (breeding) to seeds (non-breeding) might further have favoured their establishment. However, more information and, in particular, experimental approximations would be essential to properly understand the relative importance of these previously described different elements and other potential factors not studied here (e.g. behavioural flexibility, selection during invasion processes, or potential releases of competition or predation in agricultural areas) on invasion success, and to evaluate individual and population consequences.

Despite some progress, predicting invasion risk remains an important and elusive goal. Species distribution models based on ecological (Eltonian) and geographical/climatic (Grinnellian) niches in the native ranges have been shown to be a powerful tool for predicting invasion risk (Elith and Leathwick 2009). However, the temporal aspect of the niche has been neglected in the study of animal invasions (e.g. Strubbe et al. 2013, but see Larson et al. 2010). As has been clearly recognized for plant invasions (Wolkovich and Cleland 2010), our study emphasizes that a better understanding of the phenological niche and its (in)flexibility can help to understand animal invasions. Including aspects of the temporal niche might therefore improve the predictions of species distribution models, which seems especially important in the context of climate change and the ensuing changes in seasonality (Visser 2008; Hoffmann and Sgrò 2011; Penteriani et al. 2014).

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Figure 1. Monthly reproductive activity (measured as months with egg laying) of *Ploceus melanocephalus*, *Estrilda astrild* and *Euplectes afer* in their native range (grey cells, data taken from Fry et al. 2004) and invasive range (black cells, this study). The most probable countries of origin for the individuals now breeding in Spain (the source populations with >1% of exports, see Table 2) are indicated with red cells to differentiate them from the entire native range of the species. The vertical lines show the temporal overlap between the breeding season in the invasive and the native locations. (Pictures by Manuel de la Riva (*Estrilda astrild*) and Julio Blas (*Euplectes afer* and *Ploceus melanocephalus*)).

Figure 2. A greater proportion of (A) exotic species and (B) individuals among exotic species breed later in the year compared to native species. A) Monthly proportions of native and exotic species captured with an active brood patch. B) Proportions of native and exotic females captured with an active brood patch out of the total number of adults captured per month. Means and standard deviations are based on the species values. Sample size (total no. of species and individuals captured) are shown within the graph. Only species with at least 10 captures per month were considered.

Figure 3. Pattern for each species of proportion of females captured with an active brood patch out of the number of adults captured, per species. Number of individuals per species per month considered ranged between 10 and 991.

Figure 4. A) Mean ($\pm$ standard deviation) daily numbers of birds captured per month at the “Guadaira River” capture station. Note that only months with ≥ 5 capture sessions were considered. B) Mean ($\pm$ standard deviation) monthly primary production (g carbon

603 m^2/day) at the “Guadaira River” capture station and the rice fields area.

Table 1. Pearson's product-moment correlations (with p-values between brackets) between monthly values of mean primary production (PP) of rice fields or around the “Guadaira River” capture station and bird abundance, and the proportions of exotic and native species and individuals breeding. Significant correlations ($p < 0.05$) are in bold.

	Rice fields PP	Guadaira River PP	Bird abundance
Bird abundance	0.68 (p=0.043)	-0.51 (p=0.16)	-
% Exotic species	0.77 (p=0.003)	0.39 (p=0.021)	0.90 (p=0.001)
% Native species	0.63 (p=0.27)	0.82 (p=0.001)	0.14 (p=0.73)
% Exotic individuals	0.52 (p=0.09)	0.78 (p=0.003)	0.08 (p=0.84)
% Native individuals	0.41 (p=0.19)	0.80 (p=0.002)	-0.05 (p=0.90)

Table 2. Numbers (%) of *Ploceus melanocephalus*, *Euplectes afer* and *Estrilda astrild* exported to the Iberian Peninsula (Spain and Portugal) from 1986 to 2004 per African country of origin. Note that the study area is located near Portugal and all species have a continuous spatial distribution between Spain and Portugal (Sanz-Aguilar et al. 2014). Data from CITES trade database (<http://www.cites.org>), using only exports of wild, alive individuals.

Country	<i>P. melanocephalus</i>	<i>E. afer</i>	<i>E. astrild</i>
Guinea	1,763 (4.1%)	9,947 (8.6%)	21,706 (69.6%)
Senegal	41,085 (95.6%)	100,045 (86.4%)	1,660 (5.3%)
Tanzania	150 (0.3%)		1,850 (5.9%)
Ghana		300 (0.3%)	450 (1.4%)
Mali		5,250 (4.5%)	2,050 (6.6%)
Mozambique		2 (0.0%)	2,970 (9.5%)
South Africa		200 (0.2%)	
Liberia			500 (1.6%)