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Influence of habitat quality and diversity on two populations of Eurasian Curlew (*Numenius arquata*) with contrasting dynamics in Western France

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Like most shorebirds in Europe, breeding populations of Eurasian Curlew (*Numenius arquata*) are suffering from habitat loss and degradation mainly caused by changes in agricultural practices. In Deux-Sèvres (France), the number of pairs has gradually declined since the early 2000s in the main, historical breeding site, while a new breeding site has appeared recently 80 kilometres further north with increasing number of pairs through the survey period. Many wheat fields and rare dry grasslands are found in the north, whereas the landscape in the south is mainly composed of tillage plots, hay meadows, and pastures. This study aims to highlight differences in food availability and quality between the two areas. Sample series of ground-dwelling and vegetation-dwelling invertebrates were carried out during three key stages of the species breeding cycle with pitfall traps and sweep nets. Dry grasslands in the north were found to be the most favourable habitat in terms of prey availability for adults and for chicks during the brood-rearing period. Moreover, hay meadows and pastures in the south seemed to be resource-abundant feeding habitats. Therefore, the habitats of the northern site seem to offer a greater abundance of invertebrates and thus a potentially larger food resource than the southern one. It follows that the northern site likely offers better breeding conditions, especially for the growth of chicks. An increase in the area of dry grasslands in the north and the establishment of adapted agricultural management in the south would be favourable for the conservation of local curlew populations.

1. Introduction

Shorebird populations have been declining markedly worldwide for several decades (Stroud *et al*. 2006), particularly in Europe, where half of the species are classified as 'threatened' on the IUCN Red List (Butchart *et al*. 2010, Pearce-Higgins *et al*. 2017). Among the major threats involved in these declines are the loss and degradation of wintering and stopover habitats (van Roomen *et al*. 2012, Studds *et al*. 2017). However, many authors agree that falling productivity is the primary factor responsible for current population dynamics (Gregory *et al*. 2004, Macdonald & Bolton 2008, Roodbergen *et al*. 2012). Increasing predation on eggs and chicks has been evaluated as one of the main threats (Macdonald & Bolton 2008, Roodbergen *et al*. 2012, Bertholdt *et al*. 2017). It is also assumed that the modification of agricultural landscapes in recent decades has favoured access to broods by terrestrial predators such as the red fox, *Vulpes vulpes* (Bellebaum & Bock 2009, Niemczynowicz *et al*. 2017).

However, the loss and degradation of nesting habitats also explains the collapse of populations (Eglinton 2008, Zedler & Kercher 2005). Indeed, the transformation of agricultural practices in recent decades has led to the increasing scarcity and fragmentation of both wetlands, due to drainage, and grasslands, due to their conversion to arable land (Eglington 2008, Zedler & Kercher 2005). This agricultural revolution has been accompanied by a mechanisation and intensification of production methods. The frequency of mowing and density of herds have both increased and thereby led to the mechanical destruction or trampling of nests and chicks (Kruk *et al*. 1997, Kleijn *et al*. 2010).

In addition, another consequence of these modern agriculture techniques is a reduction in the availability of food resources for birds. On the one hand, the use of phytosanitary products has reduced the abundance of invertebrates, a primary food resource for insectivores such as shorebirds (Chamberlain *et al*. 2000, Clere & Bretagnolle 2001, Benton *et al*. 2002, Wilson *et al*. 2005). On the other hand, formerly favourable meadows that were characterized by a great floristic diversity and a heterogeneous vegetation structure have gradually been converted into a monospecific, fertilized sward, which is sometimes too dense to allow birds to feed in (Butler & Gillings 2004, Devereux *et al*. 2004, McCracken & Tallowin 2004, Eglington 2008). In addition, the homogenization of the vegetation structure and the simplification of plant communities have contributed to rarefaction in arthropods as well as to a reduction in their overall size (Kajak 1978, Green & Cadbury 1987, Siepel 1990, Blake *et al*. 1994, Vickery *et al*. 2001, McKeever 2003). In this context, smaller prey have become less profitable (in terms of energy gained per arthropod consumed) and therefore have increased the difficulty for adults and chicks to meet their energy needs.

The depletion of trophic resources could have major consequences on population dynamics, as reported by Kentie *et al*. (2013) for the black-tailed godwit, *Limosa limosa*, in areas of intensive agricultural areas in the Netherlands. This study reveals that chick survival was 2.5 times higher in traditionally managed grasslands (which featured late mowing, high floristic diversity, and maintenance of favourable water levels) than in intensive grasslands. These results suggest that the shift from historical management methods to intensive practices has exposed chicks to significant risk of dietary deficiency, thus decreasing their growth and potential for survival.

The Eurasian Curlew (*Numenius arquata*) is among the most threatened shorebird species in Europe, with strongly declining populations in several countries such as the UK or Ireland (48% in the UK between 1995 and 2015) (Harris *et al*. 2016). The species is now classified as vulnerable on the European IUCN Red List and benefits from an international action plan aimed at restoring its conservation status (Brown 2015). In France, the breeding population is declining moderately (Patrelle *et al*. 2017).

The French département of "Deux-Sèvres" hosts two populations of curlews with contrasted dynamics. Twenty years ago, all the breeding pairs were restricted to the southern sector, the plain of "La Mothe Saint-Heray-Lezay" (PLMSHL), an area characterized by a mixed agricultural landscape with meadows and pastures as well as a relatively well-preserved network of hedgerows. Since the early 2000s, a decrease of breeding pairs has been observed at this site. Around the same time, an increasing number of pairs have colonised two territories located 80 kilometres further north, the plain of "Oiron-Thenezay" (OITH) and the plains of Mireballais-Neuvillois (MINE) (Poirel 2017). Within these new breeding sites, the agricultural landscape is largely dominated by crops and tillage plots with only a few patches of dry grasslands.

The objective of this study is to find out whether differences in terms of habitat use and food availability between the PLMSHL and OITH sites could perhaps explain the opposing dynamics observed in the two core populations. For this purpose, a series of invertebrate samples were taken from several habitat types to determine which environments presented the most food resources for curlews. Breeding pairs were also monitored in parallel to find out which habitats the species was exploiting within both sites. We hypothesise that: (1) curlews select grasslands to feed, because (2) grassland habitats provide more important food resources than crops, and because (3) prey are more numerous and profitable in OITH than in PLMSHL considering the opposite dynamics of both populations.

2. Materials and methods

2.1. Study area

The study was carried out in a 'Zone de Protection Spéciale' or special protection area (SPA) on the plain of Oiron-Thénezay (OITH), located to the north-east of the Deux-Sèvres, as well as in a SPA on the plain of La Mothe-Saint-Héray-Lezay (PLMSHL), located to the south-east of the département (Fig.1). These sites are different in terms of landscape structure, habitat diversity, and agricultural practices (Berthomé & Turpaud-Fizzala 2012).

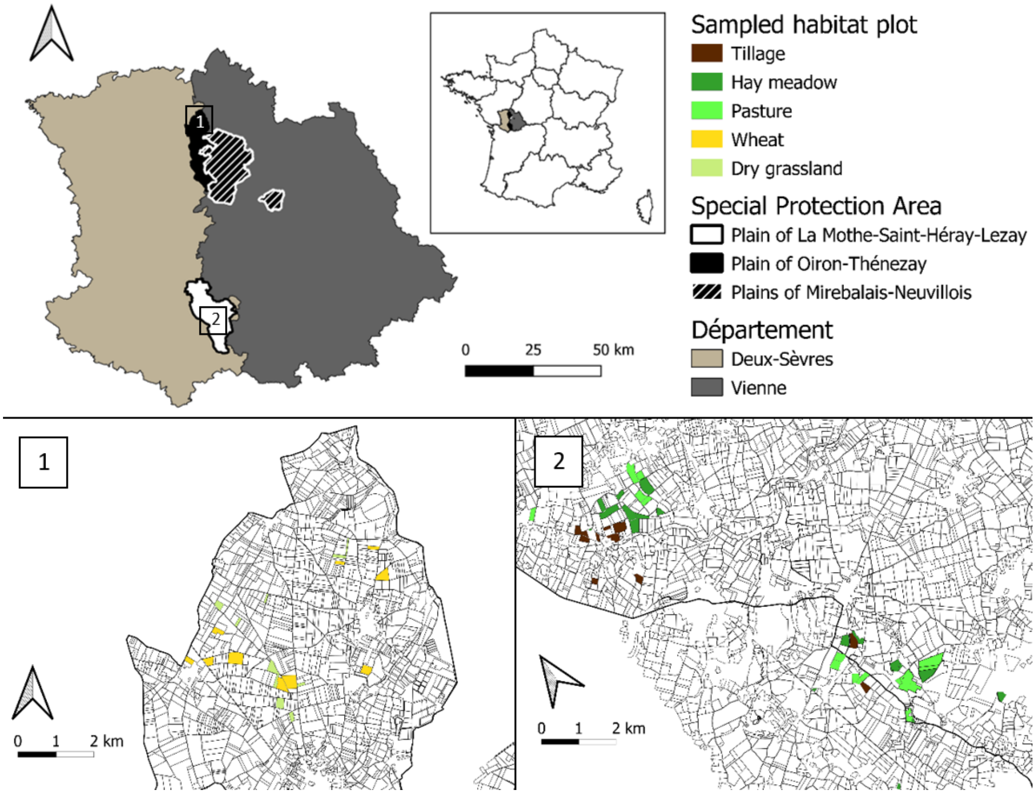

Fig. 1. Map of the Special Protection Areas of Oiron-Thénezay (OITH) in the north-east of Deux-Sèvres (black), of the Plain of La Mothe-Saint-Héray-Lezay (PLMSHL) in the south-east (white) and of the Plains of Mirebalais-Neuvillois (MINE) in the north-west of Vienne (hatched black). The plots sampled are represented in color in the two boxes at the bottom.

OITH (N 46°51'24", W 0°03'38") covers 15,580 ha. This intensive cereal-growing plain is marked by a shortage of hedgerows and by a continuous decrease of meadows since the late 1980s (Berthomé 2011). According to the latest estimates, meadows now account for only 10% of the utilised agricultural area (UAA), of which only about 3% are permanent dry grasslands. Agri-environmental management is applied to 4% of the total grassland area and allows for favourable habitats to be preserved for the breeding of the Little Bustard (*Tetrax tetrax*). This plan has been implemented since the 2000s in the département and encourages the transformation of agricultural plots into sown meadows, which favour the presence of invertebrates for improving the feeding and nesting conditions for little bustards. Benefits include delaying the mowing date from 15 May to 31 July (Bretagnolle *et al*. 2011). It should be noted that another SPA, on the plains of "Mirebalais-Neuvillois" (MINE), located in the neighbouring Vienne département, also hosts breeding pairs (Dubois 2011) (Fig. 1). MINE is adjacent to OITH (Fig. 1) and has the same types of habitats (Poirel., 2017). This is why breeding curlews in these two territories are considered to be part of the same core population. However, the study was not carried out in MINE because it is monitored by a different program. Nonetheless, data on breeding curlew numbers were provided to us to estimate the size of this core population straddling two territories.

PLMSHL (N 46°17'17", E 0°02'26"), the second study site, covers 24,451 ha. In this area, hedgerows are preserved, and grassland covers 29% of the UAA, of which 13% are permanent meadows, including rare wet meadows and some mesophilous grasslands (Berthomé & Turpaud-Fizzala 2012). Goat and cattle farming are among the reasons for the maintenance of hay meadows and pastures locally. This site is also a breeding ground for the little bustard, with 6% of the UAA of PLMSHL benefiting from agri-environmental measures (AEMs), as in OITH.

2.2. Long-term monitoring

In order to know about the temporal dynamics of the two population cores and variations in the distribution of breeding pairs within the two study sites, a compilation of historical data was carried out for 1981 to 2020 for OITH and PLMSHL. These data come from a digital naturalist database and from articles published in a local ornithological journal. A distribution map of breeding pairs was carried out for the years 2002, 2011, and 2019 by the Groupe Ornithologique des Deux-Sèvres (Gilet *et al*. 2002, Turpaud-Fizzala 2012, Lartigau 2018). It should be noted that the numbers of curlews present in MINE, the adjacent territory of OITH, were also analysed to assess the temporal dynamics of the OITH-MINE population core as a whole.

2.3. Breeding pair distribution

The monitoring of breeding pairs started from late February. To characterise breeding phenology and habitat use by birds, the territories of the pairs were surveyed from late March to early June 2019, after which the curlews were no longer expected to lay replacement eggs (Turpaud-Fizzala 2012). At both sites, observers were looking for breeding territories and tried to locate precisely the nest at least twice a week. The search areas were targeted on historical breeding areas. After every bird observation, the georeferenced location was noted. To estimate feeding habitat preferences, each individual observation was supplemented with a behaviour note as well as the habitat type on which it was observed. Behaviours such as foraging, resting, parading, mating, defending territory, and brooding were recorded. All foraging data were then compiled and the proportion of foraging curlews in each habitat type was compared to habitat availability in OITH and PLMSHL to highlight any potential habitat selection. Due to the difficulties encountered by some observers in differentiating certain types of grasslands or crops, all the observations of curlews were gathered in the following categories: 'Grasslands', 'Cereal crops', 'Tillage', and 'Other culture types'. The same gathering of habitat types was made to calculate their area in OITH and PLMSHL. The data of habitats areas were obtained from the Land Parcel Identification System (LPIS) (European Commission 2009) and calculations were made on Qgis (v3.4.2, QGIS Development Team 2017).

2.4. Invertebrate availability

Sampling of invertebrates living on the ground and in the vegetation strata was carried out at both study sites. The sampling was carried out in habitats known by local observers to be those most used by curlews in OITH and PLMSHL. It should be added that the grassland habitats were clearly different at both OITH and PLMSHL sites and therefore sampling could not be carried out on same habitats. In OITH, wheat and dry grasslands were the two habitats selected for the study (Fig. 3). Dry grasslands are calcicolous meadows with short plant formations, composed mainly of perennial herbaceous plants. In PLMSHL, tillage plots (sunflower and maize), pasture meadows, and hay meadows were sampled (Fig. 3).

In addition, two criteria had to be met for selecting a plot. First, the farmer must have given his authorization to access the land. Second, at least one sighting of curlews must have been made there in previous years.

Three series of sampling were carried out to study the availability of invertebrates throughout the breeding cycle of the species. Samples were collected from 25 April to 14 May (Session 1), from 28 May to 6 June (Session 2), and from 28 June to 8 July (Session 3). These periods correspond respectively to the peak of egg-laying, hatching, and fledgling of chicks (Turpaud-Fizzala 2012) (Fig. 2).

Ground-dwelling invertebrates living on the soil were sampled via pitfall trapping (Woodcock 2005). The traps were pots of 9 cm in diameter at their upper end and were filled with a saltwater solution (350 g of salt for 1 L of water) and a few drops of odourless washing-up liquid. They were set for 10 days. In addition, a plastic cover was suspended over each trap to prevent the pots from filling up in case of heavy rain or to protect them from excessive exposure to the sun (Woodcock 2005). The invertebrates were preserved in 70% alcohol. Each habitat was sampled in at least 10 plots with one trap each. To avoid an edge effect, the traps were placed in the plot as far as possible from adjacent plots (Clough *et al*. 2007). Each laying, mowing, or grazing event on the sampled meadows was noted.

Vegetation-dwelling invertebrates as a stratum were sampled via sweep netting (Doxon *et al*. 2011) with a net of 38 cm in diameter. For this purpose, 25 sweep movements were carried out by walking in a straight line in a predefined direction to stay as far away as possible from adjacent plots and thus limiting the possible edge effect (Puech 2014). Once trapped, the invertebrates were collected using a mouth aspirator and preserved in 70% alcohol.

All the organisms were identified to the order taxa using the identification key of Mignon *et al*. (2016), and the number of individuals was counted by order. All individuals less than 3 mm in length were excluded from the analysis as they were considered as not being able to be consumed by the curlew, according to Berg (1993) and Robson (1998). Each individual was measured

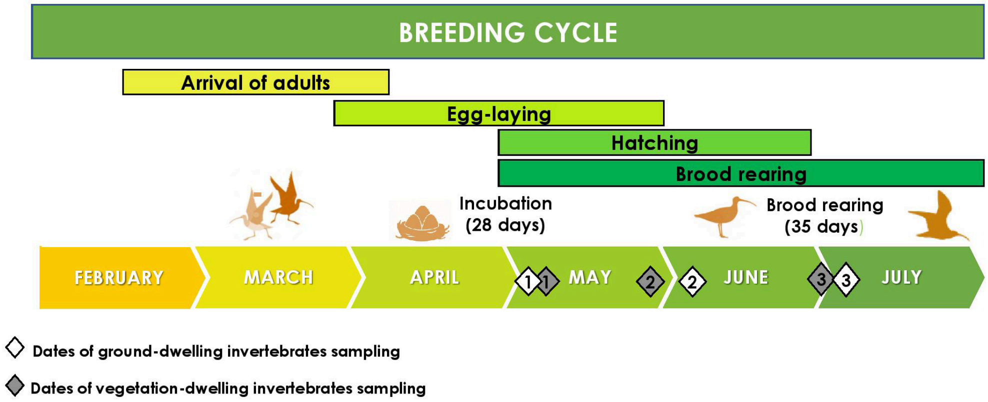

Fig. 2. Dates of ground and vegetation-dwelling invertebrates sampling according to the breeding cycle of the Eurasian Curlew in Deux-Sèvres.

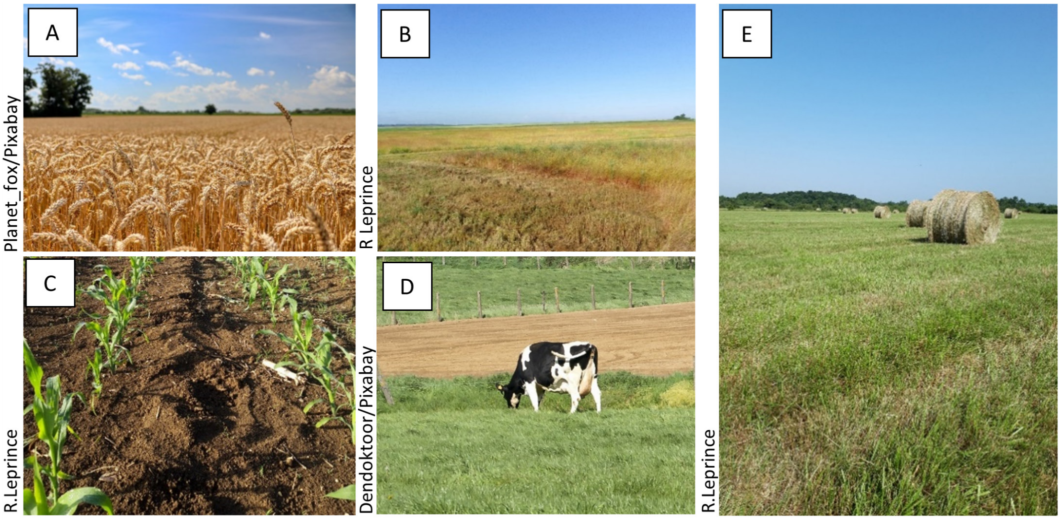

Fig. 3. Illustration of sampled habitats: A: Wheat (OITH), B: Dry grassland (OITH), C: Tillage (PLMSHL), D: Pasture (PLMSHL), E: Hay meadow (PLMSHL).

to an accuracy of 5 mm for length. Once the individuals were identified, they were collectively oven-dried at 65°C for 48 h per sample (Sabo *et al.* 2002). Dry mass (DM) was obtained using a balance with an accuracy of 0.001 g.

2.5. Statistical analyses

Habitat selection by curlew was assessed by comparing the habitat used while foraging (determined during monitoring survey) to availability (proportion of habitat present in study sites) using a χ^2 goodness-of-fit test (Zar 1999), while Bonferroni confidence intervals (Neu *et al.* 1974, Byers *et al.* 1984) were calculated to determine preference or avoidance of certain habitat types. Then, to determine the effect of the habitat type (wheat/dry grassland in OITH and tillage/hay meadow/pasture in PLMSHL) for each sampling session (1, 2, 3) on invertebrate abundance, we used likelihood ratio tests. Moreover, a type II ANOVA (Fisher 1925) was used to test the effect of that same independent variable on DM and length. When model assumptions could not be validated, non-parametric Kruskal–Wallis tests (Kruskal & Wallis 1952) were made. We used post hoc Tukey tests (Tukey 1949) for parametric methods and Dunn tests (Dunn 1964) for non-parametric methods to determine potential differences between the habitats. Furthermore, to test the effect of the sampling session in each habitat type on invertebrate abundance, DM, and length, Wald tests (Wald 1943) were used by adding the ‘plot number’ as a random factor. When model assumptions could not be validated, Friedman tests (Friedman 1939) and Wilcoxon tests for paired data (Wilcoxon 1945) were used. All the statistical tests were performed using R software (R Core Team 2019).

3. Results

3.1. Dynamic of breeding populations

The curlew population of PLMSHL has declined slightly over the past 20 years (Fig. 4). Between 24 and 28 breeding pairs were counted at this site between 2000 and 2002, while the breeding population fell to 14 to 21 pairs between 2017 and 2019 (Fig. 4). In OITH, the number of pairs has increased significantly since the recording of the first breeding pair in 2006, to reach 15 to 17 pairs between 2017 and 2019 (Fig. 4). Moreover, the emergence of breeding pairs on the plains of Mirebalais-Neuvillois (MINE) occurred at the same period as the increase at OITH. Despite some variations, the number of pairs in MINE has seemed to be stable since 2013 and varies between

4 and 8 pairs. The spatial distribution of breeding pairs slightly changed between 2002 and 2019 in PLMSHL, with the current population in 2019 more scattered than it was in 2002 (Fig. 5). In OITH, the population has clearly increased from the initial core areas that existed in 2011, except for the settlement of one pair in the southernmost part of the area. In addition, the density has increased notably (Fig. 5).

3.2. Feeding habitat selection

Regarding the availability of the different types of habitats on each study site, cereal crops represent 68.9% of the UAA in OITH and 43.7% in PLMSHL, while grasslands occupy only 10.3% in OITH and 29.7% in PLMSHL (Table 1, Supplementary Material Fig. S3). The proportions of curlews feeding in each habitat type

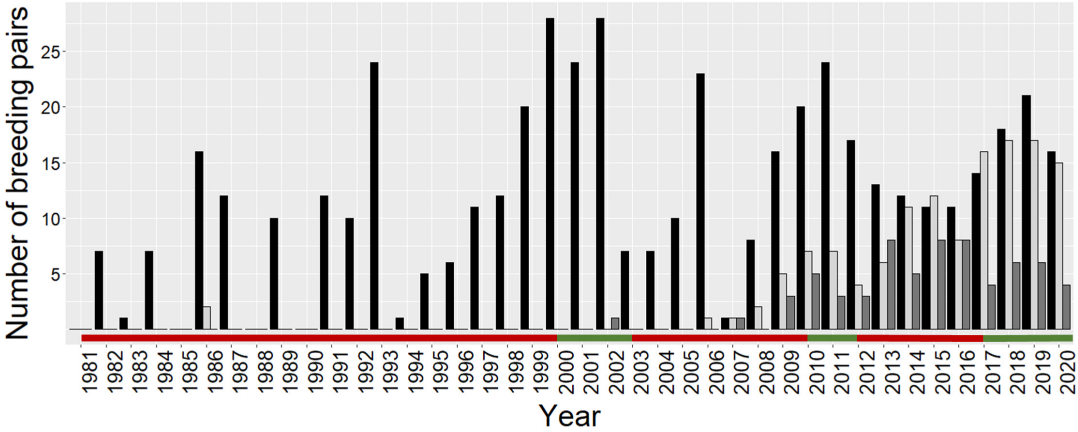

Fig. 4. Variation of the number of curlew pairs in PLMSHL in black, in OITH in light grey and in MINE in dark grey between 1981 and 2020. The periods benefiting from monitoring protocols are represented with a horizontal green bar and those not benefiting from it with a horizontal red bar.

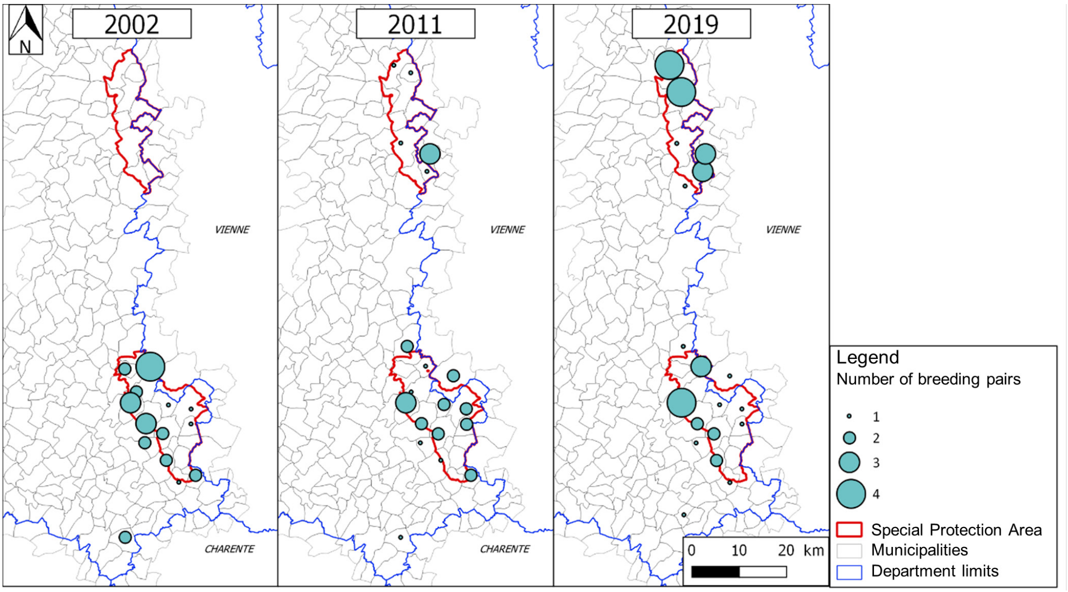

Fig. 5. Spatial dynamics of the Eurasian Curlew over PLMSHL in the south-east and OITH in the north-east of Deux-Sèvres for the years 2002, 2011 and 2019.

were found to be significantly different from the proportions expected in OITH (χ^2=1183.4, df=3, p<0.001) and in PLMSHL (χ^2=257.1, df=3, p<0.001) (Table 1). Indeed, Bonferroni confidence intervals (Table 1) showed that the curlews used the grasslands more than expected in OITH (63%, CI95=44.9-80.8%, n=374) and in PLMSHL (85%, CI95=65.6-104.8%, n=169), if we rely on their availability at the two study sites (Table 1). Conversely, cereal plots were less used in OITH (12.0%, IC95=−12.1–24.1%, n=374) and in PLMSHL (1.2%, IC95=−4.8%–7.2%, n=169) by curlews while foraging compared with their availability in the environment. On the other hand, no difference was found for tillage plots and other culture types (Table 1).

3.3. Invertebrate abundance

A total of 17 orders of Arthropoda were identified in all the samples. The two other main taxa were Gastropoda and Lumbricidae. All larvae from all orders were gathered under the category ‘Larva’. Isopods (woodlice) (35.9%), beetles (35.0%), spiders (25.4%), and hemipters (24.7%) were the taxa most represented in all the samples from the two types of traps (total n=12.505 individuals; see Supplementary Material Tables S1–S2 for taxa abundance). However, a majority of isopods (35.9%) and spiders (17.1%) were found at the ground surface (Supplementary Material Table S1) and a majority of hemipters (23.5%) and beetles (20.8%) in the vegetation stratum (Supplementary Material Table S2).

During the ‘laying’ sampling session (S1: early May), no significant differences between habitats were observed concerning the ground-living invertebrates (χ^2=8.07, df=4, p=0.089, Fig. 6a, Table 2). However, in the vegetation stratum, wheat fields (OITH) had a lower abundance of arthropods than in the dry grasslands (OITH) (Tukey post hoc test: p<0.001, Fig. 7a, Table 2) or hay meadows (PLMSHL) (Tukey post hoc test: p=0.01, Fig. 7a, Table 2). It should also be noted that the absence of vegetation in tillage plots (PLMSHL) during that session prevented any sweep netting.

During the ‘hatching’ session (S2: early June), the abundance of invertebrates increased

Table 1. Results of the comparison between the proportion of foraging curlew in each habitat (use) and the proportion of habitat areas (availability) in OITH and PLMSHL. Values obtained are shown in the chi-squared test and the Bonferroni confidence intervals. NS = no significant difference between availability and use; > = habitat used more than availability; < = habitat used less than availability.

Habitat	Chi-squared test	Proportion of foraging curlew observed	Expected proportion of use (*e.g.* proportion of habitats area)	Observation number	Bonferoni confidence intervals	Conclusion
OITH						
Grasslands	χ^2=1183.4 df=3 p<0.001	62.8%	10.3%	235	44.9–80.8%	>
Cereal crops		12.0%	68.9%	45	–12.1–24.1%	<
Tillage		15.5%	10.4%	58	2.1–29.0%	NS
Other culture types		9.63%	10.4%	36	–1.3–20.6%	NS
PLMSHL						
Grasslands	χ^2=257.1 df=3 p<0.001	85.2%	29.7%	144	65.6–104.8%	>
Cereal crops		1.2%	43.7%	2	–4.8–7.2%	<
Tillage		13.0%	23.5%	22	–5.6–31.6%	NS
Other culture types		0.6%	3.1%	1	–3.6–4.8%	NS

significantly compared with the ‘laying’ session in wheat fields (OITH), both in vegetation (Tukey post hoc test: p<0.001, Fig. 7a, Table 2) and on the ground (Tukey post hoc test: p<0.001, Fig. 6a, Table 2), while dry grasslands (OITH) became richer only in the vegetation stratum (Tukey post hoc test: p<0.001, Fig. 7a, Table 2). Moreover, vegetation-dwelling invertebrates were significantly less numerous in tillage plots (PLMSHL) than in other habitats (Tukey post hoc tests: wheat: p<0.001; dry grassland: p<0.001; hay meadow: p<0.001; pasture: p<0.001, Fig. 7a, Table 2), while ground-dwelling invertebrates were more abundant in dry grasslands (OITH) than in pastures, tillage plots (PLMSHL), and hay meadows (PLMSHL) (Tukey post hoc

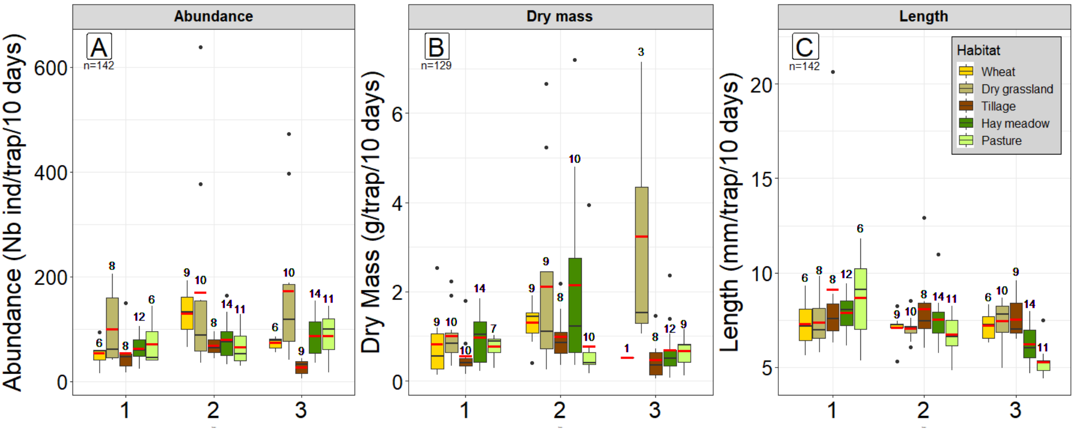

Fig. 6. Abundance of ground-dwelling invertebrates per trap (mean ± sd) (A), Dry mass of ground-dwelling invertebrates per trap (B), length of ground-dwelling invertebrates per trap (C) in the different habitats sampled for the three sampling sessions (S1: early May – laying session, S2: early June – hatching session, S3: early July-rearing session). Wheat (yellow), Dry Grassland (persimmon), Tillage (brown), Hay meadow (dark green), Pasture (light green). Means are represented by the horizontal red line. The number of samples per habitat is indicated above each box.

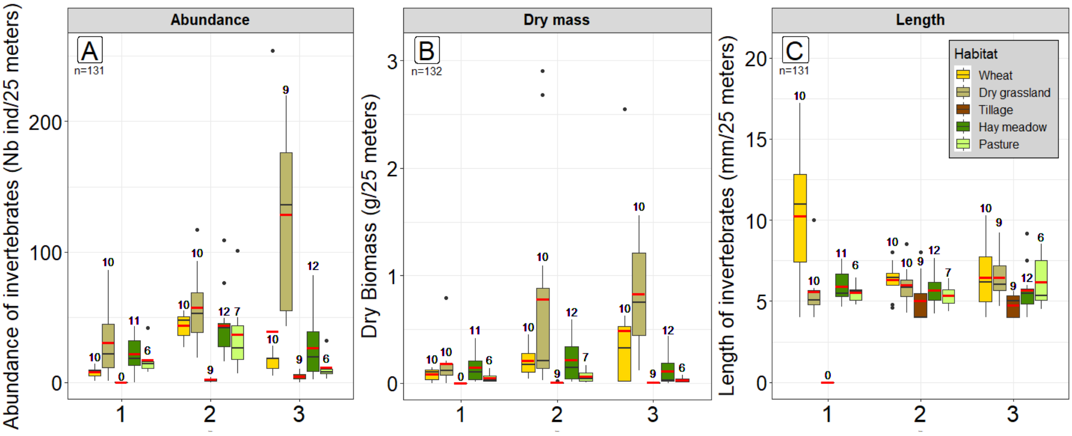

Fig. 7. Abundance of vegetation-dwelling invertebrates per 25 meters (mean ± sd) (A), Dry mass of vegetation-dwelling invertebrates per 25 meters (B), length of vegetation-dwelling invertebrates per 25 meters (C) in the different habitats sampled for the three sampling sessions (S1: early May – laying session, S2: early June – hatching session, S3: early July-rearing session). Wheat (yellow), Dry Grassland (persimmon), Tillage (brown), Hay meadow (dark green), Pasture (light green). Means are represented by the horizontal red line. The number of samples per habitat is indicated above each box.

Table 2. Average (±SE) invertebrate abundance (nb ind) and dry mass(g) per pitfall trap and per sweep-netting transect in the different habitat types sampled during the three sampling sessions. For each session, the coefficients of variation of abundance and dry mass within each habitat are given and are bold when the value is very high.

S	Study site	Habitats	Parameters	Pitfall trap		Sweep-net	
				Means	Coefficients of variation	Means	Coefficients of variation
1	OITH	Wheat	Abundance	53.8 ± 10.7	48.9%	7.9 ± 1.2	47.8%
			Dry mass	0.82 ± 0.25	90.2%	0.08 ± 0.02	75.0%
	OITH	Dry grassland	Abundance	100.4 ± 24.8	69.9%	30.0 ± 8.2	86.5%
			Dry mass	1.0 ± 0.19	61.0%	0.17 ± 0.07	**127.8%**
	PLMSHL	Tillage	Abundance	53.5 ± 14.6	77.0%	–	–
			Dry mass	0.55 ± 0.15	87.2%	–	–
	PLMSHL	Hay meadow	Abundance	62.1 ± 6.8	38.1%	21.5 ± 4.2	64.6%
			Dry mass	0.97 ± 0.14	55.7%	0.14 ± 0.04	**100.0%**
	PLMSHL	Pasture	Abundance	71.3 ± 18.3	62.8%	17.3 ± 5.1	72.3%
			Dry mass	0.77 ± 0.10	33.7%	0.05 ± 0.02	**100.0%**
2	OITH	Wheat	Abundance	129.3 ± 14.3	33.2%	43.3 ± 3.2	23.1%
			Dry mass	1.31 ± 0.16	35.8%	0.21 ± 0.05	69.9%
	OITH	Dry grassland	Abundance	169.2 ± 61.1	**114.2%**	57.5 ± 9.6	52.7%
			Dry mass	2.12 ± 0.76	**107.5%**	0.78 ± 0.35	**141.4%**
	PLMSHL	Tillage	Abundance	68.3 ± 6.8	28.3%	1.8 ± 0.5	78.9%
			Dry mass	0.99 ± 0.22	61.6%	0.06 ± 0.02	**250.0%**
	PLMSHL	Hay meadow	Abundance	79.2 ± 9.7	45.8%	43.5 ± 7.6	60.7%
			Dry mass	2.14 ± 0.71	**105.6%**	0.22 ± 0.06	99.3%
	PLMSHL	Pasture	Abundance	65.4 ± 10.1	51.1%	36.6 ± 12.1	87.4%
			Dry mass	0.78 ± 0.36	**107.5%**	0.06 ± 0.02	**96.7%**
3	OITH	Wheat	Abundance	73.5 ± 5.2	17.3%	38.8 ± 24.02	**196.1%**
			Dry mass	0.52	–	0.24 ± 0.07	89.5%
	OITH	Dry grassland	Abundance	172.7 ± 46.7	85.6%	128.6 ± 23.2	54.2%
			Dry mass	3.24 ± 1.96	104.3%	0.48 ± 0.12	73.4%
	PLMSHL	Tillage	Abundance	27.1 ± 4.8	53.1%	4.6 ± 1.2	80.0%
			Dry mass	0.48 ± 0.17	97.9%	0.01± 0.01	97.1%
	PLMSHL	Hay meadow	Abundance	86.5 ± 10.2	43.8%	26.5 ± 6.8	89.4%
			Dry mass	0.69 ± 0.18	**194.4%**	0.12 ± 0.04	**127.2%**
	PLMSHL	Pasture	Abundance	87.5 ± 13.0	49.3%	11.3 ± 4.3	92.9%
			Dry mass	0.67 ± 0.12	55.2%	0.03 ± 0.01	91.4%

tests: $p<0.001$; tillage: $p=0.003$; hay meadow: $p=0.006$, Fig. 6a, Table 2).

During the ‘rearing’ session (S3: early July), invertebrate abundance decreased at the ground level in wheat (OITH) and tillage plots (PLMSHL) compared with the “hatching” session (Tukey post hoc tests: wheat: $p=0.004$; tillage: $p=0.003$, Fig. 6a, Table 2). On the contrary, an increase was noticed in the vegetation stratum of dry grasslands (OITH) (Tukey post hoc test:

$p<0.001$, Fig. 7a, Table 2). During this period, dry grasslands (OITH) offered more invertebrates than other habitats both on the ground (Tukey post hoc tests: wheat: $p=0.02$; tillage: $p<0.001$; hay meadow: $p=0.01$; pasture: $p=0.03$, Fig. 6a, Table 2) and in the vegetation (Tukey post hoc tests: wheat: $p=0.02$; tillage: $p<0.001$; hay meadow: $p<0.001$; pasture: $p<0.001$, Fig. 7a, Table 2). Moreover, hay meadows (PLMSHL) and wheat fields (OITH) were richer than tillage plots (PLMSHL) (Tukey post hoc test: $p<0.001$, Fig. 7a, Table 2), and wheat fields (OITH) were richer than pastures (PLMSHL) in terms of vegetation, albeit not significantly (Tukey post hoc test: $p=0.06$, Fig. 7a, Table 2). On the ground, plots under tillage (PLMSHL) were poorer than the other four habitats (Tukey post hoc tests: wheat: $p=0.006$; dry grassland: $p<0.001$; pasture: $p=0.004$; hay meadow: $p<0.001$, Fig. 6a, Table 2). Every habitat showed strong variations in abundance between plots, particularly during the ‘hatching’ session and the ‘rearing’ session, especially in dry grasslands (OITH) (Fig. 6a and 7a, Table 2).

3.4. Invertebrate dry mass

Concerning the DM, no differences were observed between habitats for the ground-dwelling invertebrates (ANOVA, $F_{4.45}=1.66$, $p>0.05$, Fig. 6b, Table 2). However, a session effect was observed in wheat (OITH), where the DM per pitfall trap increased significantly between the ‘laying’ and ‘hatching’ sessions (Wilcoxon matched-pairs test: $p<0.05$, Fig. 6b, Table 2). Otherwise, none of the habitats presented differences between sessions (Friedman and Wilcoxon matched-pairs tests, $p>0.05$).

Concerning the vegetation-dwelling invertebrates, no differences were observed between the habitats during the ‘laying’ session (ANOVA, $F_{3.33}=1.28$, $p>0.05$, Fig. 7b, Table 2). Nonetheless, during the ‘hatching’ period, the DM per transect was significantly lower in tillage plots (PLMSHL) than in the four other habitats (Tukey post hoc tests: $p<0.001$, Fig. 7b, Table 2) and was higher in dry grasslands (OITH) than in pastures (PLMSHL) (Tukey post hoc test: $p=0.004$). Finally, during the ‘rearing’ session, dry grasslands presented a significantly higher DM per transect than hay meadows (PLMSHL), pastures (PLMSHL), and tillage plots (PLMSHL) (Tukey post hoc tests: $p<0.001$, Fig. 7b, Table 2) and displayed a higher, but not significant, tendency than wheat fields (Tukey post hoc test: $p=0.09$, Fig. 7b, Table 2). Moreover, wheat (OITH) presented a higher DM compared with tillage plots (PLMSHL) (Tukey post hoc test: $p<0.003$, Fig. 7b, Table 2) and displayed a higher, but not significant, tendency than pastures (PLMSHL) (Tukey post hoc test: $p=0.06$). A session effect was observed in dry grasslands (OITH), where the DM was higher in the ‘rearing’ period than in the ‘laying’ session (Wilcoxon matched-pairs test: $p=0.04$, Fig. 7b, Table 2). Finally, strong variations of DM between plots were observed, especially in dry grasslands (OITH), hay meadows (PLMSHL), and pastures (PLMSHL) during the ‘hatching’ session at the ground level and in wheat fields (OITH) during the ‘rearing’ session at the vegetation stratum (Fig. 6b and 7b).

3.5. Invertebrate size

The lengths of ground-dwelling invertebrates were similar across habitats during the “laying” and “hatching” sessions (ANOVA, $F_{4.35}=0.70$, $p>0.05$, Fig. 6c). However, during the ‘rearing’ session, they were longer in dry grasslands (OITH), tillage plots (PLMSHL), and wheat fields (OITH) than in pastures (PLMSHL) (Tukey post hoc tests: $p<0.004$, Fig. 6c). They were also longer in dry grasslands (OITH) and tillage plots (PLMSHL) than in hay meadows (PLMSHL) (Tukey post hoc test: $p\leq0.03$, Fig. 6c). Moreover, the length of ground-dwelling invertebrates decreased significantly between the ‘laying’ and ‘hatching’ sessions in pastures (PLMSHL) (Tukey post hoc test: $p=0.03$, Fig. 6c) and between the ‘hatching’ and ‘rearing’ sessions in pastures (PLMSHL) and hay meadows (PLMSHL) (Wilcoxon matched-pairs tests: $p=0.007$ and $p=0.009$, respectively). In vegetation, invertebrates were longer in wheat fields (OITH) than in dry grasslands (PLMSHL) (Wilcoxon matched-pairs test, $p=0.01$) and tended to be longer than in hay meadows (PLMSHL) and pastures (PLMSHL) (Wilcoxon matched-pairs test: $p=0.18$ and $p=0.17$, Fig. 7c) during the 'laying' session. The length then decreased significantly in wheat fields (OITH) in the 'hatching' session (Tukey post hoc test, p=0.02, Fig. 7c). No differences were observed between habitats until the 'rearing' session (ANOVA, hatching session: $F_{4.43}=2.13$, $p>0.05$; rearing session: $F_{4.40}=1.91$, $p>0.05$, Fig. 7c).

4. Discussion

The slow decline of the curlew core population observed in PLMSHL contrasts markedly with the steady increase of the core population of OITH and MINE since 2006. Various hypotheses can be proposed to explain these opposing trends. First of all, some individuals may have moved from PLMSHL to OITH and MINE. Turpaud-Fizzala (2012) estimated the number of fledglings per couple at 0.37 in PLMSHL. However, this rate was lower than the minimum productivity rate of 0.48 required to maintain populations as defined by Grant *et al.* (1999).

Consequently, it is unlikely that the adults or the few chicks produced at PLMSHL alone can explain the increase in numbers in OITH and MINE over the past 15 years. However, a few individuals of PLMSHL may have initiated colonization in OITH and MINE in the first years, with the numbers then increasing thanks to the arrival of adults or sub-adults from other populations in Europe which settled at the site during stopovers while migrating. In addition, it is possible that productivity in OITH and MINE is higher than in PLMSHL and that the chicks born there have returned to their birthplace.

Concerning the changes in distribution observed in PLMSHL, the conversion of meadows to cropland in some areas where the birds used to breed may be a cause of the movement of individuals within the area. Gilet *et al.* (2002) noted the disappearance of five out of six breeding pairs in the south of PLMSHL the year following the disappearance of large areas of grassland. Thus, the presence of grassland is probably a determining criterion for curlews to select their nesting area. Besides this factor, our study highlights the preference of the species for grassland for feeding at both study sites. Both Berg (1992) in Sweden and Valkama *et al.* (1998) in Finland have reported that curlews were concentrated mainly in grasslands in those countries, even when this habitat was poorly available in the environment. Its attractiveness can be explained by several factors, starting with the vegetation height. Indeed, depending on management practices, meadows offer a more heterogeneous vegetation structure than wheat fields and tillage plots, becoming maize or sunflower plots during the season, with 'high sward' plots, allowing curlews to escape from predators more easily, and 'low sward' plots, facilitating foraging (Pearce-Higgins & Grant 2006). In addition, in areas of intensive agriculture, grasslands constitute key feeding habitats where the food resource is more abundant and of better quality, as long as their management is not intensive (Hendrickx *et al.* 2007). Conversely, cereal fields seemed to be avoided by curlews, while no trend was observed in tillage areas. Ploughing and the repeated use of insecticides may explain the low attractiveness of these habitats due to their consequent lack of invertebrates (Chamberlain *et al.* 2000, Clere & Bretagnolle 2001). Also, once wheat has reached a certain level of development, the vegetation becomes too high and dense for birds to feed in.

The analysis of invertebrate availability and size confirms that dry grasslands often provide a better food resource in OITH, especially during the brood rearing period, although they were rarer at this site. Wheat fields also provide an important food resource, with numerous or large prey in the first half of the breeding season. In the PLMSHL, tillage plots may provide as much potential prey – or at least prey of the same size – as pastures and hay meadows at the ground level but remains a poor provider at the level of the vegetation stratum in all periods. Hay meadows and pastures seem to remain the most favourable habitats within PLMSHL, with a constant abundance of prey, although the quality declines during the breeding period due to a decrease in invertebrate size. Thus, food resources are generally higher in terms of availability and quality in the sampled habitats of OITH than those of PLMSHL, starting from the hatching period (early June), which suggests that conditions there may be more favourable for fledge growth and survival.

At the beginning of May (the laying period), parents need energy to defend their nests from predators (Turpaud-Fizzala 2012), especially since egg production during the pre-incubation period requires resources for females (Högstedt 1974, Berg 1992). In OITH, dry grasslands present more but smaller vegetation-dwelling invertebrates than wheat. Although less abundant, these prey types are therefore perhaps more profitably foraged in wheat fields because of their larger size. Moreover, hay meadows in PLMSHL offer more vegetation-dwelling invertebrates than the wheat fields of OITH while pastures display equivalent abundances of invertebrates to the dry grasslands and wheat fields of the site. Finally, tillage plots in PLMSHL seem to provide as much ground-dwelling invertebrates and of the same size as the other four habitats. Thus, both habitats sampled in OITH must be adequate for food supply, as well as in PLMSHL, hay meadows, pastures, tillage plots may be beneficial too.

From early June (the hatching period) onwards, an imbalance appears between OITH, where the quality and availability of potential prey in both sampled habitats increases, and PLMSHL, where tillage plots appears to be very poor in terms of vegetation-dwelling invertebrates and pastures host smaller ground-dwelling prey than during the laying period. Indeed, the dry grasslands and wheat fields of OITH became richer with vegetation-dwelling invertebrates than in the laying session, while ground-dwelling invertebrates became more numerous in the dry grasslands of OITH than in hay meadows, pastures, and tillage plots of PLMSHL. Dry grasslands and wheat fields are therefore two of the better-quality foraging habitats for adults and newly born chicks at this time. Hay meadows that have neither suffered a drop in abundance nor in the size of invertebrates also remain an interesting feeding habitat.

The decrease in the size of ground-dwelling invertebrates continues in early July (the rearing period), not only in pastures but also in hay meadows, where their length decreases as well. These results could be attributed to management practices employed in PLMSHL. Indeed, hay meadows are generally fertilised and mowed once or twice between May and June, while pastures begin to be grazed with a high density of livestock in the same period. Some studies have reported that intensive grazing, mowing, or fertilising may negatively affect the size of invertebrates (Blake *et al*. 1994, Birkhofer *et al*. 2015). Thus, management practices in PLMSHL might limit the availability of profitable prey for adults and chicks. In addition, early mowing is one of the main causes of reproductive failure: Turpaud-Fizzala (2012) indicated that in PLMSHL, mowing a plot close to that of the nest may be enough to cause the curlews to abandon it. Gilet *et al*. (2002) has also shown that pastures have the lowest reproductive success in Deux-Sèvres, and that this can be explained by the increased risk of eggs being trampled by cattle (Grant *et al*. 1999).

In addition, at this same period, the gap between dry grasslands in OITH and other habitats grows wider, with a greater abundance of vegetation-dwelling and ground-dwelling invertebrates than in the four other habitats and longer ground-dwelling invertebrates than in hay meadows and pastures. While prey in dry grasslands therefore become increasingly numerous and large in size in OITH through the breeding season, hay meadows and pastures decline in quality by losing their larger sized prey. It should be added that wheat fields sampled in OITH showed high abundances of invertebrates, especially in early June (hatching period). Although avoided by curlews, it seems that certain plots of wheat could provide a great abundance of invertebrates and perhaps enrich adjacent habitats with prey. It should also be noted that farmers who agreed to participate in the study were reluctant to use pesticides and herbicides. Therefore, the results of the study do not necessarily reflect the reality of all cereal fields. Collaboration with more conventional farmers would allow us to know if local wheat crops are in general as rich as those sampled in this study.

OITH seems to offer better feeding conditions during the rearing of chicks especially thanks to its dry grasslands. These results are similar to those of a local study that demonstrated that among the six special protection areas of the region, OITH was the site with the highest abundances of Orthoptera (Poirel pers. comm.). The peak of larval abundance for this order of insects being between June and July, the breeding area probably provides an important food resource for the chicks. Moreover, tillage plots (PLMSHL) was very poor for food species both on the ground and in the vegetation stratum, with very low abundance and DM from the beginning of June to July (hatching and rearing periods). Therefore, this habitat, very common within PLMSHL, seemed to limit the availability of potential prey in this territory, although curlews can benefit from higher visibility there, facilitating the detection of prey (Valkama *et al*. 1998), as well as access to endogenous fauna (such as earthworms and larvae), enabled by better penetrability of the soil (De Jong 2012).

The availability and size of potential prey are not the only parameters to be taken into account when judging the capacity of a habitat to provide a favourable food resource. Indeed, the nutritional quality of the invertebrates that a habitat offers seems to play a major role in its attractiveness to insectivorous birds (Kaspari & Joern 1993, McCarty & Winkler 1999). Razeng and Watson (2015) showed that prey with a greater energy gain for insectivorous birds contain a high proportion of crude fat and/or crude protein. An analysis of invertebrates by family would help to assess how much the habitats sampled for this study provide suitable prey for chicks. Moreover, juveniles of shorebirds do not appear to have the same requirements for prey selection. Their short bills do not yet allow them to probe the ground. For example, black-tailed godwit chicks appear to feed almost exclusively on flying insects, including several families of Diptera and Hymenoptera (Schekkerman & Beintema 2007). The abundance and size of prey within the vegetation is therefore probably a determining factor in ensuring good growth and survival conditions for young chicks.

Overall, this study encourages the implementation of new management measures. Currently, more than 1,500 ha of grassland are under AES contracts in PLMSHL and are therefore managed favourably for the conservation of lowland birds by imposing a grazing ban, mowing the grasslands between 20 May and 20 August, and applying fertilisers. However, these specifications are based on the phenology of the little bustard and therefore occur well after the first curlew eggs have been laid (Gilet *et al*. 2002, Turpaud-Fizzala 2012). Therefore, this study advises adapting these agri-environmental measures by bringing forward the date of non-intervention on the plots to improve the quality of habitats for curlew breeding and to avoid the destruction of broods (Pakanen *et al*. 2016, Sharps *et al*. 2016). In OITH, the sampled dry grasslands were all under AES contracts, but it should be noted that mowing activity is much lower in this area and that many grassland areas without AES contracts remain intact throughout the breeding season (Supplementary Material Figs. S1–S2). Therefore, practices in this sector may already be partially favourable.

In conclusion, dry grasslands have a great richness in prey for adults and the presence of suitable prey for chicks, especially during the rearing period of young curlews. This habitat, present only in OITH, may partly explain the increased attractiveness of this area for the species compared with PLMSHL. However, each habitat has considerable variability, largely related to management, probably through the use or non-use of certain pesticides, mowing intensity, or different grazing pressures. Appropriate management measures are therefore necessary to promote the availability of prey for curlews at sites where they are most likely to nest: that is, in the meadows. The increase of dry grassland areas via the introduction of new AESs would therefore be highly favourable to curlews in OITH. Moreover, introducing suitable management of the grasslands (both hay and pasture) of PLMSHL would likely favour the reproductive success of the breeding pairs and consequently maintain and increase the number of the breeding pairs. These AESs could, however, take greater account of the phenology of the species to maximise their efficiency.

Finally, given the fact that food resources appear to be more plentiful in OITH than in PLMSHL, we can hypothesise that breeding conditions for curlews are better in OITH because of the higher availability of potential prey. That said, one of the major factors in the decline of the Eurasian Curlew in Europe is predation on eggs and chicks, mainly by foxes and corvids (Roodbergen *et al*. 2012, Brown 2015). The vegetation structure (Laidlaw *et al*. 2015) or the proximity to woodlands (Douglas *et al*. 2014, Wilson *et al*. 2014) can influence the vulnerability of chicks and eggs to predators. It is therefore possible that the landscape features that oppose OITH and PLMSHL may have an influence on the predation rate and therefore on breeding success.

Pesimäympäristön laadun ja monimuotoisuuden vaikutus kuovipopulaatioihin Länsi-Ranskassa

Kuovin (*Numenius arquata*) populaatiot Euroopassa ovat pienentyneet elinympäristöjen pirstoutumisen ja laadun heikentymisen seurauksena. Syy tähän muutokseen on enimmäkseen maatalouden käytäntöjen muutokset. Ranskan Deux-Sèvresin alueella kuoviparien määrän on havaittu vähenneen vuodesta 2000 sen pääesiintymisalueella. Samaan aikaan noin 80 kilometriä pohjoiseen on ilmestynyt uusi pesimäalue, jossa parien määrä on kasvanut vastaavalla ajanjaksolla. Pohjoisella pesimäalueella on runsaasti vehnäpeltoja ja harvinaisempia kuivia ruohomaita, kun taas etelässä maatalousmaisema koostuu enimmäkseen kyntömaista, heinävaltaisista niityistä ja laitumista. Tässä tutkimuksessa pyrimme arvioimaan näiden kahden alueen eroja ravinnon saatavuuden ja laadun suhteen. Keräsimme tietoa maaperän ja kasvillisuuskerroksen selkärankaisista kuoppapyydyksillä ja haaveilla kuovien lisääntymisajanjaksolla kolmessa eri vaiheessa. Kuivien ruohomaisen havaittiin olevan ravinnon saatavuuden kannalta parhaimmat elinympäristöt pohjoisessa poikasten hoidon ajanjaksolla. Heinävaltaiset niityt ja laitumet olivat puolestaan parhaimpia elinympäristöjä eteläisellä pesimäalueella. Tulosten perusteella pohjoisen alueen elinympäristöt tarjoavat enemmän ravintoa kuoveille kuin etelän alueen elinympäristöt. Siksi pohjoisella alueella on todennäköisesti paremmat pesintäolosuhteet, erityisesti poikasten kasvun kannalta. Kuivien ruohomaiden pinta-alan lisääminen pohjoisella pesimäalueella ja toisaalta maatalouskäytäntöjen sopeuttaminen eteläisellä pesimäalueella suosisi kuovin paikallisia kantoja.

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Online supplementary material

Supplementary material available in the online version includes Figs. S1–S3 and Tables S1–S2.