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Nycthemeral movements of wintering shorebirds reveal important differences in habitat uses of feeding areas and roosts

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Abstract

Most shorebirds depend on coastal habitats for much of their life cycle. The quality and diversity of feeding areas during the wintering period directly condition their winter survival, subsequent migration, and breeding success. During their wintering in France, shorebirds use intertidal areas for feeding, both in daylight and at night, depending on the availability of mudflats during the tidal cycle. In this context, we studied whether the bar-tailed godwit (*Limosa lapponica*) shows contrasting foraging behaviors and distributions between day and night in response to differences in visual capacities, prey availability, potential predation risk, and human activities. We carried out a fine-scale GPS tracking of birds at one of their main wintering sites along the French Atlantic coast. We predicted smaller foraging home ranges at night because of limits for godwits to detect prey visually, suggesting more sediment probing and less movement. Godwits used the entire time window when they have access to intertidal areas, but they faithfully selected distinct diurnal and nocturnal feeding areas using a low number of patches. This variability in space use highlights differences in selection of habitats, such as seagrass beds selected by most of the tracked godwits by day and used much less at night. In addition, distinct feeding distributions of monitored birds revealed interindividual variability in habitat selection, even more by night, most likely to reduce intraspecific competition. We therefore urge greater consideration of the night distribution of birds, rarely evaluated in shorebirds studies, to define areas and habitats of importance to future management and conservation measures.

Keywords: Coastal ecology, coastal habitats, intertidal mudflats, GPS tracking, nocturnal foraging, *Limosa lapponica*

Introduction

According to the principle of optimal foraging, animals tend to maximize their net energy intake per unit time (Stephens and Krebs 1986) and thus forage in the best conditions to catch maximal prey with minimal energy lost. In most birds, vision is the main sense used both day and night (Martin 2012). Therefore, the majority of bird species are active during daylight, that is, when visual conditions are best for foraging (Martin 1990). However, foraging may also be influenced by, for instance, predation risk, competition, food availability, weather conditions, and human disturbance, and birds have to adapt their behavior to devise the optimum strategy toward survival (McNamara and Houston 1980; Abrahams and Dill 1989).

In coastal shorebirds feeding in intertidal areas, the quality of wintering sites, and especially of feeding areas, directly affects their winter survival, subsequent migration, and breeding success (Pitelka 1979; Piersma et al. 1993; Gunnarsson et al. 2005; West et al. 2005; Gunnarsson et al. 2006; Morrison et al. 2007). The spatiotemporal distribution of birds in intertidal areas therefore depends on prey diversity and abundance (Kelsey and Hassall 1989; VanDusen et al. 2012) as well as their availability (Colwell and Landrum 1993) to maximize the rate of energy intake over the exposure period in such areas (van Gils et al. 2003; Goss-Custard et al. 2007; Quaintenne et al. 2010). Studies on wintering shorebird activity showed a tidal pattern of space use linked with the tidal effect on the availability of intertidal trophic resources (Puttick 1984; Colwell and Landrum 1993; Granadeiro et al. 2006). Thus, shorebirds wintering on sites subject to the tidal cycle will use intertidal foraging areas when available at low tides, that is, both during daylight and night (McNeil et al. 1992; McNeil and Rodriguez 1996). This sustained feeding behavior during nocturnal low tides could allow the birds to (1) benefit from better feeding opportunities (prey activity and availability), according to the *preference hypothesis* (Dugan 1981; Evans 1987; Mouritsen 1994), or (2) meet daily energetic requirements not satisfied in daylight, according to the *supplementary hypothesis* (McNeil and

Rodriguez 1996; Smith et al. 1999; Sitters 2000). However, in addition to different diurnal and nocturnal foraging conditions, bird visual capacities, such as prey availability or predation risk (Dugan 1981; Evans 1987), could constrain bird foraging patterns and behaviors. Consequently, they should adjust their foraging activity, technique, and space use between daytime and nighttime (Mouritsen 1993; Rojas et al. 1999; Kuwae 2007). Species that can switch from sight to tactile feeding, such as the dunlin (*Calidris alpina*), the Eurasian oystercatcher (*Haematopus ostralegus*), the black-tailed godwit (*Limosa limosa*), or the *Tringa* species (Mouritsen 1994; McNeil and Rodriguez 1996; Lourenço et al. 2008) could take advantage of nocturnal feeding. Sight-feeding shorebirds could also benefit from night feeding because of the moonlight (McNeil et al. 1992) and/or physiological adaptations improving their nocturnal vision (Pienkowski 1983; Rojas et al. 1999) to maintain a high intake rate during nighttime (Pienkowski 1983; Lourenço et al. 2008). Furthermore, the higher activity and accessibility of prey at night in intertidal mudflats (McNeil et al. 1995; Esser et al. 2008), combined with the aforementioned bird capacities, could explain such an interest in nocturnal foraging behavior to satisfy wintering energetic requirements.

Both diurnal and nocturnal foraging areas are therefore important for wintering shorebirds. However, most studies focused on their daylight activity and distribution, disregarding possible important areas used only during nighttime yet also essential for adapted conservation and management measures to protect these vulnerable species. In that context, we studied the diurnal and nocturnal spatial distributions of the bar-tailed godwit (*Limosa lapponica lapponica*) wintering on Ré Island (Pertuis Charentais, Atlantic French coast), a site of national importance for the species. The population of *L. l. lapponica* is estimated at 120,000 (Delany et al. 2009), and France sees 5.8% of wintering godwits, among which about 650 (>1% of national numbers) are recorded on Ré Island in January (J-C. Lemesle, *Pers. Com.*). The bar-tailed godwit is characterized by increasing trends of the wintering population at the European

scale (BirdLife International 2015), and its numbers have been stable in France in the last 12 years (Schmaltz et al. 2019). Nonetheless, large fluctuations of the population have been observed in recent decades in France, including significant decreases during the 1980s and 1990s (Triplet et al. 2010) likely due to degraded wintering habitats and increasing human disturbance (Goeldner-Gianella 2005; Delany et al. 2009; BirdLife International 2017). In this context, we tested the hypothesis that the bar-tailed godwit shows contrasting foraging behaviors and distributions between day and night. Indeed, visual capacities, prey availability, predation risk, and human activities are all factors influencing the behavior of birds, and their variability between day and night could lead to differences in their distribution. We predicted smaller foraging home ranges at night because of birds' difficulty in visually detecting prey (Turpie and Hockey 1993), suggesting more sediment probing and therefore less movement (Pienkowski 1983; Lourenço et al. 2008). To achieve these objectives, we conducted a fine-scale GPS tracking of wintering habitat use and investigated the birds' (1) spatial distribution and foraging home ranges, (2) feeding movements, (3) habitat selection, and (4) their variation between daytime and nighttime.

Methods

Study site

Fieldwork was carried out in the Pertuis Charentais, which includes the largest area of intertidal mudflats on estuarine systems in France (Goeldner-Gianella 2005), during the wintering period (from November to March) of shorebirds in 2015–2016 and 2016–2017 (Fig. 1). We focused on Ré Island, one of the main wintering sites for bar-tailed godwits in the Pertuis Charentais. On Ré Island, godwits are known to roost in the former saltpans of the National Nature Reserve of Lilleau des Niges and use two main feeding areas on soft substrates (Aubouin 2014; Duijns et al. 2014). The first feeding site is a mudflat inside a semienclosed bay classified according to the Ramsar Convention since 2003, the "Fier d'Ars" (46°13'18"N; 1°30'29"W) (Fig. 1). A part of the "Fier d'Ars" (the western part of the bay and the high-tide roosts in saltmarshes) is also included in the Nature Reserve. The second main feeding site is "La Loge" (46°14'25"N; 1°28'42"W), a sandflat on the exposed coast north of the Island and where the foreshore remains uncovered by the tide for about four hours only, thus reducing food availability (Fig. 1). "La Loge" is part of the Ramsar labeled site "Marshes of the Fier d'Ars" but does not benefit from any protection status, and recreational activities on the beach in the summer, as well as in the winter to a lesser extent, are frequent during the day.

Capturing and tracking godwits

Bar-tailed godwits were captured using mist nets during nonmoonlight nights inside the Nature Reserve. Godwits were immediately marked with a metal ring and a unique color ring combination, and body mass (accuracy within 1.0 g), wing length (nearest 1 mm), tarsus length (nearest 0.5 mm) and bill length (nearest 0.5 mm) were measured using standard methods (Prater et al. 1977; Evans 1986). When possible, the sex (bill length: 69–90 mm for males and 86–110 mm for females; mass: 230–383 g for males and 280–455 g for females) and age (fringe

of median covert feathers is pale with brown tips in juveniles, white in adults; primary flight feathers are worn in juveniles, new in adults) of individuals were determined (Pyle 2008; Demongin 2020). The heaviest godwits captured, which were all females, were fitted with a GPS-VHF logger (STERNA VHF-SRD with solar charger, Ecotone, Gdánsk, Poland; 35 × 16 × 10 mm, 7.5 g) when the mass of the tag remained less than 3% of the bird body mass. In total, 15 individuals (11 in 2015 and 4 in 2016) were equipped with a GPS logger. Juvenile females, potentially not faithful to the study site during winter, were not selected. Tags (accuracy of ±10 m) were fixed on birds with a 2 mm Teflon harness (on the lower back) according to the "leg-loop" method (Mallory and Gilbert 2008) and were programmed to record positions every 30 minutes. Six of the 15 individuals provided a sufficient number of positions over the winter and were retained for analyses. Three individuals provided data during both winters, two others during winter 2015–2016, and a last one during winter 2016–2017. For individuals with two winter surveys, we retained the data of the winter with the best balance of GPS fixed numbers between day and night. Thus, we used the data of winter 2015–2016 for BTG01, BTG02, BTG04, and BTG05, and the data of winter 2016–2017 for BTG03 and BTG06. The monitoring period extended from November to March for four individuals and from December to March for the other two (Table 1). The data were stored and processed from a PostgreSQL/PostGIS database.

Habitat mapping

For each bird monitored, sediment core sampling was performed around the centroid of several feeding areas defined by GPS locations collected during the first two months after the birds were fitted with transmitters (see below for details). This sampling method, carried out on a grid of 9 cores spaced by 10 meters and arranged around the central reference point of the station, should describe the availability and quality of trophic resources (distribution and density of benthic macrofauna) at the feeding areas used by godwits. The samples were

collected by foot at low tide according to methods described in Bocher et al. (2007) and Bijleveld et al. (2012). Each sample consisted of a 15 cm diameter sediment core (0.01 m²), with a depth of 15 cm (maximum depth reached by foraging birds according to mean bill length of females), sieved over a 1 mm mesh size on site. Annelids were immediately preserved in 70% ethanol, and mollusks were stored at –20°C until sorted at the laboratory. Mudsnails (*Hydrobia ulvae*), a potentially small and abundant prey, were sampled through an additional core (70 mm diameter) of 0.0037 m², to a depth of 5 cm, and sieved in the laboratory over a 0.5 mm mesh. A larger sediment core sampling for mudsnails would be a time-consuming process. In the laboratory, the organisms were identified to the species level as often as possible, and mollusks were measured within a 0.1 mm accuracy.

Mean grain size (mm) and percentage of silt (fraction < 63 µm) of a sediment core for each sampling station (depth of 5 cm) was determined using a Malvern Mastersizer 2000 diffraction laser (particle sizes analyzed from 0.04 to 2,000 µm) to characterize the granulometry of the substrate. The results of the sediment's particle size characteristics helped define each sampling station in terms of habitat type and thus build a habitat map for the two study areas.

Finally, the benthic macrofauna data, sediment characteristics, and field observations allowed us to build a fine-scale map of intertidal habitat typology in the study site using the European Nature Information System (EUNIS) classification of coastal habitats as a reference (Bajjouk et al. 2015). Seagrass beds were delimitated on site using GPS Trimble GeoXH during summer 2012.

Home ranges and habitat selection

The estimation of the utilization distribution (UD), that is, the probability of finding each bird at any location (Calenge 2015), was used to analyze diurnal and nocturnal space use by godwits. Kernel density estimates (KDE) (Van Winkle 1975; Worton 1989) were used to describe UD

140 (Laver and Kelly 2008) with the "kernelUD" function from the R package "adehabitatHR"
141 (Calenge 2015). The spatial distribution of bird locations and the corresponding time spent in
142 an area are considered by KDE method to estimate the home ranges (at 95% isopleth) and core
143 areas (at 50% isopleth) of each individual (Worton 1989). To estimate the kernel home ranges,
144 a compromise between the undersmoothing of least-square cross-validation (LSCV) and the
145 over-smoothing of reference bandwidth (ad hoc) was used: a smoothing factor of 70% of the
146 minimum reference value obtained by the "ad hoc" bandwidth (Kie et al. 2010; Schuler et al.
147 2014). Using a single smoothing factor (h = 80), calculated on the set of GPS data and used to
148 estimate bird kernels, allowed us to compare UDs between individuals. Considering the
149 accuracy of the GPS positions (± 10 m), the grid size was set to 20 m. After estimating global
150 UDs, the specific foraging distribution and resting distribution were computed. Field
151 observations allowed to define a spatial delimitation on upper intertidal areas above which birds
152 were mainly at rest and not foraging. Thus, foraging distribution was estimated from the GPS
153 positions of birds located, at low tide, on intertidal areas below an elevation of 3.3 m relative to
154 the hydrographic zero. In the same way, resting distribution was computed from the GPS
155 positions of birds located on saltpans, ponds in marshes, or upper intertidal areas above an
156 elevation of 3.3 m. Sunrise and sunset data from the R package "GeoLight" were used to
157 distinguish diurnal and nocturnal positions and allowed for the computation of birds' foraging
158 and resting distribution by differentiating day and night.

159 UDs were then used to investigate the importance of foraging habitats through habitat selection
160 analysis. For this, we considered a second-order selection (design II), that is, a same availability
161 of habitats for all birds and an analysis of habitat selection at the individual scale (Johnson
162 1980). A minimum convex polygon (MCP) of foraging points from all monitored birds
163 provided an estimation of available foraging habitats for godwits. Individual kernel home
164 ranges and the habitat typology of the study area were then superimposed to perform habitat

165 selection analysis through Manly's selection ratios (Manly et al. 2002) and using the R package
166 "adehabitatHS" (Calenge 2011). We explored the interindividual variability of habitat selection
167 through an Eigen analysis of selection ratios (Calenge and Dufour 2006), a multifactorial
168 method. These analyses and other statistical tests (ANOVA, paired t-tests and chi-squared tests)
169 were performed with the software R (3.6.1).

170

Results

Day and night feeding areas

Godwits showed an extreme fidelity to their feeding grounds along the wintering period (from November to March), with a limited number of prospected areas per individual, both during daylight and night. The mean sizes of diurnal feeding home ranges (dFHR, kde 95%) and diurnal feeding core areas (dFCA, kde 50%) were 224 ± 77 ha (min–max: 125–321 ha) and 45 ± 18 ha (22–68 ha), respectively (Table 1, Fig. 2). The mean sizes of nocturnal feeding home ranges (nFHR, kde 95%) and nocturnal feeding core areas (nFCA, kde 50%) were, compared with diurnal ones, much smaller with 128±72 ha (36–226 ha) and 23 ± 12 ha (8–34 ha), respectively (dFCA/nFCA: $t = 6.535$, $df = 5$, p-value = 0.001; dFHR/nFHR: $t = 9.0391$, $df = 5$, p-value < 0.001). In addition, the overlaps between diurnal and nocturnal home ranges were low at an individual scale (Table 1). The mean individual day–night overlap was 35 ± 14% (min–max: 12%–54%) between dFHR and nFHR and 18 ± 11% (min–max: 5%–34%) between dFCA and nFCA (Table 1).

Rhythm of feeding activity

The recorded bird foraging positions indicated that godwits could start foraging mainly between 2 and 3 hours before the low tide and 3 and 4 hours after the low tide, both during daylight and night (Fig. 3). From 2 hours before and 3 hours after low tide, birds spent about 95%–100% of their time on foraging areas during daylight and 90%–95% during the night except BTG05 with 80%–85% and 75%–80%, respectively. The proportion of time spent on the foraging area during the ebb tide (*c.* 6 hours) increased continuously during daylight, from 5%–10% to 10% and 15% during the first 2 hours, to 50% during the third hour. At night, godwits spent a steady proportion of time on the foraging area (around 0%–5%) during the first 2 hours of the ebbing tide but suddenly went up to 40% between the third and fourth hours. On average, godwits

195 therefore joined the foraging areas earlier by daylight, spending significantly more time on
196 intertidal areas during the day than at night during the fourth and third hour before the low tide,
197 with an average of 11% and 12% of additional time (Fig. 3). Similarly, godwits remained longer
198 on mudflats at the end of the daylight rising tide compared to the nighttime, with 6% and 7%
199 additional time spent on the foraging areas over the third and fourth hour after low tide,
200 respectively, although differences were not significant (Fig. 3). Finally, considering the entire
201 tidal cycle (from -6 hours to 6 hours around low tide), bar-tailed godwits spent a higher percent
202 of their time on foraging grounds by day than by night (paired t-test: t = 5.35, df = 5, p-value =
203 0.003).

204 **Daylight and night local movements**

205 The distances measured between the two successive recorded locations on the feeding areas
206 were shorter at night than during daylight for all individuals (t-value = –3.82, p-value < 0.001;
207 meanNight = 298 m, meanDay = 411 m). In proportion, godwits systematically made more
208 small movements (or displacements) at night than during the daylight. For nocturnal
209 movements, 0–50 m distance class was the most represented, and most direct distances recorded
210 between two consecutive locations (30 min) were less than 100 m (Fig. 4). By day, most
211 distances between points on the feeding area exceeded 100 m, and the most represented distance
212 class was 100–150 m (Fig. 4).

213 **Habitat diversity and structure**

214 In total, 11 locations, as potential feeding habitats, were identified in the intertidal areas of the
215 study site (Fig. 5). The "Fier d'Ars" area included a large diversity of habitats, with a clear
216 dominance of seagrass beds (A2.6111 – 27% of the total intertidal site surface), bare mudflat
217 (A2.313 – 19%), and oyster parks (A2.32 – 8%) on the muddy foreshore at the center of the
218 bay (Fig 5.b). Habitat A2.6111 was characterized by a fine muddy sand substrate with an
219 abundance of *Zostera noltei* and infaunal species dominated by polychaetes (*Scoloplos armiger*

220 and *Arenaria marina),* oligochaetes, and mollusks (*Cerestoderma edule, Macoma balthica,* and
221 *Hydrobia ulvae)*. Habitat A2.313 corresponded to a littoral sandy mud, mainly characterized by
222 polychaetes (*Hediste diversicolor*) and bivalves (*M. balthica* and *Scrobicularia plana*). A2.32
223 was a muddy substrate mainly characterized by a low diversity of polychaetes and oligochaetes,
224 covered with artificial oyster grow-out tables. Another habitat well represented in the "Fier
225 d'Ars" was an intertidal muddy sandflat dominated by polychaetes (*Eteone longa*, *S. armiger*)
226 and capitellidae combined with the bivalve *C. edule* (A2.242 – 6%). Saltmarsh creeks in the
227 A2.5 coastal saltmarshes (A2.325 – 17%) surrounded the muddy bay while rocky elements, that
228 is, bedrock and boulders dominated by mussels and/or barnacle communities (A1.11 – 1%) and
229 habitats with littoral rock features (A1.41 – 6%) characterized the bay entrance.

230 The site of "La Loge" contained specific habitats not found on "Fier d'Ars" with clearly sandy
231 characteristics (Fig. 5.c). These habitats were A2.221 (17% of the total study intertidal site
232 surface), a barren coarse sandbank that can only shelter an extremely small number of
233 oligochaetes because of the constant mobility of the coarse sediment, and A2.231 (38%), a
234 littoral fine sand dominated by polychaetes including *Nephtys cirrosa* and *S. armiger*. The
235 northern part of "La Loge" was described by habitats A1.41 (composed of rocky elements and
236 sheltering littoral rockpool communities – 21%) and A2.242 (dominated by polychaetes *E.*
237 *longa*, *S. armiger,* and capitellidae, combined with the bivalve *C. edule* – 18%).

238 **Foraging habitat selection**

239 During daylight, godwits did not use available foraging habitats randomly but showed a
240 significant habitat selection, both at an individual scale ($\chi^2 = 47563.98$, df = 9.0, $p < 0.001$) and
241 when combining the six birds monitored ($\chi^2 = 51039.79$, df = 54.0, $p < 0.001$). In the diurnal
242 feeding core areas, the seagrass bed habitat (A2.6111) was selected by four godwits (BT01,
243 BTG02, BTG03, and BTG04) (Fig. 6). For BTG05 and BTG06, the most represented habitats
244 were the sandflat dominated by *C. edule* and polychaetes (A2.242) and the mudflat dominated

245 by *H. diversicolor* and *S. plana* (A2.313), respectively. Habitat A2.313 was also a prevailing
246 habitat in the core feeding areas of BTG02 and BTG05. Hence, habitat A2.6111 appeared
247 preferentially used by godwits on average, followed by A2.242 and A2.313 (global selection
248 ratios > 1) (Fig. 7). Conversely, habitat A1.31 (fucoids on sheltered shores) was globally
249 avoided by the studied birds (global selection ratios < 1) although standard errors indicate their
250 marginal use by some birds. The six remaining habitats were clearly avoided (global selection
251 ratios and SE < 1).

252 During nighttime, the birds also showed significant habitat selection when considering all birds
253 (χ^2 = 38081.9, df = 54.0, $p < 0.001$) and individuals independently (χ^2 = 31774.09, df = 9.0, p
254 < 0.001). Habitats in the nocturnal feeding core areas were more specific, with strong individual
255 patterns. The feeding core areas of BTG01, BTG02, BTG03, BTG04, BTG05, and BTG06 were
256 mainly composed of habitats of oyster parks (A2.32), bare mudflat (A2.313), intertidal muddy
257 sandflat (A2.242), littoral fine sand (A2.231), bare mudflat (A2.313), and seagrass beds
258 (A2.6111), respectively, highlighting a strong interindividual variability (Fig. 6). This
259 observation was confirmed by the result of the Manly selectivity measure, which did not allow
260 a clear identification of a habitat preferentially used by the six birds. Indeed, habitats of littoral
261 fine sand (A2.231), intertidal muddy sandflat (A2.242), bare mudflat (A2.313), oyster parks
262 (A2.32), and seagrass beds (A2.6111) all appeared selected (global selection ratios > 1) but
263 with large standard errors that well illustrate the nonidentical use of habitats by all birds (χ^2 =
264 941.584; df = 45.0; $p < 0.001$) (Fig. 7). Although seagrass beds (A2.6111) remain globally the
265 most selected habitat at night (Fig. 7), we note that all individuals showed a significant decrease
266 of its use between day and night, with a proportion decreasing from an average of 48% to 19%,
267 except BTG06, which showed an opposite trend (Fig. 6).

268 The Eigen analysis emphasized these differences between diurnal and nocturnal habitat
269 selection. During daytime, the reported positions of four individuals (BTG01, BTG02, BTG03,

and BTG04) in the space described by habitats highlighted their preferential use of seagrass beds (A2.6111) (Supplementary Material Fig. S1). The other two birds stood out from this first group, with BTG06 clearly selecting the sandflat habitat dominated by *C. edule* and polychaetes (A2.242) and BTG05 in an intermediate position between A2.6111 and A2.242. At night, each individual selected a specific foraging habitat with five different habitats, thus preferentially used by godwits at night (A2.242, A2.231, A2.313, A2.6111, and A2.32).

Roost selection

Godwits' use of roosts differed markedly between day and night. The number of roosts used by individuals was not different between day and night, with one to three main roosts according to the estimation of roost core areas (isopleth 50) (Fig. 8). However, the location clearly varied between diurnal and nocturnal stages with a mean overlapping rate of 32% for roosting home ranges (RHRs) and 8% for roosting core areas (RCAs) (Supplementary Material Table S1). By day, during high neap tide, birds preferentially roosted on the upper foreshore and used less significantly the saltpan roosts beyond dikes. At night, individuals clearly selected the saltpans of the Nature Reserve as roosts and avoided free intertidal areas during high neap tide. During spring tide, they could not stay on flooded intertidal areas and returned on saltpan roosts either by day or night.

Discussion

By analyzing the nycthemeral use of habitats by wintering bar-tailed godwits at an extremely fine spatial scale, the present study revealed distinct foraging activities in shorebirds between day and night. Previous studies showed that shorebirds could use different feeding and roosting areas depending on the time of day and according to predation risk, disturbance, and density/activity of preys (Burton and Armitage 2005; Piersma et al. 2006). Here, we went further and showed that bar-tailed godwits faithfully selected distinct diurnal and nocturnal feeding areas using a low number of main feeding patches (CA), both during daylight and nighttime, with a relatively small feeding area by individuals. Moreover, birds moved less when prospecting at night, resulting in smaller nocturnal feeding home ranges. This variability in space use underlined differences in habitat selection, such as seagrass beds strongly selected by most of the tracked godwits by day and much less used at night. In addition, the distinct feeding distributions of the monitored females revealed interindividual variability in habitat selection. We noted that all our tracked birds were females, and there could be large differences in diet and patterns of space use between males and females during day and night.

Our study highlights that bar-tailed godwits spent as much time on feeding areas at night as during the day, devoting most of it to feeding activities from two hours before to three hours after low tide, that is, during the entire time window of mudflat availability. As observed in black-tailed godwits (Lourenço et al. 2008), this result highlights the importance of nocturnal feeding in the acquisition of daily energy needs by wintering bar-tailed godwits. Night foraging activity has been reported in most shorebird species wintering on tidal coasts although the relative importance of nocturnal activity depends on the species (Dugan 1981; McNeil and Rodriguez 1996). Many species favor feeding activity during the day, with visual capabilities allowing for higher intake rate and consequently providing the major part of the daily energy needs for birds (Dodd and Colwell 1996; Kam et al. 2004; Lourenço et al. 2008). Night foraging

313 was therefore mainly considered as "supplementary" in previous studies, that is, used when
314 diurnal prey intake is not enough to offset the increased energy demands of less favorable
315 wintering conditions (McNeil and Rodriguez 1996; Smith et al. 1999; Sitters 2000). However,
316 some shorebirds could fill a significant part of their energy requirements during the night
317 (Turpie and Hockey 1993; Lourenço et al. 2008) because of physiological adaptations such as
318 better nocturnal vision for *Charadriidae* (high rod–cone ratio in the eyes) (De Azuje et al. 1993;
319 Rojas et al. 1999) or higher tactile sensitivity for *Scolopacidae* as in godwits (Cunningham et
320 al. 2013), which facilitate nocturnal foraging.

321 In our study, the space used by wintering godwits differed between day and night, both
322 during feeding and resting periods, as reported for other shorebirds in previous studies (Rompré
323 and McNeil 1996; Piersma et al. 2006; Rogers et al. 2006). Birds were highly faithful to their
324 daylight feeding grounds, with extremely restricted feeding core areas recorded over the winter.
325 Their nocturnal feeding core areas were even more restricted and mostly spatially distinct from
326 the daytime ones. These results contrast with the observations of Burton and Armitage (2005)
327 on redshanks (*Tringa tetanus*), which also used separate diurnal and nocturnal foraging areas
328 but with larger core areas and home ranges at night. In addition, the distinct distributions of bar-
329 tailed godwits between day and night were associated with a change in habitat selection, notably
330 with a strong decrease in the use of seagrass beds at night, as well as an increased use of oyster
331 parks and sandflats. Various factors that we consider below, mainly related to the characteristics
332 of wintering habitats, could explain these differences in space use between day and night.

333 Contrary to studies that highlighted an avoidance of nearshore areas by shorebirds during
334 their nocturnal foraging in response to increased predation risks (Sitters et al. 2001; Burton and
335 Armitage 2005; Piersma et al. 2006), we did not find that upper intertidal areas were less used
336 by godwits at night. Conversely, a portion of monitored birds tended to focus on strategic points
337 of the upper foreshore during nocturnal feeding, near anthropogenic illuminations. Studies

338 highlighted a positive effect of artificial light on the nocturnal foraging of shorebirds by
339 recreating full-moon conditions across the nearby intertidal areas that allow birds to maintain a
340 sight-based foraging behavior at night and improve their prey intake rate (Santos et al. 2010;
341 Dwyer et al. 2013). On Ré Island, public lighting points at the edge of the bay increase the level
342 of ambient light across mudflat areas and could attract birds by allowing them to feed by sight
343 (Lourenço et al. 2008; Santos et al. 2010).

344 Recreational and harvesting activities represent another form of disturbance related to
345 anthropogenic activities, which has already been shown to affect the habitat use and foraging
346 activity of wintering or migrating shorebirds (Lafferty 2001; Colwell et al. 2003; Navedo and
347 Masero 2007; Burger and Niles 2013). For instance, studies emphasized that recreational
348 activities on the foreshore, as well as shellfish harvesting activities, could induce a reduction of
349 foraging time, flight behavior, or even a complete avoidance of the disturbed foraging areas
350 (De Boer and Longamane 1996; Thomas et al. 2003; Navedo and Masero 2007; Burger and
351 Niles 2013). This pattern is what we observed for some godwits on Ré Island, which avoided
352 oyster parks (A2.32) and beaches (A2.231) during daytime while they commonly used these
353 habitats at night. With a high predominance of polychaetes in the macrobenthic community,
354 these habitats constitute attractive feeding areas for godwits, but the presence of oyster farmers,
355 shell fishers, and walkers during the day constitutes a significant level of disturbance (Burton
356 and Armitage 2005; Dias et al. 2008).

357 Contrasting foraging methods between day and night were also found to affect the spatial
358 distribution of shorebirds. For instance, Mouritsen (1993) found that the dunlin (*C. alpina*)
359 switched from visual feeding during the day to tactile feeding during the night, as did black-
360 tailed godwits which showed a higher rate of stitches and sweeps at night and a majority of
361 pecks during the day (Lourenço et al. 2008). Generally, the bill of the *Scolopacidae* species
362 benefits from a high number of touch-sensitive nerve endings which favors tactile feeding (De

363 Azuaje et al. 1993). Hence, we can assume that bar-tailed godwits switch from sight feeding
364 during the day to probing at night and, as observed in dunlins (*C. alpina*) by Mouritsen
365 (Mouritsen 1994), this change in behavior may induce the use of distinct feeding habitats based
366 on prey availability. This could be related to the dominance of polychaetes, more active and
367 likely more available at night (Last and Olive 2004; Kuwae 2007) in habitats A2.32 and A2.231,
368 which could explain the nocturnal use of these habitats by godwits. We did not have available
369 data to compare diurnal and nocturnal prey density, but studies underlined that polychaete
370 worms, the favored preys of bar-tailed godwits (Duijns et al. 2013), may be closer to the
371 sediment surface at night (McNeil et al. 1992; Esser et al. 2008). Such a density of prey
372 available in the top layer of the sediment could explain the nocturnal preference of polychaete-
373 dominated habitats by godwits, as observed in dunlins and redshanks (Mouritsen 1994; Burton
374 and Armitage 2005). Beyond their influence on the location of godwits' feeding areas, the
375 differences in prey availability and foraging methods between day and night also seemed to
376 affect the size of foraging areas.

377 On night foraging sites, higher prey availability could lead to better intake rates (Zharikov
378 and Skilleter 2003), resulting in an area-restricted search for tactile predators through increased
379 spatial turning rates (Dias et al. 2009). Godwits could thus use sinuous low-speed searches in
380 more profitable patches at night (Nolet and Mooij 2002) and prefer faster direct searches with
381 more step rates during the day as observed in black-tailed godwits (Lourenço et al. 2008). This
382 pattern of feeding behavior could explain the differences observed in our study in the distances
383 separating two successive foraging locations between day and night.

384 At high tide, results showed marked differences in the use of roosts between day and night
385 during neap and spring tides. Indeed, at daytime, godwits selected upper mudflat roosts as soon
386 as they were available, that is, during neap tides. However, at night, birds always used saltpans
387 in whatever tidal heights. In a previous study based on daytime observations, Rosa et al. (2006)

388 showed that wintering shorebirds, including bar-tailed godwits, preferentially select mudflats
389 to roost, and move to saltpan roosts when the upper foreshore became unavailable during
390 highest tides. This study also highlighted the effect of both raptor presence, higher in saltpans
391 than in mudflats, and visibility, lower in saltpans, on daytime shorebird roost choice (Rosa et
392 al. 2006). Others studies reported the anti-predator strategy of shorebirds avoiding some
393 specific roosting areas by nighttime because of higher predation risks (Hilton et al. 1999;
394 Rogers et al. 2006). Hence, in addition to their availability, the roost choice by shorebirds
395 between day and night in the present study could be influenced by the predation risk (Handel
396 and Gill 1992; Rohweder 2001). Birds would favor mudflats at day, less prone to overflying
397 raptors and offering better visibility of approaching predators (Rosa et al. 2006), and saltpans
398 at night, with a water barrier against nocturnal predators such as foxes or mustelids (Cramp et
399 al. 1983; Sitters et al. 2001). Further studies are nonetheless needed to validate this hypothesis
400 and better explain the pattern of use of roost sites on Ré Island, including the monitoring of
401 predator activities.

402 Our results showed that all monitored bar-tailed godwits used the entire time window during
403 which they have access to foraging grounds, both during the day and the night. Nocturnal
404 foraging thus appears crucial along the winter to allow godwits to meet their daily energy
405 requirements and is not only a "supplement" for diurnal foraging. However, nocturnal foraging
406 is probably not preferential since we did not observe more use of feeding areas at night than
407 during the day. We hypothesize that differences in biotic and abiotic environmental conditions
408 (human disturbance, predation risk, feeding methods, and prey availability) between day and
409 night all together incite birds to develop specific feeding strategies and behaviors, including the
410 selection of contrasting habitats. Bar-tailed godwits also tended to specialize in their habitat use
411 and thus in prey at an individual scale, even more by night, most likely to reduce intraspecific
412 competition. Roost choice also depended on the time of day. The visibility of approaching

predators and proximity to feeding sites, when possible, seemed to be important to the choice of daytime roosts. Finally, these results provide an important knowledge of the nonbreeding survival strategies of bar-tailed godwits on the French Atlantic coast. We therefore urge greater consideration of the night distribution of birds, rarely evaluated in shorebird studies, to define areas and habitats of importance in management and conservation. The day–night connectivity in shorebirds' space use needs to be integrated into all spatial management plans where human activities can deal with natural protected areas or their proximities.

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Table 1 Size of diurnal and nocturnal feeding areas (FCA: feeding core areas 50%, FHR: feeding home ranges 95%) and their overlap rate

					DAY			NIGHT				
Logger ID	**Mass (mm)**	**Bill lengh (mm)**	**Tracking period**	**Number of days**	**GPS fixes**	**dFCA (ha)**	**dFHR (ha)**	**GPS fixes**	**nFCA (ha)**	**nFHR (ha)**	**Overlape dFCA/nFCA (%)**	**Overlape dFHR/nFHR (%)**
BTG01	301	91.5	20 Nov. - 17 Mar.	118	557	68.3	321.8	474	34.5	226.3	17.2	39.4
BTG02	335	105	31 Dec. - 31 Mar.	90	489	31.2	212.5	418	8.7	72.9	5.9	12.2
BTG03	325	99	31 Dec. - 15 Mar.	74	138	36.3	148.7	125	24.9	89.6	17.2	32.4
BTG04	332	101	11 Nov. - 26 Mar.	136	1125	53.1	276.1	1046	29.6	168.4	5.4	43.1
BTG05	326	95	11 Nov. - 29 Mar.	139	951	22.5	125.0	872	7.9	36.0	33.6	28.4
BTG06	316	101	01 Nov. - 17 Mar.	136	1687	58.4	262.4	1809	30.8	171.8	28.3	53.4

Figure captions

Fig. 1 Map of the Pertuis Charentais (Central French Atlantic coast) and localization of the study areas on Ré Island. Dark gray corresponds to the mainland and light gray to the intertidal area

Fig. 2 Diurnal and nocturnal feeding home ranges of six bar-tailed godwits during the nonbreeding period on Ré Island. Feeding home ranges were calculated as 50% (core areas) and 95% (home ranges) kernel density contours

Fig. 3 Mean proportion of time spent by six Bar-tailed godwits on mudflats, i.e. foraging, by day and by night during the tide cycle. Significant differences between Day and Night, for each slot time around the low tide, are illustrated by the symbols '*' when $p<0.05$ and '***' when $p<0.001$.

Fig. 4 Day and night distribution of distances between two successive locations (30 min.)

Fig. 5 Habitat typology at (a) Ré Island, (b) "La Loge," and (c) "Fier d'Ars"

Fig. 6 Day and night proportion of habitat types on feeding core areas (50% kernel density contour) of each bar-tailed godwit

Fig. 7 Results of the selection ratio analysis highlighting habitat selection by six bar-tailed godwits on 10 intertidal habitat types by (a) daytime and (b) nighttime

Fig. 8 Diurnal and nocturnal roosting home ranges of six bar-tailed godwits during the nonbreeding period on Ré Island. Roosting home ranges were calculated as 50% (core areas) and 95% (home ranges) kernel density contours