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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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The wetlands of Marais breton (MB) and Marais poitevin (MP) on the French Atlantic coast are commonly used by several duck species, especially as stopover sites during the prenuptial migration. Understanding the ecological requirements of Anatidae at spring stopover sites is important to define appropriate management actions that might have a carry over effect on the subsequent reproduction success. This study focused on the Northern Shoveler (*Spatula clypeata*), a species that regularly visits the two marshes during spring and fall migrations and is highly dependent on freshwater invertebrates as the food resource. Fifteen Northern Shovelers were equipped with GPS/GSM tags and monitored during their stopover in both marshes in 2020 and 2021. The aims of the study were to understand the habitat use on stopover sites and relate home range (HR) size with characteristics of the feeding habitats (such as freshwater invertebrates' density and diversity). The HR area of the studied individuals was mainly constituted of ponds in MB (83% of the HR) and wet meadows in MP (71% of the HR). The Northern Shovelers equipped with tag spent more than 72 consecutive hours in 31 wetlands, using them during the day, at night or all day. The diurnal visited sites were deep ponds that were sparsely vegetated and dominated by microcrustaceans, whereas the nocturnal visited sites were wet meadows or ponds with high aquatic vegetation cover and high invertebrate taxonomic diversity. The 31 described sites appeared to be rich in freshwater invertebrates, with no significant difference in invertebrate densities between the diurnal and nocturnal sites. HR sizes were highly homogenous between the two study sites (MB and MP), between sexes or between age classes. In conclusion, according to this study, an appropriate HR for the Northern Shoveler at spring stopover is 8.49 ± 5.95 km² (mean ± standard error).

1. Introduction

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

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

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

Factors that influence Shovelers' use of wetlands include habitat availability, disturbance, predation but also the diversity, density, spatio-temporal dynamics (Matsubara *et al.* 1994, Guillemain *et al.* 2000) and accessibility (Bolduc & Afton 2004) of their main food resource *i.e.* freshwater invertebrates. In addition, Shovelers select foraging sites according to prey availability, prey size and energy values to maximise the net energy intake (Crome 1985, Tietje & Teer 1996). The bill with its spoon-shaped morphology and high-density, closely spaced lamellae, *i.e.* 21.48 ± 2.41 lamellae/cm² (Nudds & Bowlby 1984), is an adaptation to sieving. Shovelers filter the surface of the water to collect food giving them a specific food niche compared with other Anatidae species. The Shoveler's diet mainly consists of small freshwater invertebrates (Pirot & Pont 1987, Ankney & Afton 1988, Baldassarre & Bolen 2006) and, particularly, swimming microcrustaceans such as Cladocera and Ostracoda (DuBowy 1985, Pirot & Pont 1987, Baldassarre & Bolen 2006). Improved knowledge of Shovelers' ecology during prebreeding migration will help to determine their ecological requirements in terms of habitat and feeding.

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

2. Material and methods

2.1. Study sites

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

2.2. Capture and tagging

During the prenuptial migration period, Shovelers were captured using cage traps and attracted with live male or female Shovelers as decoys. A camera (NATURACAM – STDX2) was positioned near each trap to monitor the presence of birds in the traps, which were caught every day from the 1st of March to the 17th of March 2020, and from the 1st of March to 10th of April, 2021. In 2020, the capturing effort was stopped on the 17th of March due to the COVID-19 lockdown. In total, eight individuals were caught in the MB and 7 in the MP. All Shovelers were equipped with a GPS-GSM tag (Ornitela, OrniTrack-E10, 10 g, solar-powered GPS-GSM); these included 2 F juv (female juvenile; less than two calendar years), 2 F ad (adult; more than two calendar years), 6 M juv (male) and 5 M ad (see details in Supplementary Material Table S1). The GPS-GSM tags were attached as backpacks using a harness made of Teflon straps with rubber tubing (Klaassen *et al.* 2008, Lameris *et al.* 2017, 2018). The equipment (GPS-GSM tag, harness, and metal ring) weighed less than 3% of the body mass and we assume that the use of the GPS did not cause significant impact on ducks movements

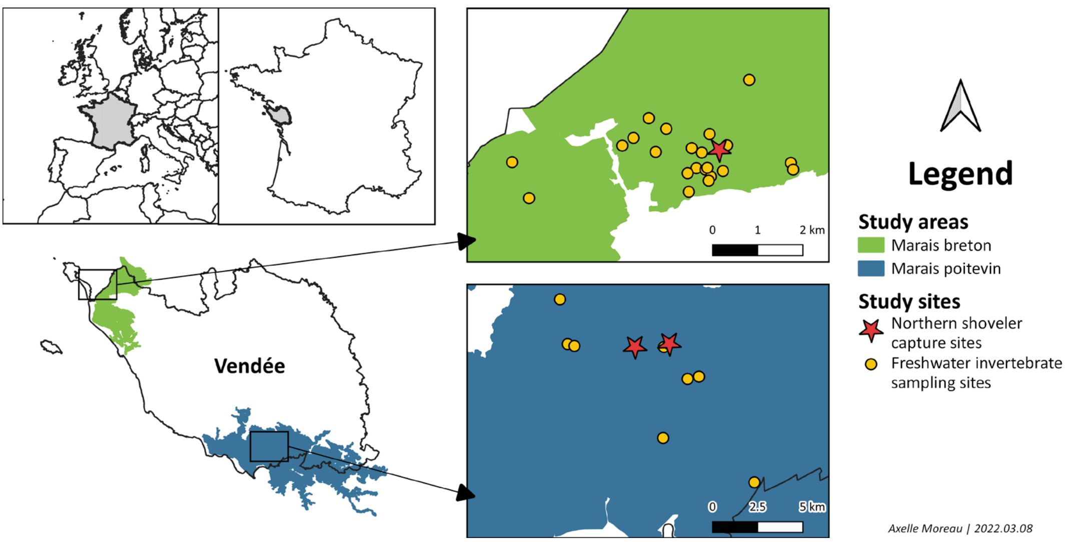

Fig. 1. Locations of the 31 sampling sites in the Marais breton (MB) and the Marais poitevin (MP) on the French Atlantic coast, France.

and behaviour. The Shovelers were captured and handled according to ethical rules edicted by French legislation (Authorization from Ministry of Ecological Transition by Research Center on the Biology of Bird Populations PP: 1821).

The location of the individuals were recorded during the prenuptial period from the 1st of March to the 30th of April in 2020 and 2021 with a frequency of 5 minutes. The location of the 15 individuals was then recorded for (14 days ± 2 days; mean ± standard error) (Table S1). No fundamental differences were observed in precipitation or hydrology between years (2020 vs. 2021) or temporal patterns within a year (*i.e.* early vs. late spring) (Moreau A., pers. comm.). None of the studied individuals attempted to breed in the studied areas.

2.3. Trophic resources at the feeding sites

The tagged individuals spent more than 72 consecutive hours in 31 sites. These sites were classified into three categories according to the habitat type: wet meadow, pond, and channel (Supplementary Material Fig. S1). From the 1st of March to 10th of April 2021, freshwater invertebrates were sampled at each site using a plankton net (mesh of 200 µm, frame size 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 feeding depth capacity (Pöysä 1983). The net contents were preserved in 70% ethanol (Balcombe *et al.* 2005) and quickly analysed at a laboratory. Invertebrates were sorted, counted and identified using a binocular magnifier (Euromex, Series Z, 7-45 x) to the family level except Copepoda, subclass; Cladocera, superorder; Hydrachnidia, suborder; and Ostracoda, class (Thorp & Rogers 2011).

2.4. Environmental parameters measurement

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

2.5. Home range and movement analysis

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

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

2.6. Statistics

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

3. Results

3.1. Home range, number of sites frequented and habitat use

The size of the minimum convex polygons (MCPs) for the 15 individuals ranged from 9.0 to 2,846.4 ha, and the estimated home ranges (HR) ranged from 2.9 to 25.4 ha (Table S1). The mean MCP areas of the individuals from MB (78.7 ± 54.1 ha, n=8) were significantly lower than those from MP (738.0 ± 10,003.0 ha, n=7; Wilcoxon test, p<0.05) while the mean HR sizes did not differ (MB = 6.2 ± 2.9 ha, n=8; MP = 11.2 ± 7.6 ha, n=7; Wilcoxon test, p>0.05) (Fig. 2). The MCP size did not differ between males

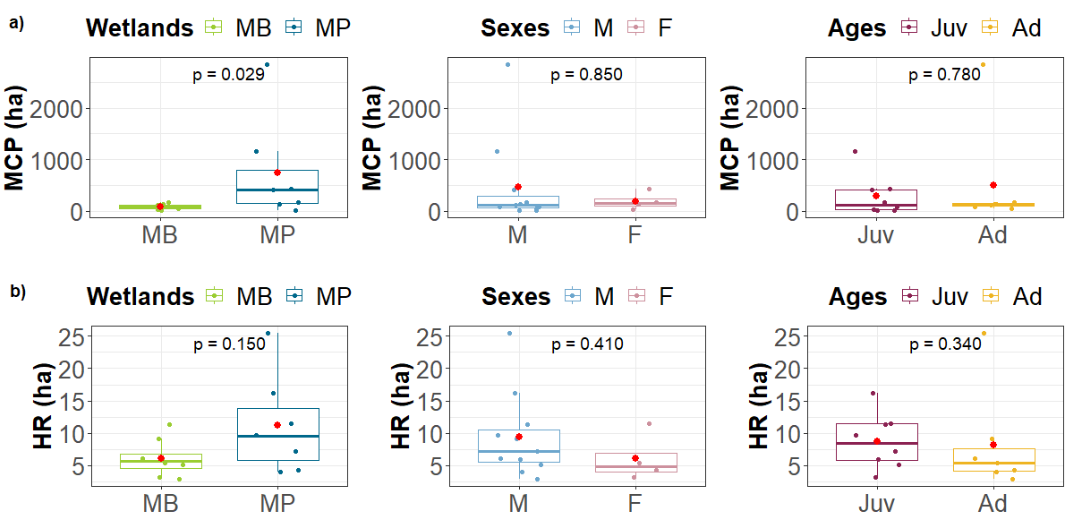

Fig. 2. Mean comparison (Wilcoxon Test) of a) the Minimum Convex Polygons (MCP) and b) the Home Range (HR) size between individuals from the Marais breton (MB, n=8) and Marais poitevin (MP, n=7), between sexes (males (M), n=11 and females (F), n=4, and between juveniles (juv, n=8) and adults (ad, n=7). The red dot corresponds to the mean value.

and females (M = 459 ± 859 ha, n=11; F = 185 ± 171 ha, n=4; Wilcoxon test, p>0.05) or between juveniles and adults (juv = 286 ± 393 ha, n=8; ad = 500 ± 1035 ha, n=7; Wilcoxon test, p>0.05) (Fig. 2). Moreover, the HR size did not differ between males and females (M = 9.4 ± 6.5 ha, n=11; F = 6.1 ± 3.7 ha, n=4; Wilcoxon test, p>0.05) or between juveniles and adults (juv = 8.8 ± 4.2 ha, n=8; ad = 8.2 ± 7.8 ha, n=7; Wilcoxon test, p>0.05) (Fig. 2).

Over the 15-day study period, the cumulative number of sites visited by the individuals increased rapidly at the MB but increased slowly at the MP (Fig. 3a). In addition, the number of sites used per day at the MB was greater than MP (Fig. 3a). However, the mean surface size of each habitat type at MP were significantly greater than those at MB, *i.e.* ponds (MB = 0.8 ± 0.8 ha, n=56; MP = 2.5 ± 3.9 ha, n=10; Wilcoxon test, p<0.05) and wet meadows (MB = 0.2 ± 0.2 ha, n=29; MP = 2.1 ± 2.3 ha, n=23; Wilcoxon test, p<0.05), except for channels (MB = 0.1 ± 0.1 ha, n=4; MP = 2.4 ± 3.2 ha, n=2; Wilcoxon test, p>0.05) (Fig. 3b). Finally, the spatial distribution showed that Shovelers used some sites only during daytime for resting or foraging, others only during nighttime for foraging, and some during both day and night (Supplementary Material Fig. S2).

Besides the significant differences in MCP sizes and number of sites visited, the utilization of habitat types also differed significantly between both marshes and individuals (Fig. 4, Table S1). In the MB, HRs mainly consisted of ponds (83 ± 15% of the HR area on average, n=8), wet meadows were the 2nd most used habitat type (16 ± 15%, n=8) and channels were very little used (1 ± 1%, n=8). At the MP, HRs mainly constituted of wet meadows (71 ± 37%, n=7) and secondly of ponds (26 ± 33%, n=7). As in the MB, channels were rarely used in MP (3 ± 7%, n=7).

3.2. Foraging habitat

The environmental characteristics of the sites were analysed using PCA (Supplementary Material Fig. S3). On Axis 1 (39%), the sediment depth, habitat type, sediment type, and slopes were negatively correlated with the emerged aquatic vegetation (Fig. S3 and confirmed by the Spearman correlation values which are –0.41, –0.51, –0.61 and –0.50 respectively). On Axis 2 (17.2%), the variables water level, submerged

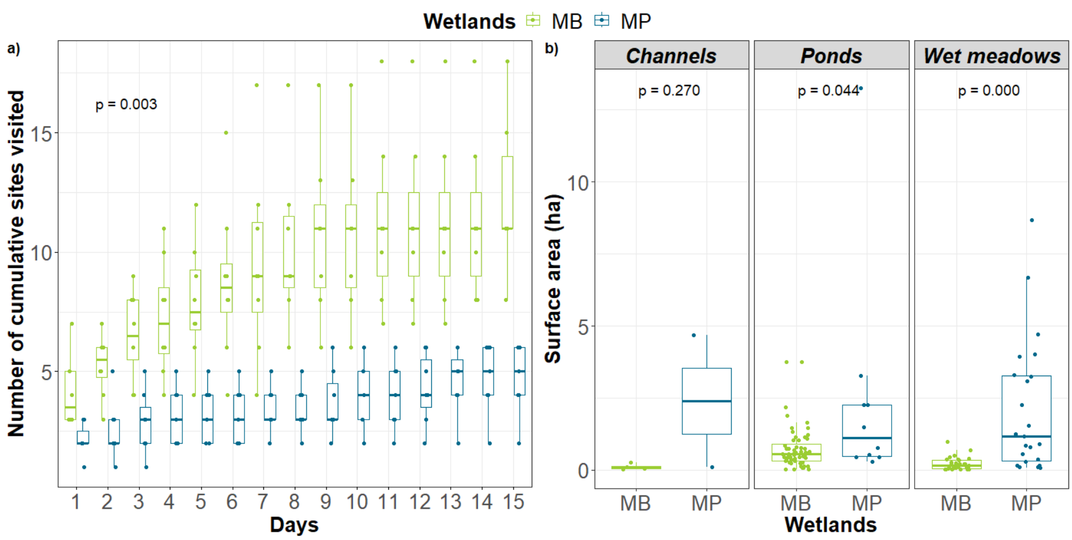

Fig. 3. (A) Mean comparison (Kruskal-Wallis test) of the cumulative sites in each wetland visited by the 15 Shovelers over the study period. (B) Mean comparison (Wilcoxon Test) of the surfaces used by the Shovelers at the three main habitats in the MB and MP.

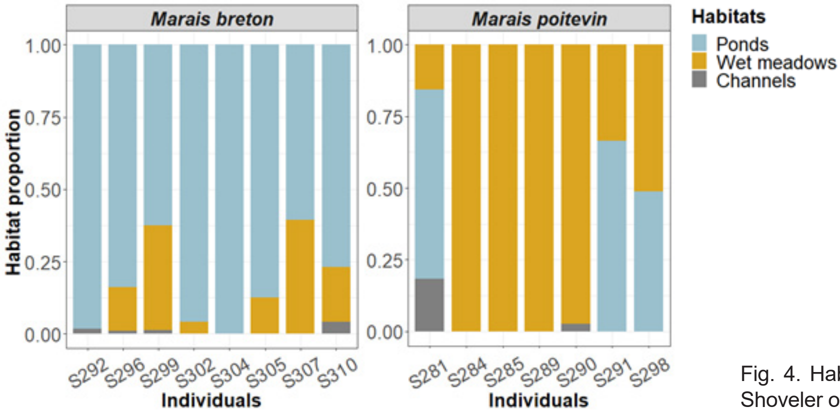

Fig. 4. Habitat proportion for each Shoveler over the study period.

aquatic vegetation, and water surface area contrasted with the invertebrate density (Fig. S3 and confirmed by the Spearman correlation values which are –0.33, –0.28 and –0.22 respectively). The other variables could not be interpreted ($\cos^2<0.4$ on the two axes).

Diurnal sites (Fig. S3 and Supplementary Material Table S2) were mainly defined by a deep water level (40.9 ± 11.1 cm), high sediment height (10.7 ± 10.7 cm), steep slopes, muddy sediment, low cover of aquatic vegetation, and a site typology corresponding to a pond. In contrast, the nocturnal sites (Fig. S3 and Table S2) were characterized by a low water level (28.2 ± 21.7 cm), low sediment height (6.3 ± 6.5 cm), loamy/muddy sediment, soft slopes, a significant cover of aquatic vegetation, and a site typology corresponding to wet meadows. Sites that were frequented at both day and nighttime were not specifically characterized by one or more environmental variables.

3.3. Trophic resources

Among the 15 taxa of freshwater invertebrates inventoried from the study sites, 12 (occurrence of ≥10% on all sites) were retained for the analysis. Five taxa were widespread (present in more than 50% of the samples). These included Copepoda and Cladocera (100% occurrence), Diptera and Hemiptera (84% occurrence), and Ostracoda (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 individuals at each site.

The invertebrate densities for all taxa combined ranged from 3,387 to 113,315 individuals/m^3 (Table S2). There was a significant difference in taxon density according to the daily use in the MB, the density in diurnal sites were lower than the density in nocturnal sites (Diurnal site = 16,106 ± 13,241 ind/m^3, n=9; Nocturnal site = 37,698 ± 31,316 ind/m^3, n=9; Wilcoxon test, $p>0.05$) (Fig. 5 and Supplementary Material Table S3). However, there was no significant difference in the density of freshwater invertebrates based on the daily use of the sites in the MP (Diurnal site = 31,899 ± 13,148 ind/m^3, n=3; Nocturnal site = 23,795 ± 15,468 ind/m^3, n=4; All day site = 19,585 ± 16,419 ind/m^3, n=2; Wilcoxon test, $p>0.05$) (Fig. 5 and Table S3). Moreover, there was a significant difference in taxon diversity according to the daily use in the MB, diurnal sites were less diversified than the other sites (Diurnal 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; Wilcoxon test, $p<0.05$) but, not in the MP (Diurnal site = 6.7 ± 0.6 taxa, n=3; Nocturnal site = 5.5 ± 2.1 taxa, n=4; All day site = 5 ± 0 taxa, n=2; Wilcoxon test, $p>0.05$) (Fig. 5 and Table S3), which was confirmed by the NMDS plot (Supplementary Material Fig. S4). Microcrustaceans (Cladocera and Copepoda) as well as Odonata, Amphipoda, Hydrachnidia, and Hemiptera were present in all the sites.

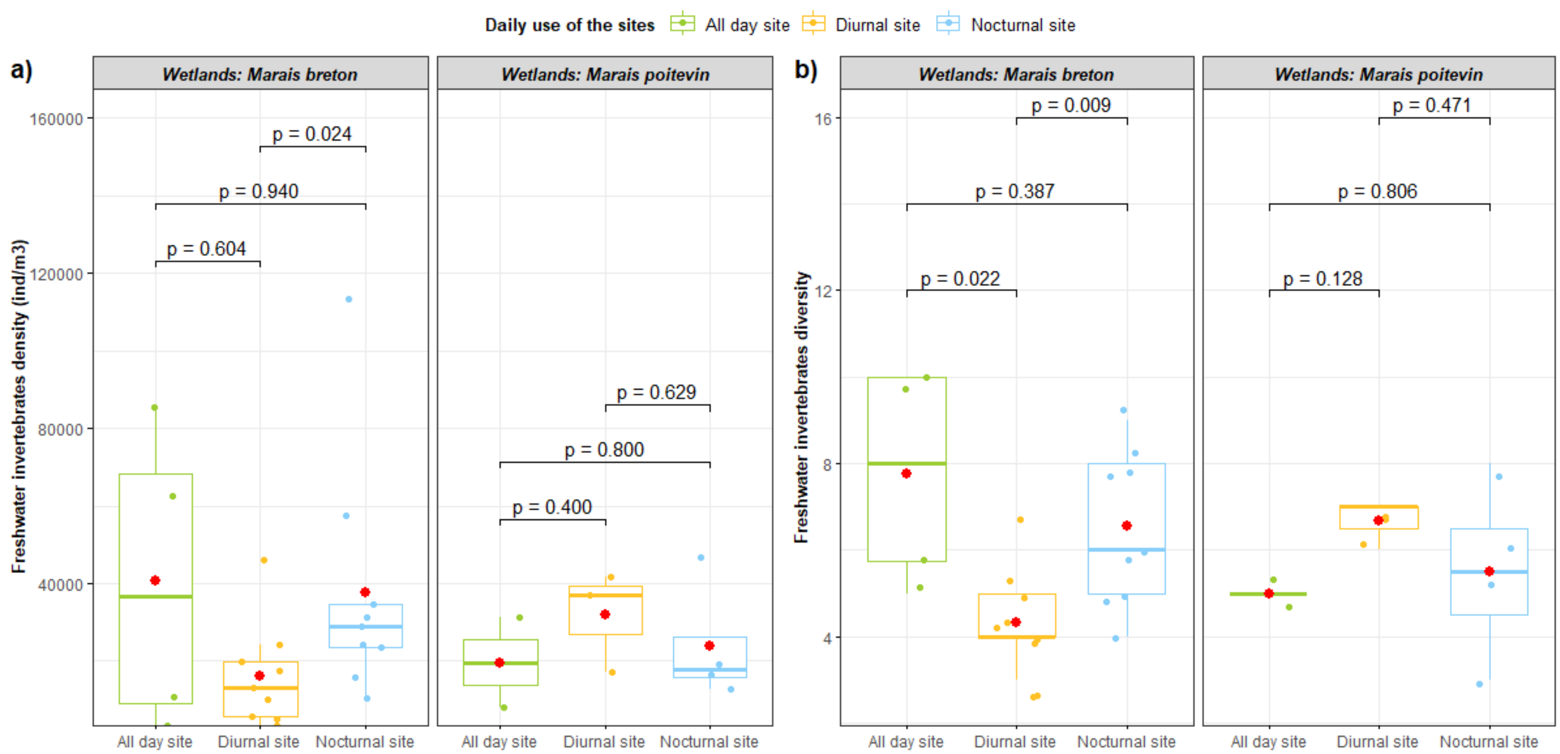

Fig. 5. Mean comparison (Wilcoxon Test) of the freshwater invertebrates a) density and b) diversity, in MB and MP, depending on daily use of the sites, i.e. diurnal site (MB, n=9; MP, n=3), all day site (MB, n=4; MP, n=2), nocturnal site (MB, n=9; MP, n=4).

4. Discussion

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

4.1. Home range, number of sites and habitats used

Heitmeyer and Vohs (1984) defined that the Shoveler preferentially uses small marshes and muddy ponds, which is consistent with the results of the present study, wherein the HR of more than half of the individuals studied (59%) contained more than 50% ponds. However, the sizes and habitat composition within the HRs were not the same across MB and MP wetlands and between individuals. Several factors can influence the HR size and shape (Rolando 2002). Species prospecting in environments that may change seasonally and contain variable food resources must adjust their distribution or space use according to resource availability to meet their energy requirement (Kirk *et al.* 2008, Kraan *et al.* 2009). In this study, no significant differences in HR sizes were observed between wetland complexes. However, the maximum total area used (Minimum Convex Polygon, MCP) was significantly larger in the MP than in the MB. Ponds and wet meadows are much more scattered in the MP than in the MB. Thus, the lower density of water areas (ponds and wet meadows) likely leads the birds to explore larger territory, possibly explaining the larger total area of the MCP in the MP. Furthermore, the lack of differences in the HR size between males and females was expected as Shovelers are considered to be 'income' breeders (Ganter & Cooke 1996, Gauthier *et al.* 2003). Accordingly, both males and females feed similarly on migratory stopovers to complete their trip to the breeding sites. This result is also supported by Arzel and Elmberg (2004), who found no sex differences in the foraging behaviour of Shovelers at the spring stopover sites (time spent feeding, day/night distribution, and feeding method). The use of sites during the stopover differed between individuals. Some individuals used up to ten different sites per day, whereas others used only two sites, although, only sites at which individuals spent more than 72 hours were kept for analysis. This variability may be due to different energy requirements and thus varied time allocated to feeding, differences in social status, or competition for access to food at some sites (Poisbleau 2005, Bengtsson *et al.* 2014). However, no interspecific competition related to food limitation has been demonstrated for the Mallard (*Anas platyrhynchos*), Eurasian Wigeon (*Mareca penelope*), Eurasian Teal (*Anas crecca*), and Shoveler (Arzel & Elmberg 2004).

4.2. Characterization of the feeding habitat during the prenuptial stopover

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

4.3. Characterization of available food resources

A predominantly invertebrate-based diet of the Shoveler in spring appears to be consistent with the temporal dynamics of this food resource. For birds that need a diet of freshwater invertebrates, there is no synchronization between their peak migration and peak density of food resources at stopover areas (Arzel & Elmberg 2004). However, the behaviour of ducks in a site is linked to fluctuations in resource density (Arzel 2006). Nevertheless, we measured high densities of freshwater invertebrates in the MB and MP during migration of Shoveler. The 31 study sites revealed a mean density of 28,298 ± 24,342 individuals/m^3 per site. In a study carried out in several wetlands in West Virginia (USA), Balcombe *et al.* (2005) reported a mean of 14,800 ± 3,060 invertebrates/m^3 in emergent waters and 2,360 ± 1,130 invertebrates/m^3 in open waters. In Delta Marsh in south-central Manitoba, Kaminski and Prince (1981) measured aquatic invertebrate densities as a function of percent cover of emergent hydrophytes (8,381 individuals/m^3 for 30% cover, 9,938 individuals/m^3 for 50% cover, and 12,190 individuals/m^3 for 70% cover). According to the present study, the particularly high density of freshwater invertebrates could explain the attractiveness of the studied sites at MB and MP for Shovelers during their prenuptial migration.

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

5. Conclusion

Regardless of wetlands, age classes or sexes and according to this study, an appropriate HR for the Shoveler at spring stopover is 8.49 ± 5.95 km² (mean ± standard error). Within its home range, the Shoveler mainly uses two habitat types with high freshwater invertebrate density: ponds (with or without vegetation) and wet meadows. Preserving deep and muddy ponds, which are used by Shovelers during the day and shallow and vegetated ponds or wet meadows, which are used during the night along the migration routes remains critical to fostering the relationship between freshwater invertebrates and the Shoveler during their prenuptial migration. Telemetric monitoring of migrating Shovelers and analysis of freshwater invertebrates in the wetlands of Vendée confirmed the processes related to this relationship during the prenuptial migration.

Lapasorsan (*Spatula clypeata*) kotialueen koko ja vuorokautinen elinympäristön käyttö kevätmuuton pysähdyspaikoilla Vendéen kosteikoilla, Länsi-Ranskassa

Ranskan Atlantin rannikolla sijaitsevat Marais Bretonin (MB) ja Marais Poitevinin (MP) alueiden kosteikot ovat tärkeitä useille sorsalajeille, erityisesti kevätmuuton aikaisina levähdyspaikkoina. Anatidae-heimon lintujen ekologisten vaatimusten ymmärtäminen näillä pysähdyspaikoilla on tärkeää, jotta voidaan määritellä hoitotoimenpiteitä, jotka voivat vaikuttaa niiden myöhempään lisääntymismenestykseen. Tämä tutkimus keskittyy lapasorsaan (*Spatula clypeata*), joka pysähtyy säännöllisesti näillä kahdella kosteikolla kevät- ja syysmuuttojen aikana ja on riippuvainen kosteikkoalueiden makean veden selkärangattomista ravintona. Viisitoista lapasorsaa varustettiin GPS/GSM-lähettimillä, ja niiden liikkeitä seurattiin näillä alueilla vuosina 2020 ja 2021. Tutkimuksen tavoitteena oli selvittää elinympäristöjen käyttöä pysähdyspaikoilla ja yhdistää kotialueen koko (*home range*, HR) ravintoympäristöjen ominaisuuksiin, kuten makean veden selkärangattomien tiheyteen ja monimuotoisuuteen.

Marais Bretonissa lapasorsien kotialueet koostuivat pääosin lammista (83 %), kun taas Marais Poitevinissa ne keskittyivät kosteille niityille (71 %). Lähettimillä varustetut linnut viettivät yli 72 tuntia yhteensä 31 eri kosteikolla, joita ne käyttivät sekä päivisin että öisin. Päivisin linnut suosivat syviä, vähäkasvustoisia lampia, joissa oli runsaasti mikroäyriäisiä, kun taas öisin ne hakeutuivat kosteille niityille tai lammille, joissa oli runsaasti vesikasveja ja selkärangattomia. Kaikki tutkitut kosteikot olivat makean veden selkärangattomien suhteen rikkaita, eikä selkärangattomien tiheyksissä havaittu merkittäviä eroja päivä- ja yöalueiden välillä. Kotialueiden koot olivat hyvin yhtenäisiä kahden tutkimusalueen, sukupuolten ja ikäluokkien välillä. Tutkimuksen mukaan lapasorsien optimaalinen kotialue keväisillä pysähdyspaikoilla on keskimäärin 8,49 ± 5,95 km².

Declaration of interest statement. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Online supplementary material

Supplementary material available in the online version includes Table S1–S3 and Figures S1–S4.