The impact of an invasive exotic bush on the stopover ecology of migrant passerines

J. Arizaga, E. Unamuno, O. Clarabuch & A. Azkona

Abstract

The impact of an invasive exotic bush on the stopover ecology of migrant passerines.— Migration is highly energy–demanding and birds often need to accumulate large fuel loads during this period. However, original habitat at stopover sites could be affected by invasive exotic plants outcompeting native vegetation. The impact of exotic plants on the stopover behavior of migrant bird species is poorly understood. As a general hypothesis, it can be supposed that habitat change due to the presence of exotic plants will affect migrants, having a negative impact on bird abundance, on avian community assemblage, and/or on fuel deposition rate. To test these predictions, we used data obtained in August 2011 at a ringing station in a coastal wetland in northern Iberia which contained both unaltered reedbeds (*Phragmites* spp.) and areas where the reedbeds had been largely replaced by the invasive saltbush (*Baccharis halimifolia*). Passerines associated with reedbeds during the migration period were used as model species, with a particular focus on sedge warblers (*Acrocephalus schoenobaenus*). The saltbush promoted a noticeable change on bird assemblage, which became enriched by species typical of woodland habitats. Sedge warblers departed with a higher fuel load, showed a higher fuel deposition rate, and stayed for longer in the control zone than in the invaded zone. Invasive plants, such as saltbush, can impose radical changes on habitat, having a direct effect on the stopover strategies of migrants. The substitution of reedbeds by saltbushes in several coastal marshes in Atlantic Europe should be regarded as a problem with potential negative consequences for the conservation of migrant bird species associated with this habitat.

Key words: *Acrocephalus* spp., Biological conservation, Biological invasion, Coastal marshes, Fuel deposition rate, Saltbush (*Baccharis halimifolia*).

Resumen

Impacto de un arbusto exótico invasor en la ecología de los puntos de parada de los paseriformes migradores.— La migración requiere un elevado gasto de energía y las aves suelen necesitar acumular grandes cantidades de grasa durante este período. Sin embargo, el hábitat original de los puntos de parada podría verse afectado por plantas exóticas invasoras que compiten con la vegetación autóctona. Se conocen poco los efectos de las plantas exóticas en el comportamiento de las especies de aves migradoras en cuanto a los puntos de parada. Como hipótesis general, puede suponerse que el cambio del hábitat debido a la presencia de plantas exóticas afectará a las aves migradoras e influirá negativamente en su abundancia, la composición de la comunidad de aves y el índice de deposición de grasa. Para comprobar estas predicciones, utilizamos los datos obtenidos en agosto de 2011 en una estación de anillamiento situada en los humedales costeros del norte de la península ibérica en los que había carrizos inalterados (*Phragmites* spp.) y en zonas en las que los carrizos habían sido sustituidos en gran parte por el bácaris invasor (*Baccharis halimifolia*). Se utilizaron como modelo a los paseriformes asociados a los carrizales durante el período de migración y se prestó especial atención al carricerín común (*Acrocephalus schoenobaenus*). El bácaris propició un cambio notable en la composición avícola, que se enriqueció con especies típicas de hábitats forestales. Los carricerines partieron con una cantidad de grasa superior, mostraron un índice de deposición de grasa más elevado y permanecieron por más tiempo en la zona de control que en la zona invadida. Las plantas invasoras, como el bácaris, pueden forzar cambios radicales en el hábitat y tener un efecto directo en las estrategias de parada de las aves migradoras. La sustitución de los carrizales por bácaris en diversas marismas de la costa atlántica de Europa debería considerarse un problema con posibles consecuencias negativas para la conservación de las especies de aves migradoras asociadas a este hábitat.

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Introduction

Migration is considered to have carry–over effects on several parameters in the life cycle of avian migrants (Newton, 2004). Suboptimal stopover places may hamper an adequate fuel deposition rate and compromise not only survival, but also future life history aspects such as mating or breeding success (Sandberg & Moore, 1996; Smith & Moore, 2003).

Generally, migrant birds cannot gain enough fuel at a single site to reach their destination areas in a single uninterrupted flight or in several flights without refuelling at en route stopovers. They therefore need to stop over periodically to accumulate sufficiently high energy stores to accomplish the next flight bout successfully. The rate of fuel accumulation at stopover sites influences speed of migration, and it has been considered to be an indicator of habitat quality at these stopover sites (Alerstam & Lindström, 1990). Accordingly, any factor that affects fuel deposition rate, such as food availability or predator disturbance, can be crucial for migrant bird species in terms of migration success or survival.

Exotic plants can displace native vegetation, causing habitat changes which are often linked to changes in biodiversity (Vitousek et al., 1997). This phenomenon also affects bird migrants when they land to refuel in an altered habitat (e.g., Cerasale & Guglielmo, 2010). The impact of exotic plants on stopover behavior of migrant bird species is, however, poorly understood (Cerasale & Guglielmo, 2010). This issue is worth taking into consideration, especially if we consider that several bird species, both at population and individual levels, tend to use the same stopover sites year after year (Newton, 2008). Habitat changes in these areas can thus have negative consequences, even though alternative stopover sites may be available.

As a global hypothesis, it can be stated that native habitat change (i.e., deterioration) due to the presence of exotic plants will have a negative impact, either in relation to bird assemblage or stopover behavior (fuel deposition rate, stopover duration, etc.), on individual migrants originally associated with native vegetation.

The predictions tested in this study were: (1) A decrease in the area covered by native vegetation will have a negative impact on bird abundance at a local scale, because these species are adapted to use their particular native habitats. Consequently, these species would not use areas heavily invaded by exotic plants. From a structural standpoint, the community may change toward species better adapted to the new conditions (e.g., Sol et al., 2002). (2) If a zone affected by an invasive exotic plant species turns into a suboptimal area (e.g., offering worse fuelling opportunities), migrants should be expected to move from this to better nearby areas with native vegetation. Thus, we expect a higher number of within–season recaptures from the affected, a priori suboptimal site (affected by exotic plants), to the unaffected site, especially if migrants are able to look for better sites at a micro–scale level within the same stopover area (Delingat & Dierschke, 2000). (3) A decrease in the

rate of fuel deposition of migrants in a zone affected by exotic vegetation as compared to a zone with only native vegetation is also expected (Cerasale & Guglielmo, 2010), either because migrants associated with native vegetation are not good foragers in a foreign habitat (in suboptimal habitats, migrants should be expected to forage less efficiently; e.g., Jenni–Eiermann et al., 2011), or because local insects (i.e., birds' food supply) cannot feed on exotic plants and, therefore, food availability is lower than that found in areas of native vegetation. Consequently, migrants departing from a stopover site affected by exotic plants should have lower fuel loads than migrants departing from an unaffected site.

The aim of this study was to evaluate the impact of exotic plants on the community structure and stopover ecology of migrant birds, particularly their effect on fuel load and fuel deposition rate. We used data obtained at a coastal wetland in southwestern Europe that had both unaltered reedbeds (Phragmites spp.) and areas where the reedbeds had been largely replaced by the invasive saltbush (Baccharis halimifolia). The study was carried out at two levels: the first level focused on bird assemblages, while the second level focused on the sedge warblers (Acrocephalus schoenobaenus) as an avian model species typical of reedbeds to compare body mass, fuel deposition rate and stopover duration in invaded and control areas.

Material and methods

Study system

Reedbeds in Europe play a relevant role as stopover sites for marsh–associated birds during migratory periods (Schaub et al., 2001; Arizaga et al., 2006). This habitat, however, has suffered a notable decline in several areas due to the saltbush (Sanz et al., 2004), a shrub originally found along the coast of eastern North America (Cronquist, 1980). Typical of plains within coastal marshes, it is currently widespread worldwide as an exotic, invasive plant that occupies wetlands with slight to moderate levels of brackish waters. The saltbush has become a problem of primary importance in many wetlands in Europe, Asia and Australia, and it has been the target of numerous (and usually costly) management plans (e.g., Palmer et al., 1993). Its eradication has thus been a priority in several projects (e.g., Life projects such as LIFE08NAT/E/000055) orientated to preserve habitats of interest in Europe.

The reed–associated warblers (Acrocephalus spp.) are a group of closely–related species of small insectivorous birds that are normally adapted to exploit vertically–structured vegetation in Europe, Africa, Asia and some parts of Oceania (Cramp, 1992; Leisler & Schulze–Hagen, 2011). A paradigmatic case of this specialization is birds such as sedge warblers, which mainly forage on aphids (Hyalopterus spp.) found in reedbeds (Bibby & Green, 1981). Sedge warblers breed in humid habitats from the west of Europe to Central Siberia (90ºE), between the July isotherms

of 12 and 30ºC (Cramp, 1992). They overwinter in tropical/southern Africa or southern Asia (Cramp, 1992). During migration (mainly from mid–July to September during the autumn migration period), they preferably occupy reedbeds, both along the coast and inland (Cramp, 1992). Sedge warblers have a direct dependence on certain aphid species on which they feed to accumulate large fuel loads before crossing the Sahara Desert in autumn (Bibby & Green, 1981). Stopover normally takes place in strategic areas with good foraging conditions (Bibby & Green, 1981; Bensch & Nielsen, 1999), so habitat changes at stopover areas could be particularly damaging to the conservation of this species.

The sedge warbler is present in northern Iberia only during the migration period (Tellería et al., 1999), when they are common in many wetlands. During the autumn migration period, the species accounts for ca. 20% of the captures obtained at a constant–effort ringing station in Urdaibai, a coastal wetland in Northern Iberia (Unamuno & Arizaga, unpubl. data). The sedge warbler is a good avian model to test the effect of invasive plants on stopover behavior of migrants associated with reedbeds, since all birds captured in Urdaibai are non–breeding, true migrants.

Study area and data collection

Data were obtained at Urdaibai, a Ramsar coastal estuary in the southeastern Bay of Biscay, northern Iberia. The wetland spreads over an area of 945 ha and has a relatively high richness of habitats, determined by tide regimens and the degree of salinity. Such habitats range from beach and dunes (situated within the lowest part of Urdaibai) to tidal flats of limes and plant species adapted to tidal flooding in the lower marsh and reedbeds and freshwater–associated vegetation in the upper marsh and nearby polders.

Birds were captured with mist nets of 16 mm mesh (144 linear m/zone) at two zones which had a different degree of invasion by saltbushes (table 1). Originally, both zones were occupied by reedbeds (as dominant vegetation) together with *Juncus* spp. and *Aster* spp., but currently the vegetation in one zone has been almost completely replaced by saltbushes. Hereafter, we will respectively call these zones 'control' and 'invaded'. Both zones are found in the upper marsh and are subject to daily tidal flooding. From July to September the area is used by warblers coming from the British Isles and Western–Central Europe (Cantos, 1998) en route to their wintering areas in tropical Africa (Cramp, 1992).

Mist nets at both zones were open daily during August 2011 for a period of 4 h starting at dawn. Since the sampling was carried out in parallel with another project, focused on finding key stopovers for the aquatic warbler (*A. paludicola*) in the bay of Biscay, we also used tape lures with the song of a male aquatic warbler (one lure per 36 linear m of mist nets) (Julliard et al., 2006). Since the sampling effort with both mist nets and lures was constant in these two zones, using tape lures would not be expected to create any bias for the comparison of stopover behavior between the two trapping sites.

Once captured, each bird was ringed and its age (first year or adult bird) was determined according to Svensson (1996). Additionally, we measured body mass (± 0.1 g) and the length of the P3 primary feather (± 0.5 mm; numbered from outermost to innermost). Following measurements, the birds were released. No bird was retained for longer than 1 h.

Statistical analyses

We compared community richness (number of birds), as well as a diversity index (*H'*) using a bootstrap procedure as calculated by the software PAST 2.1 (Hammer et al., 2001). *H'* stands for the Shannon index, which ranges from 0 (communities with only a single taxon) to high values in communities with many taxa, each with few individuals. The bootstrap procedure consisted in generating a 95% confidence interval (CI) by taking 1,000 random sub–samples from the total pooled data. The number of captures per day at each zone was compared with a *t*–test. Number of captures was log–transformed to normalize the data.

Contingency tables were used to compare the proportion of recaptures between zones, and to test whether cross–recaptures from the control zone into the invaded zone were more common than vice versa.

As body mass in excess of structural mass in migrants is mainly stored as fat and, to a lesser extent, proteins (Jenni & Jenni–Eiermann, 1998), we used body mass controlled for body size (including P3 as a covariate) as a surrogate for fuel load (*e.g.*, Arizaga et al., 2010, 2011a). Analyses of fuel load and fuel deposition rate were run only for sedge warblers.

Captures from ordinary trapping sessions at a stopover site are subject to certain constraints. In particular, the first and last captures of each individual are not always obtained on the exact dates of arrival or departure (Schaub et al., 2001). It is thus impossible to estimate daily fuel load variation for the entire stopover period of each individual. However, trapping sessions at ringing stations suffice to estimate fuel load of stopping–over migrants (Schaub & Jenni, 2000a, 2000b; Arizaga et al., 2010, 2011b). To obtain a closer estimation of fuel load both on arrival at the site and on departure, we selected the ten lightest and heaviest migrants in each zone (Ellegren & Fransson, 1992). Since migrants are expected to gain fuel whilst stopping–over at a site, the lightest birds are those most likely to have just arrived, whereas the heaviest birds are those most likely about to depart. We compared fuel loads between zones using an ANCOVA on body mass with zone and fuel category (lightest/heaviest) as factors, and P3 as a covariate that controlled for body size. Although body mass can differ between age classes (Grandío, 1999), we did not consider age as an additional factor due to the relatively low sample size, particularly in one of the zones (the invaded one). Body mass was normally distributed (K–S test: *P* > 0.05).

Table 1. Main (mean ± SE) vegetation characteristics at the two trapping stations. Statistics are calculated for a sample size of 12 nets at each trapping site. The habitat was studied within an area of 240 m² from each side of each net (*i.e.,* 480 m² around each net). The distance (straight line) from one zone to another was 300 m: * We show here the first and second dominant herbaceous plants.

*Tabla 1. Características principales (media ± EE) de la vegetación en las dos estaciones de trampeo. Los estadísticos se calcularon para un tamaño de muestra de 12 redes en cada punto de trampeo. El hábitat se estudió en una superficie de 240 m² a cada lado de las redes (es decir, 480 m² alrededor de cada red). La distancia (en línea recta) entre las dos zonas era de 300 m: * Aquí mostramos la primera y la segunda plantas herbáceas dominantes.*

	Affected by saltbush (Invaded zone) 43° 20' 43.44" N 02° 39' 44.30" W	Non–affected by saltbush (Control zone) 43° 20' 52.90" N 02° 39' 44.04" W
Vegetation cover (%)		
No vegetation (mud flats and water)	0.4 ± 0.4%	4.6 ± 1.9%
Tree	–	3.3 ± 2.2%
Bush	88.8 ± 4.7%	5.6 ± 2.8%
Herbaceous	10.8 ± 4.5%	86.5 ± 3.8%
Dominant vegetation		
Tree	–	*Tamarix*
Bush	*Baccharis*	*Baccharis*
Herbaceus*	*Juncus–Phragmites*	*Phragmites–Aster*
Vegetation height (over 12 nets)		
< 1 m	–	2/12
1–2 m	–	3/12
2–3 m	6/12	7/12
> 3 m	6/12	–

Contingency tables were also used to see whether the proportions of the first–year birds and adults differed between the control and invaded zones. This analysis was done only for sedge warblers.

The importance of a stopover site cannot be determined only in relation to how many birds a given site hosts. Consideration must also be given to sites which allow migrants to gain fuel (Alerstam & Lindström, 1990). Indeed, the fuel deposition rate is considered to reflect the habitat quality of a stopover site (Newton, 2008). To estimate fuel deposition rate, we considered the difference of body mass between the last and first capture event of each bird, divided by the number of days elapsed between these two events. To compare the fuel deposition rate between zones we used an ANCOVA on the fuel deposition rate with zone as a factor, and P3 and number of days between first and last capture as covariates. Since the estimation of the fuel deposition rate using recaptures of ringed migrants can be subject to bias due to a handling effect, especially when recaptures are obtained shortly after the first capture (Schwilch & Jenni, 2001), we repeated the analysis removing the migrants recaptured the day after their first capture event. Intermediate recaptures (in migrants recaptured more than once) were not considered in any of the analyses.

Finally, we also calculated the minimum stopover duration as: $(t_i–t_0) + 1$, where t_i and t_0 were respectively the date of the last and first capture event of each bird, respectively. The '+1' was added because sedge warblers are nocturnal migrants. We did not use a more accurate estimation of stopover duration (*e.g.* by means of the use Cormack–Jolly–Seber models, which allow separation of the survival and recapture probabilities) because our sample was too small to allow us to separately estimate survival (here, probability of a bird remaining at the site from one day to the next) and the recapture rate (Lebreton et al., 1992). We used a *t*–test assuming heteroscedasticity to test if the stopover duration differed between the control and invaded zones.

For statistical procedures, we used the software PAST 2.1. (Hammer et al., 2001), and SPSS 18.0. All means are given ± SE.

Results

Assemblage characteristics

We captured a total of 30 bird species in the invaded zone and 28 of these were passerines. In the control zone we captured 28 species and 26 were passerines. The number of captures at each zone was 529 and 558, respectively (table 2).

Bird assemblage did not differ in terms of richness, but it did differ in terms of diversity (table 3), which was lower in the control zone. Another notable aspect was that bird assemblage in the control zone was richer in species typical of reedbeds and wetlands, while in the invaded zone assemblage was richer in woodland–related species (table 3). In the control zone, six out of the ten most abundant species were clearly associated with reedbeds and wetlands (only classified as 'reed' in table 2), while conversely, in the invaded zone, six species were clearly associated with woodlands (classified as 'wood' in table 2; fig. 1). The aquatic warbler, the only species linked to wetlands and globally threatened, only appeared in the control zone ($n = 7$).

Capture rates were similar in both zones (invaded zone: 18.0 ± 2.7 cap./day, $n = 29$; control zone: 18.2 ± 3.0 cap./day, $n = 31$; $t_{58} = 0.25$, $P = 0.80$). However, the difference was significant when only captures of species clearly related to reedbeds/wetlands were considered (invaded zone: 6.2 ± 0.7 cap./day, $n = 29$; control zone: 10.0 ± 1.0 cap./day, $n = 31$; $t_{58} = 3.12$, $P = 0.003$).

Recaptures

We found 26% of the birds captured in the control zone were recaptured (at any of the study zones), while only 15% of the birds captured in the invaded zone were recaptured (at any of the study zones). This difference was significant ($\chi_1^2 = 13.04$, $P < 0.001$). Focusing on species related to reedbeds, the proportion was 38% and 25%, respectively ($\chi_1^2 = 4.71$, $P = 0.03$).

Moreover, 6% of the birds first captured in the control zone were thereafter recaptured in the invaded zone, while 24% of the birds first captured in the invaded zone were thereafter recaptured in the control zone. This difference being significant ($\chi_1^2 = 9.78$, $P = 0.002$). Focusing on species typical of reedbeds, the difference was even higher (6% *versus* 32%; $\chi_1^2 = 12.97$, $P < 0.001$), even for sedge warblers (3% *versus* 58%; $\chi_1^2 = 11.49$, $P = 0.005$), indicating that species from reedbeds tended to move to the control zone much more often than the other way around.

Body mass, fuel deposition rate, age ratios and stopover duration in sedge warblers

Sedge warblers captured in the invaded and control zone did not differ in body mass when considering only the ten lightest migrants in each zone, but there was a difference at the other end of the scale (fig. 2; ANCOVA: zone, $F_{1,39} = 20.73$, $P < 0.001$; fuel category, $F_{1,39} = 385.25$, $p < 0.001$; zone × fuel category, $F_{1,39} = 35.18$, $P < 0.001$; P3, $F_{1,39} = 0.001$, $P = 0.98$).

The body mass (controlled for body size) of the ten heaviest migrants in the control zone was higher than the body mass of the ten heaviest migrants in the invaded zone (fig. 2).

Sedge warblers last recaptured in the control zone showed significantly higher fuel deposition rates than those recaptured in the invaded zone (table 4).

The proportion of first–year birds and adults did not differ between the invaded (48.6%) and control zones (57.1%; $\chi_1^2 = 0.80$, $P = 0.37$).

Minimum stopover duration in the control zone (6.4 ± 0.9 days, $n = 32$) was longer than in the invaded zone (3.0 ± 0.6 days, $n = 3$; $t_{17.228} = 3.20$, $P = 0.005$).

Discussion

The saltbush is an exotic shrub that invades humid habitats in Europe and displaces the native vegetation (*e.g.,* reedbeds). In this work, we show that the saltbush may have a negative impact on both the abundance and stopover characteristics (fuel management and habitat use) of migrants associated with reedbeds.

Bird assemblage characteristics

The diversity index was found to reach higher values in the invaded zone than in the control zone, mainly due to the fact that in the control zone there were three passerines accounting for 70% of the captures, whilst in the invaded zone only two species were clearly dominant, making up 50% of the captures. Reedbeds constitute particular habitats where vertical vegetation is dominant. Exploitation of this type of vegetation requires high adaptation/specialization, so reedbeds constitute an adequate habitat for relatively few species (Poulin et al., 2000, 2002; Leisler & Schulze–Hagen, 2011) compared to other habitats where horizontal vegetation is dominant (*e.g.*, Arizaga et al., 2009). It is of note that in species that are typical of wooded areas and occupy reedbeds during the non–breeding period, such as robins (*Erithacus rubecula*), it is the juvenile fraction which is detected in reedbeds and wetlands (suboptimal habitats), whilst adults monopolize more suitable habitats such as forests (Figuerola et al., 2001). Thus, the captures in the control zone were mostly of species typical of reedbeds and wetlands, whereas the species detected in the invaded zone were, to a larger extent, typical of forested habitats. Moreover, reedbed–associated species were more abundant in the control zone than in the invaded zone. This result highlights that the saltbush not only had a negative impact on the abundance of reedbed–associated species, but also affected bird assemblage by facilitating the presence of woodland passerines.

Stopover behavior

The finding that the proportion of recaptures was higher for the control zone than for the invaded zone suggests that migrants tended to stay longer in the control zone. We cannot overlook the possibility that the recapture rate was site–dependent and this may have imposed some

Table 2. Number of captures/recaptures of species caught with mist nets in the invaded and control zones. Species were assigned to the specific habitats that they normally occupy during the non–breeding period, either when foraging or roosting (Cramp, 1988, 1992; Cramp & Perrins, 1994): Reed. Reedbeds and wetlands; Wood. Woodland, including shrubs, hedgerows, forested areas and parks with trees/ shrubs; Others. Urban areas, open habitats, crops. Recaptures refer to birds recaptured ≥ 1 days after the first capture event, to sites where birds were first captured (*i.e.*, a bird captured in the control zone and subsequently recaptured in the invaded area is included in the column of recaptures for the control zone), and only one recapture per bird is considered: Cp. Captures; Rcp. Recaptures.

Tabla 2. Número de capturas/recapturas de las especies atrapadas en redes japonesas en las zonas invadida y de control. Las especies se asignaron a los hábitats que suelen ocupar durante el período no reproductivo, bien mientras forrajeaban, bien mientras reposaban (Cramp, 1988, 1992; Cramp & Perrins, 1994): Reed. Carrizales y humedales; Wood. Tierras arboladas, incluidos arbustos, setos, áreas boscosas y parques con árboles y arbustos; Others. Áreas urbanas, hábitats abiertos y cultivos. Las recapturas hacen referencia a las aves que se volvieron a capturar uno o más días después de la primera captura y a los sitios en que se había capturado a las aves la primera vez (esto es, un ave capturada en la zona de control y posteriormente vuelta a capturar en la zona invadida figura en la columna de las recapturas de la zona de control); solo se tuvo en cuenta una recaptura por ave: Cp. Capturas; Rcp. Recapturas.

Specific name	Code	Main habitats	Invaded zone		Control zone	
			Cap.	Rcap.	Cap.	Rcap.
A. arundinaceus	ACRARU	Reed	0	0	1	1
A. paludicola	ACROLA	Reed	0	0	7	2
A. schoenobaenus	ACRSCH	Reed	37	7	106	40
A. scirpaceus	ACRSCI	Reed	106	22	145	56
A. caudatus	AEGCAU	Wood	17	1	0	0
A. atthis	ALCATT	Reed	9	5	7	3
C. brachydactyla	CERBRA	Wood	1	0	0	0
C. cetti	CETCET	Reed	23	13	12	4
C. juncidis	CISJUN	Others + Reed	2	0	38	9
E. rubecula	ERIRUB	Wood	21	9	5	4
F. hypoleuca	FICHYP	Wood	3	0	1	0
F. coellebs	FRICOE	Wood + Others	3	0	1	0
G. glandarius	GARGLA	Wood	1	0	0	0
H. pollyglotta	HIPPOL	Wood	6	0	7	0
J. torquilla	JYNTOR	Wood	1	0	0	0
L. collurio	LANCOL	Others + Wood	4	0	4	0
L. luscinioides	LOCLUS	Reed	0	0	1	1
L. naevia	LOCNAE	Wood + Reed	6	0	3	0
L. megarhynchos	LUSMEG	Wood	2	0	2	0
L. svecica	LUSSVE	Reed	6	0	30	13
P. caeruleus	PARCAE	Wood	10	2	8	3
P. cristatus	PARCRI	Wood	2	0	0	0
P. major	PARMAJ	Wood	5	0	6	0
P. domesticus	PASDOM	Others + Reed	3	0	1	0
P. montanus	PASMON	Wood + Reed	0	0	2	0
P. ibericus	PHYIBE	Wood	23	4	4	1
P. trochylus	PHYLUS	Wood + Reed	155	7	145	5
R. aquaticus	RALAQU	Reed	0	0	1	0

Table 2. (Cont.)

			Invaded zone		Control zone	
Specific name	Code	Main habitats	Cap.	Rcap.	Cap.	Rcap.
R. ignicapillus	REGIGN	Wood	2	1	1	0
S. torquata	SAXTOR	Wood	1	0	0	0
S. vulgaris	STUVUL	Others + Reed	0	0	1	0
S. atricapilla	SYLATR	Wood	25	1	0	0
S. borin	SYLBOR	Wood	7	0	1	0
S. communis	SYLCOM	Wood	10	0	14	0
T. troglodytes	TROTRO	Wood	11	3	4	2
T. merula	TURMER	Wood	27	4	0	0

bias in relation to the estimation of stopover duration (Schaub et al., 2001). Unfortunately, our sample was too small to separately estimate survival (here meaning the probability of a bird remaining in the site from one day to the next) and the recapture rate (Lebreton et al., 1992).

Mean fuel deposition rate in the control zone (+ 0.2 g/d) was even higher than the rate reported in another coastal reedbed in northern Iberia (+ 0.1 g/d; Grandío, 1998). In optimal stopover habitat, the species has been reported to reach mean rates of > + 0.3 g/d (Schaub & Jenni, 2000a). Thus, the rate of fuel accumulation at Urdaibai seemed high, and hence the control zone can well be considered an optimal habitat for the species. The fact that the proportion of birds that moved to the control zone from the invaded zone was higher than the opposite scenario supports the hypothesis that the saltbush area was suboptimal for migrants as compared to reedbeds. Also supporting the hypothesis that the saltbush did not provide a proper fuelling chance for migrants was the finding that the fuel deposition rate in the control zone was much higher than in the invaded zone. Together with the previous result, this is in accordance with the idea that migrants quickly depart from a site when experiencing a very low fuel accumulation rate (Alerstam & Lindström, 1990). From an evolutionary standpoint, this response allows migrants to look for better stopover places and thus have a second chance

to gain fuel during migration period. However, this flexible behavior depends on current fuel load, and birds with small fuel loads will therefore be hampered in finding a better stopover site if this is associated with long displacements. In this scenario, invasive plants imposing radical habitat changes, like the saltbush, constitute a severe problem from a fuelling standpoint. This is particularly applicable if native vegetation is replaced by exotic plants across very large areas. The substitution of reedbeds by saltbushes in several coastal marshes in the Bay of Biscay, including Urdaibai, must be regarded as a problem with unknown consequences for the conservation of migrant bird species associated with reedbeds.

The body mass of the ten heaviest and the ten lightest sedge warblers from each zone was used as a surrogate of body mass at departure and arrival, respectively (Ellegren & Fransson, 1992). The analysis of these data indicate that sedge warblers arrived at both zones with a similar fuel load, but departed with more fuel from the control zone, a result that is in accordance with the control zone favoring fuel accumulation. This result cannot be considered to be caused by a possible bias between age classes (body mass can vary between age classes; Grandío, 1999) and zones, since the proportion of each age class was constant for the invaded and control zones. Our results also support the hypothesis that a number of

Table 3. Diversity–related statistics between the invaded and control zones.

Tabla 3. Estadísticos relacionados con la diversidad entre las zonas invadida y de control.

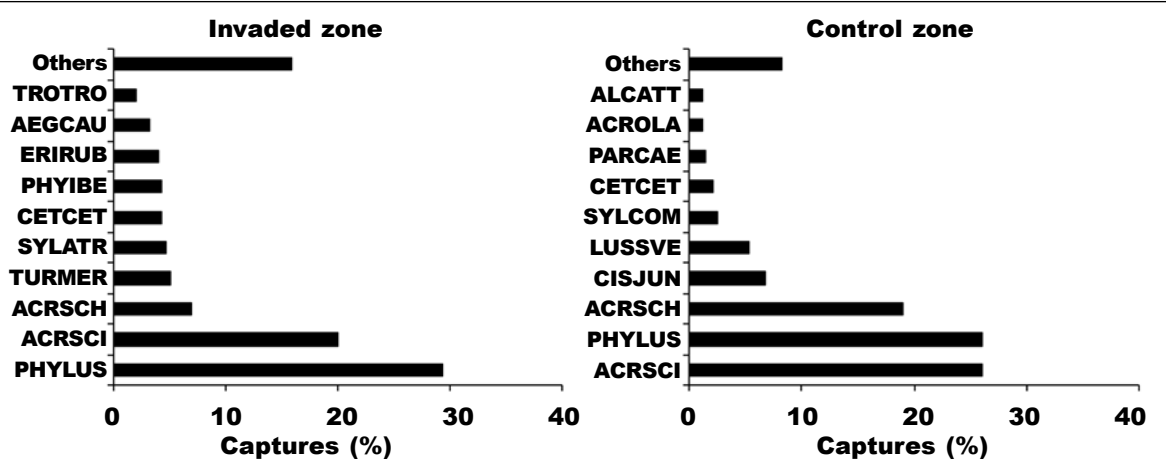|	Invaded zone	Control zone	Bootstrap (*P*–values)
Taxa (richness)	30	28	0.556
Shannon diversity index (*H'*)	2.485	2.124	< 0.001

Fig. 1. Relative number of captures (first capture event) of the ten most frequent species at each sampling zone.

Fig. 1. Número relativo de capturas (primera captura) de las diez especies más frecuentes en cada zona de muestreo.

warblers in the saltbush zone may have been able to compensate for their low fuel accumulation rate/fuel load on departure by moving to a better site (the control zone) with higher fuelling chance.

Conclusion and perspectives

The saltbush had a negative impact on several species closely associated with reedbeds, and promoted
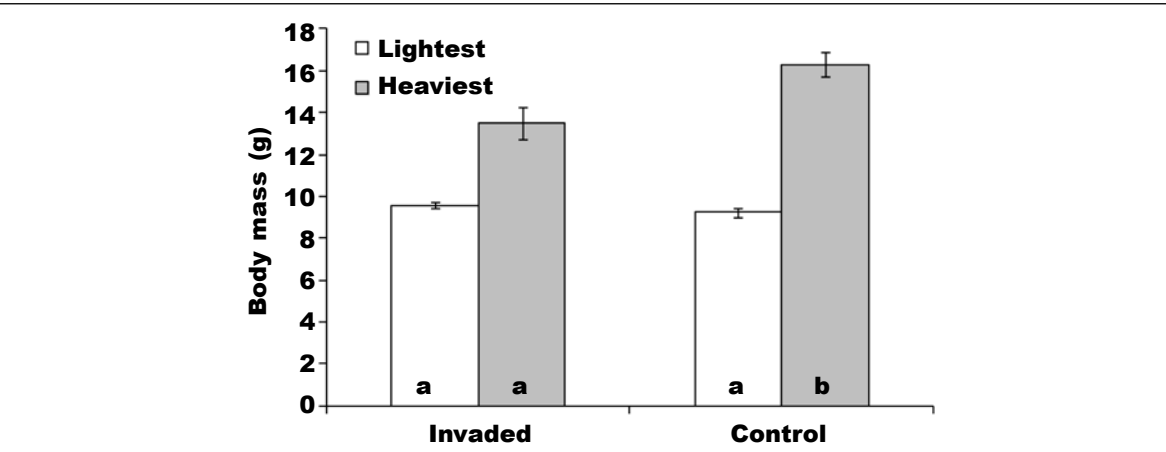

Fig. 2. Mean (± SE) body mass of sedge warblers first captured at the invaded and control zones. For each zone, we considered the ten lightest and heaviest captures of sedge warblers in each zone (ages pooled). Also within each zone, average values bearing the same letters represent non–significant differences in body mass between fuel categories (lightest/heaviest). Differences in body size were controlled including P3 as a covariate.

Fig. 2. Media (± EE) del peso corporal de los carricerines que se capturaron por primera vez en las zonas invadida y de control. Para cada zona, se tuvieron en cuenta las capturas de los diez carricerines de mayor y menor peso en cada zona (agrupadas por edad). También para cada zona, los valores medios asociados a las mismas letras representan diferencias no significativas en cuanto al peso corporal entre las categorías de cantidad de grasa (más ligero/más pesado). Las diferencias de tamaño corporal se controlaron con la inclusión de la P3 como covariable.

Table 4. Mean (± SE) fuel deposition rates for sedge warblers captured in the invaded and control zones. Sample size in brackets. Data on both zones were compared with an ANCOVA on fuel deposition rate with zone as factor and P3 and number of days elapsed between the first and last captures as covariates; we only show *F*–values used to test for the effect of zone. The number of recaptures differed from table 1 since not all birds had the P3 measured.

Tabla 4. Media (± EE) de los índices de deposición de grasa para los carricerines capturados en las zonas invadida y de control. El tamaño de la muestra se muestra entre paréntesis. Los datos de ambas zonas se compararon con una ANCOVA del índice de deposición de grasa con la zona como factor y la P3 y el número de días transcurridos entre la primera captura y la última como covariables; mostramos únicamente los valores de F utilizados para comprobar los efectos de la zona. El número de recapturas difirió de las de la tabla 1 porque no se midió la P3 a todas las aves.

Days	Invaded zone	Control zone	*F*	*P*
All	− 0.1 ± 0.1	+ 0.2 ± 0.1	0.062	0.812
	(4)	(41)		
> 1	− 0.2 ± 0.2	+ 0.1 ± 0.1	4.316	0.016
	(3)	(31)		

a noticeable change on bird assemblage, which was found to be enriched by species typical of woodland habitats. A migrant species strongly associated with reedbeds during migration period, sedge warblers captured at the control zone departed with a higher fuel load, showed a higher fuel deposition rate, and remained for longer than those that stayed at a nearby site occupied by saltbushes (an exotic invasive bush from America). Our results suggest that saltbushes reduce the habitat quality for migratory sedge warblers. Unfortunately, data comparing bird migration in the control and invaded areas before saltbushes invasion are not available. Consequently, although unlikely, it might be possible that both areas already differed in their quality before invasion. Future research with replicates will be necessary to confirm these results. Further studies are also needed to accurately quantify how the wetlands (coastal marshes) from southern Europe have been affected by saltbushes, and to better understand the ecology of migrants so as to to be able to properly evaluate the real impact of saltbushes on the stopover behavior and migratory performance of bird migrants associated with reedbeds. From a management standpoint, restoration of reedbeds must be regarded as a priority tool to preserve the optimal stopover habitat for passerines associated with this type of vegetation.

Acknowledgements

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