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# Home range sizes and nychthemeral habitat uses by the Northern Shoveler *Spatula clypeata* on prenuptial stopovers in Vendée marshes, western France

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1 **Home range sizes and nychthemeral habitat uses by the Northern Shoveler *Spatula clypeata* on prenuptial stopovers**  
2 **in Vendée marshes, western France**

3

4 Running title : Habitat uses by Shovelers on prenuptial stopovers

5

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7

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15

16 **Abstract**

17

18 The wetlands of Marais breton (MB) and Marais poitevin (MP) on the French Atlantic coast are commonly used  
19 by several duck species, especially as stopover sites during the prenuptial migration. Understanding the ecological  
20 requirements of Anatidae at spring stopover sites is important to define appropriate management actions that might  
21 have a carry over effect on the subsequent reproduction success. This study focused on the Northern Shoveler  
22 *Spatula clypeata*, a species that regularly visits the two marshes during spring and fall migrations and is highly  
23 dependent on freshwater invertebrates as the food resource. Fifteen Northern Shovelers were equipped with  
24 GPS/GSM tags and monitored during their stopover in both marshes in 2020 and 2021. The aims of the study  
25 were to understand the habitat use on stopover sites and relate home range (HR) size with characteristics of the  
26 feeding habitats (such as freshwater invertebrates' density and diversity). The HR area of the studied individuals  
27 was mainly constituted of ponds in MB (83% of the HR) and wet meadows in MP (71% of the HR). The Northern  
28 Shovelers equipped with tag spent more than 72 consecutive hours in 31 wetlands, using them during the day, at  
29 night or all day. The diurnal visited sites were deep ponds that were sparsely vegetated and dominated by  
30 microcrustaceans, whereas the nocturnal visited sites were wet meadows or ponds with high aquatic vegetation  
31 cover and high invertebrate taxonomic diversity. The 31 described sites appeared to be rich in freshwater  
32 invertebrates, with no significant difference in invertebrate densities between the diurnal and nocturnal sites. HR  
33 sizes were highly homogenous between the two study sites (MB and MP), between sexes or between age classes.  
34 In conclusion, according to this study, an appropriate HR for the Northern Shoveler at spring stopover is  $8.49 \pm$   
35  $5.95 \text{ km}^2$  (mean  $\pm$  standard error).

36

37 *Keywords:* Northern Shoveler, freshwater invertebrates, spring migration, habitat use, wetlands

38

## 39 1. Introduction

40

41 Migratory birds are dependent on different sites throughout their annual cycle, such as the wintering and breeding  
42 grounds or staging sites during the post and prenuptial migrations. Habitat selection and use are guided by several  
43 factors (Dow & Fredga 1985, Safine & Lindberg 2008, Holopainen *et al.* 2015) such as food availability, intra-  
44 and interspecific competition, predation, vegetation structure (especially for breeding birds), and extreme natural  
45 events (e.g. drought, storm). Migratory birds need to leave their wintering and then staging sites with an  
46 appropriate body condition to successfully migrate and prepare for breeding. Migratory Anatidae, are mostly  
47 considered as ‘income’ breeders’ (Ganter & Cooke 1996, Gauthier *et al.* 2003), i.e. they rely on exogenous  
48 resources to fuel their migration. Hence, they need to stop repeatedly on their way to their breeding grounds to  
49 forage. At stopover sites, they require foraging areas as well as resting places (Arzel 2006). Various studies have  
50 highlighted the crucial role of stopover areas for the survival of birds, although they are inhabited for only a short  
51 time during the annual cycle (Moore *et al.* 1990).

52

53 It is important to understand home ranges of waterfowl to direct appropriate management action plans in the face  
54 of overall degradation of suitable habitats in their flyway route (Legagneux *et al.* 2009, Ma *et al.* 2010). The home  
55 range is defined as the interaction between animals and their environment, and its size is a direct result of  
56 movement driven by habitat selection and other external factors (Börger *et al.* 2008). Hence, the home range size  
57 of migratory animals might vary seasonally pending on the conditions encountered along the migratory route  
58 (Legagneux *et al.* 2009, Verheijen *et al.* 2024). Furthermore, at a small spatial scale, *i.e.* over a defined area such  
59 as a stopover area, habitat selection and resource use influence home range size (Johnson 1980, Van Moorter *et*  
60 *al.* 2016). Home range size could also be affected by social interactions and intrinsic factors such as sex, age and  
61 health status (Börger *et al.* 2008). The habitat and the internal state of the individual can change through time and  
62 cause the size variation of the home range.

63

64 The Northern Shoveler, *Spatula clypeata* (hereafter Shoveler), is a migratory dabbling duck common throughout  
65 the Holarctic region (Cramp & Simmons 1977). This species overwintering grounds range from Western Europe  
66 to West Africa and it breeds throughout most of the Nearctic and Palearctic. The Vendée wetlands, in western  
67 France, are the major wintering and breeding sites in France. Trollet *et al.* (2016) estimated a breeding population  
68 of approximately 1,600 pairs in the Marais breton (MB) representing 80% of the French breeding population in  
69 2015 (Trollet *et al.* 2016). Further south, the Marais poitevin (MP) is also an important stopover and breeding  
70 site for waterbirds (Duncan *et al.* 1999). In 2010, 44 breeding pairs of Northern Shoveler were estimated in MP  
71 (Guéret 2010).

72

73 Factors that influence Shovelers’ use of wetlands include habitat availability, disturbance, predation but also the  
74 diversity, density, spatio-temporal dynamics (Matsubara *et al.* 1994, Guillemain *et al.* 2000) and accessibility  
75 (Bolduc & Afton 2004) of their main food resource *i.e.* freshwater invertebrates. In addition, Shovelers select  
76 foraging sites according to prey availability, prey size and energy values to maximise the net energy intake (Crome  
77 1985, Tietje & Teer 1996). The bill with its spoon-shaped morphology and high-density, closely spaced lamellae,  
78 *i.e.*  $21.48 \pm 2.41$  lamellae/cm<sup>2</sup> (Nudds & Bowlby 1984), is an adaptation to sieving. Shovelers filter the surface of

79 the water to collect food giving them a specific food niche compared with other Anatidae species. The Shoveler's  
80 diet mainly consists of small freshwater invertebrates (Pirrot & Pont 1987, Ankney & Afton 1988, Baldassarre &  
81 Bolen 2006) and, particularly, swimming microcrustaceans such as Cladocera and Ostracoda (DuBowy 1985,  
82 Pirrot & Pont 1987, Baldassarre & Bolen 2006). Improved knowledge of Shovelers' ecology during prebreeding  
83 migration will help to determine their ecological requirements in terms of habitat and feeding.

84

85 In the present study, Shovelers were equipped with GPS-GSM tags in the MB and MP . The birds were monitored  
86 for two weeks during their prenuptial migration period in order to define their stopover requirements, which are  
87 important to understand for conservation and management purposes. We hypothesize that: (1) the home range  
88 (HR) sizes of the Shoveler in the MP are larger than in the MB considering the lower density of ponds and the  
89 greater distance between them; (2) sex does not influence the HR size at stopover sites; and (3) environmental  
90 variables such as water level, presence of aquatic and riparian vegetation or water surface area, as well as  
91 invertebrate communities, energy values and size classes, contribute in shaping the size of the HR and determine  
92 movements of birds between sites.

93

## 94 **2. Material and Methods**

95

### 96 **2.1. Study Sites**

97

98 This study was carried out on the two large wetlands the MB (N2000 FR5212009 and Ramsar 2283) and the MP  
99 (N2000 FR5200659) (Fig. 1). MB and MP cover areas of approximately 32,000 ha (Trollet *et al.* 2016), and  
100 96,000 ha (Duncan *et al.* 1999), respectively. The sampling for aquatic invertebrate's areas in the two regions  
101 were limited to freshwater marshes used by the Shovelers equipped with the GPS-GSM tags. Overall, 31 sites  
102 were sampled between 1<sup>st</sup> March and 30<sup>st</sup> April 2021.

103

### 104 **2.2. Capture and Tagging**

105

106 During the prenuptial migration period, Shovelers were captured using cage traps and attracted with live male or  
107 female Shovelers as decoys. A camera (NATURACAM – STDX2) was positioned near each trap to monitor the  
108 presence of birds in the traps, which were caught every day from the 1<sup>st</sup> of March to the 17<sup>th</sup> of March 2020, and  
109 from the 1<sup>st</sup> of March to 10<sup>th</sup> of April, 2021. In 2020, the capturing effort was stopped on the 17<sup>th</sup> of March due to  
110 the COVID-19 lockdown. In total, eight individuals were caught in the MB and 7 in the MP. All Shovelers were  
111 equipped with a GPS-GSM tag (Ornitela, OrniTrack-E10, 10 g, solar-powered GPS-GSM); these included 2 F juv  
112 (female juvenile; less than two calendar years), 2 F ad (adult; more than two calendar years), 6 M juv (male) and  
113 5 M ad (see details in Table 1). The GPS-GSM tags were attached as backpacks using a harness made of Teflon  
114 straps with rubber tubing (Klaassen *et al.* 2008, Lameris *et al.* 2017, 2018). The equipment (GPS-GSM tag,  
115 harness, and metal ring) weighed less than 3% of the body mass and we assume that the use of the GPS did not  
116 cause significant impact on ducks movements and behaviour. The Shovelers were captured and handled according  
117 to ethical rules edicted by French legislation (Authorization from Ministry of Ecological Transition by Research  
118 Center on the Biology of Bird Populations PP: 1821).

119  
120 The location of the individuals were recorded during the prenuptial period from the 1<sup>st</sup> of March to the 30<sup>th</sup> of  
121 April in 2020 and 2021 with a frequency of 5 minutes. The location of the 15 individuals was then recorded for  
122 (14 days  $\pm$  2 days; mean  $\pm$  standard error) (Table 1). No fundamental differences were observed in precipitation  
123 or hydrology between years (2020 vs. 2021) or temporal patterns within a year (i.e. early vs. late spring) (Moreau  
124 A., pers. com.). None of the studied individuals attempted to breed in the studied areas.

125

### 126 **2.3. Trophic Resources at the Feeding Sites**

127 The tagged individuals spent more than 72 consecutive hours in 31 sites. These sites were classified into three  
128 categories according to the habitat type: wet meadow, pond, and channel (Fig. 2). From the 1<sup>st</sup> of March to 10<sup>th</sup> of  
129 April 2021, freshwater invertebrates were sampled at each site using a plankton net (mesh of 200  $\mu$ m, frame size  
130 of 35.5 x 15.0 cm) on a transect of 2 m at a depth of 35 cm, which corresponded to the Shovelers' maximum  
131 feeding depth capacity (Pöysä 1983). The net contents were preserved in 70% ethanol (Balcombe *et al.* 2005) and  
132 quickly analysed at a laboratory. Invertebrates were sorted, counted and identified using a binocular magnifier  
133 (Euromex, Series Z, 7-45 x) to the family level except Copepoda, subclass; Cladocera, superorder; Hydrachnidia,  
134 suborder; and Ostracoda, class (Thorp & Rogers 2011).

135

### 136 **2.4. Environmental Parameters Measurement**

137

138 The feeding sites were characterized by the following continuous environmental variables: the sediment depth (in  
139 cm), water level (in cm) (both were measured with a graduated stake), salinity (in psu, using a multiparameter  
140 probe VWR MU 6100 H Multimeter), percentage cover of riparian helophytes (*i.e.* palustrine plant that lives in  
141 the mud but whose leaves are above the waterline) and of emerged and submerged aquatic vegetation (vegetation  
142 were characterized empirically). Three environmental variables were categorized into three classes: sediment type  
143 (class 1: loamy sediment; 2: loamy / muddy; 3: muddy), slope (class 1: < 5% soft slope; 2: 5%–10% moderate  
144 slope; 3: > 10% steep slope), and habitat type (class 1: meadows; 2: ponds; 3: channels). The water surface area  
145 of each study sites was measured using Satellite images via the geographic information system QGIS (QGIS  
146 Development Team 2009).

147

### 148 **2.5. Home Range and Movement Analysis**

149

150 The time of the day during which the individuals were recorded on a study site was used to categorize the sites  
151 into 3 classes: only daytime use (from sunrise to sunset), only nighttime use (from sunset to sunrise) and all day  
152 use. Individuals were considered flying when GPS data indicated a speed greater than 14.4 km/h (Bengtsson *et al.*  
153 *et al.* 2014); the corresponding locations were excluded from the analysis. GPS coordinates with less than 5 satellites  
154 (Hulbert & French 2001), HDOP value of less than 5 (Rempel & Rodgers 1997), and altitude greater than 15 m  
155 were excluded from the analysis. Shovelers always used water for feeding and the water edges for resting, so  
156 points on land have been excluded from the analysis. Finally, the first day after capture and tagging was excluded  
157 from the analysis in case birds did not behave normally due to recent handling (Bengtsson *et al.* 2014).

158

159 The HR and the minimum convex polygon (MCP) were calculated for each individual using the ‘adehabitatHR’  
 160 package (Calenge 2006) on R software (R Core Team 2022). For the HR calculation, based on the kernel density  
 161 method (Worton 1989), 95 % of the GPS point are used whereas, for the MCP calculation, 100% of the GPS  
 162 points are used (Legagneux *et al.* 2009). The cumulative number of sites visited over the 15-day period in the HRs  
 163 was calculated per individual. The proportion of habitat type (+/- standard error) used within the HRs (wet  
 164 meadows, ponds, channels) was estimated for each individual.

165

## 166 2.6. Statistics

167

168 Statistical analyses were conducted using R software (R Core Team 2022) and considered significant when the *p*-  
 169 value was below the 5% threshold. The MCP and HR sizes were compared between individuals per sex and age  
 170 at the MB and MP using the nonparametric Wilcoxon test. The cumulative number of sites used per day by the  
 171 Shovelers were compared in MB and MP using the nonparametric Kruskal-Wallis test. The proportion of habitat  
 172 type used within the HRs (wet meadows, ponds, channels) were compared in MB and MP using the nonparametric  
 173 Wilcoxon test. A principal component analysis (PCA) was conducted to characterize the different habitats in the  
 174 sampled sites (R packages: ‘FactoMineR’ (Husson *et al.* 2024) and ‘Hmisc’(Harrell 2024)). In addition, the  
 175 invertebrate densities at the diurnal sites, all day sites, and nocturnal sites were compared using the nonparametric  
 176 Kruskal-Wallis test. To detect the differences in invertebrate community composition depending on the daily use  
 177 of the sites, a nonmetric multidimensional scaling (NMDS) was conducted to visualize the degree of overlap  
 178 between communities. This analysis focused on the density of freshwater invertebrate taxa per cubic metre in each  
 179 site. The ‘vegan’ package (Oksanen *et al.* 2024) was used for the analysis. Only groups of freshwater invertebrates  
 180 with  $\geq 10\%$  occurrence on all the sampled sites were retained for the analysis (Davis & Bidwell 2008). The two  
 181 deleted groups (Asellidae and Mysidae), with  $< 10\%$  occurrence, are not considered to be important groups in the  
 182 Shoveler diet.

183

## 184 3. Results

185

### 186 3.1. Home Range, Number of Sites Frequented, and Habitat Use

187

188 The size of the minimum convex polygons (MCPs) for the 15 individuals ranged from 9.0 to 2,846.4 ha, and the  
 189 estimated home ranges (HR) ranged from 2.9 to 25.4 ha (Table 1). The mean MCP areas of the individuals from  
 190 MB ( $78.7 \pm 54.1$  ha,  $n = 8$ ) were significantly lower than those from MP ( $738.0 \pm 10,003.0$  ha,  $n = 7$ ; Wilcoxon  
 191 test,  $p$ -value  $< 0.05$ ) while the mean HR sizes did not differ (MB =  $6.2 \pm 2.9$  ha,  $n = 8$ ; MP =  $11.2 \pm 7.6$  ha,  $n = 7$ ;  
 192 Wilcoxon test,  $p$ -value  $> 0.05$ ) (Fig. 3). The MCP size did not differ between males and females (M =  $459 \pm 859$   
 193 ha,  $n = 11$ ; F =  $185 \pm 171$  ha,  $n = 4$ ; Wilcoxon test,  $p$ -value  $> 0.05$ ) or between juveniles and adults (juv =  $286 \pm$   
 194  $393$  ha,  $n = 8$ ; ad =  $500 \pm 1035$  ha,  $n = 7$ ; Wilcoxon test,  $p$ -value  $> 0.05$ ) (Fig. 3). Moreover, the HR size did not  
 195 differ between males and females (M =  $9.4 \pm 6.5$  ha,  $n = 11$ ; F =  $6.1 \pm 3.7$  ha,  $n = 4$ ; Wilcoxon test,  $p$ -value  $>$   
 196  $0.05$ ) or between juveniles and adults (juv =  $8.8 \pm 4.2$  ha,  $n = 8$ ; ad =  $8.2 \pm 7.8$  ha,  $n = 7$ ; Wilcoxon test,  $p$ -value  
 197  $> 0.05$ ) (Fig. 3).

198

199 Over the 15-day study period, the cumulative number of sites visited by the individuals increased rapidly at the  
 200 MB but increased slowly at the MP (Fig. 5a). In addition, the number of sites used per day at the MB was greater  
 201 than MP (Fig. 5a). However, the mean surface size of each habitat type at MP were significantly greater than those  
 202 at MB, *i.e.* ponds (MB =  $0.8 \pm 0.8$  ha, n = 56; MP =  $2.5 \pm 3.9$  ha, n = 10; Wilcoxon test,  $p$ -value < 0.05) and wet  
 203 meadows (MB =  $0.2 \pm 0.2$  ha, n = 29; MP =  $2.1 \pm 2.3$  ha, n = 23; Wilcoxon test,  $p$ -value < 0.05), except for  
 204 channels (MB =  $0.1 \pm 0.1$  ha, n = 4; MP =  $2.4 \pm 3.2$  ha, n = 2; Wilcoxon test,  $p$ -value > 0.05) (Fig. 5b). Finally,  
 205 the spatial distribution showed that Shovelers used some sites only during daytime for resting or foraging, others  
 206 only during nighttime for foraging, and some during both day and night (Fig. 4).

207  
 208 Besides the significant differences in MCP sizes and number of sites visited, the utilization of habitat types also  
 209 differed significantly between both marshes and individuals (Fig. 6, Table 1). In the MB, HRs mainly consisted  
 210 of ponds ( $83 \pm 15\%$  of the HR area on average, n = 8), wet meadows were the 2<sup>nd</sup> most used habitat type ( $16 \pm$   
 211  $15\%$ , n = 8) and channels were very little used ( $1 \pm 1\%$ , n = 8). At the MP, HRs mainly constituted of wet meadows  
 212 ( $71 \pm 37\%$ , n = 7) and secondly of ponds ( $26 \pm 33\%$ , n = 7). As in the MB, channels were rarely used in MP ( $3 \pm$   
 213  $7\%$ , n = 7).

### 214 215 **3.2. Foraging Habitat**

216  
 217 The environmental characteristics of the sites were analysed using PCA (Fig. 7). On Axis 1 (39%), the sediment  
 218 depth, habitat type, sediment type, and slopes were negatively correlated with the emerged aquatic vegetation  
 219 (Fig. 7 and confirmed by the Spearman correlation values which are -0.41, -0.51, -0.61 and -0.50 respectively).  
 220 On Axis 2 (17.2%), the variables water level, submerged aquatic vegetation, and water surface area contrasted  
 221 with the invertebrate density (Fig. 7 and confirmed by the Spearman correlation values which are -0.33, -0.28 and  
 222 -0.22 respectively). The other variables could not be interpreted ( $\cos^2 < 0.4$  on the two axes).

223  
 224 Diurnal sites (Fig. 7 and Table 2) were mainly defined by a deep water level ( $40.9 \pm 11.1$  cm), high sediment  
 225 height ( $10.7 \pm 10.7$  cm), steep slopes, muddy sediment, low cover of aquatic vegetation, and a site typology  
 226 corresponding to a pond. In contrast, the nocturnal sites (Fig. 7 and Table 2) were characterized by a low water  
 227 level ( $28.2 \pm 21.7$  cm), low sediment height ( $6.3 \pm 6.5$  cm), loamy/muddy sediment, soft slopes, a significant cover  
 228 of aquatic vegetation, and a site typology corresponding to wet meadows. Sites that were frequented at both day  
 229 and nighttime were not specifically characterized by one or more environmental variables.

### 230 231 **3.3. Trophic Resources**

232  
 233 Among the 15 taxa of freshwater invertebrates inventoried from the study sites, 12 (occurrence of  $\geq 10\%$  on all  
 234 sites) were retained for the analysis. Five taxa were widespread (present in more than 50% of the samples). These  
 235 included Copepoda and Cladocera (100% occurrence), Diptera and Hemiptera (84% occurrence), and Ostracoda  
 236 (61% occurrence). The size class 0.1 to 2.5 mm was the most dominant *i.e.* 51% of the taxa and 98% of the  
 237 individuals at each site.

238



239 The invertebrate densities for all taxa combined ranged from 3,387 to 113,315 individuals/m<sup>3</sup> (Table 2). There  
 240 was a significant difference in taxon density according to the daily use in the MB, the density in diurnal sites were  
 241 lower than the density in nocturnal sites (Diurnal site = 16,106 ± 13,241 ind/m<sup>3</sup>, n = 9; Nocturnal site = 37,698 ±  
 242 31,316 ind/m<sup>3</sup>, n = 9; Wilcoxon test, *p*-value > 0.05) (Fig. 8 and Table 3). However, there was no significant  
 243 difference in the density of freshwater invertebrates based on the daily use of the sites in the MP (Diurnal site =  
 244 31,899 ± 13,148 ind/m<sup>3</sup>, n = 3; Nocturnal site = 23,795 ± 15,468 ind/m<sup>3</sup>, n = 4; All day site = 19,585 ± 16,419  
 245 ind/m<sup>3</sup>, n = 2; Wilcoxon test, *p*-value > 0.05) (Fig. 8 and Table 3). Moreover, there was a significant difference in  
 246 taxon diversity according to the daily use in the MB, diurnal sites were less diversified than the other sites (Diurnal  
 247 site = 4.3 ± 1.2 taxa per site, n = 9 sites; Nocturnal site = 6.6 ± 1.7 taxa, n = 9; All day site = 7.8 ± 2.6 taxa, n = 4;  
 248 Wilcoxon test, *p*-value < 0.05) but, not in the MP (Diurnal site = 6.7 ± 0.6 taxa, n = 3; Nocturnal site = 5.5 ± 2.1  
 249 taxa, n = 4; All day site = 5 ± 0 taxa, n = 2; Wilcoxon test, *p*-value > 0.05) (Fig. 8 and Table 3), which was  
 250 confirmed by the NMDS plot (Fig. 9). Microcrustaceans (Cladocera and Copepoda) as well as Odonata,  
 251 Amphipoda, Hydrachnidia, and Hemiptera were present in all the sites.

252

#### 253 4. Discussion

254

255 This study highlighted that the home range (HR) sizes of Shovelers did not differ between individuals from the  
 256 MB and MP, between males and females or between juveniles and adults. The proportion of the type of habitat  
 257 used differed between individuals in both marshes. Invertebrate densities did not differ between the diurnal and  
 258 nocturnal sites.

259

##### 260 4.1. Home Range, Number of Sites, and Habitats Used

261

262 Heitmeyer and Vohs (1984) defined that the Shoveler preferentially uses small marshes and muddy ponds, which  
 263 is consistent with the results of the present study, wherein the HR of more than half of the individuals studied  
 264 (59%) contained more than 50% ponds. However, the sizes and habitat composition within the HRs were not the  
 265 same across MB and MP wetlands and between individuals. Several factors can influence the HR size and shape  
 266 (Rolando 2002). Species prospecting in environments that may change seasonally and contain variable food  
 267 resources must adjust their distribution or space use according to resource availability to meet their energy  
 268 requirement (Kirk *et al.* 2008, Kraan *et al.* 2009). In this study, no significant differences in HR sizes were  
 269 observed between wetland complexes. However, the maximum total area used (Minimum Convex Polygon, MCP)  
 270 was significantly larger in the MP than in the MB. Ponds and wet meadows are much more scattered in the MP  
 271 than in the MB. Thus, the lower density of water areas (ponds and wet meadows) likely leads the birds to explore  
 272 larger territory, possibly explaining the larger total area of the MCP in the MP. Furthermore, the lack of differences  
 273 in the HR size between males and females was expected as Shovelers are considered to be ‘income’ breeders  
 274 (Ganter & Cooke 1996, Gauthier *et al.* 2003). Accordingly, both males and females feed similarly on migratory  
 275 stopovers to complete their trip to the breeding sites. This result is also supported by Arzel and Elmberg (2004),  
 276 who found no sex differences in the foraging behaviour of Shovelers at the spring stopover sites (time spent  
 277 feeding, day/night distribution, and feeding method). The use of sites during the stopover differed between  
 278 individuals. Some individuals used up to ten different sites per day, whereas others used only two sites, although,

279 only sites at which individuals spent more than 72 hours were kept for analysis. This variability may be due to  
280 different energy requirements and thus varied time allocated to feeding, differences in social status, or competition  
281 for access to food at some sites (Poisbleau 2005, Bengtsson *et al.* 2014). However, no interspecific competition  
282 related to food limitation has been demonstrated for the Mallard *Anas platyrhynchos*, Eurasian wigeon *Mareca*  
283 *penelope*, Eurasian teal *Anas crecca*, and Shoveler (Arzel & Elmberg 2004).

284

#### 285 **4.2. Characterization of the Feeding Habitat During the Prenuptial Stopover**

286

287 This study showed a distinction between the characteristics of the sites used during the day and those used during  
288 the night. During daytime, the birds were concentrated on open (unvegetated), relatively deep ponds and with a  
289 high density of freshwater invertebrates. These characteristics of the diurnal sites limit the risk of Shovelers  
290 predation during their diurnal activities, such as resting, grooming or feeding (Guillemain *et al.* 2007). Indeed,  
291 open water provides better visibility of predators (Legagneux 2007). When disturbance or predation is high at a  
292 site, birds increase their vigilance behaviour and decrease their feeding and resting times, with consequences on  
293 their energy stock (Le Corre 2009). The Marsh harrier *Circus aeruginosus* is one of the main predators on dabbling  
294 ducks in these wetlands (Fritz *et al.* 2000). The nocturnal sites had significant emergent aquatic vegetation cover  
295 and a higher freshwater diversity than the diurnal sites. The characteristics of the nocturnal sites can be explained  
296 by the fact that Shovelers feed mainly at night (Guillemain *et al.* 2002, Poisbleau 2005). Wetlands with a high  
297 percentage of vegetation cover provide a more diverse habitat structure, consequently increasing the diversity,  
298 biomass, and density of freshwater invertebrates (Olson *et al.* 1995, Broyer & Curtet 2012). However, vegetation  
299 influences wetland use by birds (Fairbairn & Dinsmore 2001). Overly dense emergent vegetation can impact  
300 feeding activity and prey detection by ducks (De Leon & Smith 1999). Webb *et al.* (2010) demonstrated the  
301 importance of a 50% open water and 50% vegetation ratio for dabbling ducks during their prenuptial migration,  
302 which allows a greater diversity of food resources, plants, and freshwater invertebrates, especially for the  
303 waterfowl. Thus, this study demonstrates that during its prenuptial migration, Shovelers need suitable habitats for  
304 resting and feeding during a complete nycthemeral cycle.

305

#### 306 **4.3. Characterization of Available Food Resources**

307

308 A predominantly invertebrate-based diet of the Shoveler in spring appears to be consistent with the temporal  
309 dynamics of this food resource. For birds that need a diet of freshwater invertebrates, there is no synchronization  
310 between their peak migration and peak density of food resources at stopover areas (Arzel & Elmberg 2004).  
311 However, the behaviour of ducks in a site is linked to fluctuations in resource density (Arzel 2006). Nevertheless,  
312 we measured high densities of freshwater invertebrates in the MB and MP during migration of Shoveler. The 31  
313 study sites revealed a mean density of  $28,298 \pm 24,342$  individuals/m<sup>3</sup> per site. In a study carried out in several  
314 wetlands in West Virginia (USA), Balcombe *et al.* (2005) reported a mean of  $14,800 \pm 3,060$  invertebrates/m<sup>3</sup> in  
315 emergent waters and  $2,360 \pm 1,130$  invertebrates/m<sup>3</sup> in open waters. In Delta Marsh in south-central Manitoba,  
316 Kaminski & Prince (1981) measured aquatic invertebrate densities as a function of percent cover of emergent  
317 hydrophytes ( $8,381$  individuals/m<sup>3</sup> for 30% cover,  $9,938$  individuals/m<sup>3</sup> for 50% cover, and  $12,190$  individuals/m<sup>3</sup>

318 for 70% cover). According to the present study, the particularly high density of freshwater invertebrates could  
319 explain the attractiveness of the studied sites at MB and MP for Shovelers during their prenuptial migration.

320

321 This study highlighted that at the diurnal and nocturnal sites, the individuals appeared to use sites abundant in  
322 Copepoda and Cladocera. These two taxa had similar abundance across diurnal and nocturnal sites. Copepoda and  
323 Cladocera do not always have a habitat preference between vegetated habitats and open water (Romare *et al.*  
324 2003); they have a high energy value, averaging 5,767 cal/g at dry weight and 5,056 cal/g at dry weight,  
325 respectively (Moreau *et al.* 2021); and they are small, averaging 1.69 mm and 1.06 mm, respectively (Moreau *et*  
326 *al.* 2021). As discussed earlier, due to its spoon-shaped bill with high-density, closely spaced lamellae, the  
327 Shovelers are particularly adapted for feeding on small prey (Nudds & Bowlby 1984). Their diet is thus composed  
328 mainly of Copepoda and Cladocera during several stages of the migratory cycle (pre and postnuptial migration,  
329 reproduction) (DuBowoy 1985, Eldridge 1990, Euliss *et al.* 1997). This is consistent with the expectations of the  
330 energy requirements related to migration (Batt *et al.* 1992). Thus, ducks appear to use sites where the food  
331 resources allow maximum energy intake while considering the safety of the site. The nocturnal sites were more  
332 diversified (in terms of taxa) than the diurnal sites. During the day, the individuals used poorly vegetated sites.  
333 Consequently, the diurnal sites had a low diversity, with a dominant presence of Copepoda and Cladocera. At  
334 night, the individuals moved to sites with a high density of microcrustaceans (Copepoda, Cladocera, and  
335 Ostracoda) as well as Coleoptera, Decapoda, Diptera, and Ephemeroptera. This higher diversity at nocturnal sites  
336 allows the Shoveler to find its preferred diet prey but also potentially more energetic prey. Indeed, one potential  
337 food source for the Shoveler is Chironomidae larvae. These organisms are predominantly benthic. Although  
338 Chironomidae densities are lower than those of microcrustaceans, their biomass is high. Chironomidae are larger  
339 organisms, *i.e.* around 2.6 to 15 mm (Moreau *et al.* 2021), and their dry weight is much higher than for  
340 microcrustaceans, *i.e.* 0.31 mg on average for Chironomidae (Moreau *et al.* 2021) versus 0.02 mg for Copepoda  
341 and Cladocera (Boreham 1994). Moreover, Chironomidae larvae are rich in protein (56%) (Baldassarre & Bolen  
342 2006).

343

## 344 5. Conclusion

345

346 Regardless of wetlands, age classes or sexes and according to this study, an appropriate HR for the Shoveler at  
347 spring stopover is  $8.49 \pm 5.95$  km<sup>2</sup> (mean  $\pm$  standard error). Within its home range, the Shoveler mainly uses two  
348 habitat types with high freshwater invertebrate density: ponds (with or without vegetation) and wet meadows.  
349 Preserving deep and muddy ponds, which are used by Shovelers during the day and shallow and vegetated ponds  
350 or wet meadows, which are used during the night along the migration routes remains critical to fostering the  
351 relationship between freshwater invertebrates and the Shoveler during their prenuptial migration. Telemetric  
352 monitoring of migrating Shovelers and analysis of freshwater invertebrates in the wetlands of Vendée confirmed  
353 the processes related to this relationship during the prenuptial migration.

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592

593 **Declaration of interest statement**

594 The authors declare that they have no known competing financial interests or personal relationships that could  
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596

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602

603 **Ethics Statement**

604 All animal capture, handling and GPS-GSM tag attachment procedures were conducted under permits from the  
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606

607 **Data availability**

608 Data generated and analyzed in this study are publically available in Dryad  
609 <https://doi.org/10.5061/dryad.kh189328n>.

610

611 **Author contributions**

612 All authors contributed to the study conception and design. Material preparation, data collection and analysis were  
613 performed by Clément Rousseau and Axelle Moreau. The first draft of the manuscript was written by Clément  
614 Rousseau and Axelle Moreau and all authors commented on previous versions of the manuscript. All authors read  
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616

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621 sampling of the freshwater invertebrates.

622

623 **Tables**

624

625 **Table 1.** Summary of the information collected per tagged individual, Home Range (HR) size, Minimum Convex  
 626 Polygon (MCP) size, and number of habitats used by the 15 Shovelers in the Marais breton (MB) and the Marais  
 627 poitevin (MP) during 2020 and 2021 (M = male, F = female, juv = juvenile, ad = adult).

Id	Sex	Age	Wetland	Year	Period	Number of locations recorded per individua	Period	HR (ha)	MCP (ha)	Total			
										number of habitats used	Channels	Ponds	Wet meadows
S292	M	juv	MB	2020	03–17 Apr	1176	03–17 Apr	6.0	9.0	4	1	3	0
S296	M	ad	MB	2020	10 Mar to 23 Apr	7477	12–26 Mar	2.9	47.3	8	1	5	2
S298	M	ad	MP	2021	30 Mar to 30 Apr	6662	01–15 Apr	4.0	128.5	6	0	2	4
S299	F	juv	MB	2021	18 Mar - 30 Apr	9471	20 Mar to 03 Apr	3.2	20.6	15	1	7	7
S302	M	juv	MB	2021	01 Mar to 30 Apr	9406	03–17 Mar	5.1	71.9	11	0	10	1
S304	M	ad	MB	2021	01–30 Apr	4925	01–15 Apr	9.1	110.0	11	0	11	0
S305	M	juv	MB	2020	05 Mar to 03 Apr	3678	7–21 Mar	11.4	167.6	11	0	7	4
S307	F	ad	MB	2020	01 Mar to 01 Apr	5278	2–16 Mar	5.4	126.7	11	0	3	8
S310	M	ad	MB	2020	01 Mar to 12 Apr	4895	03–17 Mar	6.1	76.2	18	1	10	7
S281	M	ad	MP	2021	06–23 Apr	3417	08–22 Apr	25.4	2846.4	6	1	4	1
S284	F	juv	MP	2020	11 Mar to 11 Apr	4770	13–27 Mar	11.5	424.5	6	0	0	6
S285	M	juv	MP	2020	16–31 Mar	2195	17–31 Mar	16.2	417.8	4	0	0	4
S289	M	juv	MP	2021	05 Mar to 28 Apr	9910	7–21 Mar	7.2	17.9	2	0	0	2
S290	F	ad	MP	2021	05 Mar to 07 Apr	5558	7–21 Mar	4.3	167.3	6	1	0	5
S291	M	juv	MP	2021	31 Mar to 20 Apr	4853	02–16 Apr	9.6	1161.2	5	0	4	1

628

629 **Table 2.** Mean value and standard deviation of the environmental variables depending on the daily use of the  
 630 sites (diurnal, all day, nocturnal) and the wetlands (MB, MP and both wetlands combined).

Environmental variables	Diurnal site			All day site			Nocturnal site		
	MB	MP	All sites	MB	MP	All sites	MB	MP	All sites
	(n=9)	(n=3)	(n=12)	(n=4)	(n=2)	(n=6)	(n=9)	(n=4)	(n=13)
Emergued aquatic vegetation (% cover)	10.5 ± 26.2	10 ± 17.3	10.4 ± 23.5	28.7 ± 38.3	0 ± 0	19.2 ± 33.2	35.5 ± 44.1	46.2 ± 48.1	38.8 ± 43.6
Submerged aquatic vegetation (% cover)	14.1 ± 25.8	26.6 ± 37.8	17.2 ± 27.8	44.7 ± 46.6	45 ± 63.6	44.8 ± 46.0	17.7 ± 31.5	31.2 ± 39.6	21.9 ± 33.1
Invertebrate density (ind/m <sup>3</sup> )	16,105 ± 13,241	31,898 ± 13,148	20,053 ± 14,490	40,592 ± 39,904	19,585 ± 16,419	33,590 ± 33,571	37,697 ± 31,316	23,794 ± 15,468	33,420 ± 27,535
Sediment level (cm)	12.0 ± 11.9	6.66 ± 5.45	10.7 ± 10.7	4.74 ± 2.11	11.1 ± 9.19	6.9 ± 5.5	7.27 ± 7.60	4.25 ± 1.95	6.34 ± 6.45
Site area (ha)	0.46 ± 0.27	1.80 ± 1.33	0.80 ± 0.86	0.69 ± 0.71	0.70 ± 0.48	0.7 ± 0.6	0.49 ± 0.25	1.54 ± 1.25	0.81 ± 0.82
Water level (cm)	42.2 ± 8.23	36.8 ± 19.5	40.9 ± 11.1	21.8 ± 11.6	33.6 ± 8.48	25.8 ± 11.6	30.3 ± 25.2	23.5 ± 11.9	28.2 ± 21.7

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632

633 **Table 3.** Mean value, standard deviation, and mean comparison (Wilcoxon test) of freshwater invertebrate density  
 634 ( $\text{ind}/\text{m}^3$ ) and diversity per site. Mean comparison (Wilcoxon test) was only made for the total density and diversity  
 635 of the three habitat types according to the daily use (diurnal, all day, nocturnal ) in the MB and MP. Means  
 636 followed by the same letter are not different ( $P > 0.05$ ).

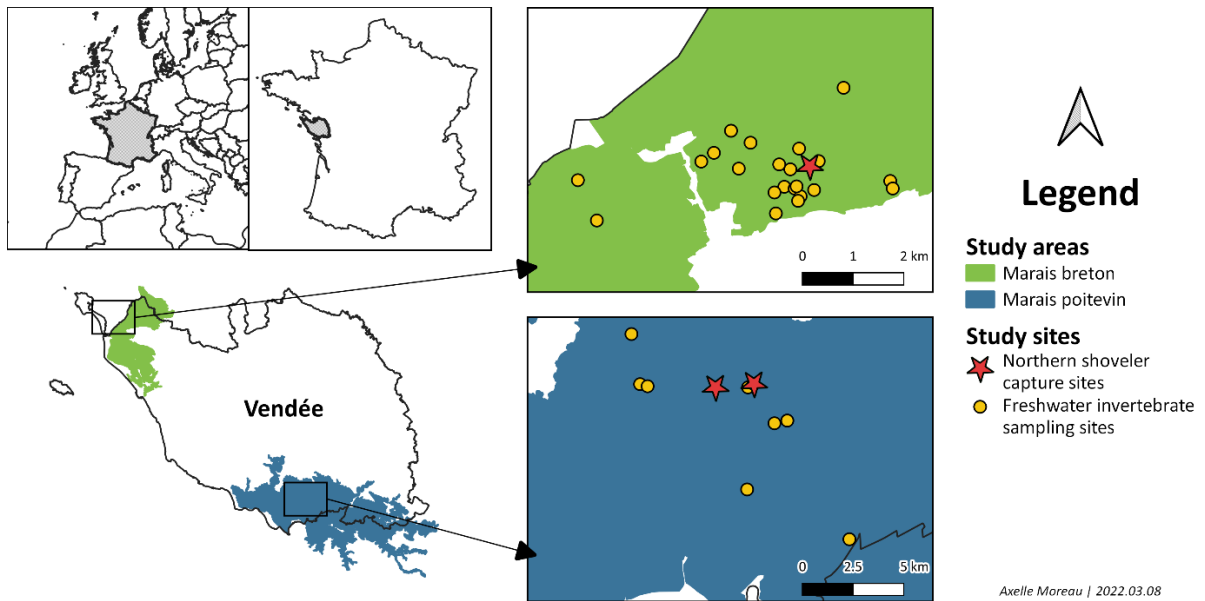
Freshwater invertebrate taxa	Diurnal site			All day site			Nocturnal site		
	MB (n=9)	MP (n=3)	All sites (n=12)	MB (n=4)	MP (n=2)	All sites (n=6)	MB (n=9)	MP (n=4)	All sites (n=13)
Amphipoda	0.0 ±	1.0 ±	0.3 ±	1.6 ± 3.1	0.0 ±	1.0 ±	25.0 ±	0.0 ± 0.0	17.3 ±
	0.0	1.8	0.9		0.0	2.6	58.4		
Cladocera	1,581.0	16,675.	5,354.0	12,038.3	3,653.0	9,243.0	18,427.0	17,521.0	18,148.0
	±	0 ±	±	±	±	±	±	±	±
Coleoptera	2,148.0	15,775.	9,757.0	17,988.5	2,563.0	14,636.	33,489.0	17,250.0	28,675.0
	0	0	0	0	0	0	0	0	0
Copepoda	0.3 ±	8.3 ±	2.3 ±	4.7 ± 9.4	0.0 ±	3.1 ±	15.3 ±	7.0 ± 8.2	12.8 ±
	1.0	14.5	7.2		0.0	7.7	22.2		
Decapoda	14,471.	14,272.	14,421.	22,484.0	15,271.	20,079.	17,221.0	3,998.0	13,153.0
	0 ±	0 ±	0 ±		0 ±	0 ±	±	±	±
Diptera	13,349.	14,061.	12,866.	23,261.0	19,675.	20,395.	13,498.0	1,588.0	12,745.0
	0	0	0		0	0	0	0	0
Ephemeroptera	0.0 ±	0.0 ±	0.0 ±	40.7 ±	0.0 ±	27.1 ±	76.9 ±	6.3 ±	55.1 ±
	0.0	0.0	0.0	35.5	0.0	34.6	194.0	12.5	162.1
Gastropoda	10.4 ±	94.9 ±	31.6 ±	108.0 ±	26.6 ±	80.9 ±	128.7 ±	918.6 ±	371.7 ±
	14.7	153.6	76.9	143.7	15.5	119.2	245.5	942.5	637.4
Hemiptera	0.0 ±	0.0 ±	0.0 ±	13.3 ±	0.0 ±	8.9 ±	52.5 ±	5.5 ±	38.0 ±
	0.0	0.0	0.0	26.6	0.0	21.7	104.4	11.0	88.4
Hydracarina	0.3 ±	138.8 ±	35.0 ±	99.4 ±	0.0 ±	66.2 ±	19.1 ±	356.0 ±	122.8 ±
	1.0	237.6	119.1	169.9	0.0	141.2	35.6	666.5	371.6
Odonata	29.9 ±	48.0 ±	34.4 ±	241.0 ±	6.3 ±	162.8 ±	141.2 ±	71.2 ±	119.7 ±
	49.1	42.7	46.4	363.9	0.0	306.9	179.6	140.3	166.0
Ostracoda	1.7 ±	1.0 ±	1.6 ±	2.3 ± 3.0	0.0 ±	1.6 ±	1.4 ± 4.2	0.0 ± 0.0	1.0 ± 3.5
	2.8	1.8	2.5		0.0	2.6			
All taxa	0.3 ±	0.0 ±	0.3 ±	0.8 ± 1.6	0.0 ±	0.5 ±	3.1 ± 8.3	0.0 ± 0.0	2.2 ± 6.9
	1.0	0.0	0.9		0.0	1.3			
All taxa	7.0 ±	659.0 ±	170.0 ±	5,558.0 ±	629.0 ±	3,915.0	1,583.0 ±	911.0 ±	1,376.0
	14.0	796.0	450.0	7,643.0	677.0	±	2,951.0	106.0	±
All taxa	16,106.	31,899.	20,054.	40,592.0	19,585.	33,590.	37,698.0	23,795.0	33,420.0
	0 ±	0 ±	0 ±	±	0 ±	0 ±	±	±	±
All taxa	13,241.	13,149.	14,490.	39,904.0	16,420.	33,571.	31,316.0	15,468.0	27,536.0
	0 b	0	0	abc	0	0	c	abc	

		abc			abc					
Diversity	4.3 ±	6.7 ±	4.9 ±	7.8 ± 2.6	5.0 ±	6.8 ±	6.6 ± 1.7	5.5 ± 2.1		
	1.2 b	0.6 a	1.5	a	0.0 ab	2.5	a	ab		6.2 ± 1.8

638 **Figures**

639

640 **Figure 1.** Locations of the 31 sampling sites in the Marais breton (MB) and the Marais poitevin (MP) on the  
 641 French Atlantic coast, France.



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644 **Figure 2.** Illustrations of the 3 studied habitat types : (A) Wet meadow, (B) pond, (C) channel.



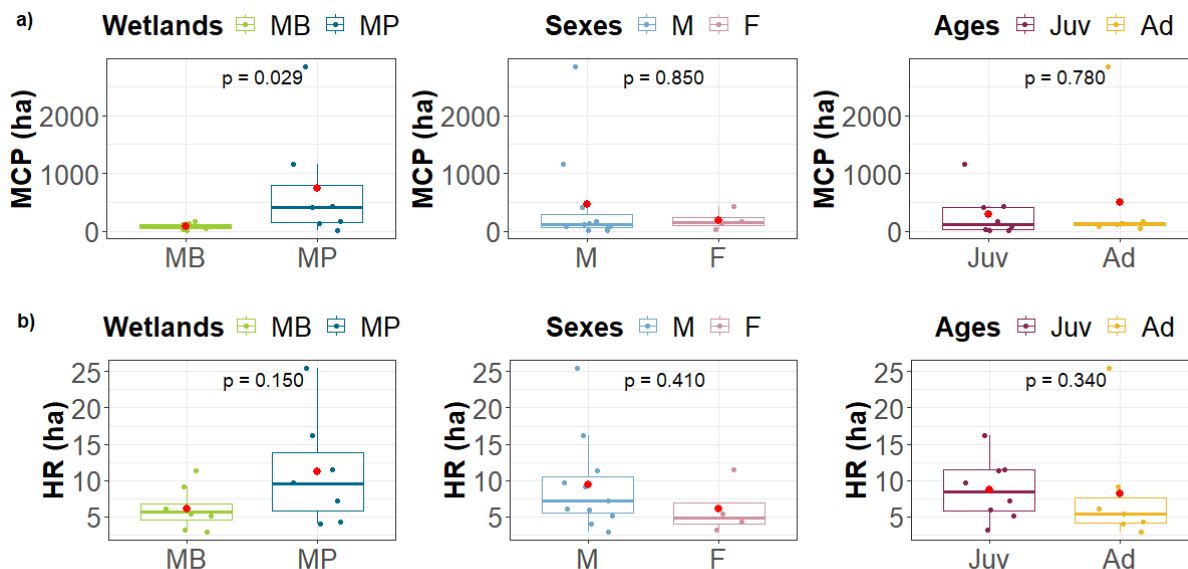
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647 **Figure 3.** Mean comparison (Wilcoxon Test) of a) the Minimum Convex Polygons (MCP) and b) the Home Range  
 648 (HR) size between individuals from the Marais breton (MB,  $n = 8$ ) and Marais poitevin (MP,  $n = 7$ ), between  
 649 sexes (males (M),  $n = 11$  and females (F),  $n = 4$ , and between juveniles (juv,  $n = 8$ ) and adults (ad,  $n = 7$ ). The  
 650 red dot corresponds to the mean value.

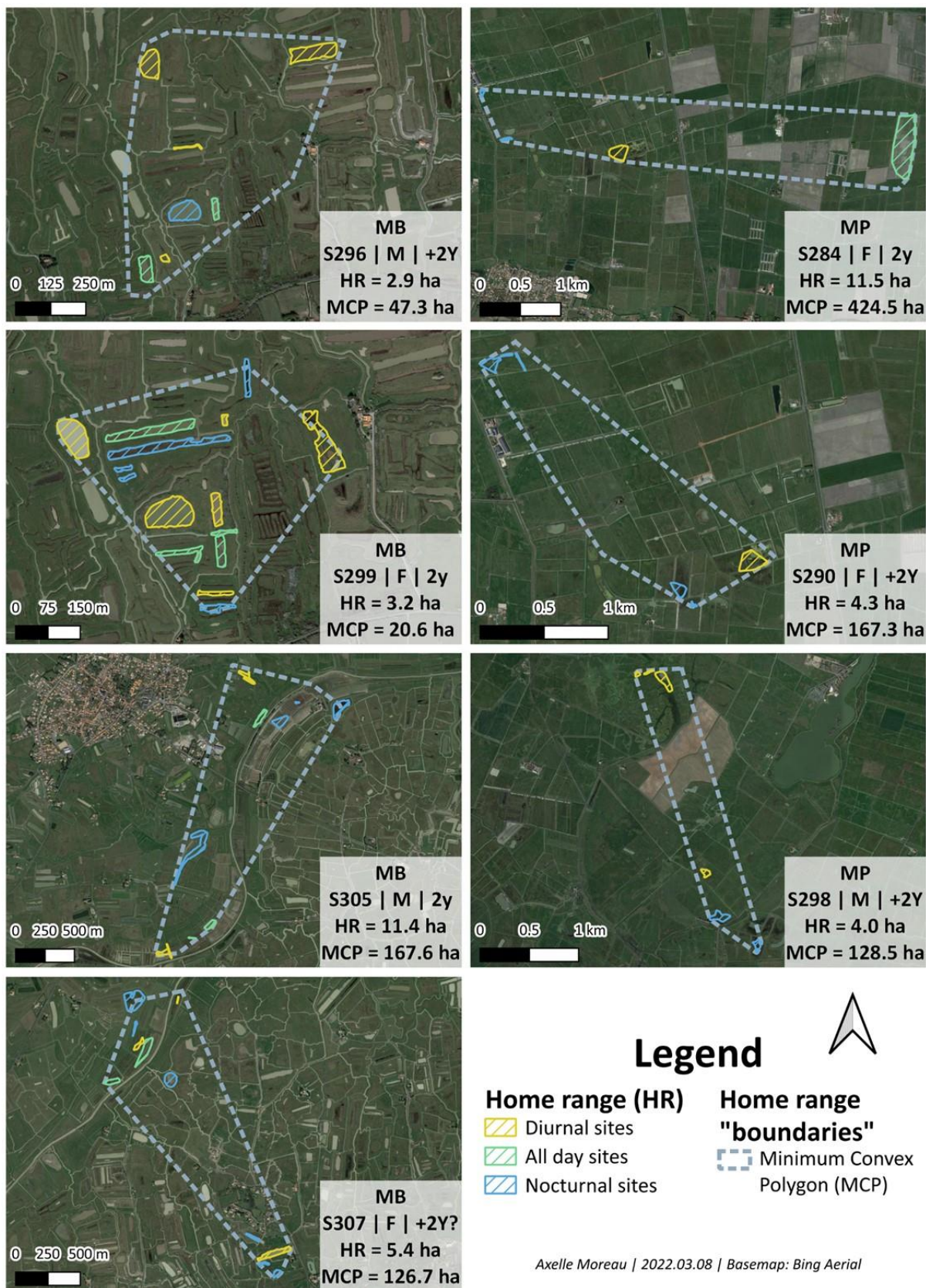
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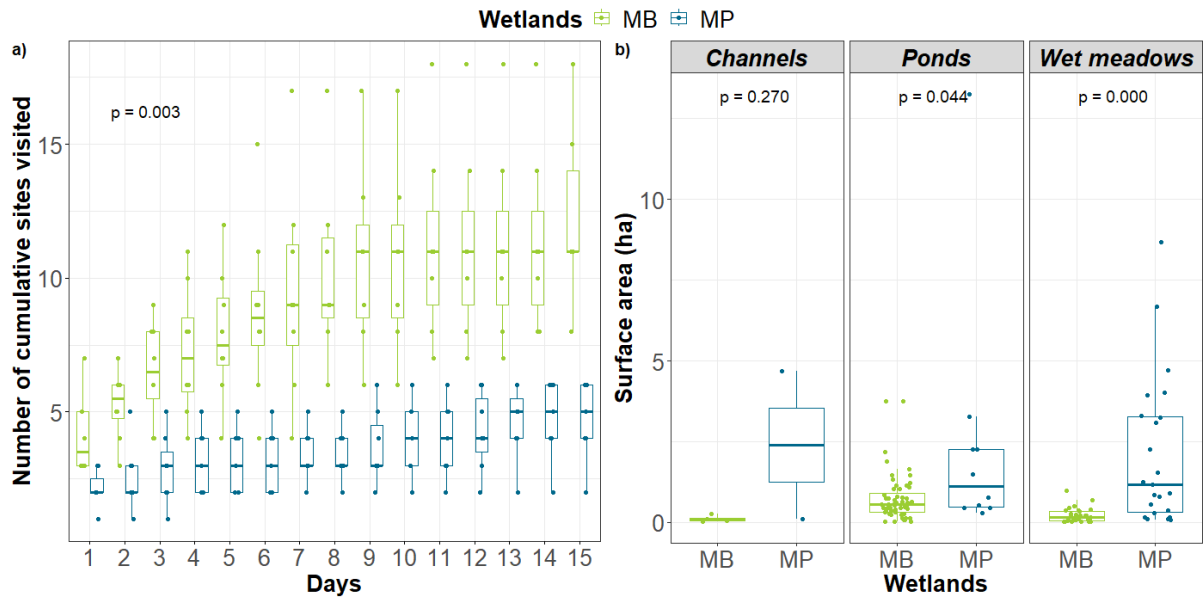
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654 **Figure 4.** Illustration of the Minimum Convex Polygons (MCP) and Home Ranges (HR) for seven individuals:  
 655 three from the Marais poitevin (MP) and four from the Marais breton (MB).



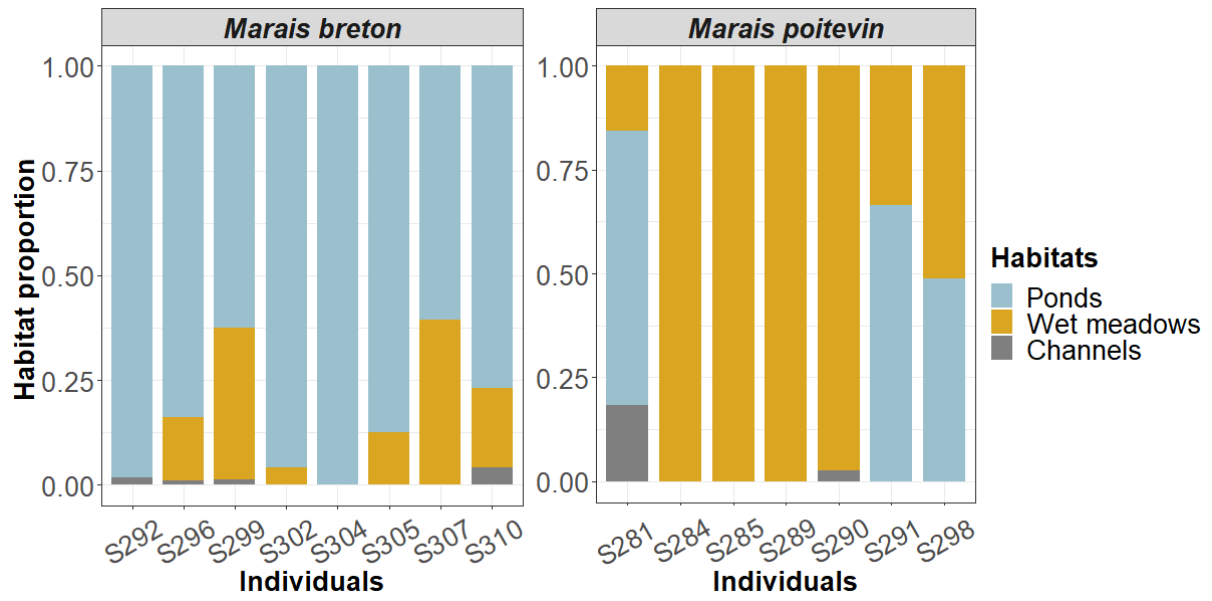
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659 **Figure 5.** (5A) Mean comparison (Kruskal-Wallis test) of the cumulative sites in each wetland visited by the 15  
 660 Shovelers over the study period. (5B) Mean comparison (Wilcoxon Test) of the surfaces used by the Shovelers at  
 661 the three main habitats in the MB and MP.  
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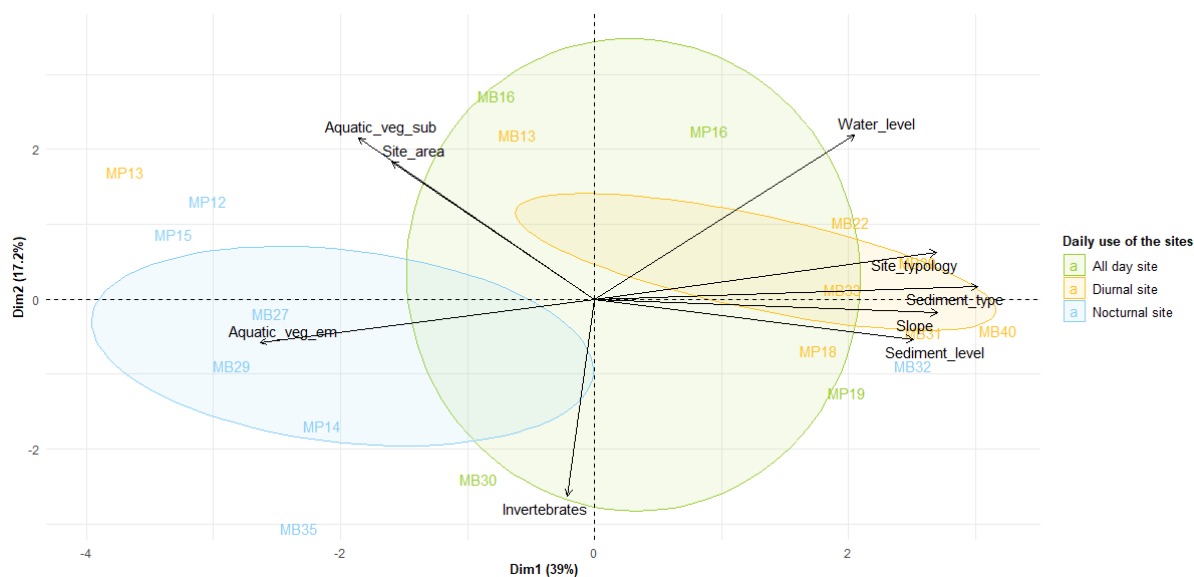
666 **Figure 6.** *Habitat proportion for each Shoveler over the study period.*



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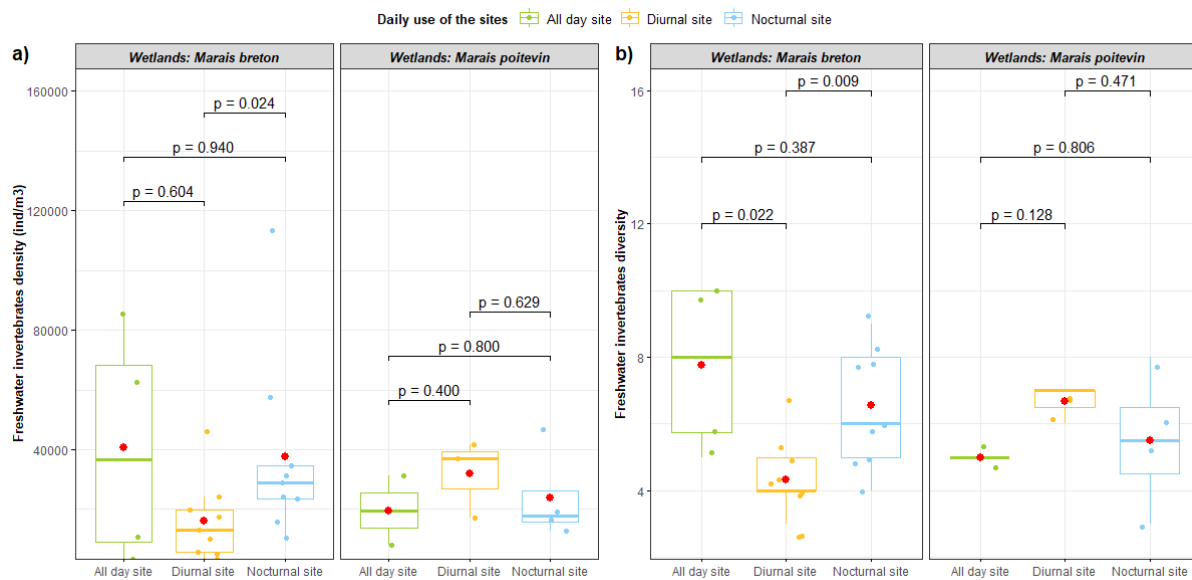
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669 **Figure 7.** Principal Component Analysis (PCA) of the environmental variables of the pre-nuptial stopover sites  
 670 used by tagged Shovelers. Dimensions 1 and 2 account for 56.2% of the total variance. Poorly represented sites  
 671 and variables ( $\cos^2 < 0.2$  on each axis) are not represented. Sites frequented by individuals during the day are  
 672 coloured in yellow, during all day in green, and during nighttime in blue. Confidence ellipses at 95 % were drawn  
 673 around each sites according to their daily use. “Invertebrates” = invertebrate density, “Slope” = slope,  
 674 “Site\_area” = water surface area, “Helophyte” = percentage cover of riparian helophytes, “Aquatic\_veg\_em”  
 675 = emerged aquatic vegetation, “Aquatic\_veg\_sub” = submerged aquatic vegetation, “Water\_level” = water  
 676 level, “Sediment\_level” = sediment depth, “Site\_typology” = habitat type, “Sediment\_type” = sediment type.



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680 **Figure 8.** Mean comparison (Wilcoxon Test) of the freshwater invertebrates a) density and b) diversity, in MB  
 681 and MP, depending on daily use of the sites, i.e. diurnal site (MB, n = 9; MP, n = 3), all day site (MB, n = 4;  
 682 MP, n = 2), nocturnal site (MB, n = 9; MP, n = 4).

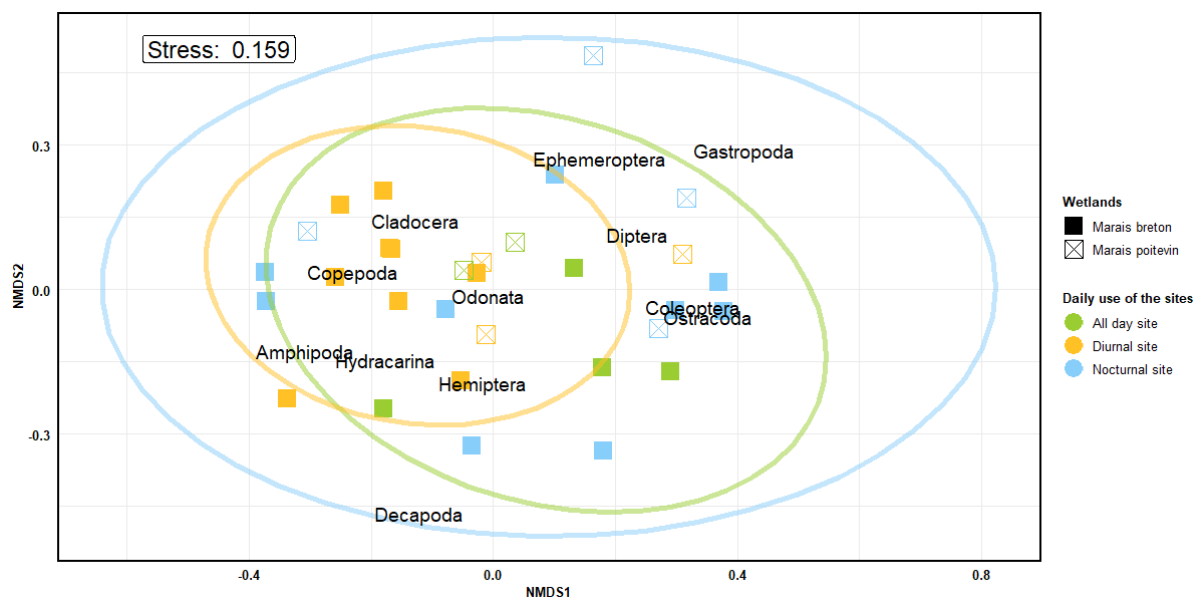


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685 **Figure 9.** Nonmetric Multidimensional Scaling Plots (NMDS) of the proportional taxonomic density with coloured  
 686 ellipses show the standard deviation of group centroids based on the daily use of the sites and the dot shapes show  
 687 the wetlands. Each points represent samples and text represents taxa (stress = 0.159).

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